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ORIGINAL PAPER

Contribution of non-native species to soft-sediment marine community structure of San Francisco Bay, California

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Abstract While non-native species (NIS) are important components in many coastal bays and estuaries, quantitative measures that characterize their effects on community structure at bay-wide scales are rare. In this study, we measure species composition and abundance for soft-sediments to assess the contribution of NIS to multiple dimensions of community structure, focusing on one of the most highly invaded bays in the world, San Francisco Bay. Benthic macrofauna was sampled in the high salinity, muddy shallow subtidal (2 m depth) across 10 sites, using replicate 0.1 m^2 Van Veen grabs. Invertebrates retained on a 1 mm sieve were identified, counted, and used to estimate the overall contribution of NIS to (a) abundance (b) species richness, and (c) community similarity. Soft-sediment communities were dominated numerically by NIS, which accounted for 76 % of all organisms detected and had a mean bay-wide abundance that was three and half-fold higher than native biota. Overall, NIS contributed to 36 % of observed taxa and 24–29 % of total estimated regional diversity. Native species accounted for 21 % of total abundance and 45 % of total species richness. Compared to native species, NIS occurred more frequently among samples and also explained more of the variation in community structure among sites. NIS dominate several key attributes of the soft-sediment infaunal community in San Francisco Bay. Percent contribution of NIS to species richness was at least two-fold higher than reported from two decades ago. Unique to this bay, these measures establish a quantitative baseline on the state of invasions and provide an important model for evaluating the extent of NIS in estuaries. Application of this approach across estuaries, with repeated measures over time, is critically needed to advance scientific understanding of invasions and also evaluation of efficacy and gaps in management to reduce new invasions.

Keywords Macrofauna · Community structure · Biological invasions · Regional diversity

Introduction

Biological invasions by non-indigenous species (NIS hereafter) are recognized as a significant force of change in ecosystems around the globe (Elton 1958; Mooney and Drake 1986; Carlton 1989; Grosholz

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2002). Despite growing knowledge about effects of invasions, the impacts of most NIS have not been evaluated (Ruiz et al. 1999, 2000; Ojaveer et al. 2015), especially at the population, community, or ecosystem levels. Moreover, even where some NIS impacts are documented, the cumulative effects of invasions on resulting community structure (including species composition and abundance) and function remains poorly understood.

In marine ecosystems, most NIS are known from bays and estuaries (Ruiz et al. 2000, 2009), which are focal points of human population and commerce. As a result, bays are exposed to extensive commercial shipping and other vectors known to transfer NIS, often in large numbers (Miller et al. 2011; Williams et al. 2013). The majority of studies have reported the prevalence of NIS on hard-substrates, including artificial structures at docks and marinas (Ruiz et al. 2009), but few quantitative data is available for soft-sediments communities. Within individual bays, previous studies have documented scores to hundreds of NIS with established populations, sometimes in high abundances (Cohen and Carlton 1995; Hewitt et al. 2004; Fofonoff et al. 2009). While considerable effort has focused on documenting NIS occurrences, relatively little quantitative information is available on how these are assembled and the net result for community structure, especially at the bay-wide scale. Yet, such measures provide insight on the potential significance of invasions for ecological processes and also serve as a critical baseline needed to evaluate changes in space or time (Ruiz and Hewitt 2002; Lee et al. 2003).

Among coastal bays, San Francisco Bay and delta has been the focus of significant research and analysis on marine NIS over many decades, having the highest documented NIS richness of any estuary in the world (Carlton 1979; Cohen and Carlton 1995, 1998; Ruiz et al. 2011). Past work has illustrated the abundance and potent effects of some NIS in soft-sediments in San Francisco Bay (Alpine and Cloern 1992; Grosholz et al. 2000; Cloern et al. 2011). In addition, Lee et al. (2003) demonstrated the relatively high abundance and richness of NIS in soft-sediments, across a range of salinities.

