RESEARCH ARTICLE

Insights into the Establishment of the Manila Clam on a Tidal Flat at the Southern End of an Introduced Range in Southern California, USA

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Abstract

Coastal ecosystem modifications have contributed to the spread of introduced species through alterations of historic disturbance regimes and resource availability, and increased propagule pressure. Frequency of occurrence of the Manila clam (*Venerupis phillipinarum*, Veneridae) in Southern California estuaries has increased from absent or sparse to common since the mid-1990s. Potential invasion vectors include seafood sales and aquaculture, and spread from established northern populations over decades. The clam's post-settlement habitat preferences are, however, uncertain in this region. Our project aimed to identify factors associated with established patches of the clam within a bay toward the southern end of this introduced range. During summer 2013, we sampled 10 tidal flat sites in Mission Bay, San Diego; each containing an area with and without hard structure (e.g., riprap, boulders). We measured likely environmental influences (e.g., sediment variables, distance to ocean). Manila clam densities across the bay were most strongly associated with site, where highest densities were located in the northern and/or back halves of the bay; and weakly correlated with lower porewater salinities. Within sites, Manila clam density was enhanced in the presence of hard structure in most sites. Prevailing currents and salinity regimes likely contribute to bay wide distributions, while hard structures may provide suitable microhabitats (refuge from predators and physical stress) and larval entrapment within sites. Results provide insights into decisions about future shoreline management efforts. Finally, we identify directions for future study to better understand and therefore predict patterns of establishment of the Manila clam in the southern portion of its introduced range.

Introduction

Humans play key roles in the spread and subsequent establishment of species from native to introduced ranges around the world [1]. Estuarine systems are, in particular, highly susceptible

to invasion [2]. Development and use of these coastal ecosystems change historic disturbance regimes and resource availability, and increase propagule pressure raising the likelihood of establishment and eventual spread of non-native species (e.g., [2–4]).

The Manila clam (*Venerupis phillipinarum*, A. Adams and Reeve, 1850), also known as the Japanese littleneck, was introduced from Asia in the 1930s to the northwest coast of North America along with Pacific oysters [5],[6]. Expansion throughout the northwest coast, from British Columbia to Northern California, has been due to planktonic larval dispersal, accidental introductions with transplanted oysters, and intentional introductions of transplanted clams for aquaculture [5–9]. While establishment and spread tend to be heaviest from San Francisco Bay northward [2],[10], the Manila clam appears to be increasing in Southern California based on comparisons among recent surveys, in which the clam was found to be relatively common (e.g., [11],[12]), and earlier studies conducted in the same areas that did not find the clam [2], [13],[14]. Vectors of spread in the southern end of this range probably include sale of live clams, aquaculture [15], and transport from the northern established populations. Influences on establishment within Southern California bays, however, remain uncertain.

In San Francisco Bay, where populations are relatively well studied [6],[10], and in Colorado Lagoon, Los Angeles County [12], the clam ranges from subtidal to high intertidal elevations. Intertidally, it is found on coarse sandy mud, gravel and cobble, and subtidally on oyster shell beds [10]. It survives salinities ranging from 13.5–35 PSU [16], grows and reproduces best within water salinities of 24–31 PSU, and can tolerate [6] or even prefer [16][17] salinities between 10–15 PSU. The clam, like other infaunal bivalves, may also be sensitive to porewater salinities [18],[19]. The surface sediments inhabited by the clam likely track the maxima of bottom water salinities [20],[21] so that only porewater water samples are analyzed in this study. In Mission Bay, as with many other embayments in Southern California, there is relatively little tidal flat area thereby limiting expanses of coarse substrate, and there are few to no dense patches of oysters or shell hash [12],[22],[23]. Salinities tend to range from seawater (34–35 PSU) near the mouth to hypersaline conditions toward the back of the bay (38–40 PSU), but this inverse gradient varies with season (i.e., amounts of precipitation and temperature) and proximity to freshwater inputs [21]. Despite the seeming lack of optimal habitat, the Manila clam has anecdotally been reported around the bay (e.g., [11],[24], C. Gramlich pers. comm.), in particular on soft substrate located next to hard structures, such as immediately adjacent to riprap and boulders (T.S. Talley pers. obs.).

