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Original Article

Persistent domoic acid in marine sediments and benthic infauna along the coast of Southern California

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ABSTRACT

Blooms of the diatom genus *Pseudo-nitzschia* occur annually in the Southern California Bight (SCB), and domoic acid (DA) associated with these events can contaminate fisheries, presenting both human and wildlife health risks. Recent studies have suggested that marine sediments may act as a reservoir for DA, extending the risk of food web contamination long after water column blooms have ended. In this study, we conducted a regional assessment of the extent and magnitude of DA in the benthic environment, and monthly observations of sediments and benthic infauna at multiple stations over a 16-month period. DA was widespread in continental shelf sediments of the SCB. The toxin was detected in 54% of all shelf habitats sampled. Detectable concentrations ranged from 0.11 ng/g to 1.36 ng/g. DA was consistently detected in benthic infauna tissues over the monthly timeseries, while the DA concentrations in sediments during the same period were commonly below detection or at low concentrations. The presence of DA in the benthic environment did not always have an apparent water column source, raising the possibility of lateral transport, retention/preservation in sediments or undetected blooms in subsurface waters. In most cases, DA was detected in tissues but not in the co-located surface sediments. Coarse taxonomic sorting of the infauna revealed that the accumulation of DA varied among taxa. We observed that DA was widespread among lower trophic level organisms in this study, potentially acting as a persistent source of DA to higher trophic levels in the benthos.

1. Introduction

Harmful algal blooms (HABs) and associated algal toxins have been a persistent and escalating issue in southern California's coastal and inland waterbodies (Anderson et al., 2006; Busse et al., 2006; Howard et al., 2021; Schnetzer et al., 2013; Shipe et al., 2008; Smith et al., 2018; Tatters et al., 2019; Umhau et al., 2018). Globally, HABs have increased in frequency, severity and spatial extent over the past decade, and anthropogenic nutrient inputs and warmer temperatures (i.e. climate change) are considered the most significant factors contributing to these increases (Anderson et al., 2021; Glibert et al., 2005; Gobler et al., 2017; Hallegraeff et al., 2004; O'Neil et al., 2012; Paerl et al., 2011).

The Southern California Bight (SCB) is a roughly 700 km portion of the U.S. West Coast that extends from Point Conception, California south to beyond the U.S. international border with Mexico. The most commonly observed HAB organisms in the SCB are species within the diatom genus *Pseudo-nitzschia*, several of which produce the neurotoxin domoic acid (DA). Annual blooms of *Pseudo-nitzschia* spp. and measurable concentrations of DA have been documented along the California coast since the 1990s and annually in the SCB since 2003. (Schnetzer et al., 2007). Trophic transfer of DA in the food web can contaminate fisheries, presenting both human and wildlife health hazards. Consumption of contaminated seafood is the cause of amnesic shellfish poisoning (ASP) in humans, resulting in symptoms of diarrhea, gastrointestinal pain, disorientation and memory loss, and in extreme cases, death (Bates et al., 1989). Stranding and mortality events in marine mammals and birds have also been attributed to exposure to DA (Fire et al., 2010; Lefebvre et al., 2002; Smith et al., 2018). DA events have

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also caused major socioeconomic impacts, including prolonged closures of key fish, bivalve and crab fisheries (McCabe et al., 2016; Moore et al., 2020).

A majority of work to date in the SCB has focused on characterizing DA within shellfish tissues and within suspended particulate material (i.e. plankton). Monitoring over the last 15 years has shown that DA has been observed in shellfish tissue on a near-annual basis in the region (Smith et al., 2018). Particulate DA concentrations observed during toxigenic blooms of *Pseudo-nitzschia* spp. in the SCB often exceed concentrations of 10 μg/L and some events have even exceeded 50 μg/L (Smith et al., 2018). Observations of dissolved DA concentrations have been more limited in the region, but recent work has indicated that

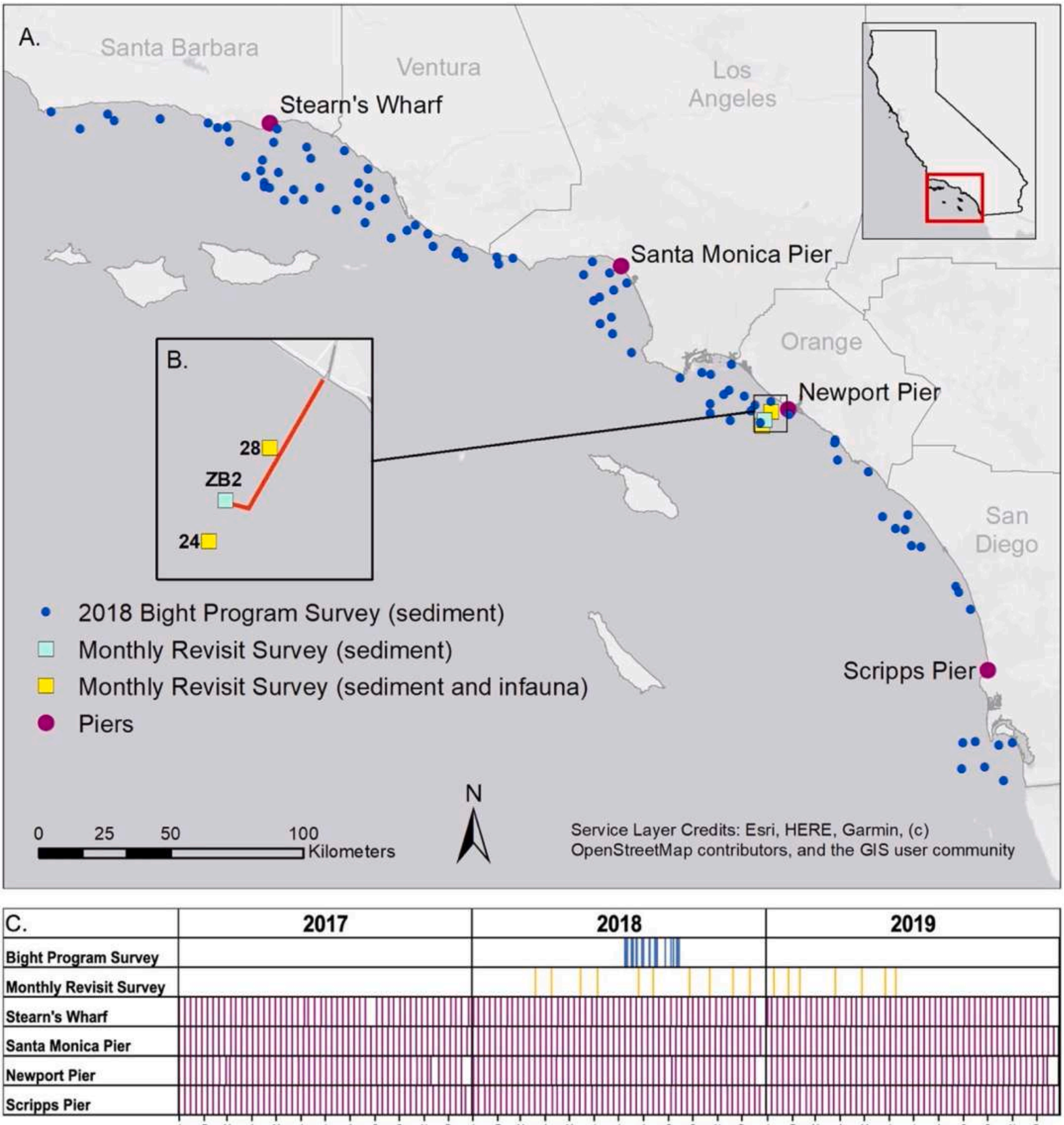

Fig. 1. Map of sampling locations for all program components. Panel A) shows an overview of the entire study area where blue circles represent the 2018 Bight Program Survey stations, yellow squares represent the Monthly Revisit Survey stations where sediment and infauna were collected, light blue squares represent the Monthly Revisit Survey stations where only sediment were collected, and purple circles represent weekly pier monitoring stations. B) Inset map of Monthly Revisit Survey stations in relation to the Orange County Sanitation District ocean outfall. Panel C) shows the temporal frequency (daily) of observations from all sampling efforts.