In this study, we quantify the overall contribution of NIS to species composition, abundance, and community similarity for soft-sediment benthic invertebrates across the shallow marine portion of San Francisco Bay. We compare our results to an earlier analysis of this community by Lee et al. (2003) and evaluate new measures (e.g. multivariate species composition, occurrences per grab/station, species accumulation curves) not previously characterized, to develop a more robust and synthetic perspective. Finally, we consider the potential application of these measures to quantify invasion patterns and the performance (efficacy) of invasion management and policy in estuaries.

Methods

Study site and sampling design

The study took place in the San Francisco Bay, California, one of the largest estuaries on the Pacific Coast of North America with a body surface area of 1000–4100 km^2 (Conomos et al. 1985; Mooi et al. 2007). We use a stratified sampling scheme to sample ten stations with muddy (versus sandy) sediments that were distributed to encompass the high salinity zone of the bay (27.88–31.42 ‰), occurring throughout the central and south part of the bay (Fig. 1, Supplemental Table S1 in Supporting Information). This particular habitat was shown by Lee et al. (2003) to have the highest NIS richness among seven distinct habitats (communities). At each station, we sampled shallow areas (2 m depth below mean low water), using replicate samples as outlined below.

Benthic invertebrate assemblages

The soft-sediment benthos was collected during 2012 summer, using a modified 0.1 m^2 Van Veen grab. Five replicate grab samples were collected at 200 m intervals at each station, generating a total of 50 samples (5 replicates *10 stations). 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). Although a smaller mesh size would retain many additional organisms, the taxonomic identification and biogeographic (i.e., native versus non-native status) resolution is generally poor for small organisms (Ruiz et al. 2000; Carlton 1979). As a result of this inverse size relationship, use of small species in community measures may alter or bias estimates of the role of NIS. We therefore focused

Fig. 1 Sampling stations in San Francisco Bay Area

on the larger species (mesh size), for which the taxonomic and biogeographic resolution are likely best.

All collected organisms were sorted and identified to the lowest taxonomic level (species in 80 % of the cases here) in the laboratory, relying largely on the extensive identification keys for fauna on the Pacific US coast (Kozloff 1996; Carlton 2007) and consulting local taxonomic experts. For each taxon, we classified the invasion status in San Francisco Bay, based upon previous analyses and using a synthesis of information in the National Exotic Marine and Estuarine Species Information System (Fofonoff et al. 2003; Ruiz et al. 2011). Four categories were used for this classification, including NIS, native, cryptogenic (of uncertain status), and unresolved, the later resulted where the condition of specimens prevented species-level identification. The resulting faunal matrix (abundances per species by sample) was used for the subsequent analyses. Data were square-root transformed in order to emphasize rare species and de-emphasize the importance of common species in the analysis (adapted from Legendre and Legendre 1998).

Data analysis

To examine the contribution of NIS to overall community composition, we characterized the observed abundance and species richness of macrofaunal invertebrates according to invasion status. Mean abundance and species richness were compared using the non-parametric Mann–Whitney test. Species accumulation curves were used to test estimate regional diversity for NIS, native species, and all species. Estimations were calculated using the software program EstimateS, version 9.1.0 (Colwell 2013). EstimateS uses Monte-Carlo resampling procedures to generate robust estimates of diversity in relation to sampling effort by randomizing sample order over a given number of replicates (in this case, 1000).

We examined community similarity using a 2D multidimensional scaling (MDS) plot of the infaunal communities based on Bray–Curtis similarities, which were generated per grab sample and station. Community composition differences among stations were tested using 1-way ANOSIM (analysis of similarity). Correlations between native, NIS and all species matrix were quantified using the Spearman correlation. SIMPER (similarity percentages) analysis was performed to define the contribution of the different species to average dissemblances between the stations (see Clarke and Ainsworth 1993). All of the multivariate analyses were performed using PRIMER v.6 (Clarke and Gorley 2006) and EstimateSWin910 (Colwell 2013).

