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BIODIVERSITY RESEARCH

Marine invasion history and vector analysis of California: a hotspot for western North America

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ABSTRACT

Aim We examine the regional dominance of California as a beachhead for marine biological invasions in western North America and assess the relative contribution of different transfer mechanisms to invasions over time.

Location Western North America (California to Alaska, excluding Mexico).

Methods We undertook extensive analysis of literature and collections records to characterize the invasion history of non-native species (invertebrates, microalgae and microorganisms) with established populations in coastal marine (tidal) waters of western North America through 2006. Using these data, we estimated (1) the proportion of first regional records of non-native species that occurred in California and (2) the relative contribution of transfer mechanisms to California invasions (or vector strength) over time.

Results Excluding vascular plants and vertebrates, we identified 290 non-native marine species with established populations in western North America, and 79% had first regional records from California. Many (40–64%) of the non-native species in adjacent states and provinces were first reported in California, suggesting northward spread. California also drives the increasing regional rate of detected invasions. Of 257 non-native species established in California, 59% had first regional records in San Francisco Bay; 57% are known from multiple estuaries, suggesting secondary spread; and a majority were attributed to vessels (ballast water or hull fouling) or oysters, in some combination, but their relative contributions are not clear. For California, more than one vector was possible for 56% of species, and the potential contribution of ballast water, hull fouling and live trade increased over time, unlike other vectors.

Main conclusions California, especially San Francisco Bay, plays a pivotal role for marine invasion dynamics for western North America, providing an entry point from which many species spread. This pattern is associated historically with high propagule supply and salinity. Any effective strategies to minimize new invasions throughout this region must (1) focus attention on California and (2) address current uncertainty and future shifts in vector strength.

Keywords

Biological invasions, California, marine invasions, non-native species, ships, vector strength.

INTRODUCTION

The study of biological invasions now spans a diverse range of disciplines, including areas of ecology, evolutionary biology, epidemiology, conservation, economics, commerce, management and policy (Mack *et al.*, 2000). Across these disciplines, from terrestrial to aquatic habitats, one broad theme of invasion research considers the risk of invasion, seeking to explain and predict the likelihood of establishment and associated impacts. The capacity to predict such risk has

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obvious implications for management and policy, motivating research aimed at reducing the probability of invasions and associated impacts.

One approach to understand invasion risk involves analysis of geographic variation in invasion patterns and factors associated with the observed patterns. Such geographic approaches often examine hotspots, consisting of sites or regions with unusually high numbers of non-native species. Analyses of such hotspots seek to (1) characterize their spatial and temporal context, and (2) understand which factors, operating alone or in combination, explain the high number of established invaders. Hotspots are selected for evaluation precisely because the factors that result in establishment are present. Past studies have examined such hotspots singly or with many other sites, with comparison among sites being either explicit or implicit.

In marine environments, most invasions are reported in bays and estuaries, due in part to the magnitude of human-mediated species transfer that is concentrated near ports and coastal population centres (Wasson *et al.*, 2005; Preisler *et al.*, 2009; Ruiz *et al.*, 2009). While bays are focal points for colonization and spread of non-native species, there is considerable variation among bays in the reported number of established non-native species (Hewitt *et al.*, 2004; Fofonoff *et al.*, 2009; Gollasch *et al.*, 2009; Ruiz & Hewitt, 2009). The factors that drive this variation have been an area of active research but remain poorly resolved.

Western North America is among the best-studied global regions for marine invasions and also exhibits the most extreme geographic variation in non-native species richness. San Francisco Bay and Estuary is known for its unusually large number of non-native species (Cohen & Carlton, 1995, 1998). A wealth of studies also exists on non-native marine species at various spatial scales from southern California to Alaska (Carlton, 1979, 2007; Cohen & Carlton, 1995; Cohen *et al.*, 1998, 2001; Wasson *et al.*, 2001; Boyd *et al.*, 2002; Sytsma *et al.*, 2005; Wonham & Carlton, 2005; Foss *et al.*, 2007; Ruiz & Hewitt, 2009). While there has been some discussion of spatial differences among sites, a regional synthesis of the resulting invasion pattern and its underlying mechanisms is not available.

In this study, we examine California's role in regional invasion dynamics for western North America. All work to date indicates that California, and especially San Francisco Bay, is the first recorded location for many non-native species in the northeastern Pacific. Here, we evaluate (1) the overall contribution of California as a focal point for known introductions to the region, (2) the invasion history for California, focusing on first-documented records of non-native species in the state, and (3) the transfer mechanisms (vectors) attributed to initial introductions to the state. Finally, against this background, we consider possible mechanisms responsible for the observed patterns.

METHODS

To generate a cumulative list of established invaders along western North America, we analysed records of non-native species that were compiled in two separate databases. The National Exotic Marine and Estuarine Species Information System (NEMESIS) is a database of non-native species records for marine and tidal waters of the continental United States. The California Aquatic Non-Native Organism Database (CANOD) includes records of non-native species for similar habitats in California. Both databases provide a synthesis of occurrence records of species, compiled from literature-based records and independent field surveys. Each database also includes information about invasion history, biogeography and vectors associated with many of the species.

For each database, we evaluated the classification and status of each species, to provide quality assurance and consistency across all occurrence records through 2006; we did not include new records after this date. Based on intensive review, we classified each species as native, non-native, or cryptogenic. Our approach used criteria for recognizing introduced species developed by Carlton (1979, 1996) and Chapman & Carlton (1991). For California, where the data records overlapped, there was generally good agreement between the NEMESIS and CANOD databases for invasion status of many species. Where there was disagreement about classification, or novel records in one data set, we re-examined the available literature on history and biogeography of the species, and consulted with experts for the respective taxonomic groups, to assign invasion status. NEMESIS was the sole source of occurrence records and invasion status classification for species in states and provinces outside of California.

We focused our analysis on invertebrates, algae, protists and microorganisms that were considered to have established populations in marine, estuarine and tidal freshwater. We excluded all vascular plants and vertebrates. We also excluded species that were clearly non-native but were not known to be established, such as those that became extinct, never established, or whose current population status is unknown. In general, we classified a species as established when (1) there were multiple records over multiple years within a region, (2) local populations were reportedly numerous and successfully reproducing, based upon age of specimens and apparent year classes, or (3) the species was reported as established in the literature or through personal communication (see Ruiz *et al.*, 2000a for discussion). In the absence of systematic field-based measures over time, there is some uncertainty about the establishment of a small subset of species.

For each individual state and province in western North America, from California to Alaska, we identified the number of non-native species that were reported and classified as established in our synthesis. For each state and province, we identified the date and location of first record of the species. We also characterized the distribution of each species, in terms of salinity range and whether they were restricted to bays and estuaries, as two key habitat variables that are readily available for all species.