The goal of our study was to increase our understanding of influences on the distribution of the Manila clam in the southern portion of its introduced range. To meet this goal, we tested two hypotheses. First, that Manila clam density throughout Mission Bay would increase with lower salinities and/or coarser sediments. Second, that within sites there would be higher clam densities on tidal flats with hard structure as compared with those without structure.

Materials and Methods

Between June 20th and July 12th 2013, we sampled ten tidal flats around Mission Bay, San Diego, California, USA (32° 46' 40.8", 117° 13' 30"), which has an average spring tide range of 1.7 meters. The tidal flats were broadly chosen to represent the geographic range of the bay, with specific sample locations haphazardly selected within region. Tidal flats were 2.2 to 8.7 km from the mouth of the bay as the water flows (Fig. 1). Each tidal flat consisted of 75–100 m stretches with no hard structure (≤5% rock or debris) and adjoining, similar sized stretches of tidal flat containing hard structure (≥75% cover of boulders or riprap). The riprap and boulders were mostly granite and/or manmade stone blocks ranging in size from 0.1–0.7 cubic meters and piled on the edge of the bay from about 0.75–1 m to over 2 m above mean lower low water (MLLW).
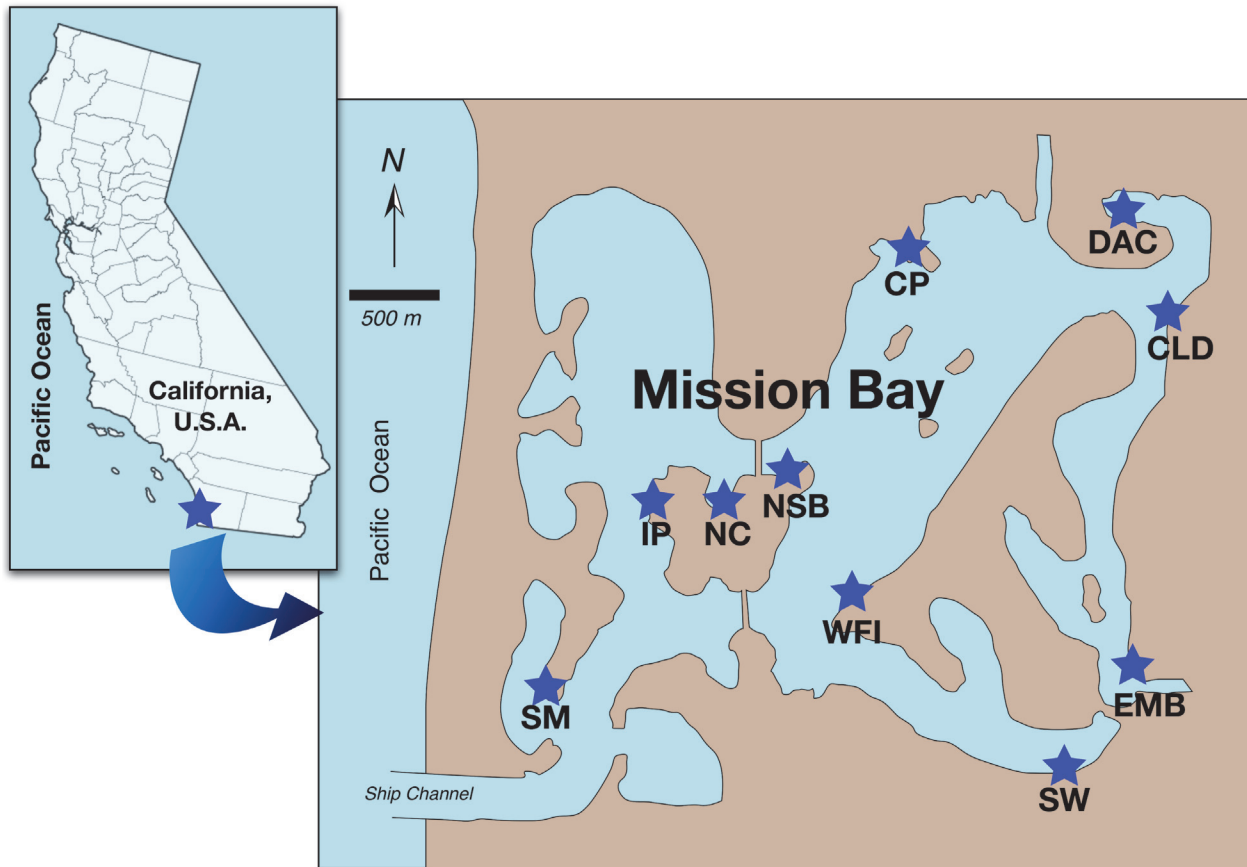
Fig 1. Map of intertidal benthic study sites within Mission Bay, San Diego, California, USA. SM = South Mission Bay, IP = Island Point, NC = North Cove, NSB = North Ski Beach, WFI = Fiesta Island, CP = Crown Point, DAC = D'Anza Cove, CLD = Clairemont Drive, EMB = East Mission Bay Drive, SW = Sea World. The Manila clam was found in all sites except SM and WFI.

