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INVASION OF COASTAL MARINE COMMUNITIES IN NORTH AMERICA: Apparent Patterns, Processes, and Biases

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■ **Abstract** Biological invasions of marine habitats have been common, and many patterns emerge from the existing literature. In North America, we identify 298 nonindigenous species (NIS) of invertebrates and algae that are established in marine and estuarine waters, generating many "apparent patterns" of invasion: (*a*) The rate of reported invasions has increased exponentially over the past 200 years; (*b*) Most NIS are crustaceans and molluscs, while NIS in taxonomic groups dominated by small organisms are rare; (*c*) Most invasions have resulted from shipping; (*d*) More NIS are present along the Pacific coast than the Atlantic and Gulf coasts; (*e*) Native and source regions of NIS differ among coasts, corresponding to trade patterns. The validity of these apparent patterns remains to be tested, because strong bias exists in the data. Overall, the emergent patterns reflect interactive effects of propagule supply, invasion resistance, and sampling bias. Understanding the relative contribution of each component remains a major challenge for invasion ecology and requires standardized, quantitative measures in space and time that we now lack.

ITRODUCTION

Biological invasions, or the establishment of species beyond their historical range, have long been of great interest to ecologists, evolutionary biologists, and paleontologists (40, 41, 50, 72, 84, 85, 135, 148). The establishment and study of small populations has generated a wide range of opportunities to understand fundamental population, community, and ecosystem processes across many taxonomic groups (38, 130, 136, 137). In recent years, invasion research has focused especially on the patterns and process of invasions themselves (25, 37, 81, 101, 108, 129), and we have witnessed a virtual explosion in the quantity and diversity of research in this topic area (104, 115, 144).

The recent growth of invasion research has been stimulated largely by an apparent increase in the rate of nonindigenous species (NIS) invasions and their effects on native populations and communities, ecosystem function, and economies, as well as human health (6, 10, 38, 61, 62, 132, 140). As a result, new information and shifting perspectives have emerged rapidly. This emergence is particularly striking for invasions of marine environments, which had historically received little attention compared to terrestrial or freshwater systems (13).

In this article we explore patterns, mechanisms and hypotheses associated with marine invasions. Although new data on marine invasions have increased rapidly, they have never been summarized, beyond analysis for single bays or estuaries (11, 29, 30, 69, 117) (JT Carlton 2000, unpublished checklist; Carlton & Wonham 2000, unpublished manuscript). Moreover, the complexities and potential biases of these data, and inferences that can be drawn from the data, have not been evaluated critically. Here, we provide such a synthesis for marine invasions of North America and begin to evaluate some of the emergent patterns and underlying mechanisms. More specifically, we wish to summarize spatial and temporal patterns of invasion and to identify (*a*) key gaps in data, (*b*) hypotheses about mechanisms, and (*c*) future directions for research. Although our analysis is specific to marine and estuarine invasions, we explore issues and approaches that are relevant generally for both invasion biology and invasion management.

TTERNS OF INVASION

ssification and Analysis

We characterized patterns of invasion for marine (including estuarine) invertebrates and algae on multiple spatial scales, focusing primarily on North America. Our focus on invertebrates and algae is intended to illustrate general issues, using a relatively large group of NIS known for North America across many phyla. Although vascular plants and fish were excluded from our analysis, these groups have contributed hundreds of additional NIS that are established in coastal bays and estuaries of North America (30, 55, 117; P Fofonoff, GM Ruiz & AH Hines, submitted, GM Ruiz, P Fofonoff, AH Hines & JT Carlton, unpublished data). Their exclusion from our analysis was pragmatic, to reduce the complexity of patterns and analyses. Furthermore, there are also many fundamental differences for vascular plants and fish, compared to invertebrates and algae, with respect to invasion patterns (e.g. transfer mechanisms, habitat distributions, dates of arrival, and biology) that warrant separate analyses.

For each of 298 NIS that are reported to be established in coastal waters of North America, we summarized available information about the distribution and invasion history for the Atlantic, Pacific, and Gulf coasts. We defined NIS as those organisms transported by human activities to coastal regions where they did not previously occur. We omitted species that underwent range expansions attributed to natural dispersal, even if some resulted from anthropogenic changes in environmental conditions (19).

We considered the marine and estuarine waters of North America to extend from outer coastlines to the limit of tidal waters within bays and estuaries, including the oligohaline and tidal freshwater reaches of estuaries. Within this coastal zone, we included all species that occurred below the mean monthly limit of spring tides. Our list therefore includes marine organisms but also some species found commonly in salt marshes and strand-lines of beaches as well as species reported from estuarine freshwater. We also included insects released for biocontrol when their host plants were reported as occurring in tidal waters. However, we excluded some "boundary species" that appeared occasionally or rarely within our study area but were found primarily in terrestrial habitats and inland freshwater (see 117 for additional discussion).

Our review and synthesis relied on four main sources of information. The primary source was published information, including especially some existing analyses of NIS for particular bays (11, 29, 30, 69, 117; JT Carlton 2000, unpublished checklist; Carlton & Wonham 2000, unpublished manuscript) as well as a diffuse collection of literature. We also reviewed unpublished reports, theses, and records from long-term monitoring efforts along each coast. In addition, we corresponded with many scientists who were expert either in particular taxonomic groups or the biota of particular geographic regions. Finally, we also conducted some limited field surveys at selected sites.

As a minimum, we sought to characterize the following attributes for each species: (*a*) Date of First Record; (*b*) Native Geographic Region; (*c*) Source Region of invasion; (*d*) Vector (*mechanism*) of introduction; (*e*) Salinity Distribution; (*f*) Geographic Distribution; (*g*) Invasion Status; and (*h*) Population Status. The information was collected separately for each coast, since some species have invaded multiple coasts and these attributes may differ among coasts. Where multiple sites of invasion for a species existed within a coast, data were always collected for the first site and date of successful introduction (as attributes such as Source Region and Vector may differ among sites). The details of this classification scheme and subsequent analyses are described below.

vasion Status

assess the invasion status of species (as below), we used a graded set of criteria, ying on the historical record, paleontological record, archaeological record, biographic distribution, dispersal mechanisms, documented introductions, and a ite of ecological and biological characteristics (26, 27, 30, 138). We assigned ecies to one of three categories of invasion status, reflecting the degree of rtainty that a species was introduced or native:

troduced species Native and introduced ranges of these species were well :ablished and provided a clear invasion history, in most cases. We considered a *v* additional species to be introductions where the evidence was very convincing; :luded here are a few intracoast invasions, for which natural dispersal is possible t highly unlikely (see below).

yptogenic species (Possible Introductions)—No definitive evidence of ei- :r native or introduced status [*sensu* Carlton (16)]. For some of these species, roduced status has been suggested or appears likely.

tive species Native range of these species was well established and provided ar evidence of native status.

Owing to intracoastal invasions, it was possible for a species to have a com- ınd assignment to two or more categories of species status. For example, the ɔked mussel (*Ischadium recurvum*) is native to the southeastern United States introduced to the northeast. Thus, this species is considered native, cryptogenic, l introduced along different regions of the Atlantic coast. In our analyses, all ormation about this species along the Atlantic coast refers to the introduced ɔulations. Although such intracoastal invasions possibly occurred for many :cies, we included only those that were clearly documented; all others were ısidered cryptogenic and thus excluded from our present analyses.

ıte of First Record

date of first record, we used the first date of collection, sighting, or documented iberate release. If these were not reported, dates of written documents or ɔlications were used; however, we recognize that these later dates may be many ırs after the date a species was first collected or sighted.

ctor

evaluated plausible mechanisms (or vectors) for each introduction, using infortion about the first date of record, life history, habitat utilization, and ecological ibutes. We assigned each species invasion to one of eight broad vector categies: Shipping; Fisheries; Biocontrol; Ornamental escape; Agricultural escape; search escape; Canals, created by humans, as a corridor for dispersal; or Multi-. Several of the broad categories are composed of subcategories. For example, Shipping vector included organisms moved on the hull, in ballast water or dry ballast, in or on cargo, on deck, on anchors, etc. Fisheries introductions involved both intentional and unintentional release, including those that resulted from aquaculture. Both Fisheries and Ornamental introductions also included species associated with the target species (e.g. fouling organisms on oysters). Although some of the subcategories are discussed further in this review, this higher resolution is the focus of a separate analysis (GM Ruiz, JT Carlton, P Fofonoff & AH Hines, submitted).

Several simultaneous mechanisms of introduction were clearly possible for many species, creating some uncertainty about the vector responsible for each invasion. In these cases, we simply classified the vector as Multiple and indicated the plausible mechanisms. For example, the green crab (*Carcinus maenas*) was recently to introduced western North America, and multiple mechanisms of introduction exist for this invasion: Shipping and Fisheries.

Sequential mechanisms of introduction also existed for some species, where the first introduction can be ascribed to a particular vector but subsequent introductions may have occurred due to additional mechanisms. To recognize this, there must exist a clear chronological sequence in the operation of the respective vectors, such that one predates any additional vectors. For example, the barnacle (*Balanus improvisus*) was introduced to western North America in the mid 19th century by Shipping, but the latter movement of oysters (Fisheries) represents an additional vector that was active afterwards. In such cases, we identified both the initial vector and additional vectors.

Native and Probable Source Region

Native Region identifies the range of each species before human transport, and Source Region identifies the likely area from which an invasion occurred. The Source Region may differ from Native Region for various reasons. First, a species may have a wide native distribution, whereas an introduction may have been most likely to occur from a particular region, based upon the prevalent trade patterns (and vectors) in operation. Second, there are many "stepping stone" invasions, where a species may invade secondarily from a previously invaded region that is outside the native range.

We assigned a probable Source Region, based upon the extent of available transfer mechanisms, known association with those mechanisms, and proximity to site of invasion. Identification of Source Region has some degree of uncertainty. This was particularly problematic for some widespread species, where many potential source regions (with operating transfer mechanisms) exist. For these species, we have indicated "Unknown" for Source Region.

For the purposes of our analysis, we classified Native and Source regions in terms of broad oceanic and continental regions. Ocean regions were used for species with strong marine affinities, whereas continental regions were used for those with primarily fresh water (or continental) distributions. The categories included: Western Atlantic, Eastern Atlantic, Amphi- (both Western and Eastern) Atlantic, Indian Ocean, Indo-West Pacific, Western Pacific, Eastern Pacific,

Amphi-Pacific, North America, Eurasia, South America, Africa, and Australia. As indicated above, Unknown was used when Source Region remained unresolved, and was also used as necessary for unresolved Native Region.