For California, we estimated vector strength, defined as the number of invasions (established non-native species) associated with each vector (Ruiz & Carlton, 2003). For each species present in California, we characterized the vector(s) associated with the initial invasion record in the state and we examined temporal patterns of vector strength. Vectors used in our analyses included (1) Ships' Fouling (or biofouling) – the hulls and underwater surfaces, including sea chests, of vessels, (2) Ships' Ballast Water – the ballast tanks (water and sediments) of ships, (3) Eastern Oysters – transfers of the Atlantic oyster *Crassostrea virginica*, (4) Asian Oysters – transfers of the Pacific oyster *Crassostrea gigas*, (5) Stocking – official, unofficial, or accidental fisheries releases, (6) Live Trade – live seafood, bait, ornamental plants, aquaria and scientific research, (7) Other Vectors – wetland restoration, biocontrol, dry ballast of ships and ships' cargo. For ships' fouling, we could not easily distinguish the roles of commercial, recreational and fishing vessels as a source of introduction; thus, our analysis treats these as one group.

Vectors were assigned to species, based on their life history (e.g. presence/absence of planktonic or attached stages), habitat, date of first record relative to human activities and other factors. For example, species discovered in California waters before 1900 were unlikely to have been introduced in ships' ballast water, as water ballast had not been widely adopted at that time. Oyster transplants were considered a possible vector for species likely to be associated with either Atlantic or Pacific oysters, for conspicuous species that were discovered close to the time of oyster transfers, or for more recently discovered and less conspicuous species that might have been overlooked. A more detailed discussion of vector assignments is given in Fofonoff *et al.* (2003).

For many non-native species, multiple vectors were considered possible, where we could not assign a sole vector. In these cases, we treated each as equally likely in our analysis. For example, some species could have arrived by ship or by oyster transfers, and species with such multiple vectors arrived to California from Asia as well as eastern North America (Cohen & Carlton, 1995; Ruiz *et al.*, 2000a).

RESULTS

Relative importance of California to invasions of western North America

We classified 290 non-native marine and estuarine species, excluding vertebrates and vascular plants, as established in western North America, from California to Alaska (see Appendix S1 in Supporting Information). Of these species, 257 (89%) are known to be established in California (see next section for further description). In contrast, far fewer (< 100) non-native species were known to occur in Oregon, Washington, or British Columbia, and only 10 non-native species were reported to be established in Alaska (Fig. 1).

California appears to be the first point of entry to the region for most non-native species. For western North America as a whole, 79% of the 290 established non-native species were first recorded in California. In contrast, 17% was reported first from Oregon to British Columbia and 0% from Alaska. Another 4% of species were reported first on the Pacific coast of Mexico, pre-dating records to the north.

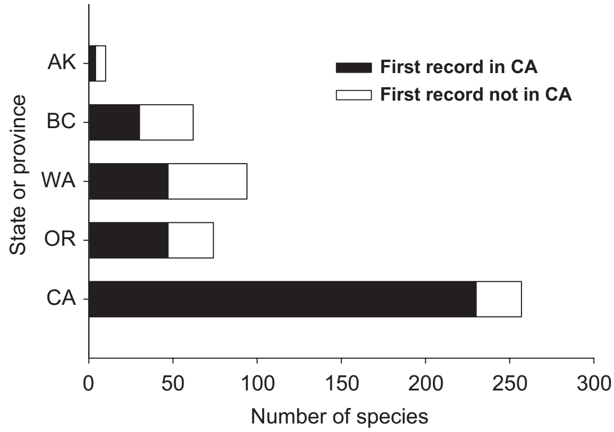

Figure 1 Number of non-native species by geographic region for western North America. For each state and province, shown is the number of non-native species known to have established populations; the number with a first record in California is indicated in black.

For non-native species established in California, most (89%) were first recorded in the state, instead of other states or provinces in western North America (Fig. 1). For other western states and provinces from Oregon to Alaska, 40–64% of non-native species were also first recorded in California. In the latter cases, it appears that California may have been the source for subsequent coastwise spread or that multiple independent introductions occurred to western North America (see Discussion).

The rate of discovery for non-native species in California showed a strong and significant increase over time, with 38% of the total (97 of 257 species) being reported since 1980 (Fig. 2). Owing to the overall contribution of California to first records in western North America, the rate of discovery in California included most species observed for western North America as a whole, accounting for a mean of 90% (SE = 4.0%) of non-native species across all time periods (Fig. 2). This dominance has shown no sign of abating, as 87% of the region's new non-native species were detected in California during the most recent time period, from 1980 to 2006.

California invasions: taxonomy, distribution and invasion history

We documented the occurrence of 257 non-native species of invertebrates, algae and protists with established populations in tidal waters of California (see Appendix S1). For these taxonomic groups, another 41 non-native species were identified with confirmed records in California's tidal waters, but their establishment was either uncertain or unsuccessful. We considered 21 species to have an uncertain establishment status, because of limited (one or few) records or highly restricted populations undergoing active eradication efforts.

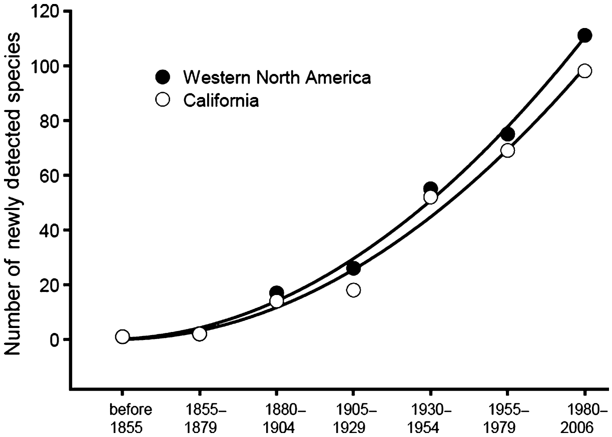

Figure 2 Rate of detection for non-native species. The number of newly reported non-native species that have established populations is shown by 25-year intervals for each (a) California and (b) western North America. Lines depict regressions for each data set, based on mid-point of each time period (California: $y = 14507 - 15.77x + 4.28x^2$, $r^2 = 0.98$; western North America: $y = 15421 - 16.79x + 4.57x^2$; $r^2 = 0.99$).

Another 18 species were classified as failed introductions, including some species with documented live introductions (e.g. the Atlantic oyster *C. virginica* Gmelin 1791, the American Lobster *Homarus americanus* H. Milne-Edwards 1837, and the Atlantic Blue Crab *Callinectes sapidus* Linnaeus 1758). Finally, two species were not considered established as a result of eradication efforts that appear successful, including the alga *Caulerpa taxifolia* Agardh 1817 and the polychaete *Terebrasabella heterouncinata* Fitzhugh & Rouse 1999.

Arthropods and molluscs account for approximately half of the 257 established invaders in California waters (Fig. 3, Appendix S1). The 87 arthropod species are dominated by crustaceans (eight decapods, 51 peracarids, 12 copepods and nine in other groups) and also include seven insects. The 41 species of molluscs include 16 bivalves and 25 gastropods (of which 11 are opisthobranchs). Among other groups of macroinvertebrates, 18–28 non-native established species were recorded for each the annelids, ascidians, cnidarians and ectoprocts. An additional 14 species of microalgae and five species of sponges were considered established.