dissolved DA may be a significant fraction of the total DA (particulate plus dissolved DA) pool with contributions as high as 50% (Umhau et al., 2018). Similarly, a few studies have demonstrated the rapid transport of DA into the benthos during bloom events in the SCB (Schnetzer et al., 2007; Sekula-Wood et al., 2011, 2009; Umhau et al., 2018), providing only limited insight into the presence or longevity of DA in benthic environments in the SCB.

The role of the benthos in extending the ecological and socioeconomic impacts of DA producing blooms is largely understudied, but recent events have underscored the need to resolve these dynamics. In 2015, a nearly West Coast wide bloom of *Pseudo-nitzschia* persisted for multiple months (Du et al., 2016; McCabe et al., 2016; Ryan et al., 2017) and resulted in extensive impacts on multiple species of marine mammals, birds, and fish (McCabe et al., 2016). The bloom also caused closures of both commercial and recreational Dungeness crab and razor clam fisheries along the U.S. West Coast that extended for over a year after the bloom ended due to prolonged contamination with DA (Ekstrom et al., 2020). The long-term impacts of the 2015 bloom were attributed to the presence of DA in the benthos. Several studies have indicated the prevalence of DA in benthic species (Kvitek et al., 2008; Lefebvre et al., 2002; Vigilant and Silver, 2007), suggesting marine sediments may be a long term reservoir for DA and temporally expand the impacts of DA producing blooms.

While the pelagic impacts of DA have been well studied, the fate and environmental persistence of DA has been historically understudied. The goal of this study was to address our knowledge gap relating to the long-term impacts and fate of DA in the coastal benthic habitat of the SCB. The overall objectives of this study were to determine the extent and magnitude of DA on the continental shelf sediments in the SCB as well as to determine how concentrations of DA vary in the sediments temporally in relation to toxin concentrations present in benthic infauna. We conducted, to our knowledge, the first regional assessment of DA presence in the benthic environment of any continental shelf ecosystem. This was complemented with a 16-month time-series to investigate how DA concentrations vary throughout the year in both the sediments and infauna.

2. Materials and Methods

2.1. Sampling design and sample collection

The areal extent of DA in SCB sediment was assessed during a field survey that was conducted between July and September 2018 as a part of the 2018 Southern California Bight Regional Marine Monitoring Program (Bight Program). The Bight Program is an integrated and collaborative monitoring program established in 1994 to provide large scale assessments of the SCB. Samples were collected from 90 stations throughout the SCB from Pt. Conception in the north to the US-Mexico international border in the south (**Fig. 1A**). The sampling effort was carried out by multiple agencies that contributed to the 2018 Bight Program. A stratified random sampling design was used to ensure an unbiased sampling approach providing areal assessments of environmental condition (Stevens, 1997). Stratification provides an appropriate number of samples (target n = 30) to characterize each stratum with adequate precision (90% confidence interval of ± 10% around estimates of areal extent assuming a binomial probability distribution and p = 0.2). Three depth strata were sampled, inner (0-30 m), middle (30-120 m) and outer (120-200 m) continental shelf. Within the SCB continental shelf, inner-shelf comprises 31% of shelf area (1.03% of area for each of the 30 stations), mid-shelf comprises 53% of the shelf area (1.77% of area for each of the 30 stations) and outer-shelf comprises 16% of the shelf area (0.53% of area for each of the 30 stations). One sampling location for the outer-shelf exceeded the outer-shelf maximum target depth of 200 m (actual sample depth was 212 m), however, for the purposes of this study, it was included as an outer-shelf sample.

The Monthly Revisit Survey was conducted off the coast of Newport Beach, CA (**Fig. 1B**) to assess shorter temporal scale changes of DA in SCB sediment and benthic infaunal tissue from March 2018 to June 2019. Samples were collected for the analysis of DA in sediment from three stations (Station 28, Station ZB2, and Station 24) and in benthic infaunal tissue samples from two stations (Station 28 and Station 24)

2.2. Sediment and infauna collection

For both the 2018 Bight Program and Monthly Revisit Survey stations, sediment samples for DA analysis were collected using tandem 0.1 m^2 Van Veen grabs. A subsample from the top 2 cm of sediment was scooped into a 250 mL amber jar and stored on ice, in the dark, until transported to the laboratory, whereupon it was kept frozen at -20°C until analysis.

Benthic infauna were collected monthly from Station 28 and Station 24. Sediment samples for benthic infauna (Monthly Revisit Survey only) from the second grab were placed on a wash tray and rinsed with filtered seawater through a 1.0 mm mesh screen. If insufficient animal biomass was obtained (target biomass was 3 g), additional drops were made to obtain enough biomass for toxin analysis. Samples were kept cool and in the dark until they were brought back to the lab, where they were rinsed further to remove remaining sediment and then sorted.

2.3. Sediment DA analysis

Sediment DA extractions were conducted according to Sekula-Wood et al. (2011). Briefly, 30 mL of 50% MeOH were added to 5 g sediment wet weight, samples were left on a shaker table at 4°C for 12-24 hours in the dark, centrifuged at 3800 RPM for 10 minutes, and filtered through a 0.2 μm filter. DA was quantified on an LC-MS/MS according to a modified Wang et al. (2012) protocol using $^{13}C_3$-caffeine as an internal standard. Minimum detection limit for these samples ranged from 0.10-0.15 ng/g depending on the analytical run.

2.4. Benthic infauna DA analyses

Infauna were sorted into major taxonomic groups or presumed feeding strategies to determine if differential accumulation of DA might be occurring. Animals were divided into four groupings. Group 1 was primarily comprised of marine worms (predominantly taxa such as polychaetes and nemerteans) and rarely non-worm taxa such as holothurians. Since this group was dominated by worm taxa, it is referred to as “marine worms”. Group 2 was primarily comprised of filter feeders (predominantly bivalves, tunicates, barnacles and minor contributions of non-filter feeding organisms such as siphonophores and scaphopods), Group 3 was primarily comprised of sediment surface feeders (predominantly urchins, sea stars, snails, shrimp, isopods and amphipods), and Group 4 comprised of brittle stars, which are also sediment surface feeders. Sorted organisms were stored in 50 mL falcon tubes or wide-mouth HDPE jars, depending on the size and number of organisms collected. The mass of each feeding group was taken, and samples were stored frozen at -20°C until analysis.