Native and Source Region categories were selected to accommodate most species and highlight general patterns. For each species, we identified distribution according to commonly used biogeographic regions (8, 134). These were then combined into our broad categories to simplify analyses (e.g. Northwestern Atlantic and Southwestern Atlantic became Western Atlantic) or to reflect species distributions that traversed boundaries (e.g. Indian Ocean and Western Pacific became Indo-West Pacific). Additional data on the known native and introduced range of each species, providing much finer resolution than presented here, are available upon request; these can also be found in associated references listed in the supplemental Appendix 1 on the Annual Reviews online website.

Population Status

To distinguish between introductions with persistent populations and those that may have failed, we classified the Population Status of each species as one of the following:

1. Established species have been documented as present and reproducing within the last 30 y. Multiple records were required for a species to be considered established. Furthermore, for species detected in the past 10 y, occurrence was necessary in at least two locations or in two consecutive years.
2. Population status was considered Unknown for introductions with no records within the past 20–30 y or for recent introductions with too few records (as above).
3. We recognized two categories of species introductions that do not appear to be established. Failed introductions are species that were reported but for which there is no evidence of establishment. In contrast, *Extinct* introductions survived and reproduced for many years before disappearing.

We did not include the extensive literature that exists on failed introductions. There are literally hundreds of species that have been released but apparently never established (see 11, 21, 69, 123, 146). Our goal was to document the history and fate of established populations, accounting also for those that were extinct or of unknown population status. Since population status can vary along a coastline, just as invasion status (above), some species were assigned to multiple categories. It is only in this context that we refer to failed introductions in our analyses.

Salinity Range

The salinity distribution of each species was classified by the Venice system of salinity zones. A species could occur in one or more of the following salinity zones: Freshwater, Limnetic (tidal freshwater, 0–0.5 ppt), Oligohaline (0.5–5 ppt salinity); Mesohaline (5–18 ppt); Polyhaline (18–30 ppt); and Euhaline (30–35 ppt). All species present in nontidal freshwater also occurred within tidal waters, occurring sometimes across a broad range of salinity. Throughout, salinity ranges were considered to be the sum of ranges for all life-stages reported for a species.

Geographic Distribution

For each species, we characterized the reported geographic distribution within North America, allowing a comparison of invasion patterns among coasts. We also compared patterns of invasion among relatively large estuaries, which included commercial ports. For comparisons among estuaries, we focused most of our attention on five locations: Prince William Sound (Alaska), Puget Sound (Washington), Coos Bay (Oregon), San Francisco Bay (California), and Chesapeake Bay (Maryland and Virginia). Most marine invasions have been reported in bay and estuarine environments (116), and these selected estuaries have been the foci of intensive analyses on the patterns and extent of invasion (11, 29, 30, 69, 117; JT Carlton 2000, unpublished checklist; Carlton & Wonham 2000, unpublished manuscript). As a result, the five estuaries offer the most complete data on spatial variation in the extent of invasions and species overlap within North America.

We also included in our comparison of NIS among estuaries data from Port Philip Bay, Australia (67). As with the focal estuaries in North America (above), patterns of NIS invasions at this site have recently received intensive analysis providing the opportunity for an initial comparison with the North American sites.

Analyses

We used the resulting database (Appendix 1) to examine patterns of marine invasion in North America by taxonomic group, date of first record, vector, source region, native region, and salinity distribution. We included all introductions that were considered established (as above). We excluded from this analysis cryptogenic species as well as boundary residents, but we discuss the importance of cryptogenic species further below. Due to the size of Appendix 1, it does not appear in this article but is available at the Annual Reviews website repository in the Supplemental Materials section.

Our primary goal is to examine patterns of invasion for the entire continent. We have also included a comparison of invasion patterns on two additional spatial scales. First, we examine concordance of patterns among the three separate coasts of North America. Second, we describe the number and overlap of NIS among estuaries, including five in North America (as above) and one in Australia (Port Philip Bay) for which invasions have been well analyzed.

Although we have characterized the current knowledge on marine invasion patterns for North America, it is important to recognize the sources and limitations in the data from which these patterns emerge. We therefore consider our analysis to outline the apparent patterns of invasion from the literature. We address both the limitations and underlying assumptions that must be tested to adequately interpret these patterns.

:nt of Marine Invasions in North America

We identified 298 NIS of invertebrates and algae that are established in coastal waters of North America (Appendix 1). The 76 established species that have successfully colonized more than one coast we designate as "repeat invaders" (also "repeat" or "secondary" invasions) in our subsequent analyses. Thus, among all three coasts of North America, there have been a total of 374 successful invasion events (= 298 initial invasions +76 repeat invasions).

An additional three species are classified as extinct invasions, and the success of another 33 species is unknown (Appendix 1). In all subsequent analyses, we have restricted our focus to species known to have successfully invaded, which are classified as established invasions.

Our data provide only a minimum estimate for established invasions of marine invertebrates and algae. We have excluded consideration of boundary residents and cryptogenic species from our estimates, and the latter group may include hundreds of NIS that have gone unrecognized as such. Furthermore, many sites and taxa within North America have received little scrutiny. Below, we discuss the potential consequences of these limitations to the overall patterns.

Although our analysis is restricted to invertebrates and algae, it is noteworthy that at least 100 species of nonindigenous fish and 200 species of nonindigenous vascular plants are known to be established within this coastal area (55, 30; P Fofonoff, GM Ruiz & AH Hines, submitted; GM Ruiz, P Fofonoff, AH Hines & JT Carlton, unpublished data). In general, the identification and knowledge of established populations is better for these groups than for invertebrates and algae, due to both the size of the organisms and the extent of research and monitoring programs. However, a relatively large proportion of boundary residents exist among the nonindigenous fish and plants, and the tendency of species to occur within estuaries can vary geographically, complicating numerical estimates of NIS (P Fofonoff, GM Ruiz & AH Hines, submitted).

:onomic Distribution of Marine Invasions North America

The NIS in our analysis were distributed among 11 phyla, with a significant difference in the contribution of each phylum to the 298 species (Figure 1A; Appendix 1; $X^2 = 224.6$, df = 10, $P < 0.001$). Half of all species were crustaceans or molluscs, accounting respectively for 28% and 22% of the initial invasions.

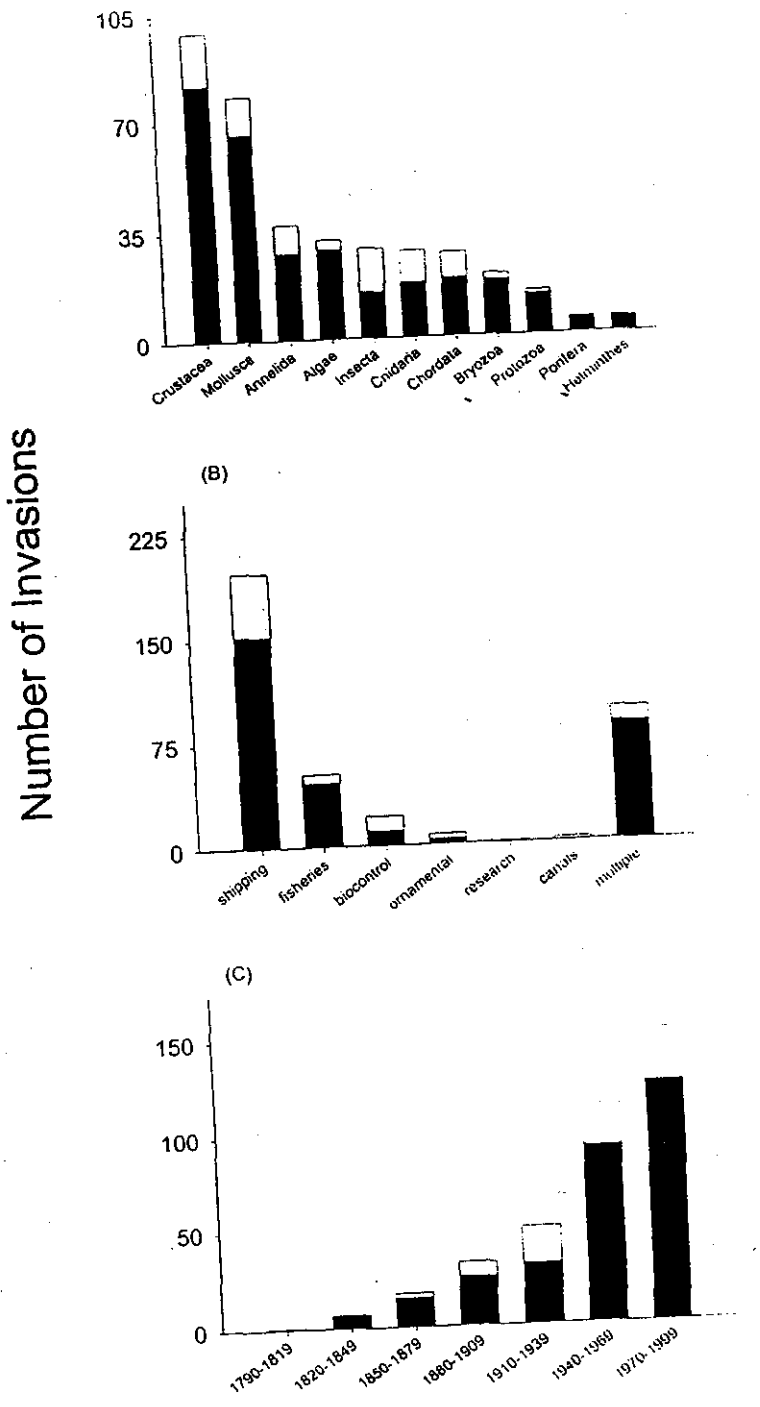
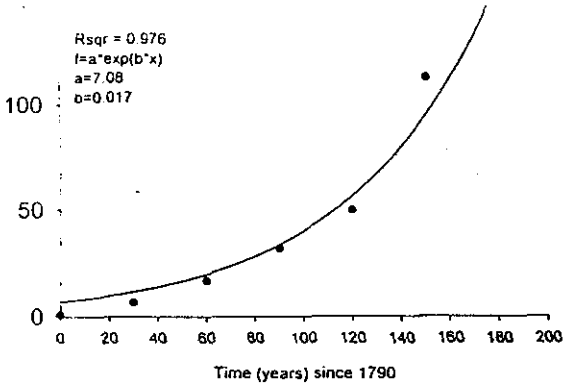
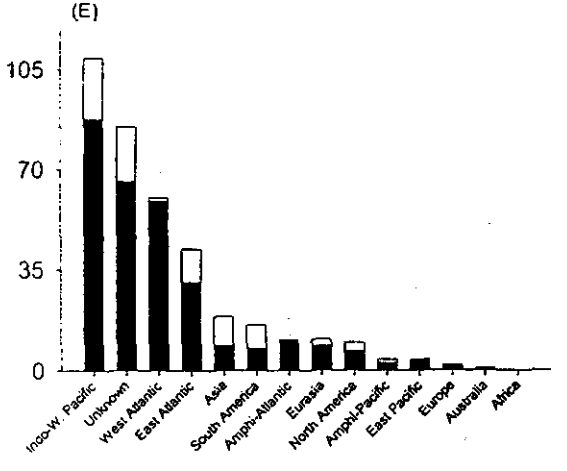
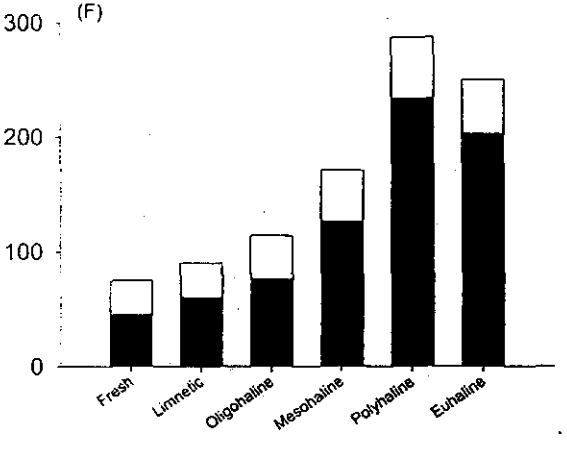