Results

Abundance

NIS were numerically dominant, accounting for a total of 76 % of the 6040 individual organisms collected across samples (Fig. 2a, Table S2). Native and cryptogenic species represented 21 and 0.9 % of the community, respectively. On average, mean abundance of NIS per grab sample was three and half-fold higher than that for native species, representing a significant difference (Mann–Whitney test U = 85.50, $p = 0.008$, Fig. 2b). There was no significant relationship between the date of introduction and the total abundance of NIS (Pearson's test $R^2 = 0.001$, $p = 0.889$) or mean occurrence ($R^2 = 0.12$, $p = 0.15$).

Overall, arthropods were numerically dominant (53 % of total abundance), followed by annelids (39.6 %) and molluscs (6.2 %). NIS contributed 97.2 % of total arthropod abundance, due almost exclusively to amphipods (see Fig. S1a and Table S2). Moreover, the most abundant single species across sites and taxa was the amphipod *Ampelisca abdita*, representing 41.9 % of total abundance and 78.8 % of arthropod abundance. NIS contributed 46.7 % of total annelid abundance, due primarily to *Sabaco elongatus*, and 95.5 % of total mollusc abundance (Figure S1, Table S2). Together, the two NIS *A. abdita* and *S. elongatus* accounted for 59.3 % of all organisms in our samples.

Species richness

The total number of species detected in our samples was higher for natives than for NIS (Fig. 2c), although mean species richness per sample was similar for native and NIS (8.8 ± 1.5 versus 9.1 ± 1.3, respectively; Mann–Whitney test U = 53.5, $p = 0.82$, Fig. 2d). Overall, we detected 61 morphospecies, from which 55 were distinct species (excluding taxa identified to genus level and non-determined taxa). NIS constituted 36 % of the observed species richness at the bay scale (gamma diversity) (Table S2). At the station level (alpha diversity) the mean percent contribution of NIS was of 45 %, ranging from 25 to 57 %. At the grab level (point diversity) the mean percent contribution of NIS was of 47 %, ranging from 17 to 80 %. For the three most speciose groups, NIS contributed 18 % (annelids), 44 % (arthropods), and 64 % (molluscs) of total species richness (Fig. S1b).

Species accumulation for NIS quickly approached an asymptote relative to those for native species and all species combined (Fig. 3). Using a variety of estimators for regional species richness indicates our sampling detected 95 to 100 % of NIS present in San Francisco Bay (for this habitat, depth, and time), but only 71–89 % of native species (Table 1). This difference in detection results in part from the relative rarity of native species, as seen in a comparison of frequency of occurrence for native species versus NIS (Fig. 4). For the 27 native taxa, 22 % were detected only in one of the 50 samples, whereas only 5 % of the 20 NIS occurred in one sample (Fig. 4a, Chi squared test $X^2 = 2.48$, $p < 0.05$). Conversely, 70 % of NIS were detected in five or more samples, compared to only 44 % of native species. For the 27 native taxa, 37 % were detected only in one stations, whereas only 10 % of the 20 NIS occurred in one sample (Fig. 4b, Chi squared test $X^2 = 6.64$, $p < 0.05$). Conversely, 60 % of NIS were detected in three or more samples, compared to only 44 % of native species.

Overall, when considering all taxa combined, including NIS and native species, estimators indicate that we detected between 74 and 91 % of total regional species richness (see Fig. 3a) from a total species pool of between 79.52 (Jack 2) and 64.72 (Bootstrap). Since the NIS richness is nearly identical between observed and estimated, and the native species richness was underestimated by our surveys, the contribution of NIS to total estimated species richness was lower