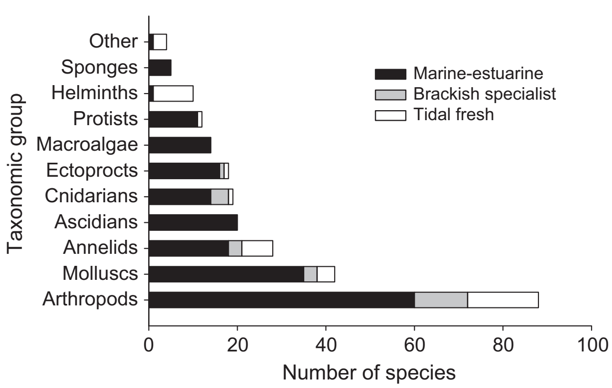

Figure 3 Taxonomic distribution of non-native species in California. For each taxonomic group, shown is the number of non-native species known to have established populations; the salinity distribution of species in each group is indicated by shading.

Species with small body sizes contributed a relatively small fraction to the total number of established non-native species documented in California. Protists accounted for 12 species, and platyhelminths (primarily fish parasites) contributed 10 species. Our total also included three nematodes and one fungus, combined in Fig. 3 as 'Other').

Most of California's marine invasions appear restricted to bays and estuaries. Of the 257 established species, 11% (29 species) have been reported on exposed outer coasts of California, and most of these species are known primarily from bays and estuaries with populations detected in immediately adjacent outer coastal areas. Overall, 75% of the non-native species occur in marine waters, 9% are brackish water specialists and 16% occur in tidal freshwater (Fig. 3, Appendix S1).

For those species established in California, 59% were first recorded within the San Francisco Bay and Estuary for the entire region of western North America (Fig. 4); this was the first recorded location in the state for 65% of the species. Invasions by freshwater and brackish species contribute to this large total in San Francisco Bay and Estuary, and similar habitats are very limited or not available in many other bays. However, even when restricting the analysis to high-salinity waters, San Francisco Bay still accounts for half (50%) of first regional records for the remaining 196 species.

Most (57%) of the non-native species first reported in California are now known to occur in multiple estuaries. This is consistent with coastwise spread from an initial site of establishment. An alternative explanation is that independent introductions have occurred from outside of the region, and such events are clearly possible for some species.

Vector strength in California

Of the 257 non-native species established in California, 44% were classified as introduced by a sole vector in our analysis, whereas more than one vector was considered possible for the remaining 56% (Fig. 5). The combined components (or subvectors) of vessels and oyster transfer are dominant signals overall. For example, species attributed exclusively to the various vessel subvectors (ballast water, hull fouling, dry ballast and cargo) in any combination, account for 48% of all taxa. When also including species for which both vessels and other vectors are possible (85 taxa), fully 81% of the 257 established species include vessels as a sole or possible (multiple) vector. Likewise, for oyster transfers, 32% of all species include oyster transfers as a sole (7%) or multiple (24%) vector.

Despite knowledge about the combination of vectors that are delivering species to California, the relative contribution of each is unresolved, especially at the level of subvector. The largest single subvectors are hull fouling and ballast water of vessels, with 18% and 9% of all species attributed to each as

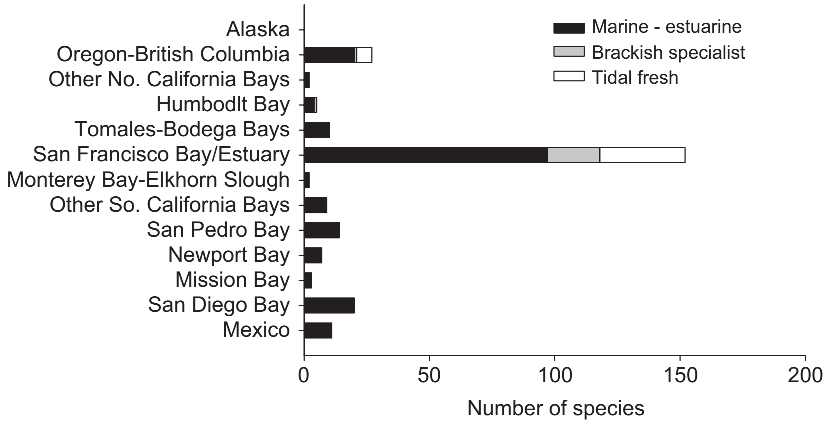

Figure 4 Locations of first records for non-native species in California. The frequency distribution of first record locations in western North America is shown for non-native species that have established populations in California; the salinity distribution of species in each group is indicated by shading.

sole mechanism of introduction, respectively (Fig. 5). Another 20% of the 257 species were attributed to both hull fouling and ballast water as the only possible vectors, and nearly all of the species assigned to multiple vectors include each hull fouling and ballast water as possible vectors. Thus, while < 20% of all species were assigned solely to each hull fouling and ballast water, 60% of all California invasions include hull fouling as a possible delivery mechanism and 53% of species have ballast water as a possible mechanism.

The uncertainty about relative contributions of each subvector results from life histories and distributions that interface with multiple vectors, creating several possible mechanisms of transfer. In the case of vessels, the introductions attributed solely to ballast water include primarily species that occur in low salinity waters or have life stages considered unlikely to be associated with hulls (or other vectors), and approximately half of these species are copepods and mysids in fresh to brackish water, often native to east Asia (see Fig. 5, top bar; Appendix S1). The solely hull-mediated introductions include species for which waterborne dispersal by ballast water was considered improbable, resulting from (1) limited dispersal capability, such as seen for ascidians that are sessile and have extremely short larval duration, or (2) sites of colonization that are not commercial ports. However, a large proportion of species possess life-history characteristics and behaviours (distributions) that allow transfer on either vessels' hulls or ballast tanks.

Other vectors contributing to established non-native species in California tidal waters were classified broadly as fisheries stocking, biocontrol, wetland restoration and live trade (Fig. 5). Fisheries stocking included unintentional introductions of organisms associated with target species (excluding oysters) used in stocking, either official or unofficial (that includes accidental releases). This category involved primarily freshwater parasites (including 10 species of platyhelminthes, three nematodes, and a copepod; shown in Fig. 3) but also a clam (*Mercenaria mercenaria* Linnaeus 1758) and a crayfish (*Procambarus clarkii* Girard 1852). Two insects (*Neochetina bruchi* Hustache 1926, *N. eichhorniae* Warner 1970) were intentionally introduced for biocontrol of water hyacinth in the San Francisco Bay delta. Wetland restoration was considered the probable source of two insects and a fungus, associated with cordgrass (*Spartina alterniflora* Loiseleur-Deslongchamps 1807) transferred to the San Francisco Bay from Georgia. Live trade included species transfers of bait, seafood, aquatic plant or pets (aquaria species), or scientific research.

Although relatively few species (1%) were associated solely with live trade, the potential contribution of live trade is much greater. As with vessels and oyster transfers, live trade is considered a possible vector for many additional species (see Fig. 5, bottom two bars), contributing up to 15% of all established invasions in California. This is exemplified by the Chinese Mitten Crab (*Eriocheir sinensis* H. Milne-Edwards 1853), which may have arrived in San Francisco Bay as live seafood or in the ballast water of ships (Cohen & Carlton, 1997).

