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Invasions in Marine Communities: Contrasting Species Richness and Community Composition Across Habitats and Salinity

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Abstract While many studies of non-native species have examined either soft-bottom or hard-bottom marine communities, including artificial structures at docks and marinas, formal comparisons across these habitat types are rare. The number of non-indigenous species (NIS) may differ among habitats, due to differences in species delivery (trade history) and susceptibility to invasions. In this study, we quantitatively compared NIS to native species richness and distribution and examined community similarity across hard-bottom and soft-sediment habitats in San Francisco Bay, California (USA). Benthic invertebrates were sampled using settlement panels (hard-bottom habitats) and sediment grabs (soft-bottom habitats) in 13 paired sites, including eight in higher salinity areas and five in lower salinity areas during 2 years. Mean NIS richness was greatest in hard-bottom habitat at high salinity, being significantly higher than each (a) native species at high salinity and (b) NIS richness at low salinity. In contrast, mean NIS richness in soft-bottom communities was not significantly different from native species richness in either high- or low-salinity waters, nor was there a difference in NIS richness between salinities. For hard-bottom communities, NIS represented an average of 79% of total species richness per sample at high salinity and 78% at low salinity, whereas the comparable values for soft bottom were 46 and 60%, respectively. On average, NIS occurred at a significantly higher frequency (percent of samples) than native species for hard-bottom habitats at both salinities, but this was not the case for soft-bottom habitats. Finally, NIS contributed significantly to the existing community structure (dissimilarity) across habitat types and salinities. Our results show that NIS richness and occurrence frequency is highest in hard-bottom and high-salinity habitat for this Bay but also that NIS contribute strongly to species richness and community structure across each habitat evaluated.

Keywords NIS · Invasions · Estuaries · Soft sediments · Hard bottoms · Community structure

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Introduction

Among all the stressors faced by coastal ecosystems, the introduction of new species is perceived as one of the major threats across many geographic regions, habitats, and taxonomic groups (Ruiz and Carlton 2003). Documented ecological effects include shifts in abundance and habitat use by native species, alteration of habitat structure by introduced ecosystem engineers (abundance, dominant species), changes in community structure and functioning, and modification of productivity and nutrient cycling (Carlton 2001; Grosholz 2002; Crooks 2002; Torchin et al. 2002).

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The process of invasions by non-native species is often likened to a series of successive filters through which a species must pass in order to successfully establish self-sustaining populations in a new region (e.g., Lockwood and Somero 2011). The exposure of specific habitats to different strengths of propagule pressure has been theorized as a major factor governing invasions (Lockwood and Somero 2011; Blackburn et al. 2011). Propagule pressure—the arriving number of individuals of a given putative invader—is a function of vector frequency and magnitude (Williamson 1996; Ruiz and Carlton 2003; Blackburn et al. 2011). In the recipient environment, propagule pressure interacts with a variety of factors that affect the success or failure of the new invader in establishing reproductive populations, including the composition of the recipient community (e.g., Levine and D'Antonio 1999; Levine et al. 2004; Stachowicz et al. 2002; Marraffini and Geller 2015) and environmental match between the new environment and the invader's native region (Elton 1958; Keane and Crawley 2002; Torchin et al. 2003; Facon et al. 2006).

Introductions of non-native species are especially common in bays and estuaries (Ruiz et al. 2000; Hewitt et al. 2004; Ruiz et al. 2009), which are focal points of human population and commerce. As a result, the number of NIS (non-indigenous species) in these areas is often large (Miller et al. 2011; Williams et al. 2013). Among the world's highly invaded estuaries and bays, the San Francisco Bay is well-known for its high number of NIS (Cohen and Carlton 1995, 1998; Ruiz et al. 2011). While numerous vectors continue to transport non-native species to the San Francisco Bay and other locations worldwide, some evidence suggests that not all habitats are equally susceptible to invasions (Wasson et al. 2005; Ruiz et al. 2009). The majority of studies have reported the prevalence of NIS on hard bottoms, including artificial structures at docks and marinas (Ruiz et al. 2009), but there are few quantitative studies designed to examine the differences between hard bottoms and other habitats such as soft sediments (Wasson et al. 2005).

The San Francisco Bay has been studied in great detail for decades, with considerable focus on NIS in both hard- and soft-bottom communities (e.g., Carlton 1979; Cohen and Carlton 1995; Lee et al. 2003; Blum et al. 2007). Extensive data indicate that NIS can be common in both benthic habitat types, especially for macro-invertebrates, and provide the opportunity to quantify differences in invasion patterns across these habitats. In general, we predict a greater number and dominance of NIS on hard bottoms than soft bottoms, based on previous invasion analyses and also the historical opportunity for transfers of hard-bottom species. However, there are no such quantitative comparisons on the relative importance of NIS to community composition across habitats in this highly invaded estuary. We expect a prevalence of NIS on hard bottoms comparing to soft bottoms due to the historical transportation of more hard-bottom species.

This study aims to quantify multiple dimensions of native and NIS diversity and distribution and to test for differences in the current contribution of NIS to soft-bottom and hard-bottom community structures in the San Francisco Bay estuary. Here, we compare results from two separate, standardized sampling programs over a period of 2 years (2012–2013), in which we quantified the richness, abundance, and geographic distribution (frequency of occurrence) of species in hard- and soft-bottom habitats in the Bay. Each program was designed explicitly to evaluate the contribution of NIS to diversity and community composition within a habitat, allowing direct cross-habitat comparisons reported here.