Figure 1 Total number of established nonindigenous species of invertebrates and algae reported in marine waters of North America shown by: (*A*) Taxonomic group, (*B*) Vector, (*C*) Date of First Record, (*D*) Rate of Invasion, (*E*) Native Region, and (*F*) Salinity zone. *Filled bar*, number of unique or initial species invasions (n = 298); *open bar*, number of repeat invasions among coasts (n = 76; see text for description). Rate of invasion was estimated for 30 y intervals, with number of new invasions shown for the first year of each interval since 1790.







Number of Invasions

These two phyla together also accounted for 38% of the 76 repeat invasions (22% of crustaceans and 16% of molluscs), which was high relative to the other phyla (mean = 7%, range = 0–18%).

Perhaps most striking is the low number of relatively small organisms recognized as NIS. A few species of protists and diatoms are recognized as NIS, but many groups of microorganisms (including bacteria, viruses, fungi, microsporidia, coccidia, etc.) are absent from our database (Appendix 1). For Chesapeake Bay alone, the number of known NIS declines significantly with size of the organism, using maximum size for all taxa other than plants and fish (117). Although there may be something fundamentally different about invasion opportunities or success for small taxa, we hypothesize that this pattern results from bias in the data (see below).

Mechanisms of Introduction for Marine Invasions in North America

Shipping and fisheries have been the dominant vectors for marine invasions in North America. Shipping was the sole vector for 51% of the 298 initial invasions, and fisheries were responsible for another 15% (Figure 1*B*; Appendix 1). Although multiple vectors were plausible for 29% of all initial invasions, 78% of these 85 invasions were attributed to shipping and fisheries as the only plausible mechanisms. Shipping and fisheries together accounted for 89% of all 298 initial invasions (= 51% shipping + 15% fisheries + 22% shipping and fisheries as multiple vectors).

Shipping and fisheries were also responsible for most (74%) of the 76 secondary or repeat invasions, occurring on coasts other than the initial coast of invasion (Figure 1*B*, Appendix 1). Shipping alone accounted for 59% of the repeat invasions, and the remaining 15% were attributed to fisheries or multiple vectors for which shipping and fisheries were the only vectors.

Despite the predominance of shipping and fisheries as vectors, there remains a great deal of uncertainty about the relative contribution or importance of each mechanism individually. This is underscored by the frequency of invasions attributed to multiple vectors, creating a wide range of importance for shipping and fisheries vectors. For example, 51% of 298 initial invasions are attributed to shipping as the sole vector, but shipping may be involved in an additional 27% of the invasions (as a possible mechanism in 94% of the 85 invasions attributed to multiple vectors; Appendix 1). It is possible to weight each vector, based upon their spatial and temporal pattern of operation, suggesting a probable vector in many cases. However, this cannot reliably exclude the other possible vectors as a mechanism for introduction. Furthermore, the multiple vectors are all in operation and may each contribute propagules to the initial or subsequent introduction of a species

A further analysis divided each vector category into subcomponents (GM Ruiz, JT Carlton, P Fofonoff & AH Hines, submitted), indicating that most invasions

n shipping resulted from ballast water and hull fouling communities, and those n fisheries were dominated by translocations of organisms associated with ters (see 14 for description). However, the relative importance of these shipping categories (hull fouling or ballast water) to the overall number of invasions iains poorly resolved, due to the existence of multiple vectors (as discussed ve), as well as multiple subcategories that were plausible within the shipping tor, in many cases.

Marine Invasions in North America

e rate of reported invasions has increased over the past 2 centuries, using the e of first record for all 374 initial and secondary invasions of North America gure 1C; Appendix 1). The increase of initial invasions is best described by exponential function (Figure 1D; $y = 7.08^{(0.017x)}$, $r^2 = 0.976$; where y is the nber of new invasions and x is time in 30y intervals, indicated as the first year the 30y interval). In contrast, although the rate of known repeat invasions is o increasing in North America, this is best described by a linear function ($y = 35x$, $r^2 = 0.874$).

The relative contribution of shipping to reported invasions has also increased er time (GM Ruiz, JT Carlton, P Fofonoff & AH Hines, submitted). The rate of asions attributed solely to shipping has increased over the past 200 y, account- ; for 62% of initial invasions in the past 30 y (Figure 2; see also Appendix 1). is increase is best described by an exponential function ($y = 1.127^{(0.024x)}$, = 0.992). In contrast, the rate of reported fisheries invasions is not increasing nsistently over time and may be declining in recent years. Only 8% of reported asions were attributed solely to fisheries in the past 30y, and the rate of fisheries asions since 1790 is best described by a slightly positive linear relationship igure 2; $y = 0.083x - 0.929$, $r^2 = 0.669$).

Finally, our temporal data indicate that 20% of initial invasions in the last 30y erval are attributed to multiple vectors, usually the combination of shipping and heries (Appendix 1). Although lower than the prevalence of multiple vectors r all time periods (29%), uncertainty exists about particular vector responsible r even many of the most recent invasions.

and Source Region of Marine Invasions th America

pproximately half of all initial invasions were classified as native to western ean margins: the Indo-West Pacific and West Atlantic regions (30% and 20%, spectively; Figure 1E; Appendix 1). Indo-West Pacific species were either from e West Pacific (69%) or shared between the Indian Ocean and West Pacific (31%; s shown in Appendix 1). In contrast, 12% of all initial invaders were considered ative to the eastern ocean margins of the Atlantic (10%) and the Pacific (1%). Continents were the native region for 12% of initial invaders, including primarily pecies of freshwater origin. Roughly 5% of the initial invaders were classified as

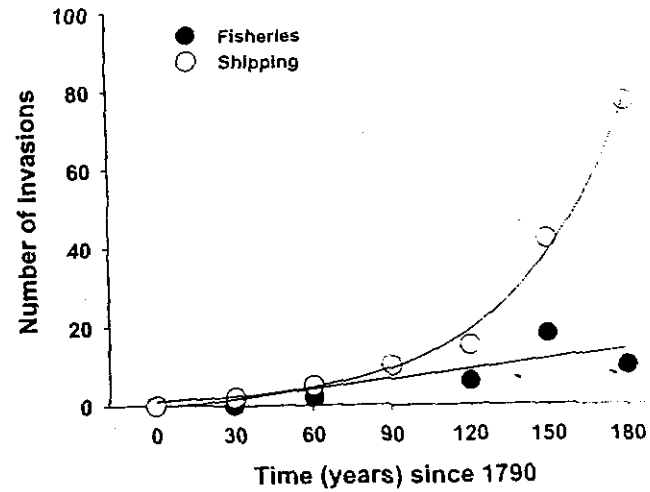


Figure 2 Rate of reported marine invasions of invertebrates and algae that were attributed to shipping and fisheries in North America since 1790. *Open circles* indicate number of new invasions associated with shipping per 30 y interval; *closed circles* indicate number of new invasions associated with fisheries per 30 y interval. Data are plotted as in Figure 1.

Amphi-Atlantic or Amphi-Pacific for native region. Surprisingly, the native region for 22% of all initial invaders was considered unknown, although the taxonomic identity was also uncertain for 33 (50%) of these 66 species.

Addition of the 76 repeat invasions has little effect on the overall prevalence of native regions (Figure 1E). However, it was notable that few repeat invaders were classified as native to the West Atlantic (2% of total for that region) and Amphi-Atlantic (0%), compared to the other regions with relatively large numbers of initial invaders (Indo-West Pacific—19%; Unknown—22%; East Atlantic—26%; Eurasia—18%). This is mostly an artifact of West Atlantic species being native to eastern North America, making it impossible to invade this coast (in our analysis) and reducing the opportunity for repeat invasions to occur.

We estimate that source and native regions were different for approximately 22% of all initial and repeat invasions (combined), excluding species classified as unknown for either region (Appendix 1). The source and native regions differed for all species with Amphi-Atlantic or Amphi-Pacific native regions, indicating that the invasion of North American sites occurred often from a limited portion of the native range. However, for all species from other native ranges, this implies a "stepping-stone" mode of invasion, where invasions are occurring from secondary populations outside the native range. Most of these cases involved secondary source populations in the East Atlantic (12 species), West Atlantic (8 species, excluding those that were Amphi-Atlantic), and North America (9 species). Furthermore, we estimate that the proportion of stepping-stone

invasions was relatively high for NIS with native regions of Indo-West Pacific (25% of 109 species) and Eurasia, Europe and Asia (31% of 32 species).

Although native region is well defined for 77% of species, source region should be considered a rough approximation. Strong evidence often underlies the choice of source region for each invasion (e.g. operation and relative strength of vectors, established populations, date of first record, etc). For example, the European green crab, *Carcinus maenas*, may have invaded western North America from multiple source regions, including: Europe, eastern North America, Australia, and South Africa. Recent genetic analyses indicate that this newly established population derived from eastern North America (3). However, in most cases, alternate sources (in and outside of the native region) cannot easily be excluded.

linity Distribution of Marine Invasions in North America

Significantly more invasions are known in high (polyhaline and euhaline) than low salinity zones, for initial invasions as well as for all invasions combined (Figure 1*F*; initial invasions: $X^2 = 245$, df = 5, $p < 0.001$; all invasions: $X^2 = 234$, df = 5, $P < 0.001$). However, repeat invasions were evenly distributed across salinity zones. Importantly, many species were reported to be euryhaline and to occur in several salinity zones. Only 18 species were considered to be restricted to one salinity category.

ographic Variation in the Extent d Patterns of Marine Invasions

Variation Among Coasts of North America

The largest number of initial invaders are known from the West Coast (187 NIS), compared to the East Coast (108 NIS) and Gulf Coast (7 NIS), representing a significant difference among coasts (Figure 3; $X^2 = 161$, df = 2, $P < 0.001$); the total number of initial invasions (302) exceeds the total number of species (298), because the initial invasion for some species occurred on more than one coast).