DA was extracted from infauna tissues by first thawing samples, and any organisms with hard parts that would not break down during homogenization were dissected to remove these parts. The material that was not homogenized included urchin tests, gastropod shells, and thick bivalve shells. In the majority of bivalves collected, the shells crushed easily with clean surgical scissors, so those remained as part of the sample. After any needed dissections, all samples were coarsely chopped with surgical scissors to aid in homogenization.

Samples were extracted based on the methods described in Litaker et al. (2008) and Kvitek et al. (2008). For samples with less than 3 g of tissue for a given sorting group, 50% MeOH was added in a 1:10 (tissue: methanol) ratio, then the sample was homogenized using an Omni Tissue homogenizer with a hard tissue plastic probe. For samples greater than 3 g, tissue was first homogenized using a hard tissue plastic probe then, 1 g of the homogenate was aliquoted into a 15 mL falcon tube and 10 mL of MeOH was then added (to maintain the 1:10 tissue:methanol ratio). All sample were homogenized and vortexed thoroughly for 1 minute. Samples were then centrifuged at 4100 rpm for 25 minutes at 4°C. The supernatant was filtered with a 0.45 µm polyethersulfone syringe filter (Litaker et al., 2008) and the extract was stored in the freezer at -20°C until analysis.

Extracts of the benthic infauna were analyzed via Enzyme-Linked ImmunoSorbent Assays (ELISA; Mercury Science DA Test Kit product #DAK-36) using the methods described in Litaker et al. (2008) for shellfish tissues. All samples were run with at least a 1:10 dilution with the sample diluent provided in the kit to mitigate any matrix effects from the methanol. This method has a minimum detection limit of 10 ng/g. A subset of samples ($n = 13$) were confirmed with LC-MS to rule out potential matrix effects. Although benthic infauna generally are not consumed by humans and are not harvested commercially in the SCB, the FDA safety level of 2.0×10^4 ng/g was used to contextualize infauna tissue toxin concentrations against concentrations that would be unsafe for commercial fish and shellfish tissues and also provide context for bioaccumulation risk in higher trophic levels.

2.5. Binning sorted benthic infauna tissue concentrations

A weighted average was calculated to bin all benthic infauna data from each sample to allow for a bulk comparison of the DA concentrations in all organisms over time. This was calculated using the following formula where the subscript denotes each of the four groups:

$$\frac{(([DA_1]*wt_1)+([DA_2]*wt_2)+([DA_3]*wt_3)+([DA_4]*wt_4))}{(wt_1+wt_2+wt_3+wt_4)}$$

The concentration from each group (denoted as $[DA_{1\text{-}4}]$) was multiplied by the weight of that group (denoted as $wt_{1\text{-}4}$) to give total mass DA. The mass of DA across all four groups was summed and divided by the total weight of benthic infauna in the sample and these numbers are reported as the sample weighted average DA in benthic infauna tissue.

Results were also calculated as concentrations present in 2 groups: DA concentrations in Group 1 (marine worms) tissues and the weighted average of Groups 2-4. Although the grouping of marine worms includes worms with varied feeding strategies and minor contributions from other taxonomic groups, there were consistently high levels of DA detected in this group throughout the timeseries compared to all other benthic organism groupings; therefore, the DA concentrations of marine worms were compared to the weighted average of the remaining three groupings which were more similar over time.

2.6. Sediment characteristics

Basic sediment characteristics including grain size, total organic carbon (TOC) and total nitrogen (TN) were characterized in all 90 samples collected during the Bight Program regional assessment. Grain size samples for this study were analyzed by the City of San Diego, Physis and Eurofins with results reported as phi size (% of sample). Phi sizes were then grouped as fine particles (Phi ≥ 5), fine sands (Phi 3-4), coarse sands (Phi 1-2) and coarse particles (Phi ≤ 0) for analysis. For TN and TOC, 200 g sediment from the top 2 cm were scooped into an 8 oz amber jar and frozen within 24 hours. Samples were analyzed by City of Los Angeles (CLA), Los Angeles County Sanitation Districts (LACSD), Orange County Sanitation District (OC San) and City of San Diego (CSD). Further details on sample collection and analysis of TN and TOC, as well as grain size, are described in the 2018 Bight Program Sediment Chemistry Report (Du et al., 2020).

2.7. Regional pier monitoring for domoic acid

Ambient monitoring for particulate DA has been conducted on a weekly basis since 2008 within the SCB as a part of the California HABMAP program (https://calhabmap.org/; Kudela et al., 2015). These observations were used to assess the presence of domoic acid producing blooms in the region in the year prior to and during the sediment and infauna sampling efforts. Particulate domoic acid (pDA) data from January 2017 to December 2019 was queried from the four pier locations within the SCB, Scripps Pier in San Diego County, Newport Beach Pier in Orange County, Santa Monica Pier in Los Angeles County and Stearn's Wharf in Santa Barbara County. The pDA analyses from these sites were conducted via ELISA using the methods described in Seubert et al. (2013). The detection limit for pDA is 0.02 µg/L.

2.8. Data analysis

Statistical analyses throughout this report were conducted in R (R Core Team, 2020) and figures were generated using ggplot2 (Wickham, 2016; excluding maps which were generated in ESRI ArcGIS software). All data below the methodological limit of detection were treated as zero.

Empirical cumulative density functions (ECDFs) were used to estimate the percent of continental shelf area containing detectable DA concentrations. The stratified random sampling design allowed for each station to represent a pre-determined fraction of the Bight continental shelf area, based on the relative area of each stratum within the whole continental shelf area. To accommodate the variable weight each station contributes to percent area, empirical cumulative density functions were calculated and visualized in R using stat_ecdf from the package ggplot2 (Wickham, 2016) with an added function to allow weighting (https://github.com/NicolasWoloszko/stat_ecdf_weighted).

Comparisons were made among DA concentrations the sediments across shelf strata using a Kruskal-Wallis rank sum test. Significant differences were tested with a post hoc Dunn's comparison test using the FSA package (Dinno, 2017; Ogle et al., 2020). Differences between infauna DA concentrations at the two Monthly Revisit Survey stations were tested using the Wilcoxon Rank Sum test using the R package stats (R Core Team, 2020). The false detection rate was controlled using the Benjamini-Hochberg adjustment and adjusted p values are reported. Spearman correlations were used to test the relationship between percent fine particles and sediment DA concentrations using the corr.test from the stats package (R Core Team, 2020). Principal components analysis (PCA) was conducted to understand sediment DA concentrations in the context of multiple variables using the package factoextra (Kassambara and Mundt, 2020).

3. Results

3.1. Domoic acid producing blooms of *Pseudo-nitzschia* in the water column

Pier-based observations of particulate DA (pDA) indicated that a significant bloom event occurred during the spring of 2017, a year prior to the start of the 2018 Bight Program and Monthly Revisit Survey. Measurements of pDA from Scripps Pier, Newport Pier, Santa Monica Pier, and Stearn's Wharf all indicated that a toxin-producing bloom of *Pseudo-nitzschia* occurred Bight-wide (**Fig. 2**). DA was detected at one or more of the piers weekly between March 13, 2017 and June 6, 2017 and detectable toxin concentrations ranged from 0.04 µg/L to 14.4 µg/L. The bloom was associated with unusual bird mortality events in Santa Barbara, Ventura and Los Angeles counties, and an influx of sea lions to marine mammal rescue centers was attributed to DA poisoning (Smith et al., 2018).