Materials and Methods

Study Site and Sampling Methods

The study took place in the San Francisco Bay, California, one of the largest estuaries on the Pacific Coast of North America (Fig. 1) with a surface area of 1000–4100 km^2 (Conomos et al. 1985; Mooi et al. 2007). The San Francisco Bay has at least two distinct geographic segments: a northern, river-dominated section consisting of the central portion of the estuary, the San Pablo Bay, and the Sacramento-San Joaquin River Delta, which drains approximately 40% of the land area of California, and the southern half of the Bay which is a blind, lagoonal embayment that receives several minor seasonal creeks but has no significant year-round source of freshwater (Conomos 1979). Due to the prevailing Mediterranean climate, the Bay region has relatively wetter winters (approximately November to March) and dry summers (June to October). The shoreline is highly modified, with most original intertidal marshland converted to hard substrates during the past century, and numerous marina basins and ports have been installed throughout the Bay (Nichols et al. 1986). Soft sediment habitats of the northern, central, and southern Bay were modified greatly by hydraulic mining during the Gold Rush in 1849, as over 850 million m^3 was deposited on the Bay floor (Barnard et al. 2013).

We sampled hard- and soft-bottom macroinvertebrate communities throughout the Bay in a paired fashion (same areas). We used a stratified sampling scheme to sample eight paired stations in the high-salinity area (mean distance of 2.5 km between hard and soft bottoms) and five paired stations in the low-salinity water of the bay (mean distance of 1.2 km), distributed in the north, central, and south parts of the Bay (Fig. 1, Electronic Supplementary Material 1 on Online Resources) during the summers of 2012 and 2013.

The soft-sediment samples were collected in shallow areas (2 m depth below MMLW), using a standard Young-modified Van Veen grab (Dauer and Lane 2005; US EPA 2009)

Fig. 1 Sites sampled for hard- and soft-bottom communities in 2012 and 2013 in the San Francisco Bay. See ESM 1 for site codes
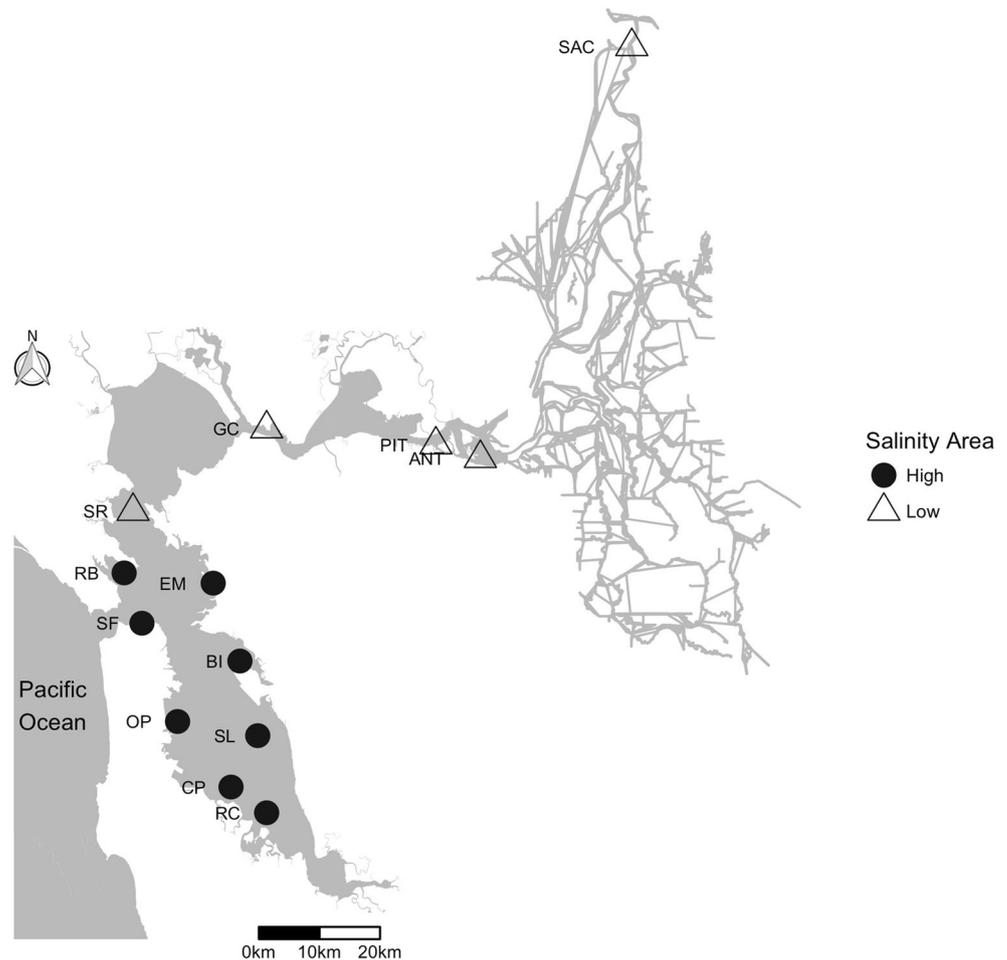
deployed via hydraulic winch, with shovels capturing grab samples with a surface area of 0.1 m². The entire grab sample was sieved on a 1-mm mesh screen, and the retained organisms were preserved in 95% ethanol (except for polychaetes and soft-bodied organisms that were preserved in 10% formalin). Five replicate grab samples were collected at 200 m intervals at each station, generating a total of 105 samples (5 replicates ∗ 8 high-salinity stations in 2012, 5 replicates ∗ 8 high-salinity stations in 2013, and 5 replicates ∗ 5 low-salinity stations in 2013).