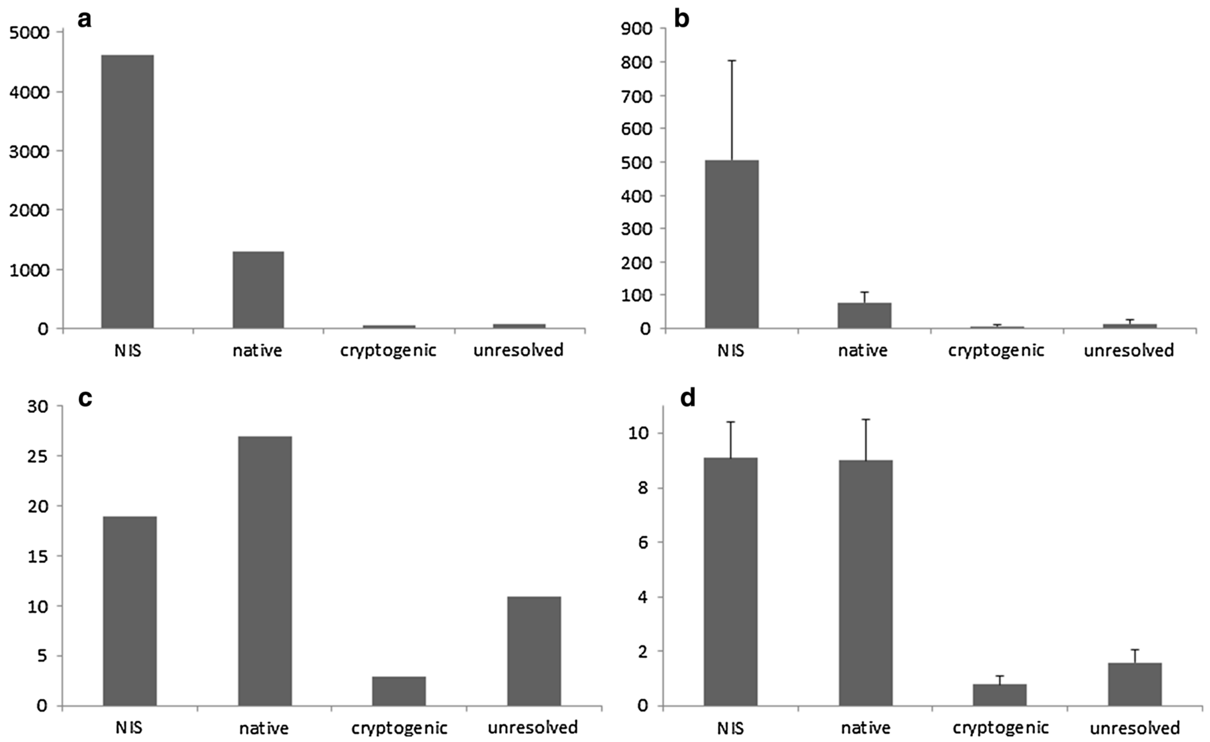

Fig. 2 Infaunal communities structure in function of species status. Total abundance (**a**), mean abundance (**b**), total species richness (**c**) and mean species richness (**d**) for NIS, native, cryptogenic and unresolved species are given

(between 24 and 29 %, depending on estimator) than that for observed species richness (36 %).

Community similarity

When considering all invertebrate taxa, species composition was highly variable and showed significant structure among stations (Fig. 5a, ANOSIM test $R = 0.767$, $p = 0.001$). NIS contributed the most to dissemblances (dissimilarity > 84 % cf. SIMPER analysis) among the stations, both individually and cumulatively (55 % vs. 38 % for NIS vs. natives, cf. Table S3). Significant structure was also observed when considering NIS alone (ANOSIM test $R = 0.729$, $p = 0.001$, Fig. 5b) and native species alone (ANOSIM test $R = 0.567$, $p = 0.001$, Fig. 5c). In addition, the correlation between all species combined and NIS was higher than between all species combined and native species (0.81 vs. 0.66 respectively), further illustrating the role of NIS in the overall community. Also of interest, the stress value was lower for NIS alone, compared to native species or all species (see Fig. 5), indicating higher similarity among samples.