Temporal variation of vector strength in California

Figure 6 shows the potential range of California introductions contributed by individual vector, or vector group, over time. As expected from above, fouling and ballast water make the largest overall contributions, when considering each sole and multiple vector categories. The number of introductions attributed to each of these two vessel subvectors also shows a strong increase over time, especially when considering the potential (multiple-vector) species. A total of 51 of the species with multiple vectors are attributed only to hull fouling and ballast water, and another 85 species include hull fouling or ballast water along with at least one non-vessel vector as a possible mechanism of introduction (see Fig. 5). Thus, our analyses highlight both (1) the increasing number of species that may be associated with hull fouling and ballast water in each time period and (2) the current level of uncertainty about the relative strength of these vectors through time.

Vectors grouped under the categories of live trade and 'other' also showed an increase in number of species (Fig. 6f,g). However, like the vessel fouling and ballast water, this increase is driven by species with multiple vectors, usually including vessels. Few species are attributed solely to these non-vessel vectors. Despite an apparent rise in possible

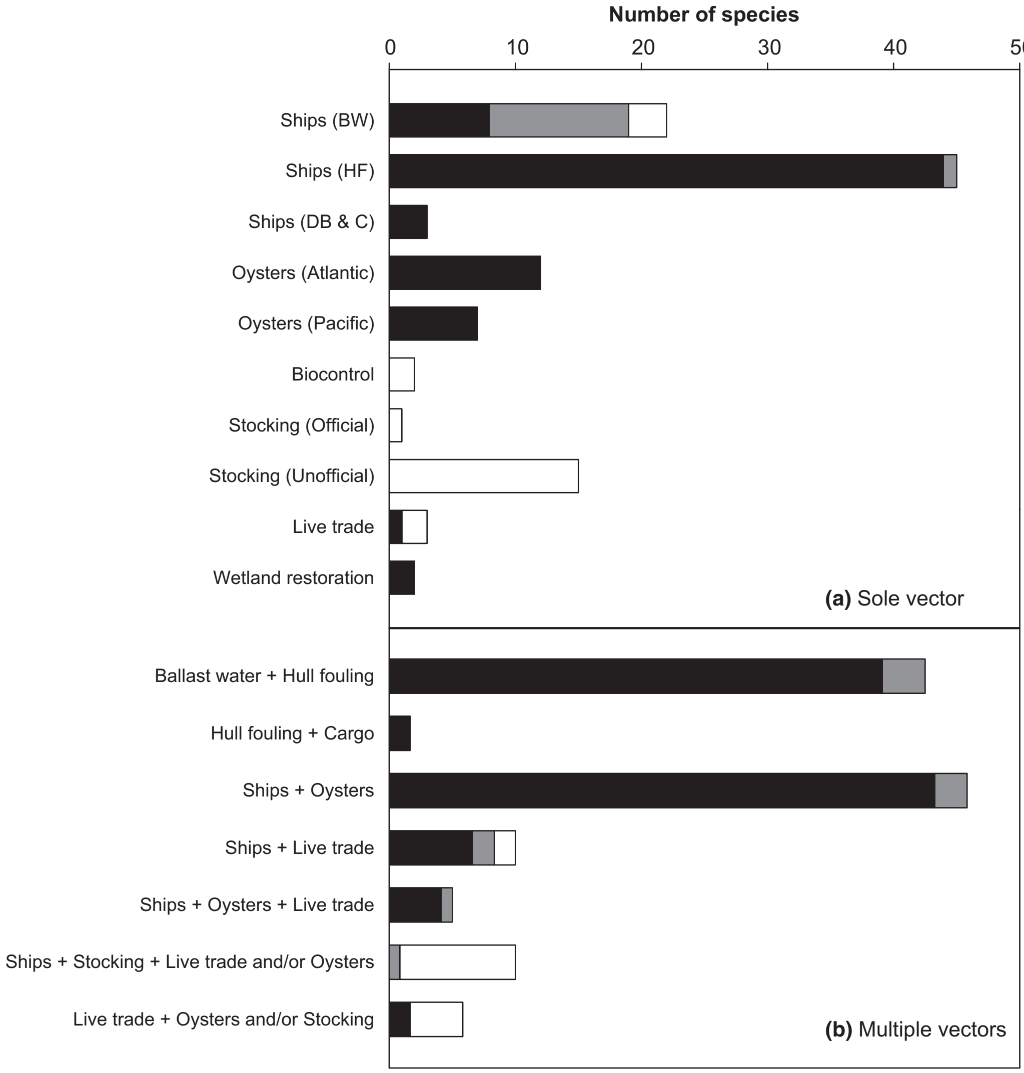

Figure 5 Vectors for established non-native species in California. Shown is the number of initial invasions by non-native species to California attributed to each vector. A species may be attributed to a single vector, or multiple vectors may be possible. The salinity distribution of species in each group is indicated by shading, as in previous figures (marine – estuarine distribution in black; brackish water in grey; tidal freshwater in white). Ships have multiple components or subvectors, including ballast water (BW), hull fouling (HF), dry ballast (DB) and cargo (C). Oysters were divided by source region as either eastern North America (Atlantic) or Asia (Pacific).

(multiple vector) invasions associated with live trade and 'other' vectors over time, their relative contributions are not clear. Although the total numbers of potential invasions in these categories are low relative to vessel-mediated invasions, it is nonetheless noteworthy that their potential contribution is relatively recent and increasing.

In contrast, the temporal trends for invasions associated with oyster transfers and stocking do not indicate an increase in species number. Not surprisingly, the number of species attributed solely to these vectors has declined, reflecting reductions and changes in the transfer of oysters as well as stocking activities over time (see Discussion). Nonetheless, these vectors were considered a possible (multiple) vector for dozens of newly detected species in the most recent time intervals. This classification reflects a possible lag-time in detection for species. This is exemplified by the foraminiferan *Trochammina hadai* Uchio 1962 and tunicate *Didemnum vexillum* Kott 2002, which may have been introduced with plantings of Japanese oysters in the 1930s but were not detected until the 1990s (McGann *et al.*, 2000; Bullard *et al.*, 2007). Thus, despite the recent date of first record for such species, many may have arrived decades earlier and simply been undetected as discussed in the following paragraph.

DISCUSSION

Geographic pattern of observed invasions

California has played a dominant role as a beachhead for marine invasions in western North America. The state is the