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The tidal flat surfaces were located at the same tidal elevation (0.75–1 m above MLLW), and the paired, adjacent flats faced the same direction.

All sites except Crown Point (CP, Fig. 1) were open to public access within Mission Bay Park so did not require special permission to enter sites. The Crown Point salt marsh creek fell within the boundaries of the University of California Kendall Frost Marsh Reserve and permission to conduct the sampling was granted from Isabelle Kay, Reserves Manager at the U.C. Natural Reserve System. All collections were conducted under the California Fish and Wildlife Scientific Collection Permit administered to T.S. Talley (Permit number SC-5295).

Within each of the 10 tidal flats, six sampling points were established: three points on tidal flats with hard structure present and three on stretches with no structure. Sampling points were 25–35 m apart and points in areas with hard structure were located immediately adjacent to the structure on the benthic surface.

At each sampling point in the field, a 0.25m² X 10 cm depth bivalve core was taken and sieved in the field through 1mm square mesh. A 10 cm diameter X 10 cm depth sediment core was taken ≤10 cm away from the bivalve core from an area with no visible debris or organisms. Both the sieved bivalve cores and the intact sediment cores were placed in separate plastic bags and frozen at -18°C until analysis.

In the lab, bivalve samples were re-sieved through 1mm square mesh using tap water to remove remaining fine sediments. Bivalves were removed using a dissecting microscope,

enumerated, measured, and identified to the lowest taxonomic level possible, usually species. Bivalve community variables of total bivalve density, species richness and density of each species were calculated. Manila clam total density, density of adults (defined as ≥2 cm diameter; [6],[7],[10]) and density of juveniles (<2 cm diameter) were also calculated and used in the statistical analyses described below.

Each sediment sample was thawed and homogenized. Pre-weighed and labeled crucibles (25 ml) were filled with sediment, dried at 55°C and reweighed to calculate dry sediment weights. Samples were then combusted and weighed once cooled in a desiccator to calculate percent organic matter content. We measured the porewater salinity by filling a 10 cc syringe containing two 1 cm diameter Whatman no. 1 filter papers with a portion of surface sediment, and squeezing the porewater on to a Leica handheld salinity refractometer. Sediment texture was measured using a Beckman-Coulter LS-230 Laser Particle Sorter that calculated the percent of particles that were in <4μm, 4–63μm, and 63μm—1 mm diameter size classes (i.e., clay, silt and sand size classes). Distance, measured as direct paths of water, between each site and the mouth of the bay at the ocean was measured using Google Earth 7.1.2.2041.

Since sampling of these somewhat motile clams occurred during low tide and we wished to obtain paired samples of bivalves and environmental conditions, we estimated salinity using the porewater water of the surface sediments, which is reflective of overlying bottom water salinities [20].

Differences in the presence (or absence) of each bivalve species among sites and between the presence and absence of structure were tested using two-way ordinal logistic ANOVA. Differences in bivalve densities and sediment variables among sites and in the presence and absence of structure were determined using two-way mixed-model ANOVA using REML (restricted maximum likelihood). Block (site) was treated as a random effect, since each site was chosen haphazardly from among a large population of potential sites across the bay [25]. The mixed-model experimental design allowed us to focus on the main effects (site and presence or absence of structure), regardless of any potential interaction between these random and fixed effects [26]. Sites in which bivalve species were absent were removed from the test of differences in abundance of that particular bivalve. Relationships between Manila clam densities and environmental variables (presence or absence of hard structure, distance from mouth, and sediment variables listed in Table 1) were tested using stepwise multiple regressions with the criteria of p≤0.05 to enter the model and both p>0.05 and r^2≤0.03 to be removed. Relationships between Manila clam density and bivalve species richness and density were tested with Pearson correlations. All analyses were run in JMP Pro 11. Data were first inspected for homogeneity of variances and normality using Kolmogorov-Smirnov and Shapiro Wilk tests, respectively; density data were 4th root transformed and fraction data were arcsin square root transformed to meet assumptions of the parametric tests.