In contrast, repeat invasions were proportionally greatest for the Gulf Coast (82% of all invasions) compared to the West Coast and East Coast (18% and 0%, respectively), resulting also in a significant difference among coasts ($X^2 = 120$, df = 2, $P < 0.001$). The lack of known repeat invaders for the East Coast is striking and underscores the asymmetry in the sequence (or direction) of repeat invasions among coasts. The high prevalence of repeat invaders for the Gulf Coast results primarily from high overlap in NIS composition with the East Coast. Of the 39 NIS on the Gulf Coast, 87% are also known invaders on the East Coast, compared to 51% on the West Coast.

The intercoast overlap appears to be much greater for NIS present on the East Coast (38% overlap with West Coast; 32% overlap with Gulf Coast) than the West Coast (18% overlap with East Coast; 9% overlap with Gulf Coast).

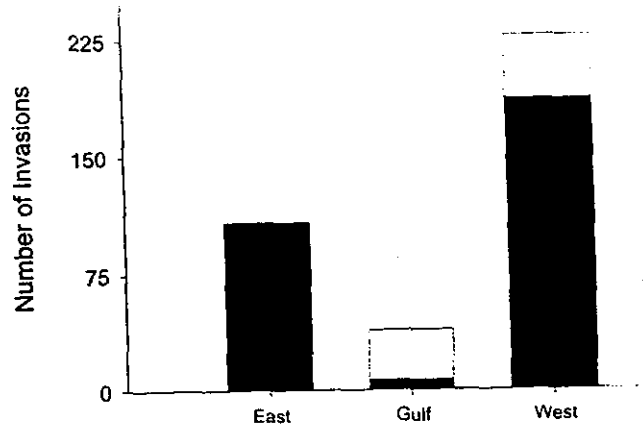


Figure 3 Total number of established nonindigenous species of invertebrates and algae reported among three coasts of North America. *Filled bar*, number of unique or initial species invasions (n = 298); *open bar*, number of repeat invasions, or the number of additional invasion events among coasts that involved a subset of initial invaders (n = 76; see text for further explanation).

However, the actual overlap of species among coasts is much greater than appears above. We have indicated overlap in a narrow sense, including only species known to be invaders to each coast. Many additional species that are native or cryptogenic to one coastal region (especially the East Coast) have invaded another coast (Appendix 1; see also Variation Among Estuaries and Data Bias Hypotheses sections for further discussion). Although these cases are excluded from our comparisons, they increase the overall overlap of biotas among regions.

Many similarities and differences exist in invasion patterns among the three coasts (GM Ruiz, JT Carlton, P Fofonoff & AH Hines, submitted; see also Appendix 1). The rate of reported invasions has increased exponentially on each coast over the past 200 y (Figure 4; West Coast, $y = 4.951^{0.0165x}$, $r^2 = 0.968$; East Coast, $y = 1.40^{0.0195x}$, $r^2 = 0.916$; Gulf Coast, $y = 0.940^{0.0160x}$, $r^2 = 0.855$). The NIS on each coast are dominated by crustaceans and molluscs, accounting together for 41–50% of the total. Shipping is the sole vector for approximately half of the known invasions on each coast: East Coast (60%), West Coast (48%), Gulf Coast (64%). However, the relative importance of fisheries as the sole vector was greater on the West Coast (19% of the total) compared to the East Coast and Gulf Coast (7% and 5%, respectively).

The native and source regions of NIS differs among coasts (GM Ruiz, JT Carlton, P Fofonoff & AH Hines, submitted; see also Appendix 1). Most West Coast NIS (53%) were native to the Indo-West Pacific and the Western Atlantic, and a smaller proportion (7%) were native to the Eastern Atlantic. In contrast, the first two of these native regions accounted for only 33% of the NIS known

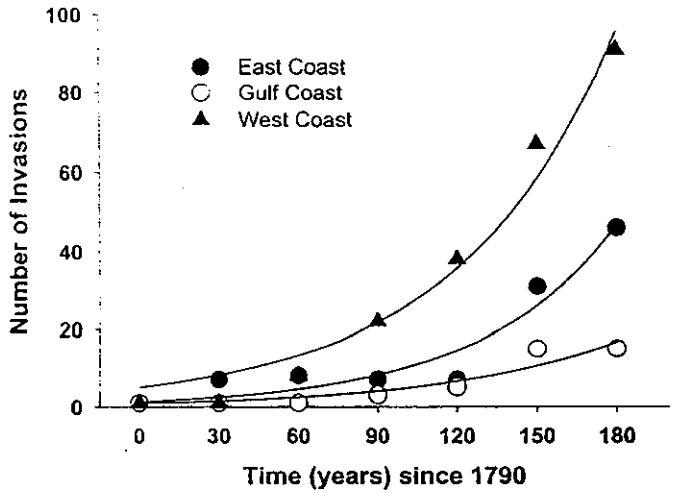


Figure 4 Rate of reported marine invasions of invertebrates and algae for each coast of North America since 1790. *Filled triangles* indicate the number of new invasions for the West Coast; those for the East Coast and Gulf Coast are indicated by *filled circles* and *open circles*, respectively. Data are plotted for 30y intervals as in Figure 1.

from the East Coast, where 19% were native to the Eastern Atlantic. Compared to the West Coast, a larger number of NIS on the East Coast were "within-coast" invasions, being introduced from one portion of the coast to another (10% of East Coast NIS compared to 1% of West Coast NIS). Finally, the disparity between native and source region was greater for the East Coast (28% of NIS had different native and source regions) than for the West Coast (15%). This results primarily from secondary invasion of the East Coast by western Pacific natives, which first invaded Europe and North America. The disparity between native and source regions was also relatively high for the Gulf Coast (38%), but finer analyses were not performed for this coast due to low sample size.

For each coast, there was a significant difference in the number of reported invasions among salinity zones (West: $X^2 = 254$, df $= 5$, $P < 0.001$; East: $X^2 = 32$, df $= 5$, $P < 0.001$; Gulf: $X^2 = 1.9$, df $= 5$, $P = 0.05$; see Appendix 1). A much greater proportion of NIS occurred in the polyhaline and euhaline zones of the West Coast (63%) compared to the East and Gulf Coasts (47% and 23%, respectively; number of NIS per salinity zone, with increasing salinity as follows: West Coast—24, 37, 54, 97, 187, 169; East Coast—33, 35, 38, 55, 75, 68; Gulf Coast—18, 18, 22, 19, 25, 22).

Variation Among Estuaries

Considerable variation exists in the number and overlap of known NIS among estuaries (11, 29, 30, 67, 69, 117; JT Carlton 2000, unpublished checklist; Carlton & Wonham 2000, unpublished manuscript; Table 1 and 2). The number of known

TABLE 1 Checklist of nonindigenous species reported as established in each of six different bays and estuaries

Phylum / Species	Site[a] SFB	CB	PS	PWS	ChB	PPB
Dinoflagellata						
Alexandrium catenella						X
Bacillariophyta						
Attheya armata		X				
Coscinodiscus wailesii					X	
Odontella sinensis					X	
Thalassiosira punctigera					X	
Phaeophyta						
Asperococcus compressus				X		X
Fucus cottoni				X		
Microspongium globosum				X		
Sargassum muticum	X	X	X			
Sorocarpus micromorus						X
Stictyosiphon soriferus						X
Striaria attenuata					X	
Undaria pinnatifida						X
Chlorophyta						
Bryopsis sp.	X					
Cladophora prolifera						X
Codium fragile ssp. *tomentosoides*	X				X	X
Ulva fasciata						X
Rhodophyta						
Antithamnionella spirographidis						X
Bonnemaisonia hamifera					X	
Callithamnion byssoides	X					
Ceramium sinicola				X		
Chondria arcuata						X
Chroodactylon ramosum				X		
Deucalion levringii						X
Gelidium vagum			X			
Gymnogongrus crenulatus						X
Lomentaria hakodatensis			X			
Medeiothamnion lyalli						X
Polysiphonia brodiaei						X
Polysiphonia denudata	X					
Polysiphonia harveyi					X	
Polysiphonia senticulosa (pungens)						X
Schottera nicaeensis						X
Solieria filiformis						X

(Continued)

TABLE 1 (*Continued*)

Phylum / Species	Site[a] SFB	CB	PS	PWS	ChB	PPB
Foraminifera						
Trochammina hadai	X		X	X		
Ciliophora						
Ancistrocoma pelseneeri	X					
Ancistrum cyclidioides	X					
Boveria teredinis	X					
Cothurnia limnoriae	X					
Lobochona prorates	X					
Mirofolliculina limnoriae	X	X				
Sphenophyra dosiniae	X					
Haplosporidia						
Haplosporidium nelsoni					X	
Porifera						
Aplysilla rosea						X
Cliona sp.	X	X	X	X		
Corticium candelabrum						X
Dysidea avara						X
Dysidea fragilis						X
Hutchondria bowerbanki	X	X				
Haliclona heterofibrosa						X
Haliclona loosanoffi	X	X				
Halisarca dujardini						X
Microciona prolifera	X					
Prosuberites sp.	X					
Cnidaria						
Amphisbetia operculata						X
Antennella secundaria						X
Blackfordia virginica	X	X			X	
Bougainvillea muscus (ramosa)						X
Cladonema radiatum			X			
Cladonema uchidae	X					
Clava multicornis	X					
Clytia hemisphaerica						X
Clytia paulensis						X
Cordylophora capsia	X	X	X		X	
Corymorpha sp.	X					
Diadumena "cincta"	X					
Diadumene franciscana	X					

TABLE 1 (*Continued*)