MDS emphasized a significant (ANOSIM test $R = 0.697$, $p = 0.001$) separation between 3 stations (San Francisco Marina, San Leandro, Ballena Isle on the right) and the rest of the stations (on the left) that was especially pronounced for all taxa and NIS (Fig. 5a, b, respectively). The molluscs *Musculista senhousia* and *Venerupis philippinarum* were more abundant at these three stations (mean values per sample: 1.1 for *M. senhousia* and 4.5 for *V. philippinarum*), compared to the other stations (mean values per sample: 0.4 for *M. senhousia* and 0.7 for *V. philippinarum*), while many other species were absent (e.g. *Theora lubrica*, *Ampelisca abdita*) or less abundant there (mean values per sample: 1.1 for *Sabaco elongatus* vs. 30.0 and 1.8 for *Harmothoe imbricata complex* vs. 3.7).

Discussion

This study provides a rare formal analysis of the effects of NIS on marine community structure, using data collected from a single estuary to control for

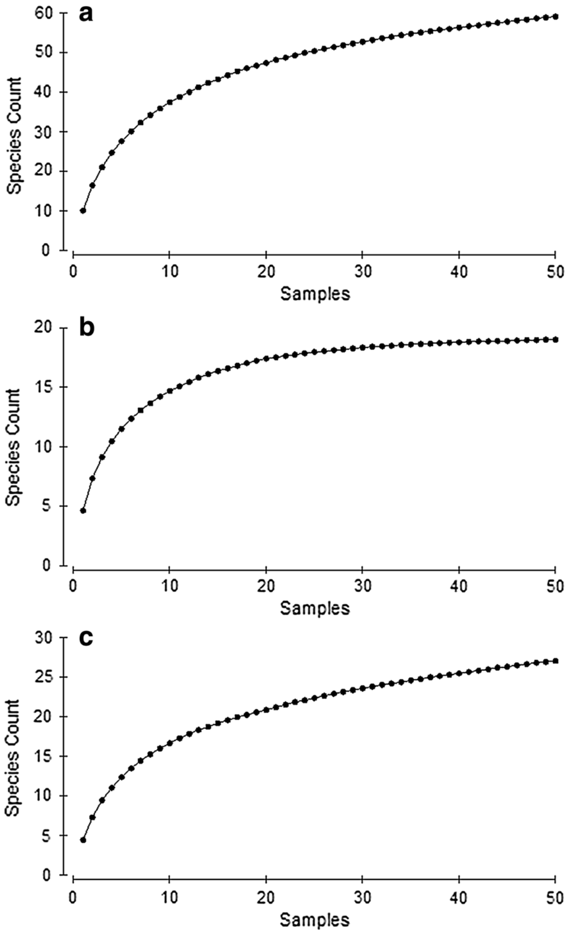

Fig. 3 Infaunal communities species accumulation curves for **a** all species combined. **b** NIS and **c** native species in San Francisco bay area

Table 1 Chao 1, Chao 2, Jack 1, Jack 2, Bootstrap and ACE indexes estimates for 50 samples given by EstimateS analyses

Species	Index	Estimate	Measured percentage (%)
Native	Chao 1	30.33	89.02
	Chao 2	32.15	83.98
	Jack 1	33.86	79.74
	Jack 2	37.76	71.50
	Bootstrap	30.07	89.79
	ACE	31.61	85.42
NIS	Chao 1	19.00	100.00
	Chao 2	19.00	100.00
	Jack 1	19.98	95.09
	Jack 2	20.00	95.00
	Bootstrap	19.61	96.89
	ACE	19.75	96.20