Results

Bay environmental conditions. Sediment texture, organic matter content and porewater salinity were similar between areas with and without hard structure, and only differed with site, but with no strong estuarine gradients from mouth to back of the bay (Table 1A, Fig. 2A). The sites with highest proportions of fine (silt and clay), organic sediments were located in areas with relatively low flushing at the back of the bay (e.g., DAC, EMB; Table 1A; Fig. 1) and/or associated with salt marsh (CP). The highest porewater salinities were also found in relatively low flow areas (DAC, EMB, CP) or at the mouth of the bay (SM), while the lowest salinities were in the mid-bay (NC, NSB, CLD; Table 1A; Fig. 1).

Table 1. Results of two-way ANOVA testing differences in sediment variables (A.) and bivalve variables (B.) between areas with and without hard structure) and among sites in Mission Bay.

| Variable	Structure				Hard structure comparison		Site differences
	p	F	df	n	present	absent	
A. Sediment variables					Average (SE)		
Porewater salinity	0.33	1.0	1	60	34.3 (2)	35.4 (1)	EMB,SM≥DAC,CP≥IP,WFI,SW≥CLD,NC,NSB
%Organic matter	0.08	3.2	1	60	1.3 (0.3)	1.2 (0.7)	EMB> all others
%Sand (63µm-1mm)	0.53	0.4	1	60	80 (4)	82 (5)	SW,SM,WFI,CLD,IP,NSB,NC>DAC,EMB>CP
%Silt (4–63 µm)	0.48	0.5	1	60	18 (4)	16 (4)	CP,EMB>DAC>all others
%Clay (<4µm)	0.90	0.0	1	60	2.3 (0.5)	2.3 (0.6)	CP,EMB,DAC>all others
B. Bivalve variables					Average no. m^{-2} (SE)		
Species richness	0.41	0.7	1	32	1.7 (0.2)	2.0 (0.3)	CLD≥CP≥NSB,EMB≥SW>DAC,NC≥SM≥IP≥WFI
Densities							
Total bivalve	**0.04**	**4.7**	**1**	**60**	**22.5 (6.4)**	**9.2 (3.0)**	CLD≥CP≥NSB,EMB≥SW,DAC≥NC≥SM≥IP,WFI
Total bivalve (minus *V.p.*)	0.56	0.4	1	60	8.3 (2.2)	7.7 (2.8)	CP≥EMB,CLD≥NSB,DAC,SW,SM≥NC≥IP,WFI
Total *V.p.*	**0.03**	**8.0**	**1**	**48**	**16.2 (5.5)**	**1.7 (0.7)**	CLD≥CP,NSB,NC,SW≥DAC,EMB,IP
Adult *V.p.*	**<0.01**	**28.0**	**1**	**36**	**14.9 (6.5)**	**0.7 (0.4)**	CP≥CLD,NSB≥DAC,NC,SW
Juvenile *V.p.*	**0.02**	**5.5**	**1**	**48**	**6.3 (2.4)**	**1.2 (0.5)**	N.S.
Chione fluctifraga (Veneridae)	0.47	0.5	1	42	0.8 (0.4)	1.3 (0.6)	N.S.
Chione undatella (Veneridae)	0.21	1.6	1	36	4.4 (1.4)	1.6 (0.6)	N.S.
Musculista senhousia (Mytilidae)	0.73	0.1	1	36	4.0 (2.1)	4.0 (2.9)	N.S.
Tagelus californianus (Cultellidae)	0.22	1.8	1	12	3.3 (2.6)	7.3 (3.6)	N.S.

Structure presence/absence was treated as a fixed variable, while site (block) was designated as a random variable. N = 60 samples (6 each per 10 sites)
V.p. = Manila clam (*Venerupis philippinarum*). Average (±standard error) of raw (untransformed) variables in the presence and absence of hard structure are shown; bold indicates significant difference between the presence and absence of structure. Significance was determined using Bonferroni adjusted alpha value (initial α = 0.05).