In a separate study designed to detect NIS in hard-bottom communities, settlement plates were deployed throughout the San Francisco Bay for a period of 3 months during the summer, the time of greatest species richness and biomass accumulation in the region. Although there is a difference in compositional age between hard-bottom communities sampled in this manner and the soft-sediment community, previous work has shown that this approach to hard-bottom communities effectively captures the NIS present in adjacent mature communities (Marraffini et al., unpublished data) as well as on natural hard bottoms (Chang et al., unpublished data). Five gray polyvinyl chloride (PVC) settlement plates

(14 × 14 cm) were suspended, from a rope tied to a floating dock, 1 m below the surface within each of 13 sites (5 replicates ∗ 8 high-salinity stations in 2012, 5 replicates ∗ 5 low-salinity stations in 2012, and 5 replicates ∗ 8 high-salinity stations in 2013). Each plate was lightly sanded to provide a rough surface for settling larvae, attached to a half-brick for weight using cable ties, and deployed with the target surface facing the bottom. Once retrieved, sessile and mobile invertebrates on the target surface (only) were collected live, sorted, and preserved in 95% ethanol for identification (except for polychaetes and other soft-bodied organisms, which were preserved in 10% formalin).

All collected organisms were identified to the lowest taxonomic level in the laboratory, using local fauna identification keys (Kozloff 1996; Carlton 2007), additional current literature, and consultation with taxonomic experts. For each taxon, we classified the invasion status in the San Francisco Bay, using a synthesis of previous analyses and information in the National Exotic Marine and Estuarine Species Information System (Ruiz et al. 2011; Fofonoff et al. 2013). Four categories were used for this classification, including NIS, native, cryptogenic (of uncertain status, sensu

Carlton 1996), and unresolved; the latter were cases where the condition or size of specimens prevented species-level identification. Unresolved taxa may be juveniles or specimens in poor condition that cannot be identified to a sufficiently fine taxonomic resolution to provide an invasion status.

Salinity and temperature were measured at the surface for each site, using a YSI 85 (Yellow Springs Instruments), and depth for soft-bottom community sites was recorded using a depth sensor on the boat. Salinity and temperature were similar between 2012 and 2013. A mean temperature of 19.6 ± 1.2 and 18.7 ± 0.7 °C was recorded in the high- and low-salinity area, respectively, for soft bottoms, while 19.2 ± 2.3 and 21.2 ± 0.9 °C was recorded in the high- and low-salinity area, respectively, for hard bottoms. Mean salinity was 30.2 ± 0.8 psu in 2012 and 30.1 ± 0.2 psu in 2013 in high-salinity area and 8.6 ± 10.4 psu in low-salinity area.

Data Analysis

We compared mean NIS and native species richness across habitats and salinities, examining the relative contribution of NIS to both number and percentage of species detected in our samples. For each NIS and native species, we also compared the frequency of occurrence for NIS and native species in each habitat type. Specifically, the frequency of occurrence of each species was estimated as a percentage of samples (number of plates or grabs) in which it was found across all samples. Mean frequency of occurrence and species richness of NIS and native species in each habitat and salinity region were compared using the non-parametric Mann–Whitney test. The benthic community composition and resemblances between high- and low-salinity stations throughout the Bay were examined at several spatial scales: across sites within years, across habitats, and across years. We calculated Bray-Curtis similarities between samples, sites, habitats, and years, and visualized these data using a 2D multidimensional scaling (MDS) plot of the invertebrate communities based on Bray-Curtis similarities, which was generated per station, year, and salinity for each habitat. Community composition differences among stations, salinity area, and years were tested using PERMANOVA (Permutational Anova). The associated R-statistic value provided the degree of difference and the p value the significance of that difference. The contribution of species to between-group similarity was assessed using a SIMPER (similarity percentages) analysis (Clarke and Warwick 1994). All multivariate analyses were performed using PRIMER v.6 (Clarke and Gorley 2006).

Results

Comparison of NIS and Native Species Richness

We detected 226 morphospecies across all samples and habitats, including 157 species from hard bottoms and 91 species from soft bottoms (see Electronic Supplementary Material 2 on Online Resources). Only 20 species (9%) occurred in both habitats (Table 1), including: 12 species arthropods, five annelids, one chordate, one mollusk, and one bryozoan. Most of the species in common were NIS (11 = 55%), followed by natives (7 = 35%), and cryptogenic (2 = 11%).

NIS richness was greatest in the hard-bottom community, especially in high-salinity waters (Fig. 2a, b). Of all 157 taxa recorded on hard bottoms, 51 (32%) were classified as NIS. This represents a minimum estimate, since an additional 15 taxa were cryptogenic and 56 taxa remain unresolved. Mean species richness of NIS was over three-fold higher than that for native species in hard-bottom habitat at high salinity, representing a significant difference (Mann–Whitney test $U = 0.0$, $p < 0.0001$). Within the hard-bottom communities, fewer NIS were detected in low- than high-salinity water (Mann–Whitney test $U = 76.0$, $p = 0.003$). Although mean richness was two-fold higher for NIS than native species in the low-salinity, hard-bottom habitat, this was not a significant difference (Mann–Whitney U test $U = 4.5$, $p = 0.106$).