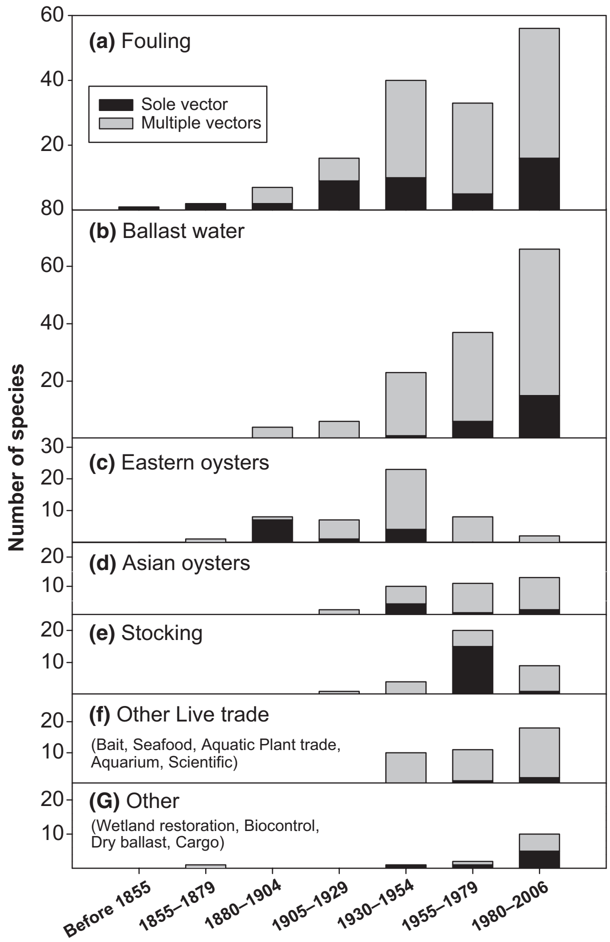

Figure 6 Temporal contribution of vectors to established non-native species in California. Shown is the number of initial invasions by non-native species to California that is attributed to each vector group by 25-year intervals. The numbers of species attributed solely to a specific vector are indicated by black bars, whereas grey bars represent the number of species for which multiple vectors are possible. Thus, the cumulative height of bars (black + grey) indicates the potential contribution of that vector.

first recorded point of entry for the majority (79%) of non-native species known to be established in the region. Following initial colonization, most species are reported in multiple estuaries. Moreover, species first recorded in California constituted a large fraction of the non-native species reported in other states and provinces to the north (see Fig. 1). The latter pattern suggests that California served as a source for northward spread for many species, following the initial introduction. This is the most parsimonious explanation for secondary populations, and studies have provided good support for such spread by selected species (Carlton & Cohen, 2003; Petersen, 2006; Yamada & Gillespie, 2008). However, the possibility of introductions from outside of western North America cannot be ruled out for some species that were first reported in California, especially as novel introductions have clearly occurred to other states and provinces (Cordell *et al.*, 1992; Sytsma *et al.*, 2005; Dudas & Dower, 2006).

On this regional scale, the increasing discovery rate of invasions observed over time also is driven by occurrence records in California. Thus, not only do first records to California dominate the cumulative number of non-native species arriving to western North America, but they have done so in each 25-year interval over the past 150 years to the present time (Fig. 2). More broadly, it is primarily because of the contribution of California that the cumulative number and rate of detection for non-native species on the Pacific coast of North America is much greater than those reported for either the Atlantic or Gulf coasts (Ruiz *et al.*, 2000a). In this sense, invasion dynamics in California disproportionately affect the overall patterns of marine invasions observed at both regional and continental scales.

The large number of recorded non-native species in California may result from a combination of factors. It appears that past propagule supply into California was far greater than other Pacific coast states and provinces, simply because of the timing, rate, and extent of commerce. Following a low intensity of European settlement and trade until the mid-1800s, there was a rapid influx and development in and around San Francisco Bay spurred by the Gold Rush (Carlton, 1979). This resulted in a large number of vessel visits, and a high frequency of abandoned vessels, compared to other ports to the north. In addition, there were massive transfers of oysters and associated biota from the eastern United States (beginning in 1859) and Japan (beginning in 1928) to San Francisco Bay and to a lesser extent in other estuaries along western North America (Carlton, 1979; Miller *et al.*, 2007). While we cannot quantitatively compare the past or cumulative propagule supply characteristics (diversity and abundance) among estuaries, there is little doubt that it was high in California compared to elsewhere on the Pacific coast (Ruiz & Hewitt, 2009).

On a finer scale, San Francisco Bay and Estuary contributed a majority of first records for non-native species documented in California (65%) and the entire west coast (52%; Appendix S1), playing a key role in the regional dominance of California as an entry point for invaders. In addition to high propagule supply, the high diversity of available habitats here also has affected opportunities for colonization. In particular, San Francisco Bay is part of a large estuary with extensive brackish and freshwater habitats, which are largely absent or greatly reduced for many other bays in the region. As a result, tidal fresh and brackish water species have been able to colonize San Francisco Bay and Estuary, comprising roughly one-third of the non-native species with first records in San Francisco Bay (Fig. 4). A lack of suitable habitat (salinity) may prevent colonization of these species in many other estuaries.

Cohen & Carlton (1995, 1998) previously reported San Francisco Bay and Estuary as a hotspot for marine invasions, and we now provide a regional framework. The earlier analysis considered the diversity and number of vectors (propagule supply), a depauperate native biota, and high level of natural and human disturbance as possible factors contributing to the high invasion number and rate for this estuary. A strong case exists for unusually high propagule supply and habitat diversity in San Francisco Bay relative to other bays in western North America. Certainly disturbance may play an important role in invasion dynamics (Elton, 1958; Ruiz *et al.*, 2000a; Piola & Johnston, 2008). However, the relative level of disturbance has not been formally examined between San Francisco and other regional estuaries, and the relative importance of this (or native diversity) across sites remains unclear.

While historically high propagule supply may explain high non-native species richness in San Francisco Bay compared to other estuaries, it is noteworthy that invasions have continued to accumulate here at a high rate for the region. This is perhaps surprising, because the number of commercial ship arrivals and the volume of ballast water discharge from foreign sources are now lower than other regional port systems (Simkanin *et al.*, 2009). This disparity may result from a combination of factors, including (1) other vectors continuing to contribute more to San Francisco than elsewhere, (2) a substantial lag-time in detection that reflects past disparities in propagule supply, and (3) greater susceptibility to invasion than other estuaries. To date, the potential contribution of these and other factors has not been tested, alone or in combination.

Finally, it is perhaps useful to consider the invasion history of California in a global context. For invertebrates and algae (the focus of our analyses), the non-native species richness for California tidal waters exceeds that reported for many regions, including the Atlantic or Gulf coasts of the United States (Ruiz *et al.*, 2000a), Laurentian Great Lakes (Ricciardi, 2006), North Sea (Gollasch *et al.*, 2009), Australia (Sliwa *et al.*, 2009), New Zealand (Hayden *et al.*, 2009), and several other countries (see Rilov & Crooks, 2009). The reported non-native species richness for each of these regions was < 200, usually by a large margin (range *c.* 30–180), even though some encompass a much larger area than California. To our knowledge, only two regions are known to have comparable numbers of established non-native species to California, when also excluding vertebrates and vascular plants: the eastern Mediterranean (*c.* 350 species; Galil, 2009) and the Hawaiian Islands (*c.* 280 species; Carlton & Eldredge, 2009). Furthermore, a large proportion of the Mediterranean species (*c.* 260) are reported to occur from Israel to Syria, with *c.* 240 species in Israel alone (Galil, 2009); a comparable spatial summary is not yet available for Hawaii (but see Carlton & Eldredge, 2009 for detailed information by species).

Such broad geographic comparisons present many challenges, and observed differences may be artefact of strong biases in sampling effort and historical knowledge (Ruiz *et al.*, 2000a; also see Interpreting the Historical Record). What can be said reliably is that only two other regions of the world are known to have comparable non-native marine species richness to California, based on available data. Interestingly, like California, both of these regions have an unusual history and magnitude of shipping, and a large proportion of the eastern Mediterranean are associated with the Suez Canal, underscoring an important role of propagule supply in creating these hotspots (Galil, 2006, 2009; Carlton & Eldredge, 2009).