In 2018 and 2019, DA was detected rarely and at low concentrations. Only two instances of detectable pDA were observed at Newport Pier in 2018 with concentrations <0.15 µg/L. In 2019, pDA was detected at relatively low concentrations at all pier stations at least once between March and June. Observed pDA concentrations ranged between 0.05 µg/

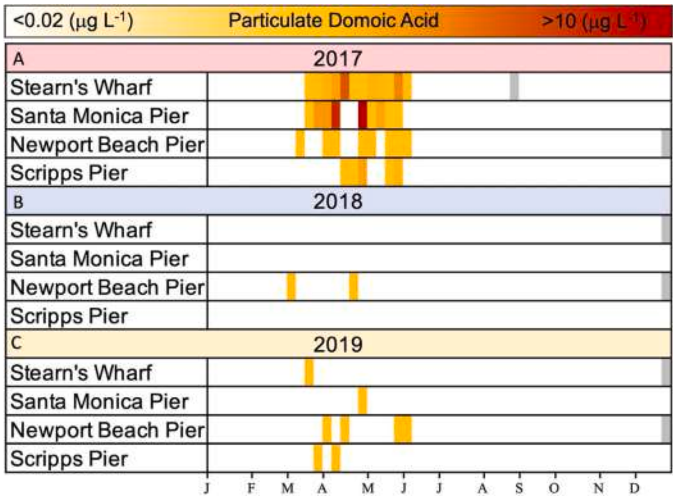

Fig. 2. Particulate domoic acid concentrations at the weekly pier monitoring stations in the Southern California Bight. Locations of the piers relative to sediment sampling locations are shown in Fig. 1. The weekly particulate domoic acid concentrations at each station are shown during (A) 2017, (B) 2018 and (C) 2019. Weeks with missing data are indicated with grey bars.

L and 0.19 μg/L (Fig. 2).

3.2. Extent and magnitude of sediment domoic acid in the Bight

Domoic acid (DA) was detected broadly across the region in this study. 54% of SCB continental shelf area in 2018 had detectable concentrations ranging from 0.11 ng/g to 1.36 ng/g (**Fig. 3**, **Fig. 4A**). The highest DA concentrations were located in sediments collected from the Santa Barbara Channel, Santa Monica Bay, and the San Pedro Shelf (**Fig. 3**). The highest concentration of 1.36 ng/g DA was collected from an outer-shelf station in the Northern Santa Barbara Channel, approximately 6 km off the coast of Gaviota.

Of the three continental shelf strata sampled, the greatest extent of DA was present in mid-shelf sediment, with DA detected in 67% of the mid-shelf area (**Fig. 4B**). The inner and outer-shelf strata had detectable DA in 27% and 40% area, respectively. DA concentration varied significantly among strata with the mid-shelf having a higher median concentration (0.18 ng/g) DA than the inner (median = 0 ng/g) or outer (median = 0 ng/g) shelves (**Fig. 4C**; Kruskall-Wallis test, $H = 9.52$, $df = 2$, $p < 0.01$). The mid-shelf DA concentrations were significantly higher than the inner-shelf concentrations (adjusted $p < 0.01$), but not significantly different than outer-shelf concentrations (adjusted $p = 0.16$), and no significant difference was found between the inner and outer-shelf (adjusted $p = 0.14$; post hoc Dunn's Multiple Comparisons test).

The presence and concentration of DA in sediments did not show any strong relationships with any of the co-sampled environmental factors. A

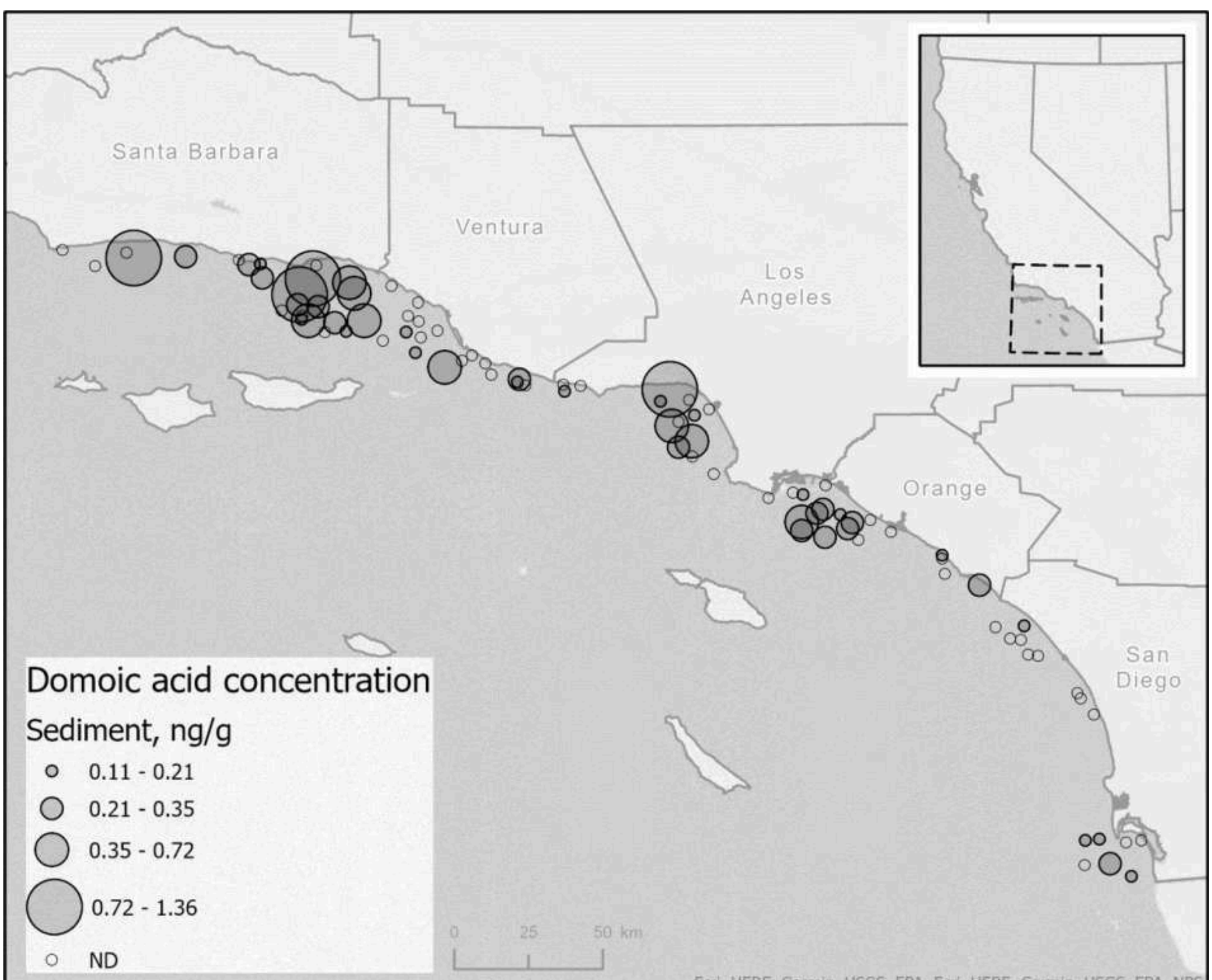

Fig. 3. Locations and concentrations of domoic acid in 90 sediment samples collected during the 2018 Bight Program. Samples span across Santa Barbara and San Diego counties. An empty circle indicates the location of stations where domoic acid was not detected.

