



Consequences of Mouth Closure and Hypoxia-Induced State Changes in Low-Inflow Estuaries: Benthic Community and Trait-Based Response

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Abstract

The southern California coastline hosts low-inflow estuaries that have mouths that periodically close. Low-inflow estuaries can become hypoxic and are then often opened mechanically. The consequences of mouth closure and hypoxia ($< 2 \text{ mg L}^{-1} \text{ O}_2$) on macrobenthic densities, species richness, diversity, composition, and biological traits were evaluated for legacy data generated by the Pacific Estuarine Research Lab for Los Peñasquitos Lagoon (LPL) (1991–2006) and Tijuana Estuary (TJE) (1988–2004). LPL closed at least annually and TJE remained open during the study period. Effects were moderated by zone within the estuary (relative to the mouth) and season. Periodic closure in LPL was associated with raised macrofaunal density and diversity, especially at the mouth, and with suppressed seasonality. Closure favored soft-bodied (non-calcified) non-bioturbating, mobile, epifaunal taxa in LPL with planktotrophic development, large branchiae, and no vision. There were more spionid and capitellid polychaetes, *Traskorchestia traskiana*, *Cerithideopsis californica*, *Tagelus californianus*, and phoronids during closure. In contrast, hypoxia ($< 2 \text{ mg L}^{-1}$) measured during faunal sampling was associated with lower densities in LPL and different taxonomic composition, but no difference in taxon richness or diversity. There were more corphiid amphipods, small snails, tubificid oligochaetes, *Palaemon macrodactylus* (shrimp), and *Trichorixa reticulata* (insects) under hypoxic conditions, and retention of taxa with very large or small bodies and with vision. TJE densities were nearly double those of LPL; taxon richness and diversity (H') were also higher in TJE. TJE hosted more burrowing, large-bodied, highly calcified taxa with planktotrophic development and no vision than LPL. Differences in composition and traits between the two estuaries disappeared in the middle and upper reaches, where ocean flushing was more limited. Historical long-term monitoring data for benthos, such as the data set analyzed here, offer a valuable baseline for evaluating ecosystem response to changes induced by climate, infrastructure development, contamination, or restoration.

Keywords Biological traits analysis · Los Peñasquitos Lagoon · Macrobenthos · Oxygen, Southern California, Tijuana Estuary

Introduction

Low-Inflow and Intermittently Closed Estuaries

Low-inflow estuaries (LIEs) experience small, episodic, and/or seasonal freshwater inflow, and they are commonly found in steep watersheds or Mediterranean climates (Largier et al. 1997, 2013; Nidzieko and Monismith 2013). Small LIEs with narrow tidal inlets along wave-dominated coastlines can experience rapid morphological changes near their mouths, including a dynamic sand and cobble sill (Clark and O'Connor 2019; Ranasinghe and Pattiaratchi 2003). In these estuaries, sill growth is driven by sediment transport into the inlet from offshore via flood tides, waves, and wave-current interactions, and from upstream via the watershed; sill breakdown is driven by ebb tides and river

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discharge driving sediment out of the inlet (Ranasinghe and Pattiaratchi 1999; Behrens et al. 2013; Rich and Keller 2013; Orescanin and Scooler 2018). The low inflow, waves, and sill height can have profound impacts on the circulation, inundation, stratification, and dissolved oxygen in these estuaries (Largier et al. 1992; Gale et al. 2007; Cousins et al. 2010; Largier 2010; Behrens et al. 2013; Harvey et al. 2022). In some of these LIEs, occasional inlet closures occur when the sill is high enough to block tidal exchange with the ocean (e.g., Elwany et al. 1998; Webb et al. 1991; Ranasinghe et al. 1999; Behrens et al. 2013; Rich and Keller 2013; Orescanin and Scooler 2018; Bertin et al. 2019). These are termed intermittently closed estuaries (ICEs) or intermittently closed/open lakes and lagoons (ICOLLs, e.g., McSweeney et al. 2017), with the former used here. ICEs are found worldwide including along the coastlines of California (Largier et al. 1997, 2013, 2019; Elwany et al. 1998), Spain (Moreno et al. 2010), Portugal (Dodet et al. 2013; Bertin et al. 2019), Australia (Ranasinghe and Pattiaratchi 1999; Roy et al. 2001; Gale et al. 2007; McSweeney et al. 2017), South Africa (Snow and Taljaard 2007; van Niekerk et al. 2020), and Chile (Bertrán et al. 2006; Dussaillant et al. 2009). Anthropogenic activities including wetland fill, beach nourishment, infrastructure placement (e.g., roads, parking lots, bridges, and jetties), and upstream dam impoundments all can have profound effects on mouth conditions, with closures becoming more frequent or prolonged where the tidal prism is reduced (Coats et al. 1989). Extended mouth closure involves reduced flushing, changes in salinity (depending on the upstream conditions and anthropogenic modifications), increased stratification, and often hypoxia (e.g., Harvey et al. 2022). For example, a decrease is seen when freshwater inflow builds up from urban runoff (White and Greer 2006).

Consequences of tidal inlet changes for restricted mouth LIE and ICE fauna are documented only sporadically, especially for broader patterns of species diversity or emergent properties such as ecological function. On long time scales, archeological and paleontological evidence have been used to examine relations between inlet condition and shelled taxa such as molluscs, forams, and ostracods (e.g., Miller 1966; Scott et al. 2011). On shorter time scales, Hadwen and Arthington (2006) reported that diversity and functioning of ICOLL communities in Australia were strongly influenced by entrance opening and closing regimes, with influence on diets of fishes and invertebrates. Mouth closure appears to reduce diversity relative to permanently open status (Pollard 1994b; Gray and Kennelly 2003), but there is conservation value to certain species associated with closed states (e.g., steelhead trout in Southern California) as well as temporally variable regimes of opening and closure (Watts and Johnson 2004; Hadwen and Arthington 2006; Bond et al. 2022). For example, in the Carretas-Pereyra Lagoon (Mexico), which closes intermittently but is artificially opened for artisanal fishers (López-Vila et al. 2021), there are half as many species reported as

in a nearby permanently open lagoon (Gómez-González et al. 2012). Functional changes are rarely studied relative to mouth closure, but López-Vila et al. (2021) observed a resilient trophic structure, favoring generalists and omnivory, that appears to withstand closures in Carretas-Pereyra Lagoon. In Carretas-Pereyra Lagoon, limited community complexity, weak species interactions, and early successional stages were considered to contribute to stability under disturbance (López-Vila et al. 2021). Prolonged closure periods, which may be extended due to changing rainfall patterns and water extraction in South Africa, are predicted to favor invasive species (Tagliarolo et al. 2018).

Southern California hosts numerous estuaries (approximately 100) of a wide range of sizes and characteristics, all of which are considered to be low inflow (Doughty et al. 2018). Anthropogenic impacts to these systems became evident soon after European colonization in the eighteenth century, starting with increased sediment loading (and therefore reduced tidal prisms) resulting from grazing cattle removing sediment-stabilizing vegetation from watersheds (Cole and Wahl 2000; Scott et al. 2011). By the early- to mid-twentieth century, these estuaries were heavily modified by urban development including roads and railways, military uses, industrial and agricultural expansion, recreation, and tourism (Zedler 1982). Most estuaries in the region have had disrupted patterns of opening and closure, with some having their mouths opened permanently via hardened structures. Others are subject to increased mouth closure due to disrupted hydrology and reduced tidal scour at the mouth, leading to buildup of sills and bars (Webb et al. 1991; White and Greer 2006; Henning et al. 2012), with impacts on circulation, stratification, and oxygenation (Elwany et al. 1998; Ranasinghe and Pattiaratchi 2003; Harvey et al. 2020, 2022). In some systems, such as Los Peñasquitos Lagoon in San Diego, California, observations that opening of the mouth could drive dramatic recovery of depauperate fauna (Bradshaw 1968; Hubbs and Whitaker 1972) helped spur the development of ecosystem-level plans that include inlet management (Los Peñasquitos Lagoon Foundation and California State Coastal Conservancy 1985). Implementation of the Los Peñasquitos Lagoon Enhancement Plan has improved conditions in the estuary (Desmond et al. 2002; Scott et al. 2011) and also established the monitoring program that generated a portion of the data used in this study.

Hypoxia in Restricted Mouth Low-Inflow and Intermittently Closed Estuaries

Hypoxia, a common and growing occurrence in coastal and estuarine waters, is usually attributed to excess nutrient loading and water column stratification. Nutrient enrichment promotes enhanced primary production followed by decay and excess oxygen consumption (Rabalais 2004).

Stratification prevents ventilation of subsurface waters (Rabalais et al. 2014; Diaz and Rosenberg 2008). Both are exacerbated by global warming (Altieri and Gedan 2015). However, hypoxia can occur in ICEs during mouth closure independent of eutrophication and warming due to diel cycling interacting with low tides, harmful algal bloom formation, or other aspects of climate change (Warwick et al. 2018). California LIEs and ICEs are susceptible to hypoxia given their location along a highly urbanized, upwelling coastline supplying ample nutrient inputs from upstream (runoff) and via oceanic inputs of upwelled water or discharged wastewater (Kessouri et al. 2021).