In contrast, mean NIS richness in soft-bottom communities was not significantly different from native species richness in either high- or low-salinity waters (Mann–Whitney U test $U = 171.5$, $p = 0.10$ and Mann–Whitney U test $U = 8.0$, $p = 0.398$, respectively), and there was also no difference in mean NIS richness between salinities (Mann–Whitney test $U = 60.5$, $p = 0.092$; Fig. 2a, b). Of all 91 soft-bottom morphospecies, 28 (31%) were classified as NIS, 35 as native, six as cryptogenic, and 22 as unresolved.

On a per-sample basis, NIS comprised an average of 42–85% total richness for each habitat and salinity, when considering NIS and native species combined (Fig. 2c, d). Percent NIS richness per sample was greatest for hard bottoms, with no statistical difference between high- and low-salinity waters (Mann–Whitney U test $U = 48.0$, $p = 0.535$). In the high-salinity area, hard-bottom communities had a greater percentage of NIS per sample than their soft-bottom counterparts (Mann–Whitney U test $U = 255.0$, $p < 0.0001$), while the percentage of NIS per sample was similar between community types in low salinity (Mann–Whitney U test $U = 18.5$, $p = 0.249$). However, there were no differences between salinities for soft-bottom samples (Mann–Whitney U test $U = 24.0$, $p = 0.200$).

Table 1 Benthic invertebrate species occurring in both soft- and hard-bottom habitats. Their phylum, invasion status, and their occurrence percentage per site are given

Phylum	Species	Status	Hard bottoms	Soft bottoms
Annelida	*Cirriformia* cf. *moorei*	Native	0.1	4.5
	Harmothoe imbricata complex	Cryptogenic	3.4	5.5
	Megasyllis nipponica	NIS	3.4	1.8
	Neoamphitrite sp. A	Cryptogenic	1.1	1.0
	Typosyllis sp.	Unresolved	0.1	0.2
Arthropoda	*Americorophium spinicorne*	Native	0.7	1.4
	Balanus crenatus	Native	0.1	2.2
	Caprella mutica	NIS	2.8	0.1
	Caprella scaura	NIS	0.3	0.3
	Gammarus daiberi	NIS	0.3	0.4
	Grandidierella japonica	NIS	1.4	2.5
	Idotea rufescens	Native	0.1	0.1
	Monocorophium acherusicum	NIS	1.4	1.1
	Monocorophium insidiosum	NIS	0.8	0.2
	Palaemon macrodactylus	NIS	0.2	0.4
	Paranthura japonica	NIS	3.5	1.0
	Photis brevipes	Native	0.1	0.7
Bryozoa	*Smittoidea prolifica*	Native	1.0	0.1
Chordata	*Molgula manhattensis*	NIS	4.5	0.9
Mollusca	*Musculista senhousia*	NIS	0.1	1.5

Species and Their Frequency of Occurrences

In soft-sediment habitats, annelids were dominant (49% of total occurrences) followed by arthropods (24%), and mollusks (19%). The most common species in high salinity were the polychaetes *Harmothoe imbricata* (6.1%), *Sabaco elongatus* (5.8%), *Glycinde picta* (5.8%), *Cirriformia moorei* (5.3%), and *Leitoscoloplos pugettensis* (3.9%), the peracarids *Sinocorophium heteroceratum* (5.7%) and *Ampelisca abdita* (5.5%), and the mollusks *Theora lubrica* (4.2%) and
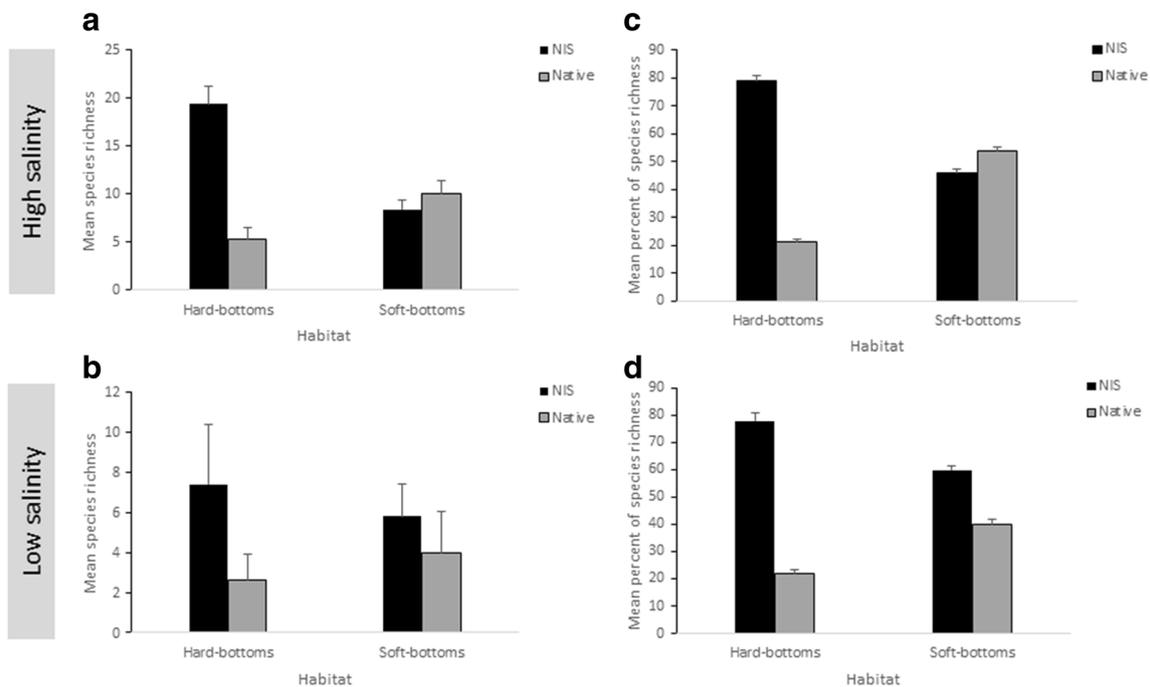