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Bivalve community. A total of five bivalve species were found during this study. Two introduced species were found—the Japanese mussel (*Musculista senhousia*) and the Manila clam. The rest were native species from the families Veneridae, Mytilidae and Cultellidae (Table 1B). Bivalves were present in samples from all sites except WFI (Fig. 1), The presence (or absence) of both *Chione undatella* and bivalves (as a taxon) varied among sites only (ordinal logistic 2 way ANOVA: chi square ≥41, n = 60, df = 19, p≤0.001) while the presence/absence of *Chione fluctafraga*, *M. senhousia* and *Tagelus californianus*, did not differ with site or structure (chi square ≤30, n = 60, p≥0.09).

The highest species richness and total bivalve density was in the northern mid to back half of the bay (CP, NSB, CLD, EMB), with no differences between areas with and without structure (Table 1B). Densities of each bivalve species except Manila clam were similar between areas with and without structure, and among sites (Table 1B.).

Bay-wide influences on the Manila clam. The presence (or absence) of Manila clam adults and juveniles was dependent on site and not on the presence or absence of structure (ordinal logistic 2 way ANOVA: chi square ≥43, n = 60, p≤0.001). Densities of the adults and juveniles were also most strongly associated with site as well as weakly negatively correlated with porewater salinity (Table 2). Of the sites where the Manila clam was present, the highest total and highest adult densities were located in the northern and back halves of the bay (CLD, CP, NSB; Fig. 1); while density of juveniles did not differ with site (Table 1B). These sites were often
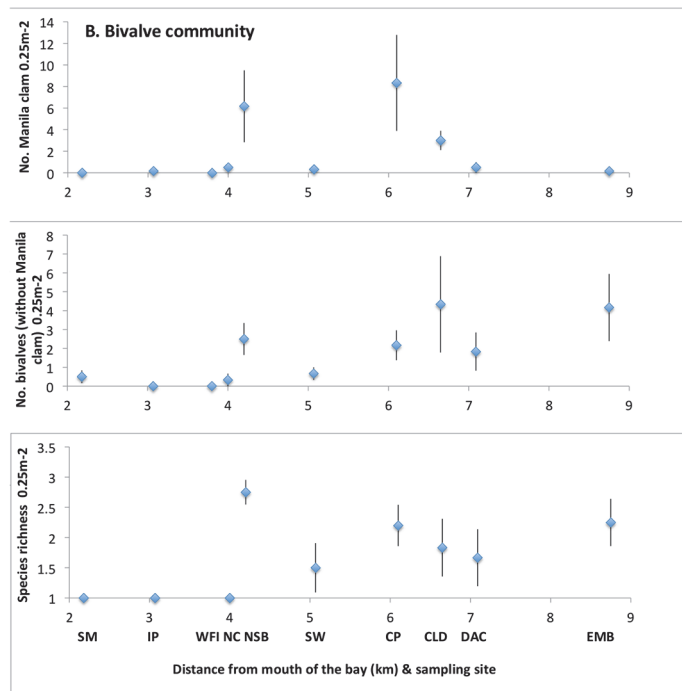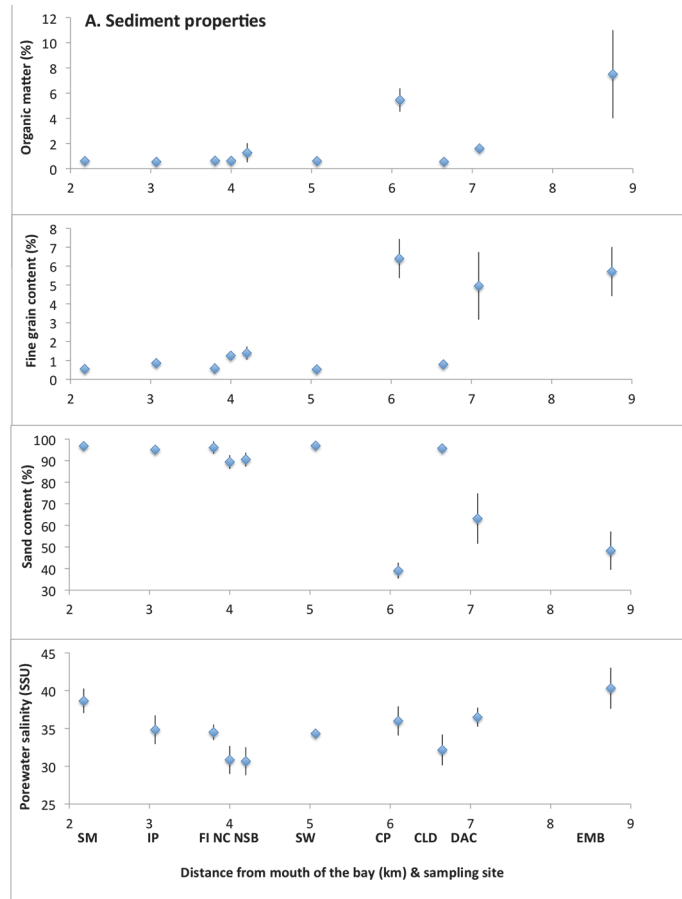
Fig 2. Average (±SE) sediment variables (A.) and bivalve community variables (B.) in each study site within Mission Bay, San Diego, California, USA. N = 6 samples per site. Fine grained sediment content refers to % silt + % clay.