Vector strength

One of the most striking results from the vector analysis is the frequency of species introductions for which multiple vectors are possible. Cohen (1997) has referred to these as polyvectic species. The high frequency of polyvectic species, which represented 56% of the 257 non-native species established in California, limits our ability to understand the relative importance of individual vectors through time. The classification of polyvectic invasions arises because many species have life stages that can interface with several transfer mechanisms that operate from potential source regions for invasion. This is perhaps best exemplified in species that have benthic and pelagic life stages that could be associated with the hulls or ballast tanks of ships, respectively (Fofonoff *et al.*, 2003). In addition, the potential lag-time in detection also contributes to the extent of polyvectic species, such as oyster transfers from decades ago that cannot be easily dismissed as a possible vector for organisms that may have gone undetected, because of size or taxonomic resolution (see Results).

Especially challenging is uncertainty about the relative importance of ballast water versus hull fouling as the source of recent invasions. Since 1980, the majority of species (61%) was attributed exclusively to a combination of hull fouling and ballast water, and 47% of these 59 vessel-only species were polyvectic for both subvectors. While both transfer mechanisms have resulted in invasions, the high degree of overlap (uncertainty) for these polyvectic species associated with shipping has significant implications for management to reduce invasion risk. Current management to prevent ship-mediated invasions has focused primarily on ballast water treatment (Ruiz & Carlton, 2003), but a large component of ship-mediated invasions may result from organisms on ships' hulls (Godwin, 2003; Coutts & Taylor, 2004; Mineur *et al.*, 2007; Davidson *et al.*, 2008). Thus, the overall effect of ballast water management on invasion dynamics will depend on the relative strength of the ballast water versus hull fouling vectors.

In a similar fashion, the strength of live trade as a vector is uncertain, and its potential importance and growth may be masked. Our analysis indicates a temporal increase in the number of species for which live trade was a possible invasion mechanism in California (Fig. 6). Several recent studies suggest a risk of species transfer with live trade to California (Chapman *et al.*, 2003; Pernet *et al.*, 2008). On a global scale, it appears that live trade is undergoing an expansion. There is growing demand for world aquaculture products (Naylor *et al.*, 2001; Minchin, 2007), and access to shipments of live organisms for a variety of purposes also may be on the rise (Weigle *et al.*, 2005; Keller & Lodge, 2007). Because there are currently few restrictions on marine species imports to the United States, or across state boundaries, live trade may be a source of increasing propagule supply and established populations for California and western North America.

Finally, we are not yet able to distinguish the relative contribution of commercial and recreational vessels for species attributed to hull-fouling. This represents another type of polyvectic transfer, for which discrimination remains challenging. It is evident that recreational, fishing and commercial vessels are each capable of transferring fouling organisms (Coutts & Taylor, 2004; Floerl *et al.*, 2005). For bays without commercial ports, it is probable that vessel-mediated transfers involved recreational or fishing vessels (Wasson *et al.*, 2001). However, where commercial ports exist, we are not presently able to separate the relative contribution of the multiple vessel types to documented hull fouling invasions.

Interpreting the historical record

We urge some caution in interpreting quantitative estimates of invasion dynamics from the historical record. It is clear that our analysis underestimates the total number of non-native species with established populations in western North America for several reasons. First, a large pool of cryptogenic species exists, because of uncertainty about taxonomic identification or biogeographic origins (Cohen & Carlton, 1995; Carlton, 1996). Second, some species with collection records are known to be non-native, but it is not evident yet whether they have established populations. Third, some non-native species have colonized but gone undetected to date.

The magnitude of this underestimate in non-native species richness is difficult to quantify and likely varies among taxonomic groups, geographic locations and habitats (Ruiz *et al.*, 2000a; Fofonoff *et al.*, 2009). For example, invasions by small organisms (especially protists, bacteria, and viruses) may be greatly underestimated relative to species with larger body sizes, because of limited search effort, taxonomic resolution and biogeographic understanding (Ruiz *et al.*, 2000b; Drake *et al.*, 2001). This may explain the pattern observed in Fig. 3, in which small organisms were rare.

Moreover, the actual date of colonization is rarely known, because lag-times exist between establishment and detection. The probability of detection for a new invasion can be very low and depends on abundance, area occupied, conspicuousness (ease of recognition and identification) and search effort (Crooks & Soulé, 1999; Costello & Solow, 2003; Solow & Costello, 2004).

In this analysis, our intent was to summarize the history for known (detected) regional invasions, examining the relative importance of California and various transfer mechanisms to the state. We did not estimate the effect of taxonomic, geographic or temporal biases on observed patterns, as reliable methods are not evident and remain a significant challenge. Nonetheless, given the unusually extensive work on invertebrate communities and invasions along western North America (see Introduction), the relative differences observed across sites appear unlikely to be an artefact of sampling bias. This conclusion is further supported by recent standardized field surveys, which detected an increasing number of non-native species from Alaska to California (Ruiz *et al.*, unpublished data; see also Ruiz & Hewitt, 2009).

CONCLUSIONS

California has consistently played a pivotal role for marine invasions in western North America over the past 150 years. This history indicates that any successful strategy to reduce new invasions on a regional scale, from southern California to Alaska, must address new incursions in California. While invasions to other states and provinces certainly occur from outside the region, these are dwarfed by the sheer number of invasions to California. Importantly, California serves as a hub for secondary spread. It appears that much of this spread is human-mediated, simply because most non-native species appear restricted to protected bays and estuaries, with relatively few species occurring offshore (Wasson *et al.*, 2005; Preisler *et al.*, 2009; Ruiz *et al.*, 2009). Moreover, a high level of connectivity exists for coastwise transfers by vessels (McGee *et al.*, 2006; Simkanin *et al.*, 2009) and other human activities.

San Francisco Bay and Estuary has been an especially important site of colonization for non-native species arriving from outside the region. Following Cohen & Carlton (1998), we hypothesize that this is attributed partly to high historical propagule supply. Today, San Francisco Bay may no longer receive unusually high propagule supply from commercial shipping (Simkanin *et al.*, 2009), and the transfer of species through commercial oyster culture also has abated. We may expect to see a shift in importance of this estuary as a focal point for invasions, if propagule supply contributed strongly to the historical pattern. Alternatively, if this site is more susceptible to invasions than other estuaries, because of disturbance or any combination of factors, its relative prominence in regional invasions may continue.

To understand the mechanisms that underpin spatial and temporal patterns of invasion, close tracking of invasions across sites is required, allowing direct comparisons for factors that may affect invasion outcome. From a management perspective, such measurements also provide the basis to assess potential shifts in importance of different vectors or different locations, providing feedback for adaptive management (Ruiz & Carlton, 2003). California has implemented a statewide survey program to achieve this goal. To our knowledge, this effort is unique within the United States, in that it was created by the state legislature (Ballast Water Management Act 1999; Marine Invasive Species Act 2003; Coastal Ecosystems Protection Act 2006) to provide a long-term and repeated survey effort needed to examine statewide status and trends for marine invasions. This strategy is critical to evaluate the efficacy of actions that aim to reduce new invasions and to identify existing (or emerging) vectors for additional action(s), and a similar approach should be adopted in many global regions to advance both invasion science and management (Ruiz & Hewitt, 2002).