At the interface between land, sea, and freshwater, estuarine benthos provides trophic support for resident and migratory fishes and birds, and plays a key role in regulating carbon burial, nutrient fluxes, and various biogeochemical processes (Levin et al. 2001). Hypoxia can cause reductions in the numbers, diversity, and size of the benthic organisms and can change the functions they provide. It also affects rates of respiration, feeding mode, bioturbation, aeration, nutrient regeneration, and even vision (Levin et al. 2009; Middelburg and Levin 2009; Conley et al. 2011; Gammal et al. 2017). To date, there have been relatively few focused studies of hypoxia or mouth closure effects on benthic fauna in Southern California's ICEs. However, Desmond et al. (2002) identified both mouth status and dissolved oxygen as influences on community structure of benthic invertebrates in three San Diego systems, including Los Peñasquitos Lagoon and a larger, more consistently open lagoonal system, the Tijuana Estuary.

In addition to traditional approaches of examining metrics of community structure such as diversity and abundance, insight into ecosystem response to changing conditions can be gained by examining functional traits. Biological traits analysis (BTA), which looks at trait structure and composition, has been increasingly used to better assess responses of coastal species in stressed ecosystems (Beukema et al. 1999; Bremner et al. 2006; Bremner 2008). BTA has also been applied to fauna subject to hydrogen sulfide stress at deep-sea methane seeps (Levin et al. 2017) and hydrothermal vents (Dykman et al. 2022). Species may be characterized by a suite of life-history, trophic, allometric, and mobility traits that link to stress vulnerability. The characteristics that allow biological species to survive and reproduce under a given set of conditions are considered to transcend specific taxonomy, and thus yield patterns generalizable across systems with different species. Use of functional trait information may inform spatial management including protected area design (Miatta et al. 2021).

The research presented here explores how benthic fauna responds to mouth closure and hypoxia-induced state changes in restricted mouth LIEs and ICEs. We use a legacy

data set for two restricted mouth LIEs, Los Peñasquitos Lagoon (LPL) and Tijuana River Estuary (TJE). Although TJE is larger, historically, these LIEs were likely more similar than they are now, with inlets that tended to stay open and biotic assemblages reflective of this (Purer 1942; Scott et al. 2011). In recent decades, the inlet condition has represented one of the largest differences between the systems, with LPL experiencing routine inlet closure and TJE experiencing only rare closure events (Harvey et al. 2020). In addition, both systems have been focal areas for long-term monitoring programs established by the Pacific Estuarine Research Laboratory (San Diego State University). Portions of these data have been previously used to explore differences in fish and invertebrates in the two systems, including relationships to disturbance and water quality factors including salinity, temperature, and oxygen (Nordby and Zedler 1991; Desmond et al. 2002). Here, we extend the use of these data to address the general questions: (i) How do traditional community-level metrics (density, diversity, taxonomic composition) and biological traits of restricted mouth LIE benthos respond to change in mouth status and hypoxia? (ii) How do location (both within and across estuary) and seasonality moderate observed responses? We suggest that these data may provide species-level or trait indicators of resistance, vulnerability, or resilience, identify gaps that exist in our knowledge, and highlight additional research that could be done to address the gaps.

To address these questions, we investigated the LPL benthos communities and their traits for (a) differences in periods when the mouth was open vs closed, (b) differential response to closure of benthos in different lagoon zones or seasons, and (c) differences under hypoxic versus normoxic conditions. We also compared the benthic communities of LPL (which closed periodically) to those of TJE which remained open continuously during the study period, examining the effects of season and location on the assemblage and trait differences.

Methods

Study Sites

This study compares macrobenthos community properties and biological traits in two LIEs, one that closes periodically (LPL) and one that remains open most of the time, including during the study period (TJE) (Figs. 1 and 2; Nordby and Zedler 1991; Desmond et al. 2002). LPL is a relatively small estuary (approx. 243 ha) in northern San Diego County, situated at the outlet of the Los Peñasquitos watershed. Historically, its three tributaries were largely dry during summer months. As the watershed developed, however, dry-weather flows into the lagoon

Fig. 1 Los Peñasquitos Lagoon mouth when open (left) and closed (right)



(i.e., urban drool) dramatically increased (Greer and Stow 2003; White and Greer 2006). Over the last 200 years, the lagoon also has been impacted by watershed alteration, local development, and alteration of tidal circulation which has severely compromised the ability of the system to re-open itself naturally (Cole and Wahl 2000; Scott et al. 2011; Henning et al. 2012). Although originally the system was probably mostly open to ocean flushing, by the mid-twentieth century, LPL was closed for extended periods with only brief openings to the sea, and the lagoon was characterized by a depauperate fauna (Miller 1966; Hubbs and Whitaker 1972; Novoa et al. 2016). Restoration activities in recent decades included installation of a new bridge at the mouth to improve tidal exchange, although the mouth still predictably closes every year during late winter or early spring (Fig. 1). The lagoon is allowed to stay closed for weeks, with conditions (including oxygen) being tracked to help guide re-opening, which typically occurs in the spring (Los Peñasquitos Lagoon Foundation 2016). LPL has been a site of long-term abiotic and biotic monitoring, which has been led since the late 1980s by Pacific Estuarine Research Laboratory and Tijuana River National Estuarine Research Reserve (TRNERR) staff.

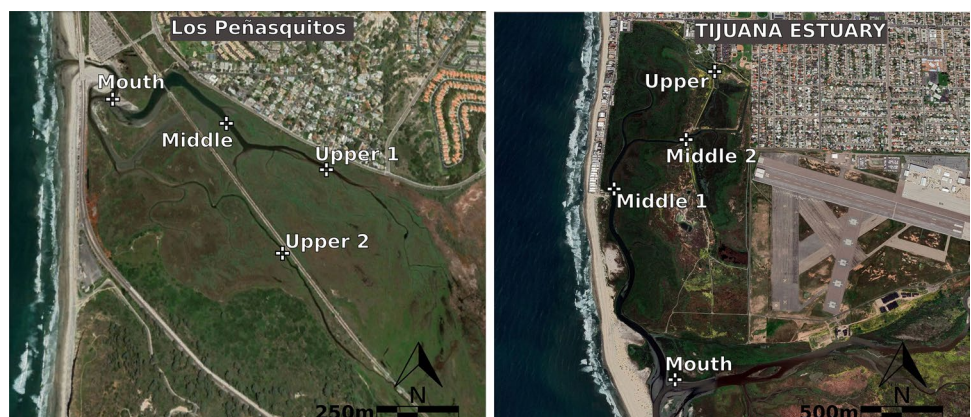
The Tijuana Estuary (TJE) sits at the terminus of a large, bi-national watershed, with 99% of surface flows entering the estuary coming from the city of Tijuana, Mexico. As

such, there can be considerable pollution associated with trans-boundary flows. The construction of a river diverter and wastewater treatment plant has helped reduce contamination, especially during dry weather. Flows associated with wet weather and sewerage failures remain a primary management concern, although plans for increased treatment are also being developed, associated with the 2020 United States Mexico Canada Agreement (USMCA). Historically, the Tijuana Estuary mouth has remained open, with only two recent closure episodes (in 1984 and 2016), both associated with elevated sea levels and large waves from El Niño (Ludka et al. 2018; Young et al. 2018; Harvey et al. 2020). Both closures resulted in major biotic impacts, including loss of endangered Ridgway's Rails and fish kills (Zedler 2010; Harvey et al. 2020). The current TJE management approach is to immediately open upon closure (unlike LPL). TJE is the site of the TRNERR.

Historical Data Acquisition and Use

Long-term benthic monitoring programs were established in TJE and LPL in the 1980s by Dr. Joy Zedler at the Pacific Estuarine Research Laboratory (PERL; San Diego State University), and were later transferred to the TRNERR. The initial goal was to characterize natural variability in benthic assemblages to inform monitoring methodologies in

Fig. 2 Macrobenthos sampling stations in Los Peñasquitos Lagoon (left) and Tijuana Estuary (right)



the context of wetland mitigation and restoration (Desmond et al. 2002). Examination of macrobenthos data from 1987 to 1998 identified streamflow and to a lesser extent dissolved oxygen as predictors of invertebrate assemblages (Desmond et al. 2002). The study reported here extends the data analysis time periods forward and for the first time considers BTA in addition to density, species composition, and diversity in relation to mouth closure and hypoxic events.

Invertebrates were collected quarterly (usually Dec., March, June, Sept.) from shallow channels by PERL from 1991 to 2006 in LPL (Fig. 2 left) and from 1988 to 2004 in TJE (Fig. 2 right). Four LPL stations were monitored that encompassed 3 zones: the upper estuary (stations 1 and 2), the middle estuary, and the lower estuary (Fig. 2 left). The lower estuary station, closest to the mouth and with the greatest ocean influence, is hereafter referred to as the mouth station, although it is set back ~300 m from the ocean (Figs. 1 left and 2 left). Four TJE locations were sampled. These were categorized as upper (tidal linkage), middle (1, East West Channel; and 2, South Coast Channel), and mouth (Fig. 2 right). The Tidal Linkage site, located in the upper estuary, was a channel created in 1997 to enhance flushing and connection between historical sewage disposal ponds and the natural marsh.

At each station, three 15-cm diameter cores (176 cm²) were taken with cylindrical clam guns, typically to a depth of 5 cm. Sediments were sieved through a 1-mm mesh and retained invertebrates were sorted, identified to species where possible and counted. We obtained the resulting invertebrate data from gray literature annual reports (www.trnerr.org). We compiled a taxon list that spans the period of 1991–2006 (Table S1), using the lowest level of identification possible. Our analyses are based on the assigned taxonomy in the reports, with minor changes to reflect subsequent name changes. We recognize that if we were able to re-evaluate this material today with genetic tools, revised taxonomy, and updated keys, it might yield somewhat different taxonomic assignments. However, our goal was to further explore and extend the use of a comprehensive legacy data set, which also has been the basis for prior analyses (Nordby and Zedler 1991; Desmond et al. 2002).