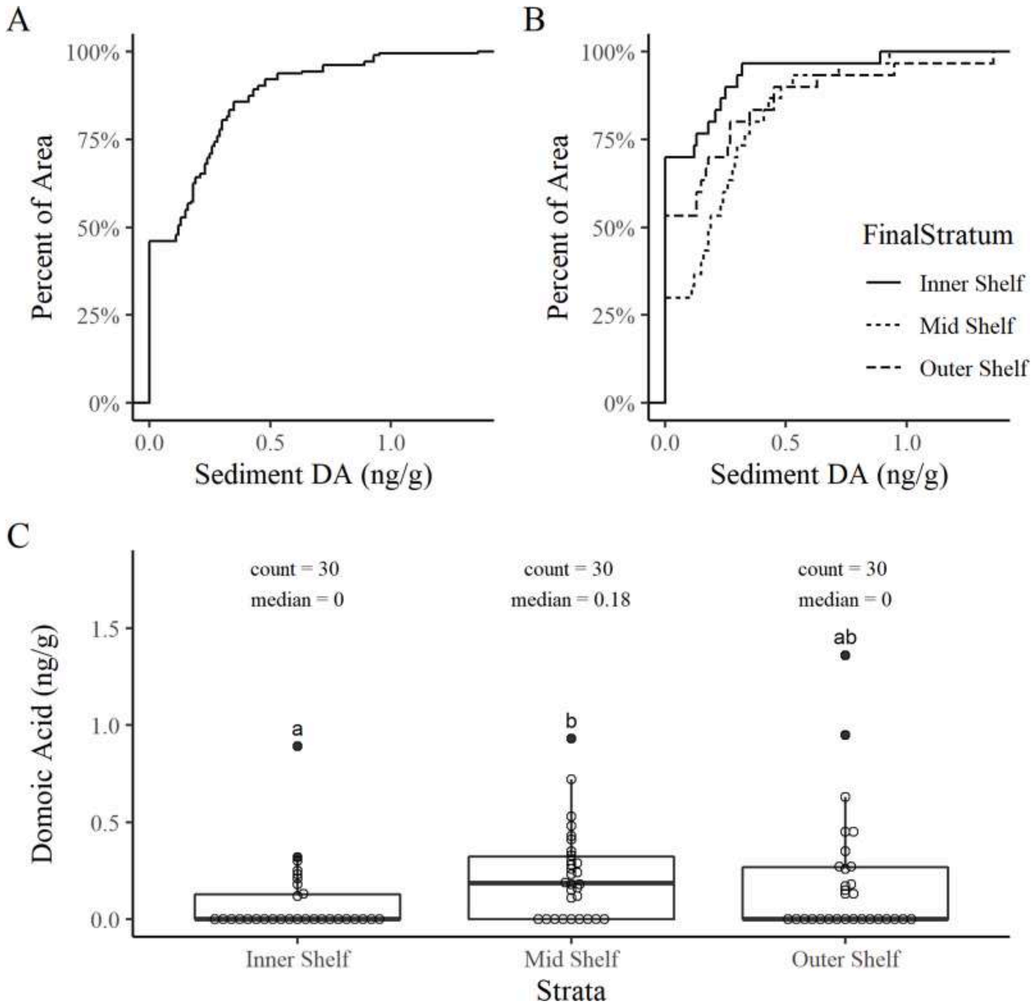

Fig. 4. Empirical cumulative distribution frequency of domoic acid concentration in A) all continental shelf sediment samples from the 2018 Bight Program and B) each of the three continental shelf strata sampled during the 2018 Bight Program; C) boxplot of the domoic acid concentrations measured in 30 samples from each continental shelf stratum, with the raw data point plotted over the box. The middle of the box is centered on the median, the lower and upper hinges correspond to the first and third quartiles, and outliers are defined as points further than 1.5 times the inner-quartile range.

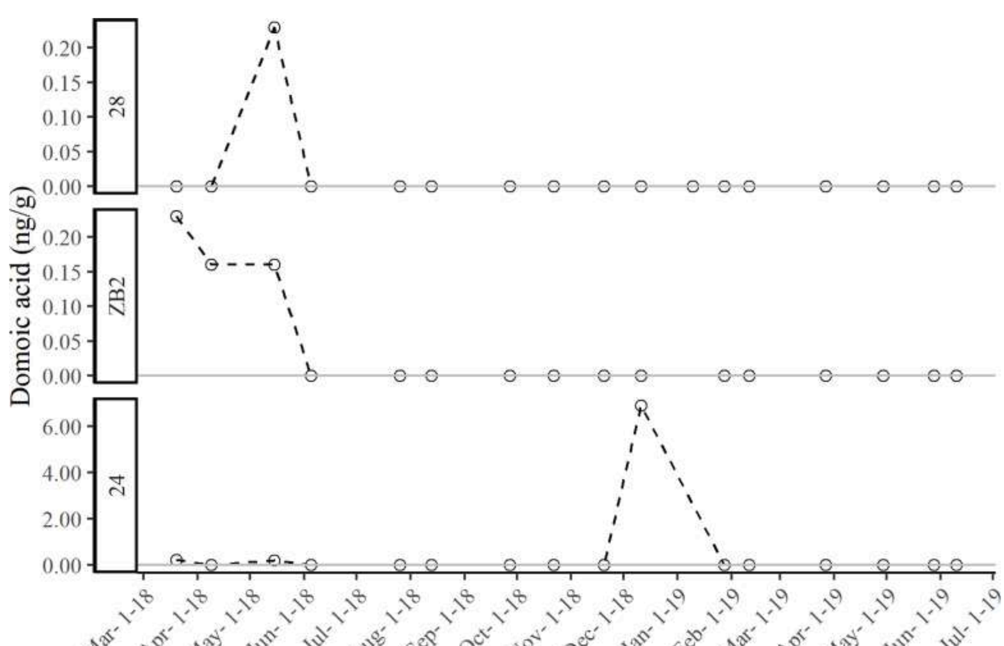

Fig. 5. Concentrations of domoic acid (ng/g) in sediment samples during the Monthly Revisit Survey at Stations 28 (32 m), ZB2 (58 m) and 24 (204 m) from Mar 2018 – Jun 2019. Note the difference in y-axis scales between stations. Depths provided are the mean station occupation depth rounded to the nearest integer.

significant but weak correlation was found between DA concentrations in samples where DA was detected (N=44) and percent fine particles (**Supplemental Fig. 1**; Spearman correlation: $\rho = 0.34$, p=0.025). A weak positive relationship was also observed between DA concentrations and percent fine particles when all samples were considered (N=90), but it was not statistically significant (**Supplemental Fig. 1**; Spearman correlation: $\rho = 0.15$, p=0.17). No significant relationships were observed between sediment DA concentrations and sediment TN or TOC, station latitude or station depth, although sediment TN and TOC showed similar positive trending relationships to that observed between sediment DA concentrations and fine particles.