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similar to those that contained the highest densities of other bivalves (Manila clam vs. other bivalve density: r = +0.42, p = 0.001, n = 60) and species richness (Manila clam density vs. species richness: r = +0.68, p<0.001, n = 60; Table 1B; Fig. 2B).

Influences of hard structure within sites on the Manila clam. Of all the bivalves found, only densities of the Manila clam were significantly higher in association with hard structure (Fig. 3); this was true of both mature (≥2 cm diameter) and juvenile (< 2 cm) individuals (Table 1B; Fig. 3).

Discussion

Bay-wide distribution

Site had the strongest association with bay-wide distributions of the Manila clam. Relationships between the clam and the environmental variables we measured were lacking or weak suggesting that site variables not measured in this study, such as rates and timing of freshwater inputs, water quality, pollutants, or predation rates, may be influencing distributions of the clam [16], [27–30]. Like other marine organisms, distribution of the clam is also likely influenced by chance associated with variability in freshwater inputs and currents, and the availability of suitable substrate at the time of transport and settlement (e.g., [31], [32]). Sites that supported mid to high densities of the Manila clam also tended to have some of the highest overall bivalve densities and species richness, a pattern that was also observed in Los Angeles County [12], signifying that those sites have properties that are broadly amenable to a variety of bivalve species. For example, these sites occur along paths of circulation in the bay likely resulting in passive transport of larvae into these areas [33]. The sites may also have environmental conditions that are suitable for a diversity of bivalve species, such as relatively low physical stress and

Table 2. Results of multiple linear regression testing relationships between densities of all Manila clam individuals (A.), juveniles only (<2 cm diameter) (B.), and adults only (C.); and environmental variables (presence/absence of hard structure, distance from bay mouth, sediment salinity, grain size and organic matter content) in Mission Bay, San Diego, California, USA.

A. All individuals					
Predictor	R^2/r^2	P/p	F	df	n
Whole model	0.44	<0.001	22.1	2,57	60
Site	0.38	<0.001			
Porewater salinity	−0.06	0.02			
B. Juveniles (<2 cm diameter)					
Predictor	R^2/r^2	P/p	F	df	n
Whole model	0.37	<0.001	16.8	2,57	60
Site	0.33	<0.001			
Porewater salinity	−0.04	0.05			
C. Adults (2 cm diameter)					
Predictor	R^2/r^2	P/p	F	df	n
Whole model	0.46	<0.001	15.9	2,57	60
Site	0.47	<0.001			
Porewater salinity	−0.06	0.02			