We identified a set of morphological, behavioral, and functional traits (Table 1) that are recognized as being linked to critical ecosystem functions and services such as secondary production, remineralization, carbon sequestration, or trophic support, and that were assignable for study species based on known morphology and lifestyles. The morphological and behavioral traits we identified correspond roughly to the “response” traits of Bolam et al. (2016) and our functional traits correspond to Bolam’s “effects” traits. These categories distinguish traits underpinning mechanisms from those determining the functional significance of structural changes. We assigned biological traits to each

species based on the lowest level taxonomic identity available (Table S2a, b). These assignments are unlikely to be compromised by taxonomic uncertainty, as closely related species typically share most traits.

Information on mouth status (open/closed) and oxygen status (hypoxic: < 2 mg L⁻¹ O₂ and normoxic: > 2 mg O₂ L⁻¹) was obtained for each LPL station on each sampling date (Table S3). Oxygen measurements from 1991 to 2004 were made manually once on each sampling date using a YSI water meter and from 2004 to 2006 every 15 min with a YSI data logger. This information was compiled from reports and research papers, but the data were not available for all sampling dates. Oxygen data were subject to immense variability associated with time of day, tidal height, and vertical sampling position in addition to mouth status. Information on LPL closure dates was obtained from the Los Peñasquitos Lagoon Foundation (Mike Hastings, pers. comm).

Statistical Analyses

The effects of open vs closed mouth status on Los Peñasquitos macrofaunal density, taxon richness, community composition, and biological traits were tested for all stations and times by zone (upper, middle, mouth) and by season. The effects of closure, location, hypoxia, season and year on faunal density, and taxon richness were analyzed using a distance-based permutational linear mixed model (Univariate PERMANOVA), which allowed us to assess the interaction and significance of a combination of factors in a single model and compensate for lack of linearity and/or normality. Community diversity metrics were calculated using Plymouth Routines in Multivariate Ecological Research (PRIMER v7; Clarke and Gorley 2015) for total species (*S*), density (*N*), Margalef’s richness index (*d*), Pielou’s evenness (*J'*), rarefaction (ES_n), and Shannon’s index ($H' \log_e$, $H' \log_{10}$). The diversity routines were calculated for whole estuaries, zones, and seasons to better explore the differences within and between TJE and LPL.

Biological Community Analysis

Community effects and differences as a function of site, station and season, mouth status, and closure were evaluated using multivariate routines. Taxon counts and abundance were 4th root transformed and a Bray–Curtis similarity resemblance matrix was produced using PRIMER v7. Community classification based on factors (location, season, mouth status) was visualized with bi-dimensional (2d) non-metric multidimensional scaling (nMDS) scatter plots. In this study (unless indicated), the statistical significance level was defined as $P < 0.05$ for all tests. In the presence of significance at the 95% confidence level, post-hoc pairwise comparison tests were used to differentiate the

Table 1 Biological trait categories used for analysis of macrofauna from Los Peñasquitos Lagoon and Tijuana Estuary

Morphological	Behavioral	Functional
Body size Large (> 2 cm) Medium (0.5–2 cm) Small (<0.5 cm)	Motility Sessile Discretely motile Motile	Bioturbation Diffusive burrower Surface bioturbator Upward conveyor Downward conveyor Non-bioturbator
Branchial morphology Branchiae or gills present—foliose Branchiae or gills present—limited No branchiae	Habitat Epifaunal Infauna shallow Infauna deep	Bioirrigation Surface pumping Infaunal pumping No pumping
Calcification Heavily calcified Lightly or partially calcified Not calcified	Dwelling mode (lifestyle) Burrower Permanent burrow Tube builder Errant Attached/sessile	
Surface area: volume High (foliose, tentacles) Medium Low (sphere)	Feeding mode Filter feeder Surface-deposit feeder Subsurface-deposit feeder Herbivore Carnivore Omnivore	
Buccal apparatus Proboscis Jaw Radula Mouth appendages	Reproductive mode (larval development) Direct development Lecithotrophic Planktotrophic Dispersal ability (in water) Adult and juvenile swimming Larval dispersal None Dependence on vision High (e.g., visual predator) Medium (eyespot or light-sensitive pigments) None	

specific differences among the means, including one-way and pairwise comparisons in the community data among factors. Ordination stress, which measures the fit of nMDS, is typically considered acceptable when < 0.20, but large sample sizes can raise stress and cause unnecessary discounting of results (Dexter et al. 2018). Based on the large number of samples in our study (117 for LPL and 201 for TJE), we have chosen to present nMDS plots with stress levels up to 0.24.

Biological Traits Analysis (BTA)

BTA was performed on both weighted and unweighted scores. Weighted analysis, which accounts for the number of individuals exhibiting each trait, provides a more accurate representation of the community functional influence. The unweighted analysis removes the influence of dominant species and might better capture the elimination of species with specific traits under conditions of

mouth closure and hypoxia. Weighted BTA scores were produced based on taxon abundance, summed across all taxa present, and square root transformed. Unweighted BTA scores were produced based on presence/absence transformation of the community data and then summed across all taxa present. A sample (rows) by trait abundance (columns) matrix was generated and used to perform the BTA. The weighted and unweighted BTA scores were analyzed using multivariate techniques with PRIMER v7. A Euclidean distance-based matrix was produced from unweighted BTA scores and Bray–Curtis similarity was used for the weighted scores. The nMDS classification method was used to produce 2-D plots. ANOSIM statistical significance testing was performed and a two-way SIMPER analysis was implemented to identify the BTAs that contributed most to the average similarity and dissimilarity between and within factors. Each of the trait groups was also analyzed separately (ANOSIM) in order to detect factor effects at a more detailed level and to enhance our understanding of the trait/factor relationship.

Results

Los Peñasquitos Lagoon

Open vs Closed Community Structure

Across the entire estuary, macrofaunal densities but not taxon richness differed as a function of mouth status, with higher mean densities when the LPL mouth was closed (2180 ± 581 ind m^{-2}) than open (1544 ± 261 ind m^{-2}) (PERMANOVA: $\text{pseudo}F_{1,116} = 1.294$; $P = 0.027$) (Fig. 3A, C). When mouth status was tested by zone within LPL, only the mouth stations exhibited effects of closure on density (PERMANOVA: $t = 2.26$, $P = 0.017$) and richness (PERMANOVA: $t = 2.62$, $P = 0.014$); the middle and upper stations did not (Fig. 3B, D). Densities were highest in fall and lowest in spring independent of closure status, but spring–fall densities were different only under open status (PERMANOVA: $t = 2.09$, $P = 0.036$) and not under closed status (PERMANOVA: $t = 1.64$, $P = 0.105$).

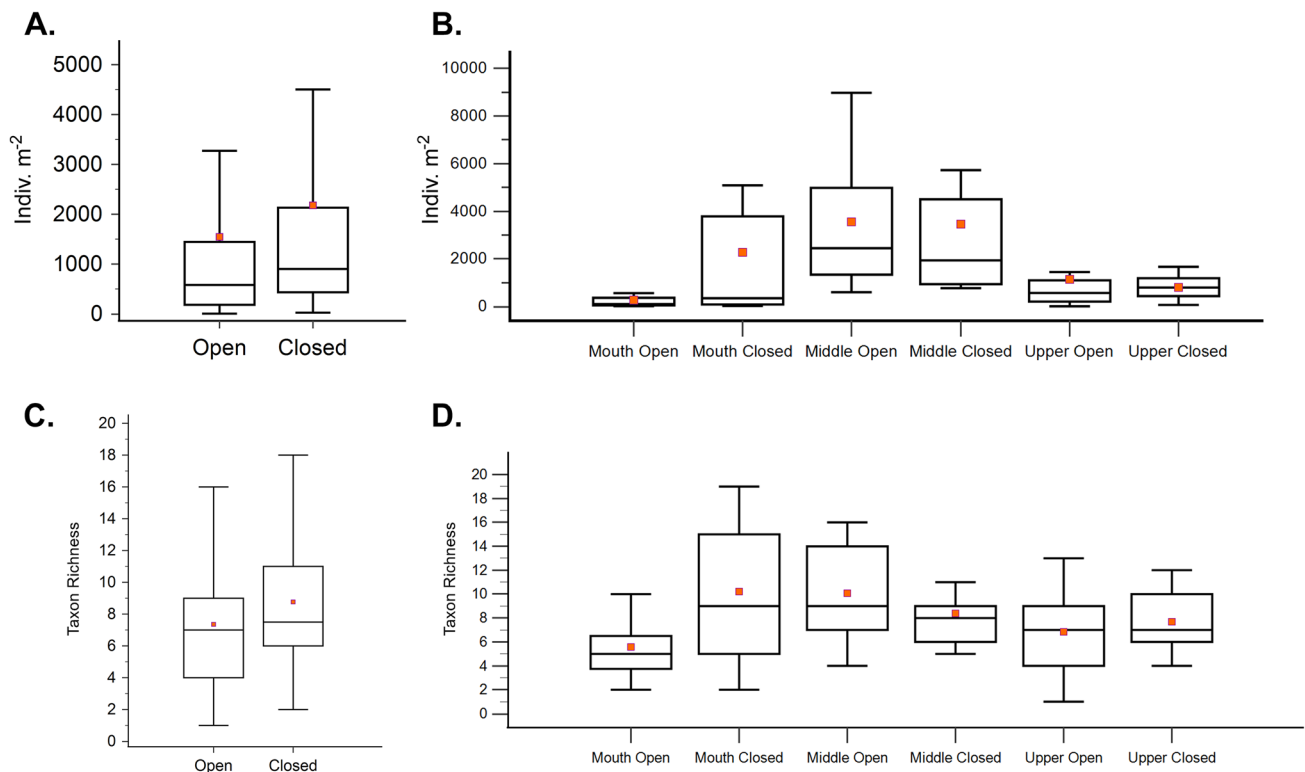


Fig. 3 Density (upper panels) and taxon richness (lower panels) of Los Peñasquitos Lagoon macrofauna as a function of mouth status for all locations combined (A, C) and for each location (B, D). Mean