Phylum / Species	Site[a] SFB	CB	PS	PWS	ChB	PPB
Diadumene leucolena	X	X				
Diadumene lineata	X	X	X		X	
Ectopleura crocea	X	X				X
Filellum serpens						X
Garveia franciscana	X				X	
Halecium delicatulum						X
Maeotias inexspectata	X				X	
Moerisia lyonsi					X	
Moerisia sp.	X					
Monotheca obliqua						X
Obelia dichotoma (australis)						X
Phialella quadrata						X
Plumularia setacea						X
Sarsia eximia						X
Turritopsis nutricula						X
Platyhelminthes						
Pseudostylochus ostreophagus			X			
Kamptozoa						
Barentsia benedeni	X	X	X		X	
Loxosomatoides laevis					X	
Urnatella gracilis	X					
Nematoda						
Anguillicola crassus					X	
Bryozoa						
Aetea anguina						X
Alcyonidium sp.	X	X				
Amathia distans						X
Anguinella palmata	X					
Bowerbankia gracilis	X	X	X			
Bowerbankia spp.						X
Bugula "neritina"	X	X				X
Bugula calathus						X
Bugula flabellata						X
Bugula simplex						X
Bugula sp. 1			X			
Bugula sp. 2			X			
Bugula stolonifera	X		X			X
Celleporella hyalina						X
Conopeum reticulum						X
Conopeum tenuissimum	X	X				

(*Continued*)

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TABLE 1 (*Continued*)

hylum / Species	Site[a] SFB	CB	PS	PWS	ChB	PPB
Cryptosula pallasiana	X	X	X			X
Electra pilosa						X
Fenestrulina malusii						X
Membranipora membranacea						X
Microporella ciliata						X
Schizoporella unicornis	X	X	X	X		X
Scruparia ambigua						X
Scrupocellaria bertholetti						X
Scrupocellaria scrupea						X
Scrupocellaria scruposa						X
Tricellaria occidentalis						X
Victorella pavida	X					
Watersipora "subtorquata"	X	X				X
Watersipora arcuata						X
Zoobotryon verticillatum	X					
Mollusca						
Aplysiopsis formosa						X
Batillaria attramentaria			X			
Bithynia tentaculata					X	
Boonea bisuturalis	X					
Busycotypus canaliculatus	X					
Catriona rickettsi	X					
Cecina manchurica			X			
Cipangopaludina chinensis	X				X	
Corbicula fluminea	X	X			X	
Corbula gibba						X
Crassostrea virginica			X			
Crepidula convexa	X					
Crepidula fornicata			X			
Crepidula plana	X		X			
Cuthona perca	X				X	
Cyrenoida floridana					X	
Eubranchus misakiensis	X					
Gemma gemma	X					
Geukensia demissa	X					
Ilyanassa obsoleta	X		X			
Janolus hyalinus						X
Littorina littorea					X	
Littornia saxatilis	X					
Lyrodus pedicellatus	X					
Macoma petalum	X					
Melanoides tuberculata	X					

TABLE 1 (*Continued*)

Phylum / Species	Site[a] SFB	CB	PS	PWS	ChB	PPB
Mercenaria mercenaria			X			X
Musculista senhousia	X		X			
Mya arenaria	X	X	X	X		
Myosotella myosotis	X	X	X		X	
Mytilus galloprovinicialis	X	X	X			
Nassarius fraterculus			X			
Nuttallia obscurata			X			
Ocinebrellus inornatus			X			
Okenia plana	X					
Petricolaria pholadiformis	X					
Philine auriformis	X	X				
Potomocorbula amurensis	X					X
Raeta pulchella					X	
Rangia cuneata					X	
Rapana venosa						
Sukuraeolis enosimesis	X				X	
Stramonita haemostoma						
Tenellia adspersa	X	X				
Teredo navalis	X	X			X	
Theora lubrica (fragilis)	X					X
Urosalpinx cinerea	X		X			
Venerupis (Ruditapes) philippinarum	X	X	X			
Viviparus georgianus					X	
Annelida						
Boccardia proboscidea						X
Boccardiella ligerica	X					
Branchiura sowerbyi	X				X	X
Demonax leucaspis						X
Eteone sp.		X				
Euchone limnicola						X
Ficopomatus engimaticus	X				X	X
Heteromastus filiformis	X	X		X		
Hydroides elegans						X
Limnodrilus monothecus	X					
Manayunkia speciosa	X					
Marenzellaria viridis	X					
Marphysa "sanguinea"	X					
Myxicola infundibulum						X
Nereis succinea	X	X	X			X
Paranais frici	X					
Potamilla sp.	X					
Potamothrix bavaricus	X					

(*Continued*)

TABLE 1 (*Continued*)

Phylum	Site[a]					
Species	**SFB**	**CB**	**PS**	**PWS**	**ChB**	**PPB**
Pseudopolydora paucibranchiata						X
Sabaco elongatus	X					
Sabella spallanzanii						X
Streblospio benedicti	X	X	X			
Tubificoides apectinatus	X					
Tubificoides brownae	X	X				
Tubificoides diazi		X	X			
Tubificoides wasselli	X					
Variachaetadrilus angustipenis	X					
Crustacea						
Acanthomysis aspera	X					
Acanthomysis bowmani	X					
Acartiella sinensis	X					
Ampelisca abdita	X					
Ampithoe valida	X	X	X			
Argulus japonicus					X	
Balanus amphitrite	X				X	X
Balanus improvisus	X	X				
Caprella mutica	X	X	X			
Carcinus maenas	X	X			X	X
Chelura terebrans	X					
Cirolana harfordi						X
Corophium acherusicum	X	X	X			X
Corophium alienense	X					
Corophium heteroceratum	X					
Corophium insidiosum	X	X	X			X
Corophium sextonae						X
Deltamysis holmquistae	X					
Dynoides dentisinus	X					
Eobrolgus spinosus		X	X			
Eochelidium sp.			X			
Epinebalia sp.	X					
Eriocheir sinensis	X					
Eurylana arcuata	X					
Eusarsiella zostericola	X					
Gammarus daiberi	X					
Gitanopsis sp.					X	X
Grandierella japonica	X	X	X			
Hemigrapsus sanguineus					X	X
Iais californica	X	X				
Ilyocryptus agilis					X	X
Jassa marmorata	X	X	X			X

TABLE 1 (*Continued*)

Phylum	Site[a]					
Species	**SFB**	**CB**	**PS**	**PWS**	**ChB**	**PPB**
Lernaea cyprinacea	X					
Leucothoe sp.	X					
Ligia exotica					X	
Limnoithona sinensis	X					
Limnoithona tetraspina	X					
Limnoria quadripunctata	X					
Limnoria tripunctata	X	X	X			
Loxothylacus panopaei					X	
Melita nitida	X	X	X			
Melita sp.	X					
Mytilicola orientalis	X		X			
Nippoleucon hinumensis	X	X	X			
Oithona davisae	X					
Orconectes virilis	X				X	X
Pacifastcus leniusculus	X					
Palaemon macrodactylus	X	X				
Paracerceis sculpta						X
Paradexamine sp.	X					
Paranthura sp.	X					
Parapleustes derzhavini	X	X	X			
Procambarus clarkii	X				X	
Pseudodiaptomus forbesi	X					
Pseudodiaptomus inopinus		X	X			
Pseudodiaptomus marinus	X		X			
Pyromaia tuberculata						X
Rhithropanopeus harrisii	X	X				
Sinelobus sp.	X	X				
Sinocalanus doerri	X					
Sphaeroma quoyanum	X	X				
Stenothoe valida	X					
Stephos pacificus			X			
Stephos sp.			X			
Synidotea laevidorsalis	X					
Tortanus dextrilobatus	X					
Transorchestia engimatica	X					
Hexapoda (Insecta)						
Anisolabis maritima	X				X	
Conchopus borealis	X					
Galerucella calmariensis					X	
Galerucella pusilla					X	
Hylobius transversovittatus					X	
Neochetina bruchi	X					
Neochetina eichornia	X					

(*Continued*)

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TABLE 1 (*Continued*)

Phylum / *Species*	SFB	CB	PS	PWS	ChB	PPB
				Site[a]		
Procancace diannae					X	X
Trignotylus uhleri	X					
Echinodermata						
Asterias amurensis						X
Chordata						
Ascidia sp.	X					
Ascidiella aspersa						X
Botrylloides leachi						X
Botrylloides sp.	X					
Botrylloides violaceus	X	X	X	X		
Botryllus schlosseri	X	X	X		X	X
Ciona intestinalis	X					X
Ciona savignyi	X		X			
Diplosoma listerianum		X				
Ecteinascidia turbinata					X	
Molgula manhattensis	X	X	X			X
Styela clava	X	X	X			X
Styela plicata						X
Totals	157	55	57	10	49	91

Abbreviations and primary literature sources for each site are as follows:
San Francisco Bay (SFB, 30)
Coos Bay (CB, JT Carlton 2000, unpublished checklist)
Puget Sound (PS, JT Carlton & M Wonham, unpublished manuscript)
Prince William Sound (PWS, 69)
Chesapeake Bay (ChB, 117)
Port Philip Bay (PPB, 67)

S per estuary ranges from 10 to 157, and the percent overlap of NIS between irs of estuaries varies between 0% and 90%. The percent overlap was often ymmetrical between estuary pairs, especially where a disparity existed in total mber of NIS. Estuaries with relatively few NIS had the greatest overlap with uaries with a larger number of invaders. As discussed above, the total number species shared among estuaries is much greater than it appears, when native and ptogenic species are included.

Although it may not be surprising to find relatively high NIS overlap among est Coast estuaries from California to Washington, the degree of overlap among more distant estuaries (e.g. across oceans or continents) is notable. The pairse overlap ranges from 6% to 41% among San Francisco Bay, Chesapeake Bay, d Port Philip Bay (Australia), as shown in Table 2. Five species are known invaders in all three estuaries, and twenty NIS are established in both San ancisco Bay and Chesapeake Bay (Appendix 1). An additional 43 established

TABLE 2 Overlap of established nonindigenous species reported among six different estuaries, shown as number and percent (parentheses)[b]

	SFB	CB	PS	PWS	ChB	PPB
SFB	157 (100)	51 (32.5)	37 (23.6)	6 (3.8)	20 (12.7)	20 (12.7)
CB	51 (89.5)	57 (100)	31 (54.4)	5 (8.8)	9 (15.8)	13 (22.8)
PS	37 (64.9)	31 (54.4)	57 (100)	5 (8.8)	5 (8.8)	11 (19.3)
PWS	6 (60.0)	5 (50.0)	5 (50.0)	10 (100)	0 (0.0)	1 (10.0)
ChB	20 (40.8)	9 (18.4)	5 (10.2)	0 (0.0)	49 (100)	5 (10.2)
PPB	20 (22)	13 (14.3)	11 (12.1)	1 (1.1)	5 (5.5)	91 (100)

[a]See Table 1 for abbreviations.