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REFERENCES

Boyd, M., Mulligan, T. & Shaughnessy, F. (2002) *Non-indigenous marine species of Humboldt Bay, California*. Final report, California Department of Fish and Game, Sacramento.

Bullard, S., Lambert, G., Carman, M., Byrnes, J., Whitlatch, R., Ruiz, G., Miller, R., Harris, L., Valentine, P., Collie, J., Pederson, J., McNaught, D., Cohen, A., Asch, R., Dijkstra, J. & Heinonen, K. (2007) The colonial ascidian *Didemnum* sp. A: current distribution, basic biology and potential threat to marine communities of the northeast and west coasts of North America. *Journal of Experimental Marine Biology and Ecology*, **342**, 99–108.

Carlton, J. (1979) History, biogeography, and ecology of the introduced marine and estuarine invertebrates of the Pacific Coast of North America. PhD dissertation, University of California, Davis.

Carlton, J. (1996) Biological invasions and cryptogenic species. *Ecology*, **77**, 1653–1655.

Carlton J. (ed.) (2007) *The Light and Smith manual: intertidal invertebrates from central California to Oregon*. University of California Press, Berkeley.

Carlton, J. & Cohen, A. (2003) Episodic global dispersal in shallow water marine organisms: the case history of the European shore crabs, *Carcinus maenas* and *C. aestuarii*. *Journal of Biogeography*, **30**, 1809–1820.

Carlton, J. & Eldredge, L. (2009) *Marine bioinvasions of Hawai'i*. Bishop Museum bulletin in cultural and environmental studies 4. Bishop Museum Press, Honolulu.

Chapman, J. & Carlton, J. (1991) A test of the criteria for introduced species: the global invasion by the isopod *Synidotea laevidorsalis* (Miers, 1881). *Journal of Crustacean Biology*, **11**, 386–400.

Chapman, J., Miller, T. & Coan, E. (2003) Live seafood species as recipes for invasion. *Conservation Biology*, **17**, 1386–1395.

Cohen, A. (1997) Have claw, will travel. *Aquatic Nuisance Species (ANS) Digest*, **2**, 16–17.

Cohen, A. & Carlton, J. (1995) Nonindigenous aquatic species in a United States estuary: a case study of the biological invasions of the San Francisco Bay and Delta. U.S. Fish and Wildlife Service and National Sea Grant College Program (Connecticut Sea Grant), Washington.

Cohen, A. & Carlton, J. (1997) Transoceanic transport mechanisms: introduction of the Chinese mitten crab, *Eriocheir sinensis*, to California. *Pacific Science*, **51**, 1–11.

Cohen, A. & Carlton, J. (1998) Accelerating invasion rate in a highly invaded estuary. *Science*, **279**, 555–558.

Cohen, A., Mills, C., Berry, H., Wonham, M., Bingham, B., Bookheim, B., Carlton, J., Chapman, J., Cordell, J., Harris, L., Klinger, T., Kohn, A., Lambert, C., Lambert, G., Li, K., Secord, D. & Toft, J. (1998) *Puget sound expedition: a rapid assessment survey of non-indigenous species in the shallow waters of Puget Sound*. Final report, Washington State Department of Natural Resources, Olympia.

Cohen, A., Berry, H., Mills, C. *et al.* (2001) *Washington state exotics expedition 2000: a rapid survey of exotic species in the shallow waters of Elliott Bay, Totten and Eld inlets, and Willapa Bay*. Final report, Washington State Department of Natural Resources, Olympia.

Cordell, J., Morgan, C. & Simenstad, C. (1992) Occurrence of the Asian calanoid copepod *Pseudodiaptomus inopinus* in the zooplankton of the Columbia River Estuary. *Journal of Crustacean Biology*, **12**, 260–269.

Costello, C. & Solow, A. (2003) On the pattern of discovery of introduced species. *Proceedings of the National Academy of Sciences USA*, **100**, 3321–3323.

Coutts, A. & Taylor, M. (2004) A preliminary investigation of biosecurity risks associated with biofouling on merchant vessels in New Zealand. *New Zealand Journal of Marine and Freshwater Research*, **38**, 215–229.

Crooks, J. & Soulé, M. (1999) Lag times in population explosions of invasive species: causes and implications. *Invasive species and biodiversity management* (ed. by O.T. Sandlund, P.J. Schei and Å. Viken), pp. 103–125, Kluwer Academic Publishers, Dordrecht.

Davidson, I., Sytsma, M., Fofonoff, P., McCann, L. & Ruiz, G. (2008) Assessing the potential for hull-mediated species transfers by obsolete ships on their final voyages. *Diversity and Distributions*, **14**, 518–529.

Drake, L., Choi, K., Ruiz, G. & Dobbs, F. (2001) Global redistribution of bacterioplankton and virioplankton communities. *Biological Invasions*, **3**, 193–199.

Dudas, S. & Dower, J. (2006) Reproductive ecology and dispersal potential of varnish clam *Nuttallia obscurata*, a recent invader in the Northeast Pacific Ocean. *Marine Ecology Progress Series*, **320**, 190–205.

Elton, C. (1958) *The ecology of invasions by animals and plants*. Methuen & Co. Ltd., London.

Floerl, O., Inglis, G. & Hayden, B. (2005) A risk-based predictive tool to prevent accidental introductions of nonindigenous marine species. *Environmental Management*, **35**, 765–778.

Fofonoff, P., Ruiz, G., Steves, B. & Carlton, J. (2003) In ships or on ships? Mechanisms of transfer and invasion for non-native species to the coasts of North America. *Invasive species: vector and management strategies* (ed. by G. Ruiz and J. Carlton), pp. 152–182, Island Press, Washington.

Fofonoff, P., Ruiz, G., Hines, A., Steves, B. & Carlton, J. (2009) Four centuries of estuarine biological invasions in the Chesapeake Bay region. *Biological invasions in marine ecosystems: ecological, management, and geographic perspectives* (ed. by G. Rilov and J.A. Crooks), pp. 479–506, Springer-Verlag, Berlin.

Foss, S., Ode, P., Sowby, M. & Ashe, M. (2007) Non-indigenous aquatic organisms in the coastal waters of California. *California Fish and Game*, **93**, 111–129.

Galil, B. (2006) The marine caravan – the Suez Canal and the Erythrean invasion. *Bridging divides: maritime canals as invasion corridors* (ed. by S. Gollasch, B.S. Galil and A.N. Cohen), pp. 207–302, Springer Press, Dordrecht.

Galil, B. (2009) Taking stock: inventory of alien species in the Mediterranean Sea. *Biological Invasions*, **11**, 359–372.

Godwin, S. (2003) Hull fouling of maritime vessels as a pathway for marine species invasions to the Hawaiian Islands. *Biofouling*, **19**(Suppl), 123–131.

Gollasch, S., Haydar, D., Minchin, D., Wolff, W. & Reise, K. (2009) Introduced aquatic species of the North Sea coasts and adjacent brackish waters. *Biological invasions in marine ecosystems: ecological, management, and geographic perspectives* (ed. by G. Rilov and J.A. Crooks), pp. 507–528, Springer-Verlag, Berlin.