(orange square), median (horizontal line), two hinges (the 25th and 75th percentiles), and whiskers extend from the hinge to the largest/smallest value at $1.5 \times$ the inter-quartile range

Differences in density and taxon richness among LPL locations were a function of mouth status. When the lagoon mouth was open, the mouth station had lower densities than middle stations (PERMANOVA: $t = 0.008$, $P = 0.0001$) and the upper station had lower richness than middle stations (PERMANOVA: $t = 3.22$, $P = 0.002$) (Fig. 3B, D). When the lagoon mouth was closed, the upper station had lower density than the middle station (PERMANOVA: $t = 2.16$, $P = 0.005$), but richness did not differ among locations (Fig. 3B, D). Overall, closed stations exhibited higher richness, ES(200) and H' than the open stations (Table 2). In the year 1991, which had the longest continuous closure period, the densities in the mouth were much higher than at the inner zones.

Assessed together, LPL stations sampled during periods with an open lagoon mouth had benthic community composition different (85% SIMPER dissimilarity) than during closure (ANOSIM: $R = 0.279$; $P = 0.001$) (Fig. 4A; note stress level of 0.23 reflects poor fit). The most similarity between open and closed stations was detected in 1994, shortly after LPL emerged from extended and frequent periods of closure. Communities differed during open versus closed periods when tested separately for each zone (ANOSIM: upper $R = 0.169$, $P = 0.027$; middle $R = 0.305$, $P = 0.0004$; mouth $R = 0.207$, $P = 0.005$) (Fig. 4B, note stress level of 0.23 reflects poor fit) and season (PERMANOVA: winter $t = 2.86$, $P = 0.0001$; spring $t = 1.51$, $P = 0.039$; summer $t = 2.32$, $P = 0.0001$; fall $t = 1.62$, $P = 0.048$) (Fig. S1)). Based on SIMPER analysis, taxa that contributed to differences during open and closed periods were primarily non-*Capitella* capitellids, *Traskorchestia traskiana*, *Polydora* complex (including *Boccardia* spp., *Polydora nuchalis*, other *Polydora* spp., *Dipolydora* spp., and *Pseudopolydora* sp.), *Cerithideopsis californica*, *Tagelus californianus*, and phoronids, which dominated in closed conditions, and Tubificidae, *Streblospio benedicti* (an invasive species), microgastropods (e.g., *Acteocina inculta*), and amphipods (Corophiidae, *Grandidierella japonica* which is another invasive, and unidentified amphipods), which dominated in open conditions (Fig. 5; Tables S4 and S5). Notably, seasonality was suppressed during closure, such that seasonal differences were not detected in community composition during closures. In contrast, during open periods, pairwise seasonal comparisons yielded community differences between all seasons except spring and fall (Fig. S1).

Open vs Closed Biological Traits Analysis

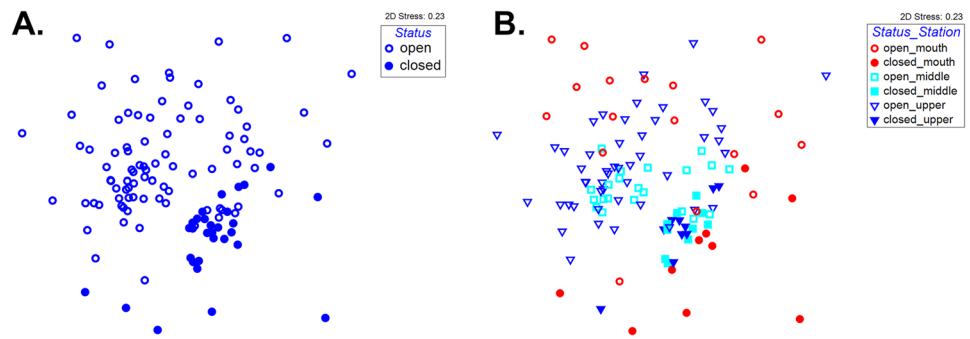
Biological traits did not differ in LPL open vs closed communities when weighted for taxon abundance. This was true for all stations combined (ANOSIM: $R = 0.009$, $P = 0.590$) and for stations compared separately within upper, middle, and mouth zones. In unweighted analyses (focused on

Table 2 Mean diversity statistics for macrofauna of Los Peñasquitos Lagoon (LPL) (A) during periods when the mouth is open versus closed; (B) during hypoxic and normoxic conditions; (C) for all sites combined, mouth, middle, and upper zones; (D) for Tijuana Estuary (TJE) for all sites combined and for SC (= middle 1) and EW (= middle 2), M = mouth, TL=upper. d , Margalef's index; J' , Pielou's evenness; $ES(200)$, rarefaction index; H' , Shannon–Wiener index; SE , standard error

	d	J'	ES(200)	$H'(\log_e)$	$H'(\log_{10})$
A					
LPL closed	0.96	0.66	6.61	1.23	0.53
SE	0.05	0.02	0.32	0.05	0.02
LPL open	1.12	0.61	7.37	1.25	0.54
SE	0.09	0.03	0.55	0.08	0.04
B					
LPL_Normoxia (mean)	1.06	0.68	6.98	1.22	0.53
SE	0.13	0.05	0.82	0.10	0.04
LPL_Hypoxia (mean)	0.96	0.61	6.87	1.23	0.53
SE	0.05	0.02	0.32	0.06	0.03
C					
LPL_ALL (mean)	1.00	0.65	6.80	1.23	0.54
SE	0.04	0.02	0.28	0.04	0.02
LPL-Mouth (mean)	1.082	0.731	6.513	1.252	0.544
SE	0.11	0.04	0.69	0.09	0.04
LPL-Middle (mean)	1.09	0.62	7.77	1.37	0.59
SE	0.07	0.03	0.43	0.07	0.03
LPL-Upper (mean)	0.924	0.626	6.425	1.155	0.501
SE	0.06	0.03	0.37	0.07	0.03
D					
TJE_ALL (mean)	1.58	0.66	11.91	1.69	0.73
SE	0.04	0.01	0.31	0.03	0.02
TJE-Mouth (mean)	1.43	0.66	11.04	1.61	0.7
SE	0.08	0.02	0.56	0.07	0.03
TJE-SC (mean)	1.74	0.68	13	1.77	0.77
SE	0.09	0.02	0.61	0.06	0.03
TJE-EW (mean)	1.77	0.66	13.2	1.81	0.79
SE	0.08	0.02	0.57	0.06	0.03
TJE-TL (mean)	1.18	0.61	8.96	1.43	0.62
SE	0.06	0.03	0.45	0.07	0.03

taxon occurrence), open vs closed stations had different traits both for all stations combined (ANOSIM: $R = 0.102$; $P = 0.025$) (Fig. 6A) and for the mouth station alone (ANOSIM: $R = 0.26$, $P = 0.009$) (Fig. 6B and Table S6). The upper and middle stations did not exhibit effects of closure on unweighted traits. When zones were combined and analyzed by season, there were no mouth status effects on unweighted or weighted traits (ANOSIM: all $P > 0.05$). Key trait response to mouth closure varied depending on estuarine zone and mouth status (Fig. 7). Closure events appear to suppress carnivory in the upper and middle zones, and deep burrowing, high vision dependence, and calcification

Fig. 4 nMDS plots of community composition in Los Peñasquitos Lagoon as a function of **A** mouth status and **B** zone and mouth status



at the mouth. However, in the mouth zone, closure seems to benefit the traits that negatively respond to mouth closure in the middle and upper estuarine zones (Fig. 7). Perhaps, this reflects down-estuary migration of individuals with these traits from the upper zones.

There was an effect of season on weighted traits (ANOSIM: $R=0.076$, $P=0.024$), with differences between spring and fall (ANOSIM: $R=0.106$, $P=0.025$; 38% SIMPER dissimilarity) and summer and winter ($R=0.046$, $P=0.044$; 33% SIMPER dissimilarity). Most of the spring-fall trait differences involve higher numbers in fall of shallow infauna, burrowers/subsurface-deposit feeders, lecithotrophs, infaunal pumping, and species without branchiae, vision, or

calcification. Fall traits resembled many of those linked to closed status—planktotrophic development, larval dispersal, no vision, errant, epifaunal/high motility, no bioturbation, large branchiae, and high surface area. Only high calcification and medium body size were distinctive from the “closed”-status traits. Most of the winter-summer trait differences involve higher numbers in summer of individuals with no bioturbation, dispersal or vision, small bodies, infaunal pumping, small surface area, and shallow burrowing. Notably, seasonality with closure status as a cofactor did not affect traits (ANOSIM: $R=0.067$; $P=0.085$).