Fig. 2 Mean species richness (**a**, **b**) and mean species richness percentage (**b**, **d**) in each habitat for high- (**a**, **c**) and low- (**c**, **d**) salinity areas. NIS in *black* and natives in *gray*

Ruditapes philippinarum (3.9%). Combined, these accounted for a total of ~50% of occurrences, and NIS represented 25%. In low salinity, the most common species were the mollusks *Corbicula fluminea* (8.9%) and *Corbula amurensis* (4.7%), the peracarids *Americorophium spinicorne* (8.3%) and *A. abdita* (6.5%), and the polychaete *Marenzeriella viridis* (5.9%). Combined, these accounted for a total of ~50% of occurrences, and NIS represented 26%.

On hard-bottom habitats, tunicates, arthropods, bryozoans, and annelids were dominant (37, 25, 19, and 16%, respectively). The most common species in high salinity were the bryozoans *Bugula neritina* (4.6%) and *Bugulina stolonifera* (3.8%), the tunicates *Molgula manhattensis* (4.4% of occurrences) and *Ascidia zara* (3.9%), the peracarids *Paranthura japonica* (3.9%) and *Caprella mutica* (3.1%), and the polychaetes *Megasyllis nipponica* (3.7%) and *Harmothoe imbricata complex* (3.7%). Together, these species accounted for 31% of all hard-bottom community occurrences, of which NIS represented 28%. The most common species in low salinity were the peracarids *Gnorimosphaeroma oregonensis* (7.1%), *A. spinicorne* (6.4%), *Grandidierella japonica* (5.1%), *Uromunna* sp. (5.1%), *Sinelobus* sp. (4.5%),

Ampithoe valida (3.2%), and *Incisocalliope derzhavini* (3.2%), the tunicate *M. manhattensis* (4.5% of occurrences), the bryozoans *B. stolonifera* (3.8%), *Fredericella* sp. (3.2%), *Membranipora chesapeakensis* (3.2%), and *Pectinatella magnifica* (3.2%), and the polychaetes *Ficopomatus enigmatus* (3.2%) and *H. imbricata complex* (3.7%). Together, these species accounted for 55% of all hard-bottom community occurrences, of which NIS represented 37%.

Overall, NIS on average comprised ~50% of each sample, with some variation among habitats and salinity areas. In hard-bottom habitats, NIS accounted for a total mean percentage of 79% and 64% of taxa found in each sample in high and low salinity, respectively (Fig. 3a, b). On average, mean occurrence of frequency is six-fold higher than that for native species, representing significant differences (Mann–Whitney test $U = 546.5$, $p = 0.002$ in high-salinity area and $U = 667.5$, $p = 0.025$ in low-salinity area). A similar pattern was seen for both hard- and soft-bottom communities at low salinity (Fig. 3b; Mann–Whitney test $U = 349.5$, $p = 0.015$), although the disparity was not as great as it was between NIS and native species occurrence frequencies. For soft-bottom communities