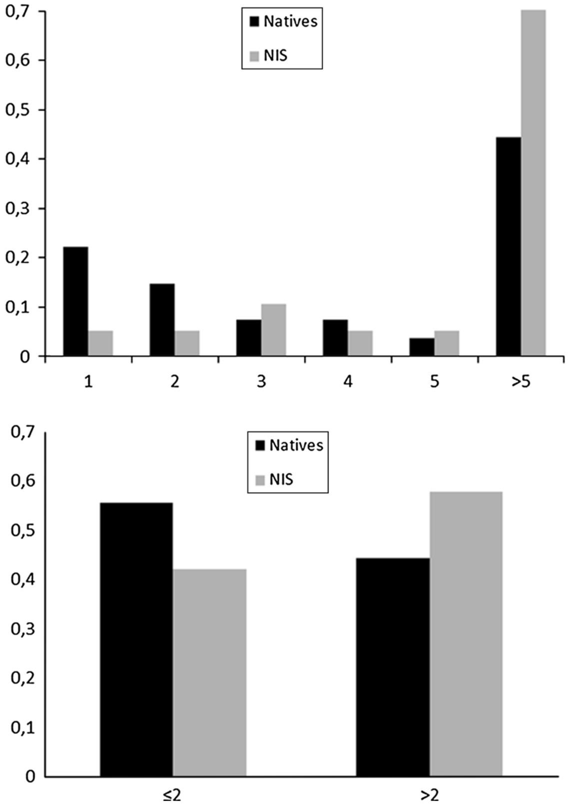

Fig. 4 Occurrence of the number of species found per sample for natives and NIS species. The proportions of the number of species present in 1, 2, 3, 4, 5 and more than 5 grabs over the total number of natives (27) and NIS (19) are given

habitat (salinity, depth, and substrate) and season. Our analyses show that the shallow, marine soft-sediment invertebrate community of San Francisco Bay is dominated by NIS, in terms of both abundance and structure (Figs. 2 and 5). NIS represented 36 % of total observed species across samples and 50 % of mean species richness per grab sample. We also show that NIS are over-dispersed, having a much higher frequency of occurrence among samples, compared to native species. As a consequence of this dispersion, species accumulation models predict that our sampling effort, within the selected habitat type and depth, detected $\geq$95 % of NIS present and that NIS represented >24 % of the total estimated regional species richness.

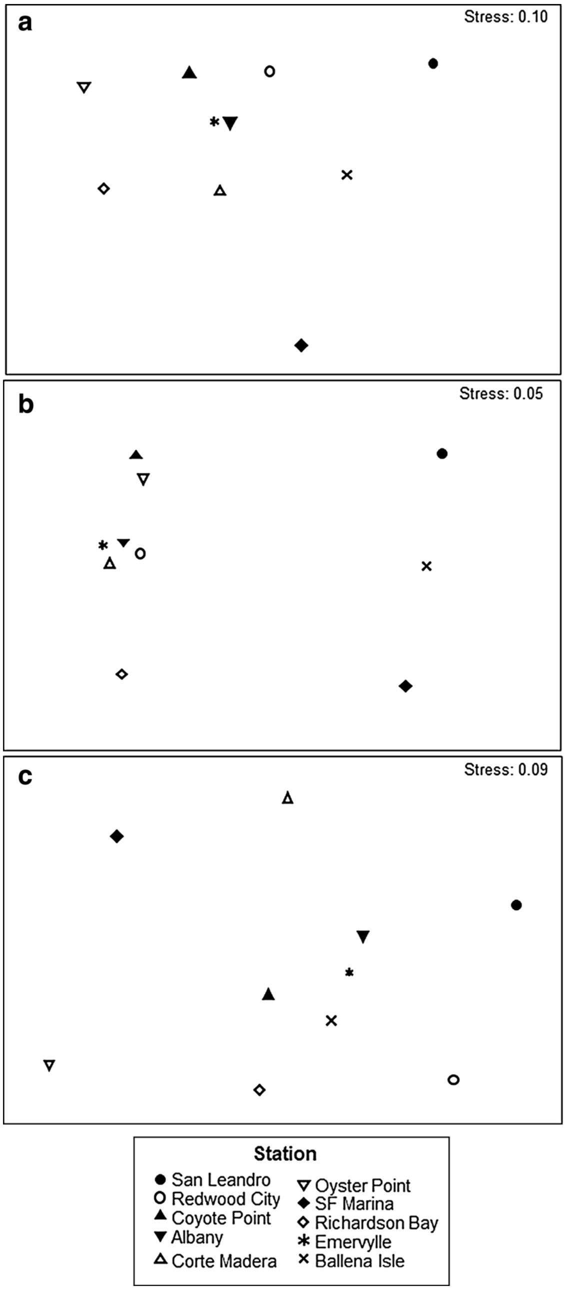

Fig. 5 Species composition of infaunal communities in San Francisco bay area projected on a multi-dimensional scaling (MDS) **a** for all species, **b** for NIS species and **c** native species. Stress value gives the representation of spatial dispersion based on resemblances among samples