3.3. Temporal and spatial variation of domoic acid in sediment and benthic infauna

Concentrations of DA were mostly below or near the detection limit (0.10-0.25 ng/g) in the 49 sediment samples collected from three stations off the coast of Newport Beach over the course of the 16 month Monthly Revisit Survey (Fig. 1**B**, Fig. 5). DA was not detected in 88% of sediment samples collected. Of the six samples in which DA was detected, concentrations ranged from 0.16 to 6.9 ng/g with the highest DA concentration observed at the farthest offshore Station 24. During the 16 months of sampling, DA was detected in 6% (1/17) of samples at Station 28, 13% (2/16) of samples at Station ZB2 and 19% (3/16) of samples at Station 24. A majority of sediment samples with detectable DA were collected between March 2018 and June 2018.

In contrast to DA levels in the Monthly Revisit Survey sediment samples, DA was detected in all co-located benthic infaunal samples at Stations 24 and 28 (Fig. 6**A**). The weighted average of DA concentrations in tissues ranged from 70 ng/g to 1.8×10^3 ng/g at Station 28 and from 7.0×10^3 ng/g to 7.0×10^4 ng/g at Station 24. Weighted DA concentrations in benthic infauna tissue was significantly higher at Station 24 (median 1.8×10^4 ng/g), compared to the concentrations observed at Station 28 (Fig. 6**B,** median 2.9×10^2 ng/g; Wilcoxon Rank Sum test, W = 0, p<0.01). Additionally, the weighted average of DA in benthic infauna tissue exceeded the FDA safety level of 2.0×10^4 ng/g in 44% of samples collected at Station 24, while the weighted average DA concentration at Station 28 never exceeded 2.0×10^4 ng/g.

Among the sorted groups of benthic infauna, Group 1 (marine worms, which included other taxonomic groups as well) had consistently higher body burdens of DA (Fig. 7). At Station 28, DA concentrations in marine worms (median 4.4×10^2 ng/g) ranged from 1.0×10^2 ng/g - 6.5×10^3 ng/g and was significantly higher than weighted average DA concentration of the remaining organisms (median 70 ng/g), which ranged from 20 ng/g – 6.0×10^2 ng/g (Fig. 7**B**; Wilcoxon Rank Sum test, W=265, p<0.01). At Station 24, DA concentrations in marine

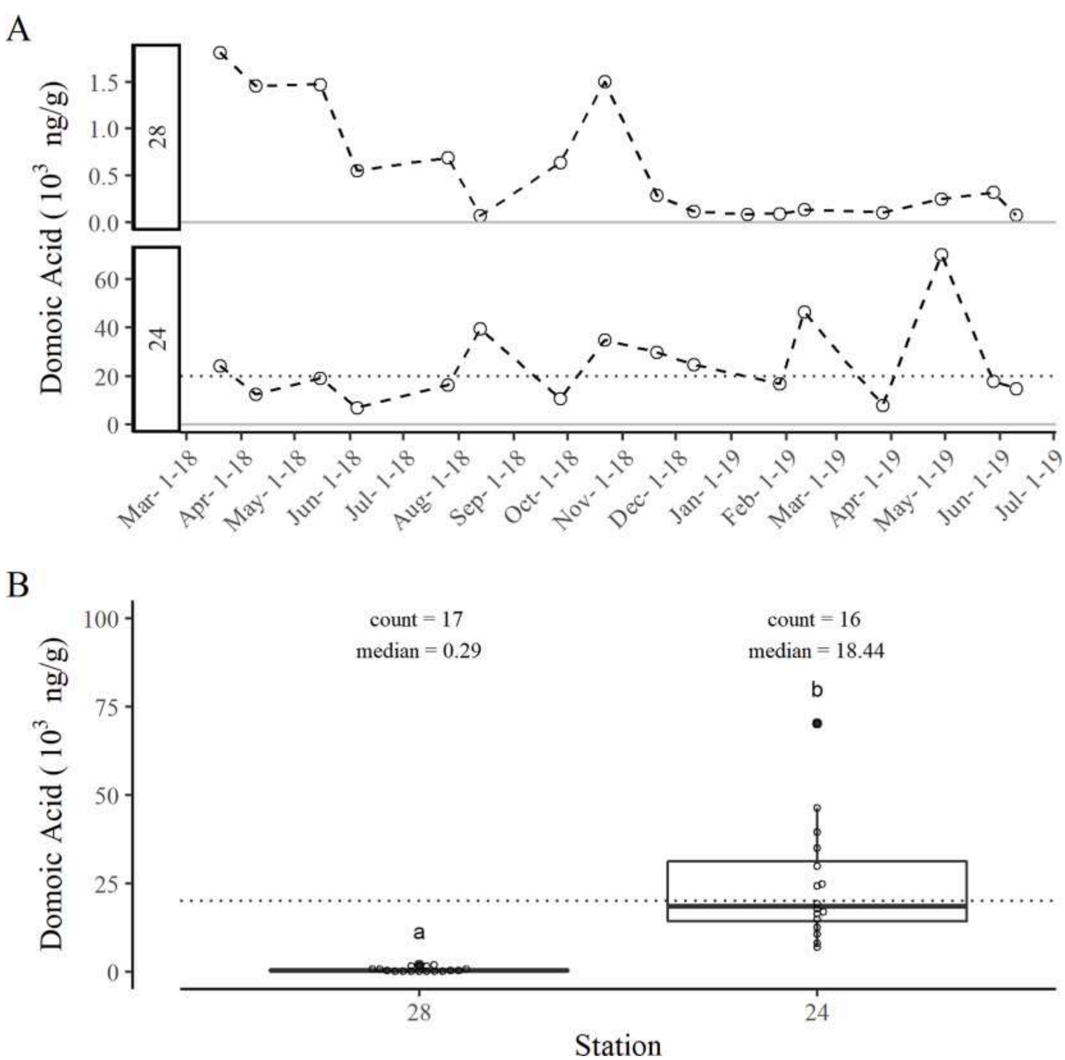

Fig. 6. Tissue domoic acid concentrations (10^3 ng/g) in benthic infaunal tissue collected during the Monthly Revisit Survey, March 2018-June 2019. A) Time series of domoic acid at Stations 28 and 24 and B) boxplot comparing weighted average domoic acid concentration between Station 28 and Station 24. Black dashed line indicates the FDA safety level domoic acid concentration of 2.0×10^4 ng/g.