Fig. 3 Mean percentage of occurrences of NIS and native species per habitat in high- (a) and low- (b) salinity areas
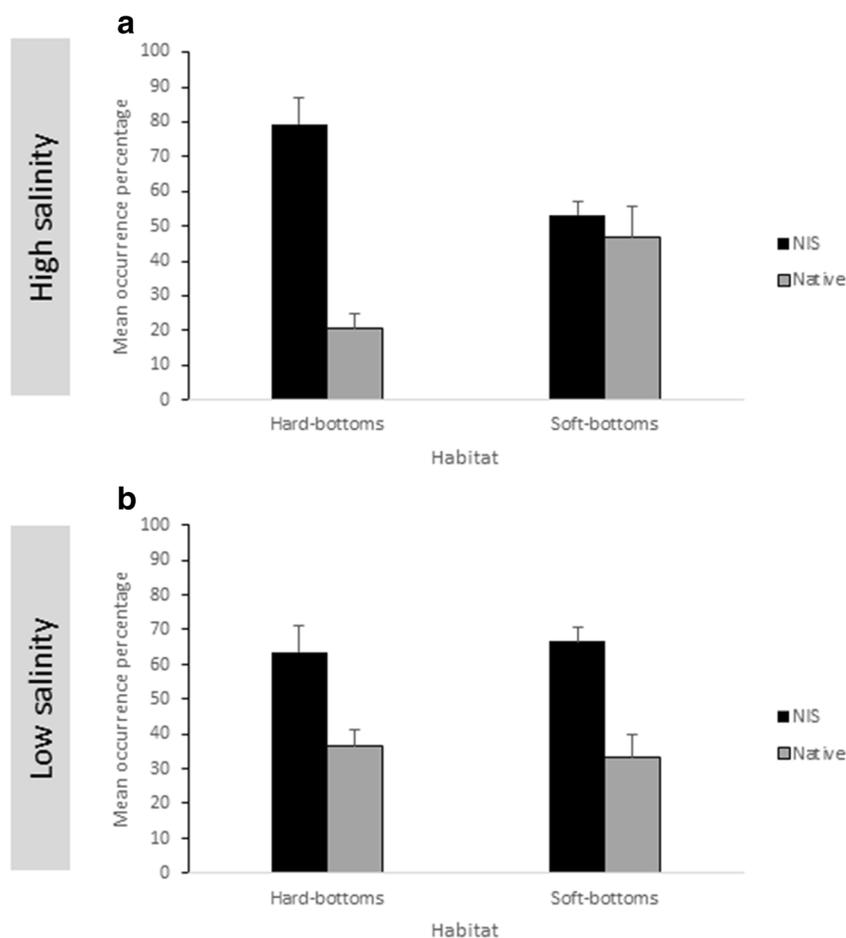
at high salinity, however, there was no difference in the prevalence of NIS and native species across samples (Mann–Whitney test $U = 512.0$, $p = 0.900$).

NIS Contribution to Similarities in Invertebrate Assemblages Across Habitats and Salinities

Comparisons of sample similarity of hard-bottom samples (Fig. 4a) and soft-bottom samples (Fig. 4b) revealed significant differences (PERMANOVA test Pseudo-$F = 3.51$, p-perm = 0.001 and Pseudo-$F = 5.45$, p-perm = 0.001, respectively) between low-salinity sites (open symbols) and high-

salinity sites (plain symbols). No significant differences between the years were detected (PERMANOVA test Pseudo-$F = 1.85$, p-perm = 0.091 and Pseudo-$F = 2.42$, p-perm = 0.061 for hard bottoms and soft bottoms, respectively).

High-salinity sites in each habitat were more similar to each other (47 and 45% for hard bottoms and soft bottoms, respectively) than were low-salinity sites (14 and 25%, from SIMPER). The dissimilarity between high- and low-salinity areas was of approximately 85% for both habitats and mostly due to a relatively small number of species in each habitat (Table 2). Most of these differentiating key species were restricted to either the high- or the low-salinity area (Table 2).

Fig. 4 Species composition of hard-bottom (**a**) and soft-bottom (**b**) communities in the San Francisco Bay estuary based on a matrix of Bray-Curtis similarities projected on a multi-dimensional scaling (MDS) plot showing high-salinity (filled symbols) and low-salinity (open symbols) stations in 2012 (*black*) and 2013 (*gray*). Each point represents the average composition of a site's community in a given year. Stress value gives the representation of spatial dispersion based on resemblances among samples
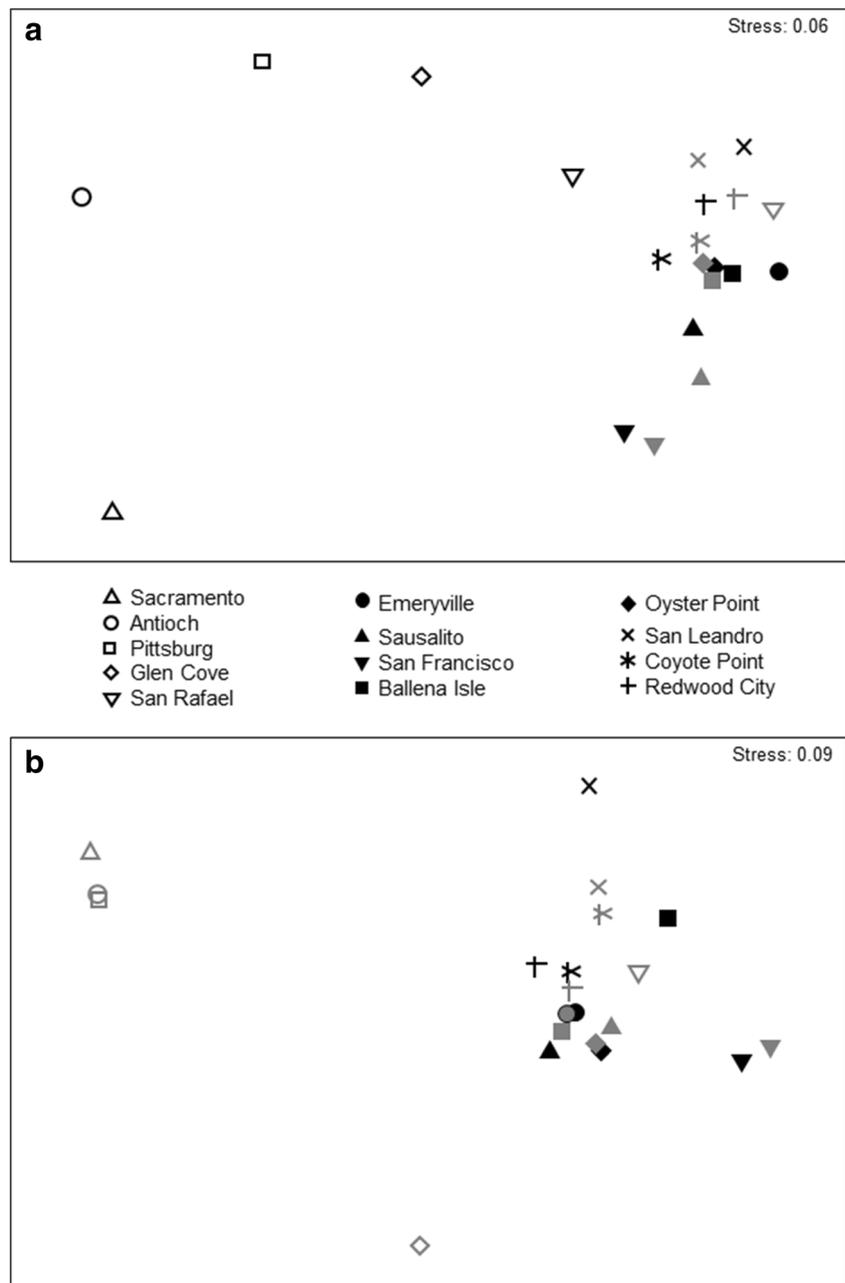
Table 2 Species contributing to the dissimilarity between high- and low-salinity areas in each habitat (from SIMPER analysis). The percentage contribution is given for each species