Multiple studies have explored both the abundance and richness of NIS in soft-sediments of San Francisco Bay (Carlton 1979; Nichols and Thompson 1985; Thompson and Nichols 1984; Lee et al. 2003), and our results provide the first contemporary community measures at a bay-scale in nearly 20 years and also several novel dimensions, including estimates of total species richness of NIS and native species (Fig. 3; Table 1) as well as effects of NIS community similarity (Fig. 5; Table S3). Using historical data from 1992 to 1997, Lee et al. (2003) conducted the most detailed previous analysis of NIS abundance and richness for soft-sediment invertebrates, examining multiple spatial scales. For the entire bay, they found NIS species richness accounted for 11 % of detected 533 species, which included samples from all salinities (freshwater to marine), substrate types, depths, and seasons that were collected with a 0.5 mm sieve. Total NIS richness was highest at high salinity sites with muddy sediments (n = 81 samples), which was considered a distinct community where 37 NIS were documented, representing approximately 11 % of species richness and 75 % of total abundance within this habitat type. Finally, the authors reported percent contribution of NIS to species richness was (a) related inversely to spatial scale, suggesting broader distribution across environmental gradients for NIS than native species, and (b) potentially underestimated by up to 100 % in some habitat types, due to uncertainty of status (classification) of cryptogenic and indeterminate species.

In comparison to Lee et al. (2003), our analysis focused on the same high salinity and muddy habitat, where they observed peak NIS richness, but was restricted to a shallow depth (2 m) and season within a single year, to control for potential effects of these variables on community structure. We also used a larger mesh (1.0 mm) sieve, in an attempt to reduce uncertainty for both identification and biogeographic origin of organisms, since this is related generally to organism size (Ruiz et al. 2000). While the contribution of NIS to abundance of organisms for this habitat was remarkably similar in the two studies, we found a much higher percent contribution of NIS to species richness than the previous study, at both the habitat level (36 vs. ~11 % of total richness) and the grab sample level (47 vs. ~25 % in mean richness). Both studies found that frequency of occurrence among samples was greater for NIS than native species, although Lee et al. (2003) reported a range observed among seven habitats and did not provide values or statistical comparisons for specific habitats, including the one in our analysis.

The high contribution of NIS to species richness in our analyses, relative to that reported earlier, may result from multiple factors. First, we focused on larger organisms (1.0 vs. 0.5 mm sieve size), which may differ from smaller organisms in the percent of NIS or size-dependent differences (bias) in detection associated with taxonomic and biogeographic knowledge (Ruiz et al. 2000). Second, our study was more narrowly focused on a particular depth range and season. It is possible that NIS richness is higher (proportionally) within this depth and season, but we cannot yet evaluate this possibility. This narrower spatial and temporal scope also reduced the total species pool compared to the previous study. One assumption of this is that percent NIS may be expected to decline with increasing area, due to the different dispersion of NIS versus native species, such that the total native species number increases faster with spatial scale (Lee et al. 2003) and possibly time. While the scale may contribute to observed differences in percent NIS of the total (cumulative) species richness, there was still a two-fold difference between studies in percent NIS per grab sample. We therefore surmise that spatial scale alone cannot explain observed differences, especially at small spatial scales. Third, data for the two studies were collected nearly two decades apart, and time may contribute to observed differences. Three (15 %) of NIS in our study were detected in California after 1997 (Table S2), during or after sample collection for the earlier study, so increasing NIS richness over time (due to invasions or detection) may contribute to a higher percent NIS in the recent study. Also, the most common NIS found in our study and by Lee et al. (2003) were similar among the amphipods (*Ampelisca abdita*, *Monocorophium acherusicum* and *Sinocorophium heteroceratum*) and polychaetes (*Euchone limnicola*). *Streblospio benedicti* (second most common polychaete for Lee et al. 2003) was not recorded in our survey due to the small size of the species not recorded in our study using a 1 mm mesh screen. The major difference found between Lee et al. (2003) and this study is the prevalence of the polychaete *Sabaco elongatus* in our survey, while Lee et al. (2003) didn't record this species among the most common NIS. It could be a function of the sampling method, or of the sampling period (1992–1996). This species was introduced in San Francisco Bay in 1960. It has been recorded by Carlton (1979) and Cohen and Carlton (1995). This maldanidae worm is now widespread in the bay and very abundant (total abundance of 1061 see Appendix Table S2). This worm builds muddy tubs and can potentially modify drastically the habitat itself.