Trait modalities (categories) analyzed separately were unaffected by open vs closed mouth status when weighted (by numbers of individuals), but, when unweighted (occurrence only), body size (ANOSIM: $R=0.094$; $P=0.04$) and reproductive mode (ANOSIM: $R=0.102$, $P=0.03$) varied with mouth status. Relative to open conditions, under closure, there were fewer small but more medium and large taxa, as well as more species with planktotrophic larvae, non-bioturbators, surface bioturbators, and taxa with large branchiae.

Hypoxia

Macrobenthos densities in LPL were generally lower under hypoxic than normoxic conditions (ANOVA: $F_{6, 89} = 2.59$; $P=0.0415$) (Fig. 8). Community composition trended towards difference under hypoxia relative to normoxia (ANOSIM: $R=0.182$; $P=0.06$) (Fig. 9A, note stress level of 0.24 reflects poor fit). These composition differences were associated with higher representation of corophiid amphipods, microgastropods (e.g., *Acteocina inculata*), tubificids, the invasive shrimp *Palaemon macrodactylus* and *Trichorixa reticulata* under hypoxia, and better representation of *Polydora* spp., capitellids, *Grandidierella japonica*, *Streblospio benedicti*, *Traskorchestia traskiana*, *Tagelus californianus*, and *Acteocina culcitella* under normoxia (SIMPER; Table S7). Unexpectedly, the taxa prevalent under hypoxia (measured instantaneously) included many of those characteristic of open-mouth status, largely because the limited hypoxia records occurred during periods when the mouth was open, primarily in winter.

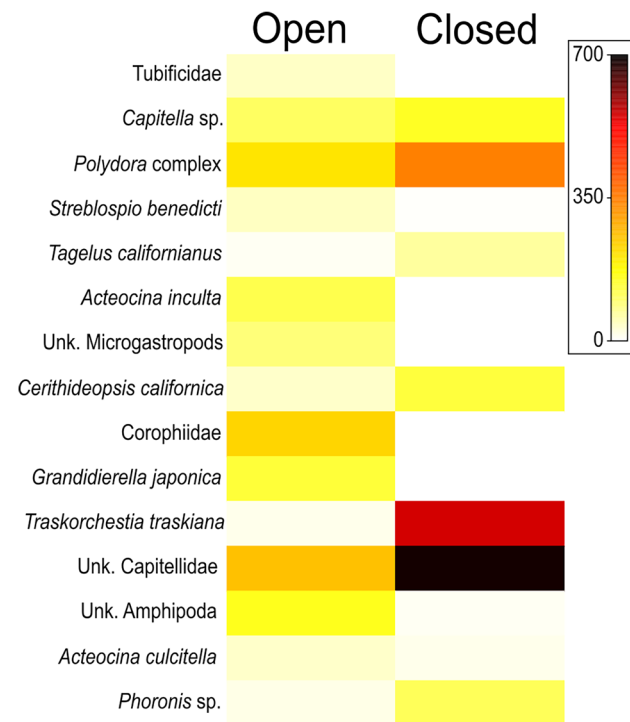
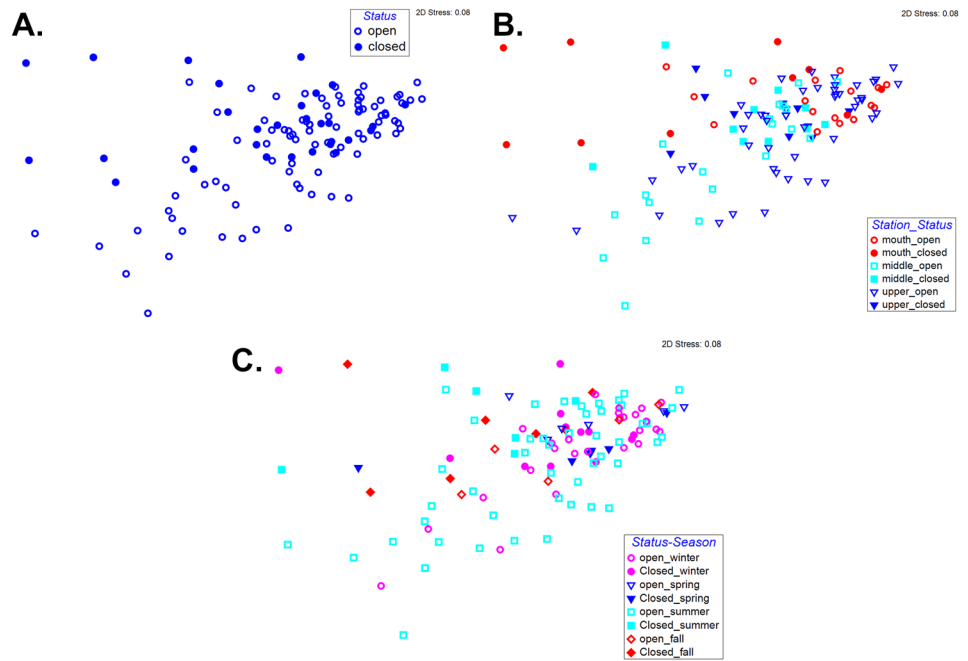


Fig. 5 Heatmap depicting effects of mouth closure on individuals comprising > 1% of total for all stations combined at Los Peñasquitos Lagoon. Scale = ind. m⁻²

Fig. 6 nMDS plot of unweighted BTA for macrofauna at Los Peñasquitos Lagoon as a function of **A** mouth status, **B** zone and mouth status, and **C** season and mouth status



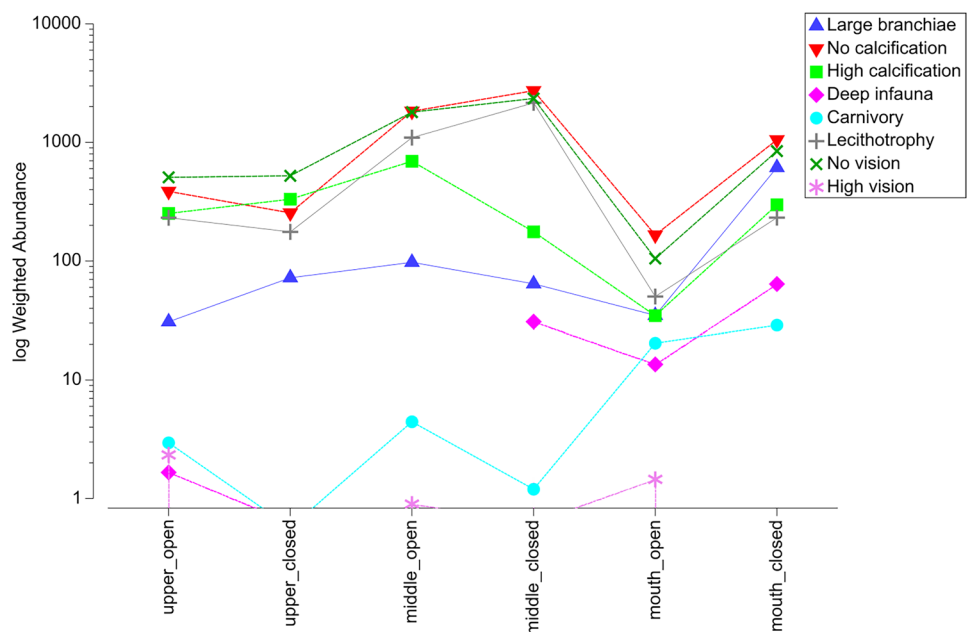
Hypoxia had no influence on unweighted biological trait modalities (ANOSIM: $R=0.066$, $P=0.183$), but when weighted by abundances (Fig. 9B), hypoxia exhibited influence on body size (ANOSIM: $R=0.165$, $P=0.03$) and vision (ANOSIM: $R=0.279$, $P=0.02$), with borderline influence on calcification (ANOSIM: $R=0.124$, $P=0.06$). Representation of mid-size individuals, medium and no-vision individuals, and non-calcified individuals was lower under hypoxic conditions than under normoxic conditions.

Los Peñasquitos Lagoon Compared to Tijuana Estuary

Density, Diversity, and Composition

A comparison of LPL with TJE offers potential insight into long-term effects of differing mouth status. In whole-estuary analyses, TJE macrobenthos differed from LPL macrobenthos in having about threefold higher density (ANOVA:

Fig. 7 Effects of mouth closure on macrofaunal biological traits (weighted by abundance, log-transformed) in different Los Peñasquitos Lagoon zones



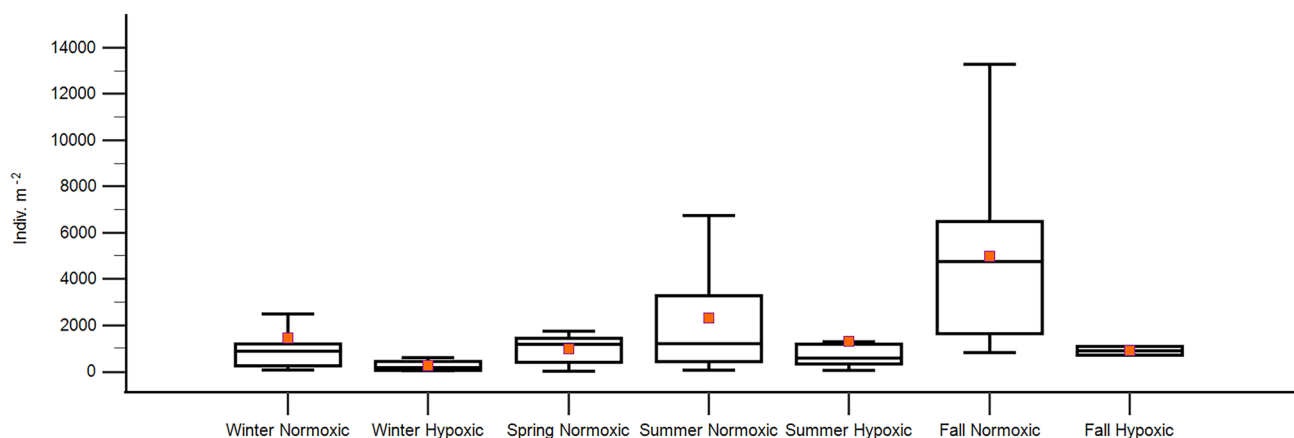


Fig. 8 Density of Los Peñasquitos Lagoon macrofauna as a function of season and oxygen status. Mean (orange square), median (horizontal line), two hinges (the 25th and 75th percentiles), and whiskers extend from the hinge to the largest/smallest value at $1.5 \times$ the inter-quartile range