Hard-bottom species	Contribution (%)	Soft-bottom species	Contribution (%)
Bugula neritina[a]	2.53	*Glycinde picta*	3.49
Paranthura japonica[a]	2.46	*Harmothoe imbricata complex*	3.46
Caprella mutica[a]	2.46	*Sabaco elongatus*[a]	3.41
Ascidia zara[a]	2.45	*Corbicula fluminea*	3.37
Megasyllis nipponica[a]	2.43	*Americorophium spinicorne*	3.26
Didemnum vexillum[a]	2.23	*Cirriformia moorei*	3.26
Bugulina stolonifera[a]	2.22	*Corophium heteroceratum*[a]	2.93
Caprella simia[a]	2.06	*Venerupis philippinarum*[a]	2.85
Molgula manhattensis[a]	2.05	*Theora lubrica*[a]	2.75
Harmothoe imbricata complex	2.00	*Ampelisca abdita*[a]	2.66
Botryllinae unk	1.93	*Zaolutus actius*	2.65
Botrylloides violaceus[a]	1.88	*Oligochaeta unk*	2.65
Botryllus schlosseri[a]	1.87	*Euchone limnicola*	2.45
Ciona savignyi[a]	1.78	*Americorophium stimpsoni*	2.41
Balanus crenatus	1.78	*Nereididae unk*	2.20
Total	32.13		43.8

[a] NIS

Discussion and Conclusion

Cross-habitat comparisons of NIS invasion patterns are relatively rare (see Wasson et al. 2005) and can be challenging to perform due to the expense and expertise required across multiple habitats, salinities, and taxonomic groups. This study provides a rare quantitative analysis of the contribution of NIS to marine community structure in two major habitats (hard and soft bottoms) in the San Francisco Bay. Our results are conservative and may underestimate the true number of NIS in samples, due to the presence of a significant number of cryptogenic (10 and 5% in hard and soft bottoms, respectively) and unresolved taxa (33 and 22%) in both habitats. Nevertheless, our analyses show contrasting patterns of invasions between these habitats that are likely attributable to differences in both species introduction vectors and habitat modification.

The prevalence of NIS differed strikingly between habitats. NIS were dominant in hard-bottom habitats, representing on average 73–85% of total richness per sample and 32% of all species detected (see Fig. 2). In contrast, native species are more diverse than NIS (39 vs. 31%) and exhibit similar total number of specimens (46 vs. 54% and 60 vs. 40% in high and low salinity, respectively) in soft-bottom habitats. This result is consistent with that of Wasson et al. (2005), who found that NIS were most dominant in hard-bottom communities, constituting 52 and 21% of total species richness in hard- and soft-bottom habitats and 58 and 23% of total abundances in hard and soft bottoms, respectively, in Elkhorn Slough, CA. However, we also note that NIS richness was greater

in the San Francisco Bay, in terms of number and percentage of NIS, especially for the hard-bottom communities. Wasson et al. 2005 reported a total number of NIS (12 in hard bottoms and 7 in soft bottoms) that was roughly 25% below that found in our study (51 in hard bottoms and 28 in soft bottoms).

This difference between estuaries likely reflects differences in the extent of invasions, driven by historical differences in (a) the magnitude of propagule delivery, (b) disturbance regime and amount of artificial substrate, and (c) the size and environmental characteristics (see Cohen and Carlton 1998; Ruiz et al. 2000, 2011; Wasson et al. 2005; Glasby et al. 2007). Our estimates are also more recent in time, with more extensive sampling effort, expanding the NIS richness reported by Cohen and Carlton (1995) for the San Francisco Bay. Despite the disparity in total numbers between estuaries, approximately twice as many NIS were reported for hard-bottom than soft-bottom communities.