Hayden, B., Inglis, G. & Schiel, D. (2009) Marine invasions in New Zealand: a history of complex supply-side dynamics. *Biological invasions in marine ecosystems: ecological, management, and geographic perspectives* (ed. by G. Rilov and J.A. Crooks), pp. 409–423, Springer-Verlag, Berlin.

Hewitt, C., Campbell, M., Thresher, R., Martin, R., Boyd, S., Cohen, B., Currie, D., Gomon, M., Keough, M., Lewis, J., Lockett, M., Mays, N., McArthur, M., O'Hara, T., Poore, G., Ross, J., Storey, M., Watson, J. & Wilson, R. (2004) Introduced and cryptogenic and species in Port Phillip Bay, Victoria, Australia. *Marine Biology*, **144**, 183–202.

Keller, R. & Lodge, D. (2007) Species invasions from commerce in live aquatic organisms: problems and possible solutions. *BioScience*, **57**, 428–436.

Mack, R., Simberloff, D., Lonsdale, W., Evans, H., Clout, M. & Bazzaz, F. (2000) Biotic invasions: causes epidemiology, global consequences, and control. *Ecological Applications*, **10**, 689–710.

McGann, M., Sloan, D. & Cohen, A. (2000) Invasion by a Japanese marine microorganism in Western North America. *Hydrobiologia*, **421**, 25–30.

McGee, S., Piorkowski, R. & Ruiz, G. (2006) Analysis of recent vessel arrivals and ballast water discharge in Alaska: toward assessing ship-mediated invasion risk. *Marine Pollution Bulletin*, **52**, 1634–1645.

Miller, A., Ruiz, G., Minton, M. & Ambrose, R. (2007) Differentiating successful from failed molluscan invaders in estuarine ecosystems. *Marine Ecology Progress Series*, **32**, 41–51.

Minchin, D. (2007) Aquaculture and transport in a changing environment: overlap and links in the spread of alien biota. *Marine Pollution Bulletin*, **55**, 302–313.

Mineur, F., Johnson, M., Maggs, C. & Stegenga, H. (2007) Hull fouling on commercial ships as a vector of macroalgal introduction. *Marine Biology*, **151**, 1299–1307.

Naylor, R., Williams, S. & Strong, D. (2001) Aquaculture – a gateway for exotic species. *Science*, **294**, 1655–1656.

Pernet, B., Deconinck, A., Llaban, A. & Archie, J. (2008) Evaluating risks associated with transport of the ghost shrimp *Neotrypaea californensis* as live bait. *Marine Biology*, **153**, 1127–1140.

Petersen, C. (2006) Range expansion in the northeast Pacific by an estuary mud crab – a molecular study. *Biological Invasions*, **8**, 565–576.

Piola, R. & Johnston, E. (2008) Pollution reduces native diversity and increases invader dominance in marine hard-substrate communities. *Diversity & Distributions*, **14**, 329–342.

Preisler, R., Wasson, K., Wolff, W. & Tyrell, M. (2009) Invasion of estuaries vs the adjacent open coast: a global perspective. *Biological invasions in marine ecosystems: ecological, management, and geographic perspectives* (ed. by G. Rilov and J.A. Crooks), pp. 587–617, Springer-Verlag, Berlin, Heidelberg.

Ricciardi, A. (2006) Patterns of invasion in the Laurentian Great Lakes in relation to changes in vector activity. *Diversity and Distributions*, **12**, 425–433.

Rilov, G. & Crooks, J. (2009) *Biological invasions in marine ecosystems: ecological, management, and geographic perspectives*. Springer-Verlag, Berlin.

Ruiz, G. & Carlton, J. (2003) Invasion vectors: a conceptual framework for management. *Invasive species: vectors and management strategies* (ed. by G. Ruiz and J. Carlton), pp. 459–504, Island Press, Washington.

Ruiz, G. & Hewitt, C. (2002) Toward understanding patterns of coastal marine invasions: a prospectus. *Invasive aquatic species of Europe* (ed. by E. Leppakoski, S. Olenin and S. Gollasch), pp. 529–547, Kluwer Academic Publishers, Dordrecht.

Ruiz, G. & Hewitt, C. (2009) Latitudinal patterns of biological invasions in marine ecosystems: a polar perspective. *Smithsonian at the poles: contributions to international polar year science* (ed. by I. Krupnik, M.A. Lang and S.E. Miller), pp. 347–358, Smithsonian Institution Scholarly Press, Washington.

Ruiz, G., Fofonoff, P., Carlton, J., Wonham, M. & Hines, A. (2000a) Invasion of coastal marine communities in North America: apparent patterns, processes, and biases. *Annual Review of Ecology and Systematics*, **31**, 481–531.

Ruiz, G., Rawlings, T., Dobbs, F., Drake, L., Mullady, T., Huq, A. & Colwell, R. (2000b) Global spread of microorganisms by ships. *Nature*, **408**, 49–50.

Ruiz, G., Freestone, A., Fofonoff, P. & Simkanin, C. (2009) Habitat distribution and heterogeneity in marine invasion dynamics: the importance of hard substrate and artificial structure. *Marine hard bottom communities* (ed. by M. Wahl), pp. 321–332, Springer-Verlag, Berlin.

Simkanin, C., Davidson, I., Falkner, M., Sytsma, M. & Ruiz, G. (2009) Intra-coastal ballast water flux and the potential for secondary spread of non-native species on the US West Coast. *Marine Pollution Bulletin*, **58**, 366–374.

Sliwa, C., Migus, S., McEnnulty, F. & Hayes, K. (2009) Marine bioinvasions in Australia. *Biological invasions in marine ecosystems: ecological, management, and geographic perspectives* (ed. by G. Rilov and J.A. Crooks), pp. 425–437, Springer-Verlag, Berlin.

Solow, A. & Costello, C. (2004) Estimating the rate of species introductions from the discovery record. *Ecology*, **85**, 1822–1825.

Sytsma, M., Cordell, J., Chapman, J. & Draheim, R. (2005) *Lower Columbia river aquatic nonindigenous species survey 2001–2004*. Final report, United States Coast Guard & United States Fish and Wildlife Service, Washington.

Wasson, K., Zabin, C., Bedinger, L., Diaz, M. & Pearse, J. (2001) Biological invasions of estuaries without international shipping: the importance of intraregional transport. *Biological Conservation*, **102**, 143–153.

Wasson, K., Fenn, K. & Pearse, J. (2005) Habitat differences in marine invasions of central California. *Biological Invasions*, **7**, 935–946.

Weigle, S., Smith, D., Carlton, J. & Pederson, J. (2005) Assessing the risk of introducing exotic species via the live marine species trade. *Conservation Biology*, **19**, 213–223.

Wonham, M. & Carlton, J. (2005) Trends in marine biological invasions at local and regional scales: the Northeast Pacific Ocean as a model system. *Biological Invasions*, **7**, 369–392.

Yamada, S. & Gillespie, G. (2008) Will the European green crab (*Carcinus maenas*) persist in the Pacific Northwest? *ICES Journal of Marine Science*, **65**, 725–729.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Non-native invertebrates and algae recorded for western North America before 2007, including (a) date and location of first records and (b) vector attributed to introduction into California.

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