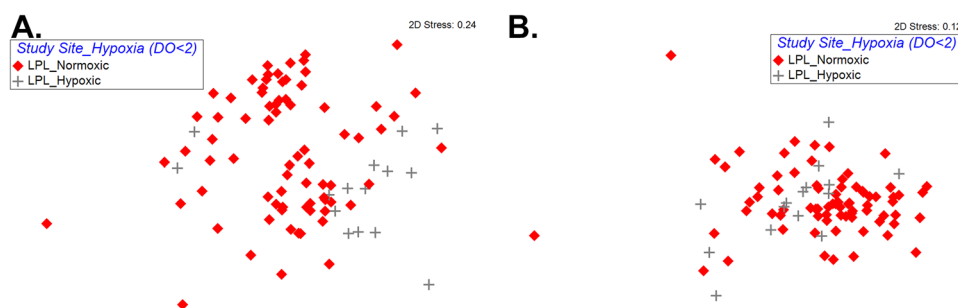
$F_{1,317} = 28.8$; $P = 0.0001$) (Fig. 10A), nearly double the taxon richness (ANOVA: $F_{1,317} = 116.52$; $P = 0.0001$) (Fig. 10C and Table 2), and distinct community composition (ANOSIM: $R = 0.366$; $P = 0.001$) (Fig. S2A). The two lagoons also differed in biological traits for both weighted (ANOSIM: $R = 0.379$; $P = 0.0001$) and unweighted (ANOSIM: $R = 0.185$; $P = 0.001$) analyses. When evaluated by zone however, there were some similarities between estuaries. Notably, TJE densities at the mouth and middle stations did not differ from the LPL middle stations (Fig. 10B, D). TJE exhibited higher taxon richness and diversity across a range of indices than LPL in mouth, middle, and upper zones (Table 2); however, taxon richness was similar at TJE upper and LPL middle stations. For all stations combined, evenness (J') was similar at LPL (0.65 ± 0.02) and TJE (0.66 ± 0.01). At the mouth, LPL tended to have greater evenness (0.73 ± 0.04) than TJE (0.66 ± 0.02); J' did not differ between LPL and TJE in upper zones. Notably, the TJE upper station (Tidal Linkage) had the lowest taxon richness and diversity within TJE and was most similar to those at LPL (especially the middle station), possibly because the Tidal Linkage site, created in 1997, was initially in an early successional stage.

When compared on a zone-by-zone basis (mouth, middle and upper), TJE and LPL community composition differed between estuaries in the mouth and middle zones, but not in the upper zone (TJE Tidal Linkage vs LPL Upper) (Fig. S2B). TJE had better representation of *Protothaca staminea*, other Capitellidae, *Polydora* complex, *Grandidiarella japonica*, *Acteocina inculca*, *Cerithiopsis californica*, *Streblospio benedicti*, the invasive mussel *Musculista senhousia*, *Tagelus californianus*, and *Capitella* sp. (SIMPER; Table S1). LPL had more *Trasorchestia* when closed and more corophiid amphipods when open than TJE (Table S4).

Biological Traits

In whole-estuary analyses, biological traits differed between TJE and LPL for unweighted (ANOSIM: $R = 0.185$; $P = 0.001$) (Fig. 11A) and weighted (ANOSIM: $R = 0.379$; $P = 0.0001$) analyses (Fig. 11B); similar differences were observed when TJE was compared to LPL during open (ANOSIM: $R = 0.454$; $P = 0.0001$) and closed periods (ANOSIM: $R = 0.387$; $P = 0.0001$) in weighted analyses (Fig. 11A), so the difference between estuaries is not linked directly to mouth state at the time of sampling. Unexpectedly

Fig. 9 nMDS plot of macrofauna at Los Peñasquitos Lagoon (LPL) reflecting **A** composition and **B** weighted BTA during normoxia ($O_2 > 2 \text{ mg L}^{-1}$) versus hypoxia ($O_2 < 2 \text{ mg L}^{-1}$)



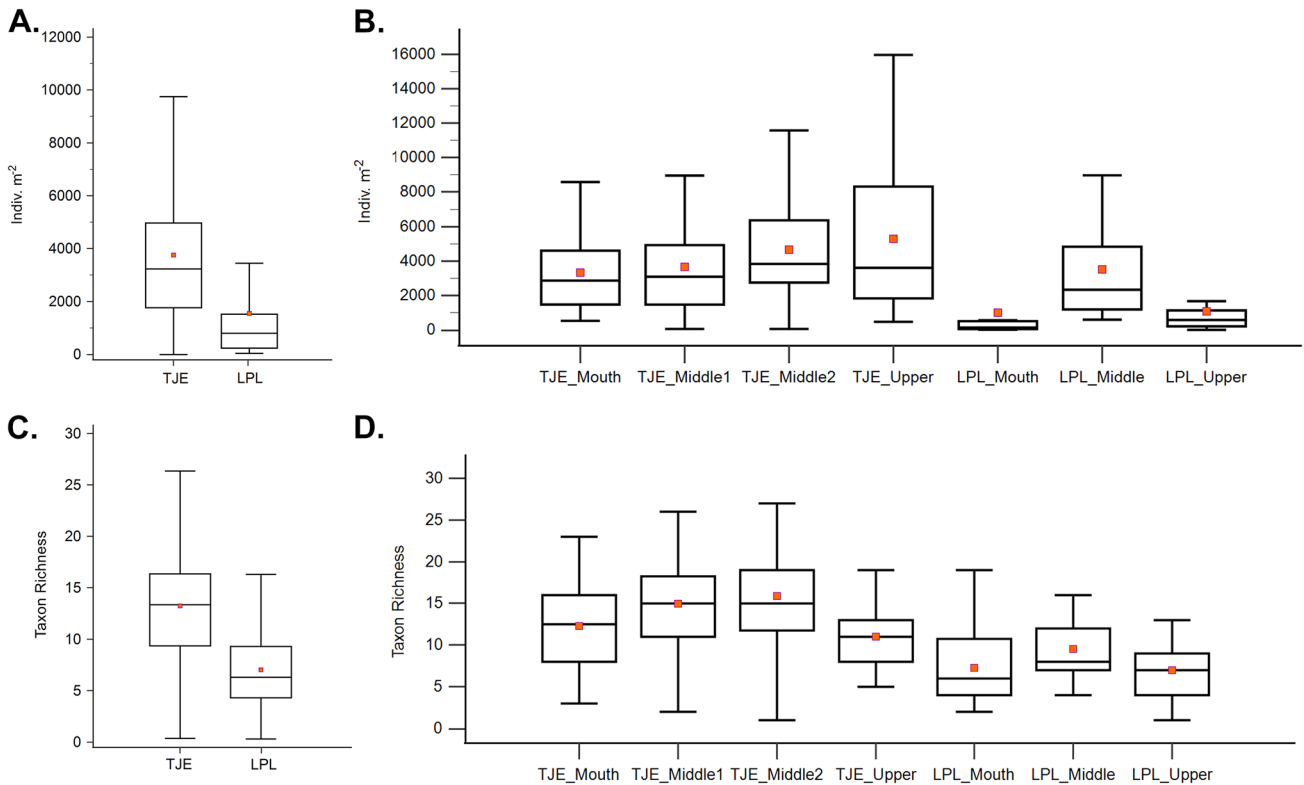


Fig. 10 Comparison of density (**A, B**) and taxon richness (**C, D**) between the Tijuana Estuary (TJE) and the Los Peñasquitos Lagoon (LPL) for the whole estuary (**A, C**) and by location (**B, D**). Mean

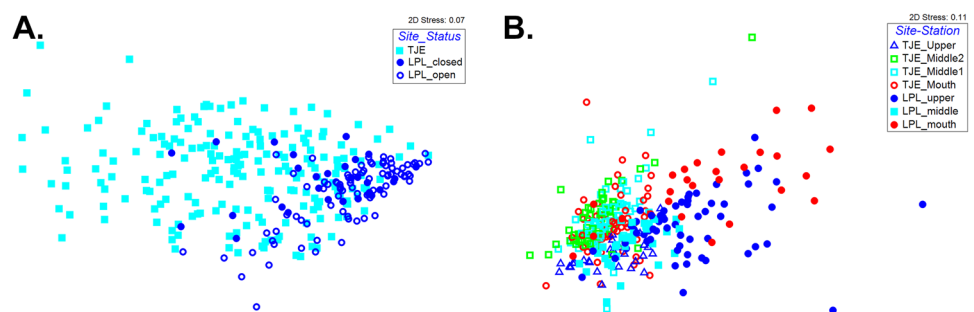
(orange square), median (horizontal line), two hinges (the 25th and 75th percentiles), and whiskers extend from the hinge to the largest/smallest value at $1.5 \times$ the inter-quartile range

however, in unweighted analyses, TJE and LPL traits differed only when LPL was open, not when it was closed. Traits more prevalent in TJE than LPL (when both open and closed) were planktotrophic larval dispersal, large surface area, no vision, buccal appendages, large branchiae, large body, higher calcification, and burrowing (based on unweighted analyses). Weighted analyses detected several different dominant traits in TJE relative to LPL: high calcification, discretely motile, large body size, surface bioturbation, surface pumping, surface-deposit feeding, large branchiae, no vision, both planktonic larval dispersal and no dispersal, large surface area, burrowing, shallow infauna, no bioturbation, and presence of a radula.