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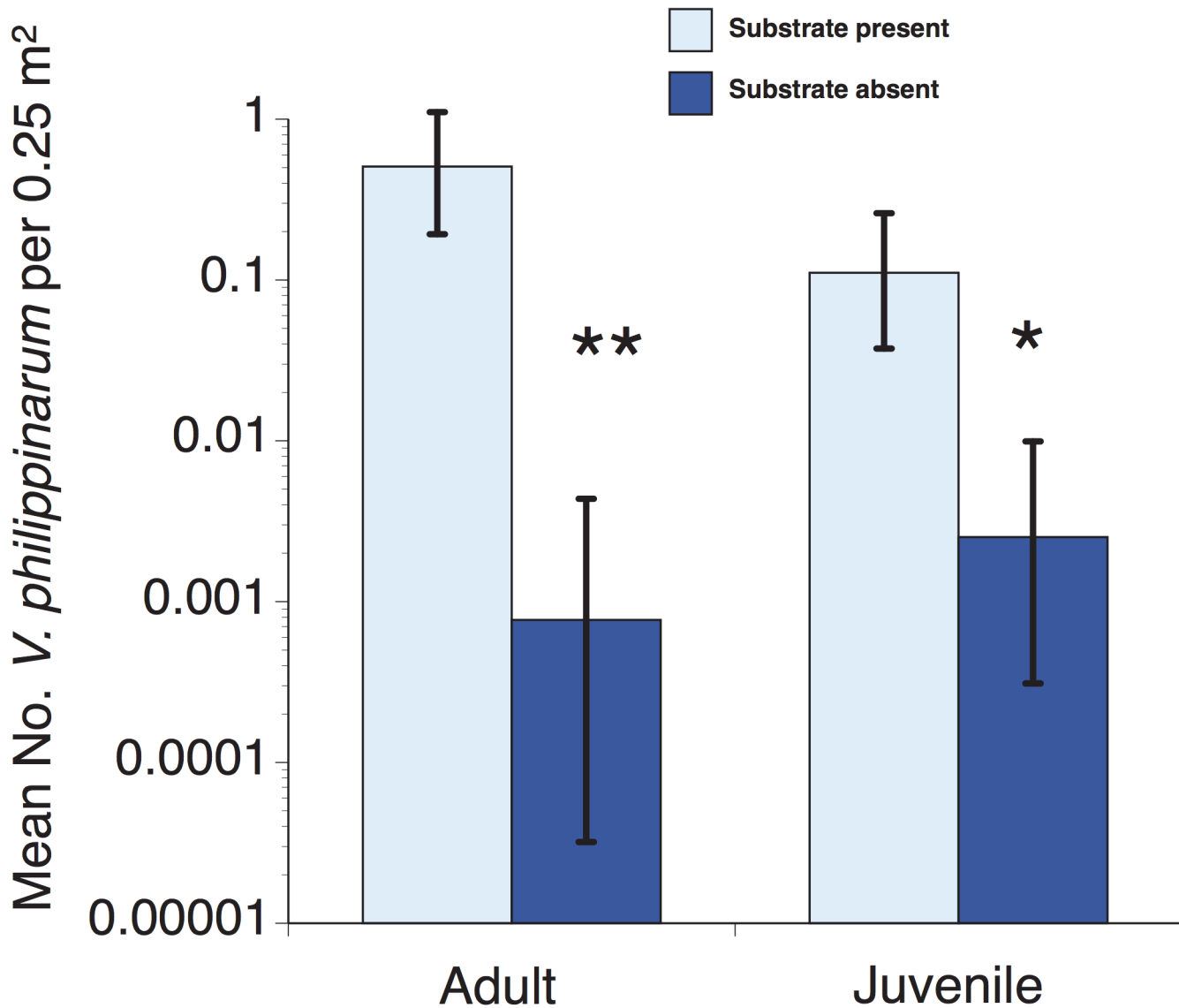
Fig 3. Backtransformed average (±SE) density of the Manila clam in benthic cores taken from beside hard substrate (rip rap) and in adjacent areas without significant hard substrate in Mission Bay, San Diego, California, USA. n = 10 paired sites. * = 0.01<p<0.05, ** = p<0.01.

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disturbance (e.g., little desiccation, salt stress or sedimentation; [34]), acceptable water quality, and/or moderate to high productivity (e.g., [35]).

Salinity is well-documented as influencing larval retention and settlement rates [17],[36], which is consistent with our finding of salinity being a correlate of juvenile and adult clam density, albeit weak. Porewater salinity in Mission Bay ranged from about 30–40 PSU, which reflects an overlap with the optimal growth range of 24–31 PSU of seawater [6],[10]. Observed salinities did not reveal the dips in salinity (13–17 PSU) associated with increased retention

and settlement rates revealed in lab [17] and modeling [36] studies. However, our average summertime, shallow porewater salinities of 35 PSU (i.e., average ocean salinity) or less found in six sites indicate influence of freshwater inputs with potential salinity dips during the rainy season [21] that may aid larval retention and settlement. Areas within a passive transport range but without salinity reductions had much lower larval retention rates due to larval behavior and subsequently lower adult densities [36]. Therefore, spatially and temporally dynamic patterns of salinity associated with freshwater inflows, tidal influence, and bay currents may influence dispersal patterns, rates of retention, settlement and establishment, and ultimately distributions of the Manila clam.