[b]Diagonal (in black) indicates the number of nonindigenous species in each estuary. Numbers below diagonal (gray) indicate the overlap as the percentage of species at the row site that also occur at the column sites. Numbers above the diagonal (clear) indicate overlap as the percentage of species at the column site that also occur at the row site.

species introduced to San Francisco Bay occur as natives in Chesapeake Bay, and at least 6 other species (*Boccardiella ligerica, Bowerbankia gracilis, Halichondria bowerbankia, Molgula manhattensis*, and *Tenellia adspersa*) are cryptogenic in Chesapeake Bay and introduced to San Francisco Bay; both of these groups are not included in our estimates for Table 2 (which requires the species be introduced in both systems). However, there are only two cases of species cryptogenic or native on the west coast, including San Francisco Bay, and introduced into Chesapeake Bay (the diatoms *Coscinodiscus wailesii* and *Thalassiosira punctigera*).

The data for West Coast estuaries show an intriguing latitudinal pattern, with number of NIS increasing significantly from north to south (for Prince William Sound, Puget Sound, Coos Bay, and San Francisco Bay: $y = -5.51x - 332.7$, $r^2 = 0.762$, $P < 0.01$, where degrees latitude is the independent variable; see Tables 1 and 2). Fewer invasions are, however, known from southern California (n = 35) than San Francisco Bay (n = 157) (35) (Table 2). Importantly, intensive analysis of NIS invasions is not yet available for any bay in Southern California, similar to that for other estuaries in Table 1.

Recent analysis of Pearl Harbor, Hawaii, indicates that a relatively high number of that NIS are established in this low latitude embayment. Although not yet complete for direct comparison in our analyses, Carlton and Eldridge (20) report 156 NIS of invertebrates and algae are established at this site, increasing an earlier initial estimate (32). This result appears consistent with the latitudinal pattern above. However, island sites may differ from continental ones in many respects (83, 91)

that could confound interpretation of latitudinal effects. Analysis of additional island sites, both tropical and temperate, is necessary to partition the relative effects of latitude versus land area (i.e. mainland versus island sites) on invasion number.

The five focal estuaries (Table 1) display both similarities and differences with respect to invasion patterns, as described in recent analyses (30, 31, 67, 117; Carlton & Wonham 2000, unpublished manuscript). Most display a strong increase in the reported rate of invasions. The NIS among sites are dominated by crustaceans and molluscs, and most invasions are attributed to shipping or the combination of shipping and fisheries. Native and source regions of the NIS are highly variable, particularly across continents or oceans. Although some sites do not exhibit a large range in salinity (e.g. Port Philip Bay, Puget Sound), the other estuaries exhibit contrasting salinity patterns of invasion. For example, the total number of NIS increases three- to fourfold from low to high salinity in San Francisco Bay, peaking in the polyhaline zone; whereas in Chesapeake Bay, the total number varies much less among zones (up to twofold) and peaks in the mesohaline zone. In contrast, the number of NIS in the fouling community increases with salinity in Chesapeake Bay but decreases with salinity in Coos Bay (46, 117; GM Ruiz, AH Hines, LD McCann & JA Crooks, unpublished data).

Most data about the extent and patterns of marine invasion in North America and elsewhere come from protected bays and estuaries, and we have presented data from a small number of sites. Although data on marine invasion patterns exist for other global regions, (e.g. 2, 33, 51, 59, 67, 73, 94, 102, 103, 105, 109, 150; G Pauley, pers. comm.), these are not directly comparable to the sites evaluated in North America, differing substantially in area (e.g. entire seas), habitat type, or intensity of analysis. Our analyses therefore represent only a subset of existing latitudes, habitat types, as well as continents. A clear next step is to test the robustness or generality of emerging patterns across these additional scales.

)ERSTANDING PATTERNS OF INVASION

Hypotheses that could explain the observed patterns of invasion may be grouped into three general categories related to: (*a*) variation in propagule supply characteristics; (*b*) variation among recipient regions in susceptibility or resistance to invasion; or (*c*) bias in the quantity or quality of existing data. These hypotheses are not mutually exclusive and have been advanced in various forms and combinations to account for invasion patterns by space, time, taxonomic group, habitat type, and donor region (34, 50, 81, 82, 84, 101, 116, 121, 129, 143). Below, we review these hypotheses in more detail and evaluate existing support for them in marine communities, discussing ways in which these hypotheses may operate to generate observed patterns.

Another theme in invasion ecology has been the invasion potential or capacity of a species to invade (5, 39, 43, 52, 66, 93, 101, 107, 120, 121, 142). This theme focuses on the applicant pool of species, examining a range of questions, such as which species will invade, what makes a good invader, and which attributes of species contribute to differential invasion success? A general view is that life history attributes such as the intrinsic rate of population increase, r, play a significant role in determining which species succeed, although empirical data in support of this hypothesis are often confounded by other variables (52, 120). Geographic range, which integrates environmental tolerance and a variety of population characteristics, has also emerged as a predictor of invasion success and has some empirical support (143). In this review, variation in invasion potential has been considered as a component of the above three hypotheses, because our focus is on patterns of NIS richness, not individual species characteristics. Thus, for our purposes, we consider invasion potential as a component of propagule supply (as described below under Different Donor Regions's, and Condition of Propagules), which may modify the relationship between supply and invasion success.

Progagule Supply Hypotheses

Supply hypotheses propose that variation in propagule delivery accounts for variation in invasion patterns. In its basic form, propagule supply is portrayed as the quantity of arriving propagules (propagule pressure), with the number of invasions increasing as a function of total propagule quantity (84, 119, 120, 143). Supply hypotheses by themselves predict that the same propagule pressure in space or time would result in approximately the same number of invasions. Thus, the relationship between propagule supply and invasions would be described by a single function across spatial and temporal scales (82, 143).

Propagule supply can be broken down into component parts that each may affect the invasion outcome, including the following:

Total Quantity (Propagule Pressure)

The quantity of propagules released may be correlated significantly to invasion success. Studies of propagule pressure have (*a*) correlated estimates of the rate of propagule arrival and invasion or (*b*) measured the success of intentional introductions as a function of propagule number (10, 84, 114, 119, 120, 143).

Inoculation Density, Frequency, and Duration

The spatial dispersion and tempo of supply may have important consequences. The same quantity of propagules can be distributed differently in space and time, affecting invasion success (112, 121, 142). In particular, inoculation characteristics that result in consistently low propagule densities may produce different success rates compared to those resulting in high local propagule densities (1, 100).

Different Donor Regions

The source of propagules may influence invasion success, due to a number of differences in the donor region. These include different species pools, differing genotypes of the same species, as well as differences in density and condition

(i.e. "inoculation density" and "condition" as discussed elsewhere). Propagules from two donor regions may therefore differ in their physiological, life-history, and ecological characteristics that can modify capacity to invade the same recipient environment (37, 43, 101, 135). Discussions of such variation among donor regions are often accompanied by consideration of "environmental matching" or "biotic resistance" in the recipient region (see below).

Condition of Propagules

The physiological condition of propagules upon arrival to various recipient regions may vary, depending upon the individual organisms (e.g. life stage or age) and the history of transfer (e.g. vector, food, temperature, season, length of journey, etc). In turn, this may affect performance of propagules and their invasion success (69, 96, 97, 123, 147).

For marine and estuarine habitats, these aspects of propagule supply exhibit considerable spatial and temporal variation that may contribute to observed invasion patterns. The strongest evidence for supply hypotheses derives from increased propagule pressure and a corresponding increase in the rate of reported invasions. In general, the transfer rate of marine organisms is thought to have increased, especially during the twentieth century, due to changes in the size, speed, and operation of global shipping traffic (17, 116). Ship size is correlated positively to the volume of ballast water (within vessel class) and the surface area of hulls and seachests (24; GM Ruiz, AW Miller, B Steves, RA Everett & AH Hines, unpublished data). The increase in ship sizes could result in increasing propagule pressure. The increased speed of vessels over time may have further increased the number and condition of arriving propagules, especially in ballast water where survivorship of organisms during transit is often time-dependent (58, 77, 123, 147; LD Smith, GM Ruiz, AH Hines, BSS Galil & JT Carlton, unpublished data). With expanding global trade, both the number of arriving vessels and the number of source regions (i.e. last ports of call) have increased at many recipient ports. This combination of factors may increase the overall number of propagules arriving to ports over time as well as the diversity of species and genotypes involved. Furthermore, as invasions continue to accrue at the source ports, the diversity of exported propagules may further expand and promote a positive feedback of "stepping-stone" invasions (17, 69, 77).

Working against this presumptive increase in transfer rate, however, is the probable decline in ship fouling communities that characterized wooden vessels for many centuries, as well as steel and iron vessels up to the mid-twentieth century (12, 22). Several factors are thought to be involved in a decline, including the development of anti-fouling paints, lower port residencies (leading to reduced settlement of fouling organisms), and greater speeds at sea (leading to more species being washed away by shear forces, while also facilitating potential survivorship for those organisms that remain, as noted above). The balance among these various processes, operating to both enhance and depress transfer rates by ships over time, remains to be quantified.

A large portion of observed spatial variation in the origin (i.e. native and source regions) and vectors of NIS clearly reflects qualitative differences in propagule supply. This is most evident in comparison of West Coast and East Coast patterns (Appendix 1). Most marine invasions to the West Coast originate from the Indo-West Pacific (including Western Pacific) and Western Atlantic, having the same native and source regions. In contrast, most invasions to the East Coast originate from Eastern Atlantic, although many of these species are native to the Pacific. These patterns correspond directly to the dominant trade corridors for the respective coasts in historical time (12, 24, 30, 117; US Maritime Administration, unpublished data). Furthermore, although shipping was identified as the probable vector for most invasions along each coast of North America, many more invertebrate species arrived via fisheries to the West Coast compared to the East Coast (30, 117; Appendix 1). This difference in introductions via fisheries corresponds to a marked difference in supply of oysters between coasts: the West Coast received extensive shipments of oysters from the western Atlantic and the western Pacific, whereas oyster transfers to East Coast fisheries have been minor by comparison and primarily intracoastal (14, 117).

Any quantitative relationships between propagule supply and spatial invasion patterns are much less evident. For example, despite the disparity in number of NIS between the East and West coasts, or between San Francisco Bay and Chesapeake Bay (Figure 3, Table 2), there is no evidence that propagule supply has been greater for the West Coast compared to the East Coast, or for San Francisco Bay compared to Chesapeake Bay. Estimates of the present number of ship arrivals and the total volume of ships' ballast water arriving from overseas are negatively associated with apparent invasion patterns. For 1997–1999, more vessels arrived from overseas to the East Coast, as well as the Gulf Coast, than the West Coast (U.S. Maritime Administration, unpublished data; GM Ruiz, AW Miller, B Steves, RA Everett & AH Hines, unpublished data). Carlton et al (24) estimated that the largest volumes of ballast water discharged at selected ports from foreign arrivals in 1991 occurred on the Gulf Coast (New Orleans) and East Coast (Chesapeake Bay), whereas discharge volumes to West Coast ports (including San Francisco Bay) were relatively low; however, total volume estimates are not yet available for the entire coasts. Furthermore, the cumulative supply of exotic propagules over historic time (which is unknown) may also be greatest for the East Coast, reflecting temporal differences in the development of extensive European colonization and oceanic trade among North American coasts (GM Ruiz, JT Carlton, P Fofonoff & AH Hines, submitted).