We suggest that the contrasting patterns of invasion that we observed across soft sediment and hard substrates are the result of the interacting effects of differing invasion vectors to these habitats and patterns of habitat modification. The soft-sediment and hard-bottom habitats of the San Francisco Bay have received very different inoculations of NIS in terms of number and type of major vectors transporting species and duration of vector operation, as there have probably more opportunities for transfer of hard-bottom species across multiple vectors. A large number of vessels whose hulls were colonized by multitudes of fouling species arrived in the San Francisco Bay during the California Gold Rush, providing a supply of novel propagules of predominantly hard substrate-

colonizing NIS on a scale rarely paralleled in human history (Carlton 1979). In addition, massive transfers of oysters and associated biota from the eastern United States (approximately from 1869 to 1940) and Japan (approximately from 1928 to 1950s) to the San Francisco Bay, which transferred soft-sediment species as well as hard-substrate dwellers living on oyster shells (Carlton 1979; Miller et al. 2011). Ballast water also transports both hard-bottom and soft-bottom species, and the importance of this vector has increased over time in California and the San Francisco Bay (Ruiz et al. 2011).

Invader success and invasion patterns can be driven as much by habitat changes in the recipient environment as by the vectors transporting NIS to the region (Williams et al. 2013), and alteration of the San Francisco Bay soft-sediment and hard-substrate habitats have undoubtedly played an important role in the relative success of invaders in each community. Since the advent of the California Gold Rush, the area occupied by hard substrates in the San Francisco Bay has increased greatly, with large amounts of artificial substrates (e.g., pontoons, docks, breakwaters, riprap, pilings) added to the environment, creating new habitat for potential invaders (Nichols et al. 1986). These surfaces frequently represent beachheads for many NIS and can enhance the spread and establishment of NIS in estuaries (Glasby et al. 2007; Ruiz et al. 2009). In contrast, soft-bottom habitats in the San Francisco Bay were most strongly modified by the destruction or alteration of the sedimentary environment when vast quantities of sediment were discharged into the San Francisco Bay watersheds from large-scale hydraulic gold mining operations in the Sierra Nevada from 1852 to 1884 (Nichols et al. 1986; Barnard et al. 2013). These destructive forces may have reduced populations of native species, possibly affording newly arrived invaders good opportunities to colonize and establish self-sustaining populations. The relative impact of habitat modification on the success of NIS in each habitat is not clear, but changes to both habitats undoubtedly had an enormous effect on the survival of both resident biota and in the provision of opportunities for new invaders.

The two major habitats studied have little overlap in species composition, as expected (only 20 species in common out of 226 detected; Table 1). Amphipods, which are relatively mobile, comprised most of the species found in both habitats, a result also reported by Wasson et al. (2005) in Elkhorn Slough, CA. Some of the overlapping species, such as the solitary tunicate *M. manhattensis* and the encrusting bryozoan *Smittoidea prolifica*, are not usually soft-bottom species, but they were found on dead oyster shells on soft bottoms. This small overlap highlights the importance of sampling across habitats when quantifying the contribution of NIS to regional diversity, as does the very large difference in species composition between high- and low-salinity sites (Fig. 4). Most species

were restricted to one salinity area (high or low), likely because of physiological limitations.

While the difference in the relative ages of the communities sampled could affect differences in overall community composition between the two habitats, previous works suggest that these results reflect the relative prevalence of NIS in each habitat more than the age of the communities sampled. Hard-substrate communities on both artificial and natural substrates in the San Francisco Bay are subject to relatively frequent disturbances (periodic floods; e.g., Cheng et al. 2016; Chang 2009) that "reset" the community, and extensive previous sampling suggests that 3-month settlement plate surveys during the summer capture all or nearly all NIS present in the community. PERMANOVA analyses showed no differences in community composition among persistent hard substrates surveyed using scuba and panels deployed for 3 months during the summer, while generalized linear models of species richness indicated no difference in the number of species detected using each method (Marraffini et al., unpublished data). While additional species will show up with longer duration exposure, these are a relatively low proportion of the community (Chang 2009). Hard-substrate communities undergo dramatic seasonal biomass fluctuations, and the summer deployment period used here is designed to capture the period of maximum summer growth and species richness. In addition, Marraffini et al. (unpublished data) compared the prevalence of NIS and native taxa on 3-month summer settlement plates to samples scraped from adjacent floating docks and piling structures, finding that the plates captured nearly all NIS and the majority of taxa that were detected in the dock samples. Overall, unlike soft-sediment communities, the hard-substrate communities in the San Francisco Bay have long been known to be largely dominated by NIS, with a remarkable paucity of native taxa (Carlton 1979; Cohen and Carlton 1995).

Our results have several important implications for the management of NIS. The contrasting invasion pattern observed between hard- and soft-bottom habitats illustrates the importance of sampling across multiple habitat types. First, surveys based only on one or a limited selection of habitat types may under- or overestimate the true total proportion of NIS in the estuary, depending on the estuary's complement of habitat types and invasion vector history (Ruiz et al. 2011). Second, our results agree with previous analyses indicating greater NIS colonization of hard-bottom than soft-bottom communities (Wasson et al. 2005; Ruiz et al. 2009). Third, the differing patterns of invasion across habitats recorded here may interact in unexpected ways with our changing climate and further habitat changes. Shifting environmental conditions and further habitat changes will affect both existing and incoming potential NIS. For example, changes to freshwater flow have been shown to play a large role in the distribution and abundance of invaders on hard substrate,

but less so in soft sediments. Management strategies to limit invasions must therefore consider effects both habitat alteration and environmental forcing functions on susceptibility to invasions.

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