While the Manila clam is often associated with coarse substrates, such as sand, gravel and shell [6],[10],[37], sediment grain size had no observed effect on distributions of the Manila clam in this study where grain sizes were ≤1 mm diameter. This was consistent with the results of lab trials revealing a lack of influence of sand grain size classes ranging from 63 μm to 2 mm diameter on settlement rates [17]. When larger materials such as gravel or shell hash are offered, however, survival rates and density are greater than on natural mudflat substrates [37]. The lack of these coarse substrates from Mission Bay and other Southern California bays, however, does not appear to limit invasion of the clam indicating that the habitat requirements which are filled by coarse substrate may also be filled by large, hard structures.

Hard structure effects

Within tidal flat sites, the presence of hard structure had the strongest positive influence on Manila clam density in this study. It is well known that the addition of hard structure to a soft environment, such as riprap or pier pilings, can change the community through provision of substrate for fouling and open coast organisms [38],[39]. Hard structure may also alter the underlying sediment surface through loss of area, shading, refuge creation, and changes to hydrodynamic and sediment transport patterns, all of which influence the benthic community beneath and adjacent to the structure [37],[40–42].

The specific mechanism for facilitation of the Manila clam by riprap in this study is uncertain, but could include some of these explanations. Hard structure can have a number of indirect influences on species establishment. Depending on the shape and location of the structure relative to currents, structure can lead to increased turbulence, scour and coarser sediments [40], or baffling of currents and accumulation of fine sediment particles and organics [43]. Slowing of currents may also increase the likelihood of larval entrapment and/or settlement [44], and creation of "seasoned" substrate where thin layers of fine particles and organic debris that settle on coarse gravel and shell substrate increase larval settlement rates [37]. Furthermore, the cover provided by hard structure may act as predator and physical stress refuge for the shallow, sometimes mid-intertidal dwelling Manila clam. The clam is subject to heavy shorebird predation in some regions [28] and likely experiences predation by rays and crabs [6], [10], [29]. The overhangs and crevices of hard structures may also provide shade and trap moisture likely reducing desiccation risk for the clam.

While the mechanism is unclear, these results demonstrate that human alteration of the habitat, specifically the addition of hard structure, facilitates the Manila clams' presence in Mission Bay. With sea level rise adaptation planning underway in this and many areas, the prevalence of armored shorelines may be on the rise, and existing terrestrial hard structure will increasingly come in contact with the intertidal. The addition of more hard structure on our soft shorelines has the potential to facilitate this benthic dweller, in addition to other introduced species (e.g., [45]). Alternatively, proposals of living shorelines, such as introduction of native oyster beds on tidal flats throughout this region [46], [47], may also provide coarse

substrates that could facilitate spread (e.g., [6]). More information is needed on the distributions and spreading potential of the Manila clam in its southern range to make informed decisions.

In particular, we need more information on the life history and growth of the clam in its southern range, where warmer conditions may lead to faster growth and more frequent spawning [7],[48]. We also need to better understand dispersal, settlement and establishment patterns in space and time as related to freshwater pulses, other environmental variables (e.g., water quality, pollution, disturbance, parasite load; [28],[49], and behavior [34],[50]. A regional approach to data collection is needed throughout the Southern end of this introduced range to better understand how these factors change with location and conditions, and to document current distribution against which to measure spread.

While effects of the Manila clam on other species along the west coast of North America are only recently starting to emerge [51], studies from Europe reveal potential dramatic ecosystem-level effects associated with dense beds of the clam [52],[53]. Dense beds and dominance by this clam have been documented in San Francisco Bay and Colorado Lagoon in Los Angeles County (e.g., about 800–1000 m^{-2} in productive beds, [10],[12]), and several relatively dense patches have been observed in other estuaries throughout Southern California ([24], H.M. Page pers. comm.). Tracking the habitat requirements, spread and establishment of the Manila clam will inform management priorities and actions in this and other regions, which is especially important given the various plans being considered to adapt with climate change.

Acknowledgments

Author Contributions

Conceived and designed the experiments: DMT TST. Performed the experiments: AB DMT TST. Analyzed the data: DMT. Contributed reagents/materials/analysis tools: DMT TST. Wrote the paper: DMT TST AB.

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