Although it appears that total propagule supply in these pairwise comparisons may run counter to the number of known invasions, ships now arriving at the West Coast (relative to the East Coast) may include fewer donor ports (24; Ruiz et al., unpublished data). A relatively limited number of donor sites would perhaps result in repeated inoculations of the same species more frequently to the West Coast than to the East Coast, and this could increase invasion success (24, 112, 123). Furthermore, the donor ports for ships arriving to the West Coast are from different regions

than those arriving to the East Coast (US Maritime Administration, unpublished data), and may also differ in the diversity and densities of arriving propagules. We do not know the extent to which the spatial and temporal patterns of these progagule supply characteristics differ among coasts.

The relationship between supply and taxonomic distribution of known marine invasions has received little consideration (however see 146). In general, we expect that the number and diversity of propagules released into marine environments by humans is inversely correlated with organism size, reflecting the general availability of organisms in their natural environment as well as the abundance of organisms measured in ballast water of ships (9, 56, 60). For example, it is not unusual to detect bacteria in the range of 10^7–10^8 cells per liter in ballast water, compared to densities of 10^2–10^3 crustaceans per liter (47, 69, 123; GM Ruiz, FC Dobbs, TK Rawlings, LA Drake, TH Mullady, A Huq & RR Colwell, unpublished data). However, the relative number of reported invasions for small organisms, and taxonomic groups dominated by small organisms, is perhaps not surprisingly counter to this expectation (as discussed in Data Bias Hypotheses section, below).

The relationship between supply and salinity distribution of invaders is also poorly resolved. It is clear that propagules have arrived frequently from high salinity zones of donor regions (14, 21, 30, 69, 123; GM Ruiz, LD Smith, AH Hines & JT Carlton, unpublished data). We speculate that most ballast water (and entrained propagules) arriving in North America from overseas is of relatively high salinity, as described for Chesapeake Bay (123) and Coos Bay (21), but this is not at all clear. Since species richness often increases with salinity in estuaries (7, 42), this may increase the species pool arriving in ballast of higher salinity. For marine invertebrates and algae, we hypothesize that both species richness and absolute number of human-transferred propagules have generally been greatest from high salinity zones of donor regions, corresponding to the pattern of invasion for North America. If true, however, this would not explain the observed difference in salinity distribution of NIS between the East Coast and West Coast, or between Chesapeake Bay and San Francisco Bay.

So far, we have limited our discussion of the supply-invasion relationship to species richness and patterns of delivery, but variation in invasion potential may exist among donor regions, taxonomic groups, and time periods that can modify this relationship. There is reason to believe that invasion potential differs among donor regions and taxonomic groups, corresponding to size, life history characteristics, and environmental requirements of organisms (43, 66, 100, 101, 135, 143; see also below). Furthermore, the condition of propagules at the donor region or during transfer may change over time and influence their capacity to invade, independent of invasion resistance among recipient regions (17). Although an intriguing possibility, we presently lack the data to critically evaluate variation in invasion potential or its importance to patterns of marine invasion.

We have identified some possible associations between propagule supply and invasion patterns, based primarily upon qualitative data. Some quantitative data exist on propagule supply in particular marine systems (21, 28, 56, 58, 61, 63, 64, 69, 76, 86, 99, 123, 127, 141, 146, 149). However, these data have not been collected in a standard fashion or compared directly to invasion patterns to test for specific associations. Comparative data on propagule supply among sites largely remain to be collected and should include measures of diversity, frequency, density, and condition of propagules (as above). Until such quantitative measures of propagule supply are available, we cannot adequately and formally test the various relationships between supply and invasion in marine systems (82, 143).

Invasion Resistance Hypotheses

Resistance hypotheses hold that invasion patterns result from variation in characteristics of recipient environments that prevent (or facilitate) survival and establishment of NIS. Lonsdale (82) has effectively illustrated this concept with a simple equation: $E = IS$. Here, the number of successful invasions at a site (E) is the product of number of exotic species that are introduced (I) and the survival rate of these species at this site (S); we assume that the term I controls for density, frequency, and tempo of introductions (as discussed above). Supply hypotheses assume that S is approximately constant, whereas resistance hypotheses do not. Instead, the latter predict that given the same supply characteristics (I), the resulting number of invasions (E) will differ among sites or times due to variation in survivorship (S). When controlling for supply, such differences in the number of successful invasions are considered to result from differences in invasion resistance (*i.e.*, susceptibility or invasibility). Invasion resistance is therefore a relative term, which arises from variation in S and can only be defined by measuring residuals from the relationship between I and S (82, 143). As a practical matter, survivorship is often equated with invasibility (the inverse of resistance), since survivorship is the response variable to resistance that is difficult to quantify. Unfortunately, equating survivorship with invasibility may obscure rigorous analysis of resistance as an independent attribute of the recipient system, which regulates the survivorship response.

As with propagule supply, resistance hypotheses can be divided among categories based upon factors causing variation in survivorship. Lonsdale (82) suggested survivorship (S) is a product of multiple survivorship functions: $S = S_1S_2S_3...S_n$, where S_{1-n} represents survivorship due to different attributes (1...n) of the recipient environment (e.g. environmental conditions, predators, pathogens, etc.). Thus, resistance can result from any one or a combination of attributes that affect survivorship of propagules differently among recipient environments.

For our discussion of resistance hypotheses in marine habitats, we divide resistance into two general components: abiotic and biotic. The abiotic component includes environmental conditions, such as habitat distribution and availability, that affect mortality; this is roughly equivalent to mortality resulting from maladaptation (82). For example, tropical species arriving in polar ecosystems may experience very poor survival compared to those arriving in temperate or tropical ecosystems. We consider this difference in survivorship and invasion success to result from differences in abiotic resistance. The biotic component includes variation

in mortality due to biological interactions (e.g. competition, predation, disease, parasitism, etc), and differences in the strength of interactions among sites may result in differences in biotic resistance. The roles of biotic and abiotic resistance to invasion success have been explored using a variety of quantitative and theoretical approaches, providing strong support for both (4, 25, 101, 106, 111, 128–130, 133; see also 79, 110). In addition, an extensive literature since Elton (50) also indicates that disturbance can significantly affect invasion resistance (54, 70, 71, 100; but see also 126). We consider disturbance to either facilitate or inhibit invasion through changes in biological and environmental conditions, affecting biotic and abiotic resistance respectively.

Considering known differences in the biological and environmental attributes among marine systems throughout the world (8, 48, 134), variation in resistance to invasion is virtually certain. Furthermore, temporal variation in invasion resistance is an expected outcome of the broadscale changes and disturbance in recipient coastal ecosystems resulting from habitat alteration, freshwater diversion, eutrophication, fisheries exploitation, sedimentation, anoxia, chemical pollution, and invasion (25, 45, 54, 70, 101, 112, 118, 122). Many, if not most, considerations of disturbance suggest that invasion resistance should diminish with increasing magnitude and frequency of change over time (6, 62, 89, 90, 95).

Despite these predictions, tests of biotic or abiotic resistance to invasion are extremely rare in marine systems compared to terrestrial systems. Smith et al 123) showed that most propagules released in Chesapeake Bay with the ballast water of ships derive from high salinity environments and are faced with low salinity conditions upon release, suggesting that abiotic resistance may be relatively high and limit many potential invasions. In addition, an experimental study has shown that species richness had a significant effect on establishment and survivorship of exotic marine species, using pre-assembled fouling communities exposed to natural rates of recruitment at field sites (125). In this case, it appears that the outcome was mediated by resource (space) competition, as space became more limiting with increasing species richness. A similar outcome may result from disturbance events that reduce diversity and space occupation, allowing more species to become established and persist (98, 124; but see also 79). Despite some support for effects of species richness on invasibility in freshwater and terrestrial systems, the interaction between species richness and invasibility has been variable among communities, suggesting that the interactions are often complex and any generalizations are premature (78, 79, 82, 110, 145; see also 80 for review).

Climatic differences between the respective coasts may also contribute to differences in abiotic resistance (8, 134). Although there is a growing literature about the use of environmental matching to predict invasibility, or abiotic resistance to invasion (59, 68, 143), we urge caution. To date, there are no clear demonstrations of this approach as a predictive tool in marine systems. For example, it is tempting to suggest that the paucity of NIS known from Prince William Sound, Alaska, is a large part a result of environmental resistance, which may be intrinsic to high latitude ecosystems. We surmise that relative propagule pressure to this region historically has been low. Propagule supply to Prince William Sound increased markedly in the latter half of the twentieth century, as oil tankers have delivered annually since 1977 an estimated 20 million metric tons of ballast water to the area (69). Most of this ballast water and associated plankton originates from western U.S. ports, including San Francisco Bay, that are invaded by NIS. Recent field surveys in Prince William Sound have failed to detect many new invasions (69). Although the low number of NIS is consistent with an environmental resistance hypothesis, there may be significant time lags in detection of recent invasions. More fundamentally, we lack comparisons of invasion success among sites that control for propagule supply, providing the necessary reference point(s) to estimate resistance.

Despite the current lack of data to evaluate invasion resistance, we suggest that variation in invasion success among sites is probably the rule rather than the exception. In our view, the question is not whether biotic or abiotic resistance exists but how much variation exists in space and time. Furthermore, given the plethora of missing data and potential confounding factors in analysis of correlative field data (82; see also above), we advocate an experimental and theoretical approach to explore both the variation in invasion resistance and its role in observed invasion patterns.

Data Bias Hypotheses

Many potential biases exist in the observed patterns of marine invasions. Potential biases may result from three fundamental aspects of the present data:

1. The search effort for NIS is unevenly distributed spatially, temporally, and taxonomically. All of the data used in our analyses, and those of existing compilations for the well-studied estuaries, are derived primarily from literature-based syntheses (11, 20, 30, 117; JT Carlton 2000, unpublished checklist; Carlton & Wonham 2000, unpublished manuscript; but see 67). These data represent "by-catch" from a wide spectrum of research, surveys, and observations. The focus (habitats, salinity zones, taxonomic groups), resolution (taxonomic expertise and level of identification), and extent (sampling effort, areal coverage, number) of analyses are therefore uneven in space and time. Thus, data for analyses are not directly comparable (especially among sites, times, or taxonomic groups), as they result primarily from the accumulation of historical analyses that were conducted for a diverse variety of reasons.
2. The quality of systematic and biogeographic information is unevenly distributed taxonomically. There is an inherent bias in the quality of information available among taxonomic groups. Some organisms are relatively large and conspicuous, with hard parts that are preserved in the fossil record (e.g., molluscs, crustaceans). In general, the systematics and biogeography of these groups are well known relative to smaller organisms

(e.g. nematodes, annelids, dinoflagellates, and microorganisms) for which the historical surveys and paleontological records are much more limited and the systematics are often poorly resolved.