Discussion

Benthic fauna has long been sampled for assessments of estuarine condition (reviewed by Diaz et al. 2004), and approaches such as traditional species-based assessments and examination of traits can allow for distinguishing systems with differing environmental conditions (Brauko et al. 2020). The analyses of historical benthic data in LPL and TJE, coupled with available information on conditions such as mouth status, reveal that there are observable differences on relatively short time and small spatial scales, both within and across systems. Many interacting factors beyond those examined here (e.g., salinity, sediment properties,

Fig. 11 nMDS plots of **A** unweighted BTA at Tijuana Estuary (TJE) and Los Peñasquitos Lagoon (LPL) with mouth open vs closed and **B** weighted BTA in TJE and LPL as a function of location (see Fig. 2)



and circulation) are likely at work in producing observed patterns, and furthermore, detailed studies (including manipulative experiments) would be warranted to increase predictability and mechanistic understanding. However, the recognition that there are discernable differences correlated to factors of keen management interest such as mouth status and dissolved oxygen highlights the value of long-term monitoring programs in the complex, altered, and highly managed lagoonal systems of southern California.

Mouth Status and Community Structure

Tidal inlet dynamics in many restricted mouth LIEs and ICEs, especially in urbanized areas, has been greatly modified, and mechanical mouth opening is now a common management strategy in many temporarily closed estuaries in South Africa (Whitfield et al. 2012; Adams and Van Niekerk 2020), Australia (Roy et al. 2001), and California (Elwany et al. 1998). Such activities can have effects on intertidal biota, both through direct effects associated with disturbance during opening (such as occurs with bulldozing beaches, Peterson et al. 2000) and changing flow regimes (Van Niekerk et al. 2005). The finding that LPL supported higher densities and diversity at the mouth when closed than open may be due to loss of accumulated organic matter, larvae, and benthic individuals upon breaching. It is also possible that fewer species can tolerate the morphodynamic activity, strong waves, and highly variable salinities experienced when the mouth is open. In a comparison of permanently open LIEs and temporarily open/closed estuaries of South Africa, Teske and Wooldridge (2001) observed higher macrofaunal diversity in open systems, and higher densities in closed systems. Carrasco et al. (2010) found that zooplankton abundances were highest during closure for South African estuarine ecosystems that are seasonally connected to the sea; often biomass and accumulated organic matter are lost after estuaries open (Flores-Verdugo et al. 1987; Netto et al. 2012). Pollard (1994a) in a comparison of a permanently open and intermittently open lagoon in New South Wales Australia found higher fish diversity in the open system, but higher biomass and fisheries resources in the system that closed periodically. The trends in these studies are consistent with our observations of higher densities during closure in LPL, and higher diversity in TJE than LPL, but not with higher overall densities in TJE than LPL. We note, however, that higher densities or species richness are not necessarily an indicator of system health, including in southern California estuaries. For example, high abundances are often characteristic of enriched or degraded areas in estuaries (Pearson and Rosenberg 1978; Dexter and Crooks 2000). Southern California is heavily invaded by non-native species which can increase local species counts, and most invaders are found in the region's estuaries (Crooks and Suarez 2006; Priesler et al. 2009; Crooks et al. 2016).

Mechanical opening of LIEs to the ocean can lead to loss of taxa (particularly freshwater species) or lead to fish kills

resulting from algae-induced low dissolved oxygen (Pollard 1994b). In April 2020, red tide waters (*Lingulodinium polyedra*) originating in open coast waters were trapped in LPL after mouth closure. Within days, production and decay led to severe oxygen loss with faunal density decline (S. Giddings personal observation; Neira et al. 2022). Breaching of a temporarily closed estuary in southern Brazil led to an initial 90% loss of macroinvertebrate density and 50% loss of biomass but limited effect on diversity (Netto et al. 2012). In the Southern Baltic, Jamno Lagoon loss of seawater inflow triggered 50% loss of invertebrate density and 60% loss of biomass, but no effect on Shannon diversity (Obolewski et al. 2018). In South Africa, breaching by river flooding leads to population crashes that do not recover until closure (Whitfield et al. 2012). However, as we found in LPL, proximity to the mouth determines variability and response to breaching for most taxa; these breaching effects are mediated by salinity and microphytobenthic biomass in Brazil (Netto et al. 2012) and by chlorophyll *a*, pH, and salinity in the Baltic (Obolewski et al. 2018). Notably, closure can also lead to harmful algal blooms and onset of hypoxia (e.g., Lemley and Adams 2020; Harvey et al. 2022).

The diversity patterns observed within an estuary under open vs closed mouth status do not necessarily mirror differences between permanently open vs intermittently closed estuaries. For example, LPL had reduced taxon richness relative to the permanently open TJE, but LPL exhibited higher richness overall when its mouth was closed than when the mouth was open. Collectively, ICEs often have reduced diversity relative to permanently open ones (Teske and Wooldridge 2001). However, as a group, LIE heterogeneity in both space and time (driven by mouth opening) can support high combined biodiversity, highlighting their conservation significance (Watts and Johnson 2004). Isotopic analyses indicate that even during periods of closure, lagoon fauna typically use more marine than terrestrial carbon food sources as they are likely more labile (Hadwen and Arthington 2006).

We documented 153 taxa in TJE and 68 at LPL. These values bracket the 87 taxa recorded in the permanently open Mhlathuze Estuary in South Africa (Izegaegbe et al. 2020). TJE and LPL taxon richness is generally higher than reported by Whitfield et al. (2008, 2012), who noted that permanently open estuaries in South Africa typically have 42–62 species, whereas those with strong freshwater influence have only 23–32 species. High dominance was seen in both TJE (11 taxa accounting for 80% of individuals) and LPL (9 taxa accounting for 80%). Although richness is much higher in southern California, likely in part due to high numbers of invasive species, the doubling of taxon richness in permanently open relative to periodically closed estuaries is similar to those in South Africa. Thirty years ago, Nordby and Zedler (1991) documented 58 benthic invertebrate taxa in TJE with equal representation of polychaetes and bivalves. In LPL,

they noted reduced salinity due to hydrologic disturbance which most strongly affects bivalves. We observed greater densities of snails (including *Cerithideopsis californica*), *Grandidierella japonica*, and spionids as well as the bivalve *Protothaca staminea* in TJE than LPL. Nordby and Zedler (1991) documented relatively few spatial patterns in fish and benthic invertebrate distribution within LPL. Prevalent taxa were those tolerant of salinity shock and hypoxia, which were easily reintroduced during brief periods of mouth opening, or from freshwater inflows. Our analyses of these same estuaries, which extended to 2006 and examined LPL dynamics at much higher spatial and temporal resolution, documented distinctions between mouth, middle, and upper stations during both open and closed phases.

A key finding was that different regions or zones of an estuary will experience different degrees of ocean flushing and thus may experience effects of mouth closure very differently. Within LPL, community composition at the mouth differed from that in the upper and middle zones, but the upper and middle zones had similar community structure to each other and to the communities in Tijuana Estuary (Fig. S2B). In contrast, the biological traits of each LPL zone differed from each other and from the TJE zones, in both weighted and unweighted analyses (Fig. 11). Similar to Netto et al. (2012), we note an interaction of mouth status and site, suggesting that mouth management decisions may need to incorporate spatial heterogeneity within ICEs as well as among ICEs. Oligochaetes, chironomids, and corophiid amphipods have been identified as key responders to mouth status (Netto et al. 2012; Obolewski et al. 2018). In LPL, corophiid amphipods were indicative of open-mouth status.

Because Mediterranean climate restricted mouth LIEs and ICEs are often small, their diversity may be highly vulnerable to loss from sea-level rise. Doughty et al. (2018) suggest that 1.7 m of sea-level rise could lead to loss of most of the intermittently closing estuaries along the southern California (USA) coast. Our results, which show significant spatial heterogeneity, also point to a potential vulnerability at even smaller magnitudes of sea-level rise, and zonation relative to the mouth will likely shift.

Biological Traits and Function Under Mouth Closure and Hypoxia

We are unaware of any previous BTA studies on the effects of mouth closure on estuarine biota. Many of the traits responding to mouth closure in LPL were both response traits such as morphological features, dwelling habitat, motility, and sediment position, and functional traits such as size, development mode, feeding mode, and bioturbation, based on Bolam et al.'s (2016) categorization. Depending on the zone, mouth closure in LPL favored species response traits involving presence of a proboscis and large branchial

structures, both high and low calcification, no vision, burrowing, or tube building, and functional traits involving loss of carnivory, more or less deep dwelling habit, upward conveyor feeding, subsurface-deposit feeding, bioirrigation (infaunal pumping), shallow infaunal habit, medium size, lecithotrophic development, and larval dispersal. Notably, seasonality also affects functional traits in LPL (Fig. 6C), creating higher representation in summer and fall of many bioturbation- and dispersal-associated traits that unexpectedly dominated under closed conditions.