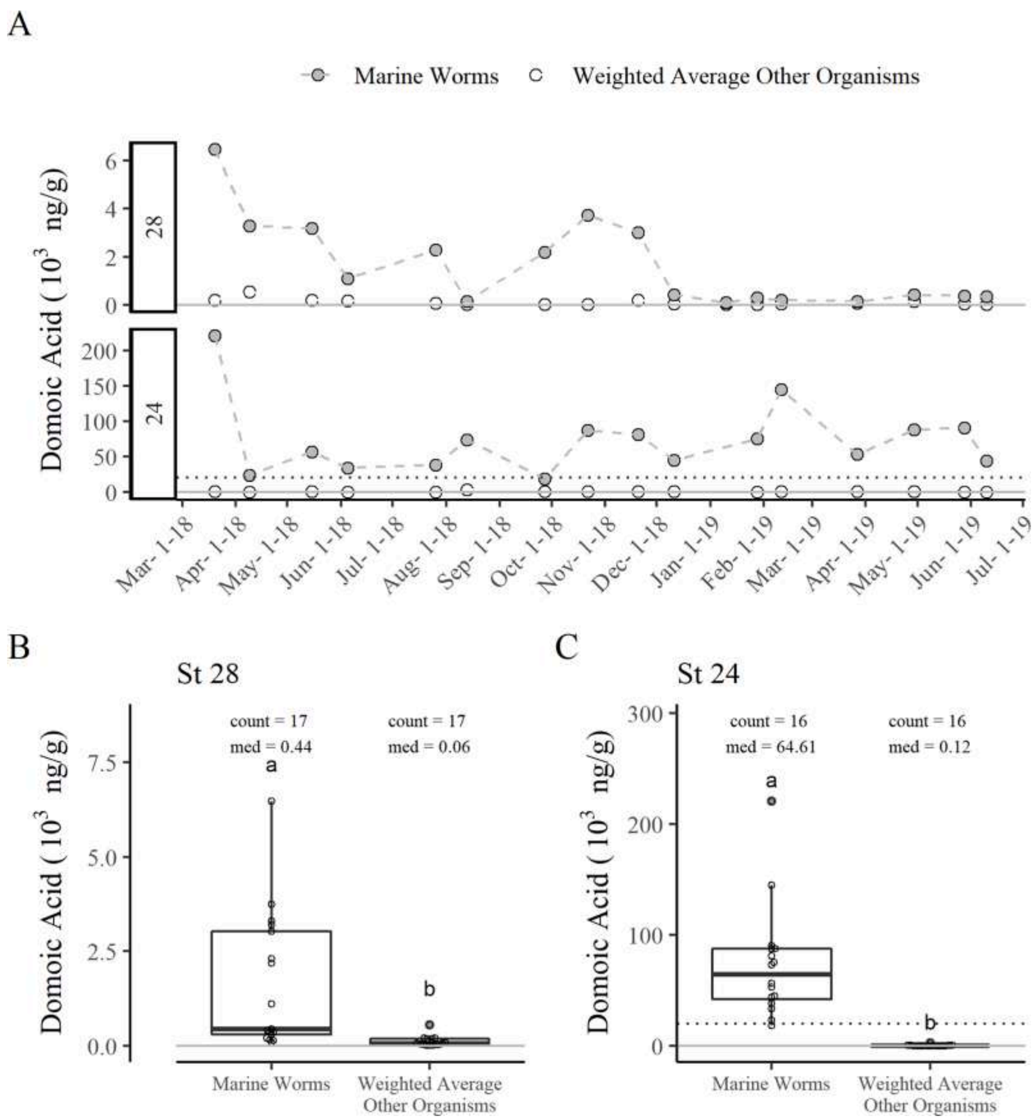

Fig. 7. Domoic acid concentrations (10^3 ng/g) in tissues of marine worms collected during the Monthly Revisit Survey compared to the weighted average of all other organisms, Mar 2018 – Jun 2019 presented as A) a time series and (B, C) boxplots for each station.

worms (median 6.5×10^4 ng/g) ranged from 1.8×10^4 ng/g to 2.2×10^5 ng/g and was significantly higher than the weighted average DA concentration of the remaining organisms (median 1.2×10^2 ng/g), which ranged from $< 10 – 2.6 \times 10^3$ ng/g (Fig. 7C, Wilcoxon Rank Sum test, W=256, $p<0.01$). Marine worms consistently exhibited detectable body burdens of DA throughout the time series study. At Station 24, marine worm tissues were above the FDA safety level of 2.0×10^4 ng/g in 94% (15/16) of samples collected during the time series.

Measured sediment DA concentrations did not directly correlate with DA concentrations in the tissue of co-located benthic infauna (Fig. 8). DA was routinely detected in benthic infauna throughout the 16-month study period, but largely not detected in co-located sediment samples.

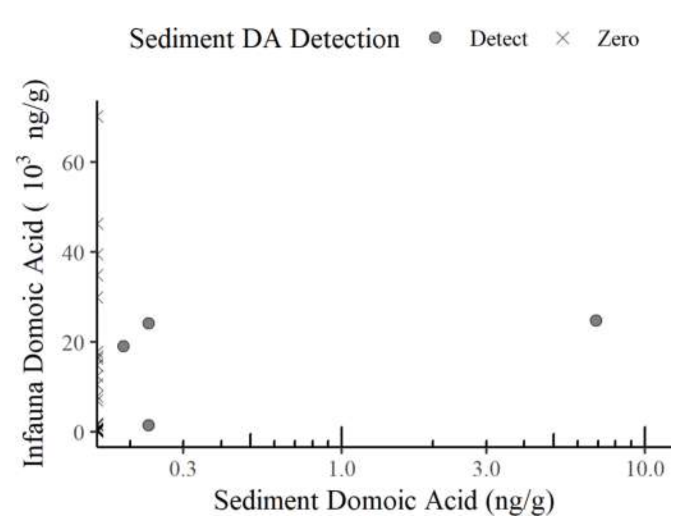

Fig. 8. Sediment domoic acid (ng/g) versus infauna tissue domoic acid (10^3 ng/g) from co-located samples collected during the Monthly Revisit Survey. Note x-axis is plotted on a log scale.

4. Discussion

4.1. Domoic acid in sediments and linkages to surface blooms

The 2018 Bight Program sampling documented geographically widespread presence of DA throughout the SCB, with detectable DA in the sediments in 54% of the continental shelf area. Reports of DA in sediments prior to the present study have been geographically limited to a few stations within the Santa Barbara Basin and the San Pedro Basin.

Between 2001 and 2005, 11 surficial sediment samples (0 - 2cm) collected from 2 stations in the Santa Barbara Basin and San Pedro Basin had concentrations ranging from 17 to 38 ng/g DA in dried sediment (Sekula-Wood et al., 2009). A 28-station survey of surficial sediment samples conducted in the Santa Barbara Basin as part of the Bight '08 Program detected DA at 8 stations, with observed concentrations that ranged from 1.2 to 8.0 ng DA per gram sediment (Sekula-Wood et al., 2011).

The results of the present study identified shelf strata where DA concentrations and presence were higher relative to the continental shelf area as a whole. DA was most commonly observed in the mid-shelf stratum (67% of the mid-shelf area) compared to the spatial extent of DA observed in inner (27% of inner-shelf area) and outer-shelf strata (40% of outer-shelf area). These observations, for the most part, align with onshore to offshore patterns in DA distributions observed during blooms. Multiple studies have reported offshore concentrations of DA are generally higher than those observed at nearshore monitoring stations (Smith et al., 2018; Umhau et al., 2018). This may partly account for the lower observations of DA in the inner-shelf, although given this pattern it might be expected that the spatial extent of DA observed in the mid-shelf and outer-shelf strata might be more comparable. The reduced spatial extent of DA in the outer-shelf sediments may be a result of increased horizontal transport at the outer-shelf stations compared to the mid-shelf stations. It is also possible that the decomposition rates of DA may vary with depth.