While the detection rate of NIS has increased dramatically over time for this and many other bays (Cohen and Carlton 1998; Fofonoff et al. 2009; Hewitt et al. 2004), robust measures of marine NIS richness and abundance over time are largely lacking (Ruiz et al. 2000; Costello and Solow 2003; National Research Council 2011). Specifically, there is a paucity of standardized, quantitative measures for soft-sediment communities that provide statistical confidence in estimates of NIS at a bay-scale, and these have not been repeated over time. The lack of these measures results in uncertainty about the actual rate of invasion in coastal bays and estuaries, as well as variation among different bays, that limits scientific understanding of invasion patterns and processes as well as the ability to evaluate efficacy of management and policy aimed at reducing new invasions (Ruiz and Hewitt 2002; Ruiz and Carlton 2003; National Research Council 2011).

San Francisco Bay is among the best studied estuaries in the world, and provides an important model for approaches to address this critical gap. Lee et al. (2003) provide a valuable quantitative measure and discussion of NIS metrics from collections nearly 20 years ago. However, these have not been repeated, and it is difficult to make direct comparisons with our contemporary measures, due to multiple differences in both methods and scale (as noted earlier). It is especially challenging to sustain repeated measures over time with the high level of sampling effort in this previous study, which drew upon multiple historical programs that collected extensive data (for a variety of objectives) over multiple years.

The approach used in our study offers one solution by constraining the focus to one key habitat (high salinity, marine muddy sediment, and 2 m depth) and one season (summer). We further constrained analysis to macrofauna (retained by 1 mm sieve), allowing more rapid analysis as well as less uncertainty about taxonomic identity and biogeographic origin compared to smaller sized organisms. Our standardized survey do a good job capturing the abundance and diversity of NIS in a given habitat. It is repeatable and can be used as a baseline for comparisons to future studies, as well as to compare to previous work. Our results demonstrate good statistical confidence among grab samples in species richness and abundance measures (Fig. 2) which could detect change over time. In addition, the total NIS species estimates indicate that nearly all NIS present in this habitat were detected (Fig. 3; Table 1) and provide an additional, robust metric to evaluate change through time.

Our study provides a useful baseline and approach to evaluate both NIS richness and abundance. The metrics used to quantify the relative contribution of NIS are easy to measure, can be applied to various taxa, are independent of scale, comparable across regions, repeatable though time and their interpretation is straightforward as already shown by Catford et al. (2012). We are now applying this approach to multiple estuaries and also evaluating performance of repeated measures across years in San Francisco Bay. In contrast to the study by Lee et al. (2003), we are not capturing invasion dynamics in the entire estuary. Instead, we are trading broad-based measures across habitat types and smaller organisms for higher resolution, fidelity, and feasibility (i.e., a modest and sustainable effort) for one key habitat where NIS richness and abundance is known to be high. This focused strategy can allow us to establish time-series of quantitative and robust community measures at the bay scale that are now missing, characterizing temporal changes in NIS (and native species) and responses to existing biosecurity management and policy.

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