Several studies have applied BTA to understand effects of hypoxia on marine benthos. Key effects of hypoxia observed in LPL involved body size, vision, and calcification. In a comparison of normoxic and hypoxic habitats off Chile, Pacheco et al. (2011) found hypoxia to favor small size, short lives, asexual reproduction, soft-body design, burrowing, infaunal tube building, filter and subsurface-deposit feeding, and sessile lifestyles. Traits associated with the shallow, normoxic habitat were large and medium size, high longevity, hard-exoskeleton and shell, temporary burrows, free living, epizoic/epiphytic, or crevice habitat, surface-dwelling habit, high motility, omnivory/carnivory, and attachment site provision. Gogina et al. (2020) examined temporal changes in community traits in the SW Baltic over time under differing hypoxia regimes, and was able to identify site differences, specific years, and phases of hypoxia development where oxygenation was associated with specific suites of traits. In general, hypoxic years were associated with sedentary habit, suspension feeding, formation of epibenthic structures, globulose form, medium to large size, longevity over 10 years, and benthic (non-dispersing) larvae. Conley et al. (2011) reported episodic hypoxia in the Baltic favoring species with limited motility and sedentary lifestyles, while free-living species and tube- and burrow-dwelling species, deposit feeders, and predators declined under hypoxia through departure or mortality. Short-lived species with planktonic larvae (i.e., r-strategy) prevailed in oxygen-rich years. Hypoxia-tolerant traits common to these studies include limited mobility/sessile lifestyle and limited dispersal; but longevity and body size patterns differed among investigations. In general, the southern California findings presented here exhibit few parallels with the Chile and Baltic studies.

Long-Term Historical Data and Data Mining

The data sets used in this analysis, collected by PERL, are unusual in that they represent a relatively long (> 15 year) time series, generated in an era when continuous monitoring was generally underappreciated and hard to fund. Although portions of these lagoon data have been subject to excellent analysis in previous decades (e.g., Nordby and Zedler 1991; Desmond et al. 2002), from today's perspective, these data

represent a valuable historical picture of past conditions and assemblages against a backdrop of rapidly changing wetlands subject to climate change, coastal squeeze, habitat degradation, and contaminants. But these estuaries are also currently undergoing restoration and adaptation, and the 1990s and 2000s baseline data can help index the relative success of enhancement activities. Like the California Cooperative Fisheries Investigation (CALCOFI) program, another visionary southern California long-term monitoring program that recognized the importance of integrated environmental and ecological monitoring (Gallo et al. 2019), the PERL sampling of LPL generating the data reported in this study provides valuable input for ecosystem-based management and solution-oriented policy in southern California LIEs going forward (Callaway et al. 2000). Since the PERL data were collected, benthic biologists have recognized that mesh sizes < 1.0 mm are needed to collect juveniles and small species, identify cryptic species, document effects of vegetation on animal distributions, and recognize the critical importance of meiofauna in LIE food webs. They also acknowledge the need for continuous measurement of environmental data that overlaps benthic faunal sampling. Advances in deployed instrumentation for collection of time series data, telemetry of real-time data, and publicly available online data repositories allow increasing accessibility to information that can support management action in southern California LIEs, including rapid response to mouth closure and hypoxia (Mills et al. 2008). Future benthic faunal monitoring in the region's LIEs could embrace all of these opportunities.

LIE Management and Benthos

Managing LIEs, especially ones subject to closure, is complicated but best informed by both detailed information and broad perspectives. The recent fauna of LPL and TJE appears to be quite different, although historically it is likely that the biota would have been more comparable as both were systems characterized by relatively open tidal inlets that supported comparable habitat types (Purer 1942; Scott et al. 2011). While both estuaries have been heavily impacted by anthropogenic activities, the opening/closure dynamics of LPL have been much more severely disrupted, which has caused marked changes in biotic assemblages over the last century. By the 1960s and 1970s, species once common to both TJE and LPL had largely disappeared from the latter due to prolonged closures, fueled in large part by human modification to the watershed, lagoon, and beach (Miller 1966; Hubbs and Whitaker 1972 I; Novoa et al. 2016). For example, the California hornshell (*Cerithideopsis californica*), a nearly ubiquitous member of local intertidal marsh systems which has been present in LPL in recent decades, was noted in 1972 as being “conspicuously absent” in the LPL (Hubbs and Whitaker 1972). Although

long-term monitoring data reveal that LPL had lower densities and diversity than TJE (Fig. 10), and some of this pattern might be attributed to the legacy of a dramatically impoverished fauna just several decades prior, there has been at least partial recovery of many formerly missing taxa in LPL. This in part has been attributed to the management program aimed at tidal inlet maintenance (Bradshaw 1968; Hubbs and Whitaker 1972; Los Peñasquitos Lagoon Foundation and California State Coastal Conservancy 1985; Nordby and Zedler 1991).

Despite the potential benefits of opening closed lagoons such as LPL, tidal inlets and their management are extremely complex, and mechanical opening of tidal inlets is one of the most contentious management issues associated with ICEs (Jacobs et al. 2011; Clark and O'Connor 2019; Largier et al. 2019; Stein et al. 2021). It is clear that naturally closing systems provide a variety of unique functions and services (e.g., support for anadromous fish) that artificial opening can compromise, especially when intermittent systems are made to be permanently open (Jacobs et al. 2011). However, without mechanical opening of inlets, anthropogenically impacted lagoons such as LPL can experience unnatural, prolonged closures as well as watershed inputs that affect biota, including invertebrate communities. Prolonged closure decreases the ability of the system to provide services such as water quality improvement, decreased flood risk, and abatement of mosquito vectors often associated with ponded water. In general, mouth opening should be viewed in the context of trade-offs that inevitably arise with such actions and be informed by both detailed assessment of estuarine condition (including benthic fauna) and broader consideration of socio-ecological factors (Southern California Wetlands Recovery Project 2018).

Stein et al. (2021) highlighted a series of management recommendations for ICEs including the need to (1) develop tools that measure function and identify thresholds for “healthy” systems; (2) identify cumulative and interacting effects of management actions (such as increased flushing) on functions; (3) develop strategies for monitoring, assessment, and adaptive management of flows to inform ongoing management and improve performance of models; and (4) identify sensitive ecological indicators. Fundamental to this is the availability of long-term data to assess the consequences of management action (or inaction), including mouth management, changes to watershed inputs, or use of compensatory mitigation to offset impacts to ICE habitats and functions (Zedler and Callaway 2000; Desmond et al. 2002). Ideally, biotic data can be coupled with high-resolution monitoring of abiotic factors such as water quality, as one limitation of the current study is the relatively infrequent assessment of dissolved oxygen (given that much of these data were collected before widespread use of deployed dataloggers).

Our findings suggest that the definition of healthy may differ for mouth, middle, and upper stations, with different taxa and traits present in each zone. While largely open LIEs may support higher diversity, intermittently closed systems contribute to broader patterns of richness. In terms of potential indicator taxa, some amphipods and gastropods appear to be highly sensitive to mouth status, with densities of some taxa higher under closure and others under open conditions. Amphipods are typically a more taxonomically difficult group, although even higher taxonomic levels have discriminatory ability (e.g., Corophiidae, Fig. 5). Some local amphipods are relatively distinguishable, such as the invasive *Grandidierella japonica*, which has been widely used as a sentinel species for toxicity studies (e.g., Hiki et al. 2019). Molluscs also represent good candidates as indicators (e.g., Novoa et al. 2016). The California hornshell snail, *Cerithideopsis californica*, showed density differences in open and closed conditions (Table S4), and its disappearance from LPL in the 1960s was attributed to prolonged closures (Hubbs and Whitaker 1972). The large-bodied cloudy bubble snail, *Bulla gouldiana*, was more abundant in TJE than LPL (Table S1), and observations of dead, floating shells after mouth closure and hypoxia in the latter system (JAC pers. obs.) suggest its use as a qualitative indicator of degraded conditions. Another conspicuous species, the invasive shrimp *Palaemon macrondactylus*, although rare in the samples (due to its high mobility), did demonstrate increased abundances with hypoxia. This species also has been identified as being indicative of freshwater influence in LPL (Bierzychudek 2022), and this again highlights that there are likely many factors operating simultaneously to affect the distribution and abundance of resident biota in LIEs.

The biological trait analysis conducted suggests that management of mouth status (and thus hypoxia) in LPL affects both response and functional attributes. Changes in sensitive traits such as body size, vision, calcification, carnivory, dwelling habit, bioturbation, and dispersal could affect LIE services such as trophic support for resident and migratory fish and birds, nutrient remineralization, and carbon burial and sequestration. BTA revealed more large-bodied taxa in TJE than LPL, which could imply that regular flushing is required to support high-biomass species. Superimposed on the mouth-related flushing dynamics are changing regional climatic conditions—altered rainfall intensity, warming temperatures, ocean acidification, and rising sea levels—and likely increasing incidence and intensity of red tides. It is unclear whether climate-induced environmental changes that occurred during the 1990s and 2000s contributed to or confounded any of the taxonomic or functional patterns observed. LIE monitoring strategies going forward will need to link community structure and ecosystem function to watershed, ocean, and atmospheric forcing of

hydrology within the estuary. The ability to efficiently and effectively use scientific information in decision-making will become ever more relevant with the rapidly changing global and local conditions already upon us.

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Declarations

Competing Interests The authors declare no competing interests.

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