The mechanisms governing DA dispersal patterns to the benthos need to be better characterized to accurately estimate toxin transport to determine where benthic DA hot spots may exist. While blooms of *Pseudo-nitzschia* have been observed throughout the Bight, some sub-regions of the Bight have been identified as regions where DA concentrations and *Pseudo-nitzschia* cell abundances are seasonally high, presumably due to retentive circulation patterns and other factors conducive to bloom development. Such regions include the Santa Barbara Channel (Anderson et al., 2009; Anderson et al., 2006; Umhau et al., 2018), Santa Monica Bay (Seubert et al., 2013; Shipe et al., 2008), the San Pedro Shelf (Schnetzer et al., 2013; Schnetzer et al., 2007; Seubert et al., 2013; Smith et al., 2018) and San Diego (Busse et al., 2006). The results of this study suggested that there may be geographic benthic hotspots that correspond generally to these regions, but additional observations are needed to establish long term patterns (**Fig. 3**). Like many diatoms, toxin containing cells of *Pseudo-nitzschia* form aggregates at the time of bloom termination, facilitating transport from surface waters to the benthos and thereby providing a source of DA to benthic environments (Schnetzer et al., 2017; Sekula-Wood et al., 2011, 2009; Thornton, 2002; Umhau et al., 2018). Sediment trap studies have indicated that transport of surface cells to depth is relatively rapid, with transport rates between 50 to >100 m per day (Schnetzer et al., 2017; Sekula-Wood et al., 2009). Given the reported transport rates of *Pseudo-nitzschia* cells, it is possible that sub-regions with intensified water column blooms may also have increased prevalence and concentrations of DA in the sediments.

The persistence and stability of DA in marine sediments is not well understood. It is possible that DA occurrence in sediments is related to both near term sources and historical deposition. Minimal bloom activity was detected at the pier monitoring locations throughout the SCB in 2018, although 2017 experienced a significant bloom event (**Fig. 2**). Despite that pattern, DA was still prevalent across the Bight-wide survey in 2018 (44% of samples and 54% of shelf area). Therefore, it is possible that the distribution patterns observed Bight-wide in 2018 were still strongly influenced by the water column bloom observed in 2017. Previous work has indicated that DA can adsorb to sediments and clays with adsorption varying based on the composition (Burns and Ferry, 2007). We speculate that that behavior might result in prolonged retention of DA in the sediments. A weak positive trending relationship between DA concentration and percent of fine particles in the present study was observed (**Supplemental Fig. 1**), however focused studies to better explain the occurrence patterns of DA in sediments are warranted.

Interestingly, the presence of DA in sampled sediments was more sporadic across shorter monthly timescales during the 16 months of observations in the Central Bight (March 2018 to June 2019). Concentrations of DA were generally low in samples collected from March 2018 through June 2019 and DA was generally not observed at these stations after the summer of 2018 (**Fig. 2, Fig. 5**). The time-series observations in the spring of 2018 may be showing DA degradation at these locations following the large water column bloom in 2017. This is not fully possible to resolve however, since there are not recurrent observations of the sediment DA concentrations immediately following the bloom event. Additionally, water column sources of DA to the sediments during the Monthly Revisit Survey were not fully characterized given that the water column observation collected at the pier locations only capture very nearshore dynamics and are unable to detect any offshore or subsurface blooms of *Pseudo-nitzschia* that may provide a source of DA to these locations. Previous work in the region points to the occurrence of subsurface *Pseudo-nitzschia* blooms (Seegers et al., 2015). These subsurface blooms might provide a cryptic source of DA to the benthos. Future studies focused on resolving the presence of DA in the water column offshore and in the benthic environment will help resolve these patterns.

4.2. Persistent domoic acid concentrations in benthic infauna and linkages to the food web

DA was consistently observed in the tissues of benthic infauna throughout the duration of the study, even at times when DA was not detected in sediments. Weighted average DA concentrations exceeded the FDA safety level of 2.0×10^4 ng/g at seven timepoints in the monthly samples (**Fig. 6A**), and even more frequently in the marine worm grouping (**Fig. 7A**). The sources of DA to these organisms is unclear given the poor relationship between DA in the sediments and in the co-located infauna (**Fig. 8**). Significant spatial and temporal variability was observed in the DA concentrations present in the infaunal tissues collected over 16 months in the Central Bight. Significantly higher tissue concentrations were observed at Station 24 compared to Station 28. These stations differ in that Station 24 is situated farther offshore, while Station 28 is more nearshore and had an increased terrestrial influence from the nearby Santa Ana River. The differences in the infaunal DA concentration presumably reflect these differences between stations, which raises questions about the environmental factors that may contribute to increased site-specific risks for exposure to DA.

There are multiple possible sources of contamination of benthic infauna with DA. Given that the uptake and depuration rates of DA for most organisms are not known, the consistent presence of DA in infaunal tissues could reflect long term retention of DA by multiple taxa. Alternatively, our observations may be a result of the bioaccumulation of sub-nanogram concentrations of DA in the sediments that are below the detection limits of the methods used in this study. In an 11 month study in Monterey Bay, CA, DA was detected in 91% of solid phase adsorption tracking samplers (SPATT, a type of passive sampler) deployed at the sediment-water interface while DA was only detected in 9% of the co-located sediment samples (Ziccarelli, 2014). SPATT samplers are time-integrative and sensitive (Kudela, 2017), meaning this result indicates that DA may be persistent at low concentrations, or that DA might be more prevalent in the dissolved phase at the sediment-water interface than bound to the sediments.

When infauna DA concentrations were compared across groups, the marine worms had temporally persistent DA present in tissues. The marine worms also had the highest tissue concentrations compared to bulk-weighted average of all organisms in the other groupings, indicating they might be a major repository for DA in the benthic environment. Although the resolution of the infauna sorting was taxonomically coarse, a number of studies indicate that benthic infauna organisms may differentially acquire and retain *Pseudo-nitzschia* cells and DA. A study in the Gulf of Mexico concluded that the polychaete *Paraprionospio pinnata* was a major vector of DA after finding elevated abundances of *Pseudo-nitzschia* cells in the guts of organisms (Baustian et al., 2018). Observations in Monterey Bay demonstrated the presence of DA in infaunal tissue long after blooms in overlying waters subsided, similar to this study, with particularly high concentrations observed in innkeeper worms (*Urechis caupo*) over multiple years (Kvitek et al., 2008). DA was also prevalent in benthic-feeding flatfish compared to planktivorous species caught at the same time in Monterey Bay (Vigilant and Silver, 2007). Curlfin turbot (*Pleuronicthys decurrens*) had the highest observed concentrations of DA of all the species sampled, and those fish feed primarily on polychaetes which suggests these organisms are a potential vector of toxin transfer (Vigilant and Silver, 2007). Together the observations of the present study and others suggest that characterizing the uptake and depuration rates of specific infauna species could lend a greater understanding of cycling of DA in the benthos and increase the understanding of the routes of transfer to higher trophic levels.

5. Summary

Our study demonstrated that DA is geographically widespread in the continental shelf sediments of the SCB, even in the absence of a water column bloom event. In 2018, over one year after a significant bloom event, DA was present in sediments from 54% of continental shelf area. These observations indicate that DA may persist in the sediment long after water column blooms end. Our study also points to the importance of better characterizing the sources of DA the benthos, along with rates and mechanisms of DA degradation that may contribute to the longevity of the toxin in these environments. Monthly observations of DA in sediment and infauna also revealed that DA may be present in benthic infauna tissues, even when not detected in co-located sediment. The sources of DA to the infauna were not resolved in our study, but the consistent presence of DA in infauna may pose a risk for DA transfer to higher trophic levels. Coarse taxonomic sorting of samples also indicated that DA might accumulate differentially in across taxa and that different taxa may pose different risks for transfer to higher trophic levels. Given that differential DA accumulation may occur, it is also important to identify which benthic taxa have the greatest and most persistent tissue DA concentrations. Without this understanding, it will remain difficult to quantitatively assess bioaccumulation risk to higher trophic levels.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

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