3. The quality of biogeographic information is unevenly distributed among sites and regions. The extent and timing of search efforts differ relative to the onset of intensive propagule pressure. For example, intensive shipping began in Chesapeake Bay approximately four centuries ago, predating surveys of many taxonomic groups by decades to centuries. In contrast, intensive propagule pressure in San Francisco Bay commenced about 1850, and major biological surveys of this region commenced within approximately 60 y (rather than the 300 y lag-time evident for many groups in the Chesapeake). The relative timing of these activities may have affected our ability to differentiate early invaders from native species (18, 53, 117).

Although we are confident about the information presented for the 298 NIS Appendix 1), providing a minimum level of invasions on the coasts, the uneven uality of data may cause invasions to go undetected and thereby influence ob- erved invasion patterns. It is for this reason that we have characterized our analysis f existing data as "apparent" patterns. Here, we evaluate further some biases that ıay exist for many of the patterns discussed above.

patial Patterns of Invasion

/e hypothesize that significant bias exists in the apparent spatial patterns of in- ıasion in our analyses. As suggested above, this may result primarily from two ›urces. First, the search effort among sites is uneven (#1 above). For example, the search effort for San Francisco Bay is undoubtedly greater than that for Prince 'illiam Sound, and effort for individual taxonomic groups also varies among sites. econd, and possibly more significant, the quality of historical baseline informa- ›n on biotic communities is highly variable among sites (#3 above). We expect ›th the search effort and quality of baseline to affect the number of NIS detected ithin each site.

There are no standardized, quantitative measures across sites to evaluate (or ntrol for) the effect of variable search effort on spatial invasion patterns. It is so difficult to compare or normalize prior search effort among sites, because e historical information results from a variety of studies and methods. We esently know of no approach to control for these missing data, short of conducting rveys.

On the level of coasts, we hypothesize that the relatively low number of in- ders known for the Gulf coast results from bias in search effort: (*a*) there has en no "case study" of invasions for a Gulf Coast estuary, similar to those San Francisco Bay or Chesapeake Bay, and (*b*) the extent of historical re- arch on marine invertebrate communities is lowest for the Gulf coast. On the el of estuaries, similar potential for strong bias clearly exists, especially for sites like Prince William Sound compared to other estuaries. A recent survey of Prince William Sound resulted in 20 new species records for the region, including 3 NIS and many additional species that were native or cryptogenic (69). This suggests that the biota remains poorly described. Although the poor records of local biota may result in bias, this survey also did not detect many of the NIS that have been evident at other West Coast estuaries. In contrast, a similar set of surveys in Chesapeake Bay detected five new NIS for that region (117). We therefore hypothesize that the observed numerical differences in NIS among estuaries in Table 2 does not result from differences in search effort.

While it is possible to test for bias due to search effort by implementing standardized surveys, the issue of uneven historical baseline information among sites is more difficult to resolve. For each estuary and coast, there are cryptogenic species that may be either native or non-native (30, 69, 117; Carlton & Wonham 2000, unpublished manuscript). Some cryptogenic marine species are conspicuous, structurally and functionally, but the historical record is ambiguous about their distribution prior to ocean trade (Table 3). There is strong reason to believe that the extent of cryptogenic species is unevenly distributed among sites and coasts, corresponding to the extent of biotic surveys prior to the onset of intense propagule supply (18, 117). We therefore predict that the number of invasions that are cryptogenic is greater for the East and Gulf Coasts compared to the West Coast, and for Prince William Sound compared to other West Coast estuaries.

To explore the potential magnitude of cryptogenic species, Fofonoff et al (53) found that approximately 34% of 780 species from the Chesapeake Bay also occur in Europe. Although a few (5%) of these species are known invaders to the Chesapeake or Europe, the invasion status of most have never been evaluated, suggesting that 30% of 739 species should be considered cryptogenic at present. The first records for many of these taxa follow by decades to centuries the initiation of extensive commerce with Europe. Fofonoff et al surmise that many NIS may have arrived with early trade and are now included in this unevaluated group of species. We suggest that the extent of overlap between West Coast estuaries and the western Pacific may be lower, due in part to the timing of trade and surveys. The extent of cryptogenic species may also be lower along the West than East Coast. It would be instructive to quantify and test for such asymmetry among coasts with comparable data sets.

To further explore this possible bias in the observed pattern of invasion, we examined spatial patterns of invasion for molluscs, which are relatively conspicuous and well studied, have a fossil record, and are presumably less prone to be missed as invaders. Despite our predictions about bias due to cryptogenic species, the distribution of invasions for molluscs shows the same general spatial patterns that we reported across all taxonomic groups (15). Specifically, the data indicate that the largest number of mollusc invasions are known from the West Coast (47 NIS) compared to the East and Gulf Coasts (28 and 8 NIS, respectively; Appendix 1).

TABLE 3 Examples of cryptogenic marine and estuarine species present in North America[a]

Species[b]	Phylum	Present World Distribution	Date of 1st North American Record	Distribution[c]
Pathogens & Parasites				
Vibrio cholerae	Omnibacteria	Cosmopolitan	Unknown	East, West, Gulf
Labyrinthula zosterae	Labyrinthulamycota	N Atlantic, NW Pacific	1930s	East
Perkinsus marinus	Apicomplexa	NW Atlantic	1920s	East[1]
Minchinia teredinis	Haplosporida	NW Atlantic	1976	East
Phytoplankton				
Pseudo-nitzschia australis	Bacillariophyta	SW Pacific, NE Pacific	1930s	West
Gyrodinium "aureolum"	Dinophyta	Cosmopolitan	1957	East
Pfiesteria piscicida	" "	NW Atlantic	1991	East, Gulf
Heterosigma akashiwo	Raphidophyta	Pacific, Atlantic	1950s	East, West
Fibrocapsa japonica	Raphidophyta	W Pacific, N Atlantic	1980s	East
Aureococcus anophagefferens	Chrysophyta	NW Atlantic	1985	East
Macroalgae				
Enteromorpha "intestinalis"	Chlorophyta	Cosmopolitan	1858	East, Gulf, West
Ulva "lactuca"	" "	Cosmopolitan	1858	East, Gulf, West
Cladophora spp.	" "	Cosmopolitan	1858	East, Gulf, West
Myriocladia loveni	Phaeophyta	N Atlantic	Unknown	East
Zooplankton				
Tintinnopsis "corniger"	Ciliophora	NW Pacific, Gulf of Mexico	1968	Gulf, West[2]
Eurytemora "affinis"	Crustacea	Circumboreal	1906	East, Gulf, West
Americamysis almyra	" "	Gulf of Mexico, NW Atlantic	1977	Gulf, East[3]
Benthic Invertebrates				
Ectopleura dumortieri	Cnidaria	NE Atlantic, NW Atlantic	1862	East
Obelia spp.	" "	Cosmopolitan	1857	East, West
Protohydra leuckarti	" "	Cosmopolitan	1939	East, West
Nematostella vectensis	" "	N Atlantic, NE Pacific	1939	East, Gulf, West
Limnodrilus hoffmeisteri	Annelida	Cosmopolitan	Unknown	East, West
Capitella "capitata"	" "	Cosmopolitan	Unknown	East, Gulf, West
Harmothoe "imbricata"	" "	Circumboreal	1881	East, West
Namanereis "littoralis"	" "	Cosmopolitan	1942	East, West
Polydora "cornuta"	" "	Cosmopolitan	1820	East, Gulf, West

(*Continued*)

TABLE 3 (*Continued*)

Species[b]	Phylum	Present World Distribution	Date of 1st North American Record	Distribution[c]
Pygospio "elegans"	" "	Circumpolar	Unknown	East, West
Spiophanes "bombyx"	" "	Cosmopolitan	1881	East, West
Siphonaria pectinata	Mollusca	N Atlantic, S Atlantic	1841	East, Gulf
Alderia modesta	" "	Cosmopolitan	1848	East, Gulf, West
Teredo clappi	" "	Cosmopolitan	1923	East, Gulf
Leptochelia "dubia"	Crustacea	Cosmopolitan	1901	East, Gulf, West
Limnoria lignorum	" "	Circumboreal	1841	East, West
Caprella "equilibria"	" "	Cosmopolitan	1818	East, Gulf, West
Caprella "penantis"	" "	Cosmopolitan	1818	East, Gulf, West
Platorchestia platensis	" "	Cosmopolitan	1873	East, Gulf, West
Aetea anguina	Bryozoa	Cosmopolitan	1891	East, West
Alcyonidium parasiticum	Bryozoa	N Atlantic, N Pacific	1873	East, West
Molgula manhattensis	Chordata	Cosmopolitan	1843	East, West[4]

[a]References for each species published in reference 117.
[b]Quotation marks indicate possible species complexes.
[c]North American Distribution.
[1]Cryptogenic in Chesapeake Bay and southward, but introduced to Delaware-Maine.
[2]Collected from ballast water only on the West Coast.
[3]We consider this species native on the Gulf Coast, where it was described from specimens collected in 1953, but cryptogenic on the Atlantic Coast (Florida-Maryland), where it was first reported in 1977.
[4]Cryptogenic on the Atlantic Coast, but introduced on West Coast.

Temporal Patterns of Invasion

The number of established marine NIS is increasing over time, but the actual rate of invasions warrants further scrutiny and discussion. Based upon current data, the rate of invasion appears to have increased over the past 200 y for North America as well as for multiple estuaries (31, 67, 117). A similar pattern has also been observed for freshwater and terrestrial ecosystems, across many taxonomic groups (55, 87, 88; GM Ruiz & JT Carlton, submitted). Although the signal is consistent and appears robust, two sources of bias may contribute to this temporal pattern. First, many early invasions may simply be undetected and are considered cryptogenic species. Second, the search effort has increased over time, due to (*a*) to increased level of research activity and publications, both generally and specifically on invasions, (*b*) increased public interest and search effort, and (*c*) improved tools for systematic analyses (e.g. molecular techniques).

These three sources of bias would serve to increase the apparent rate of invasions, but their relative importance has not been explored (115). It would be useful to standardize rate of past detection against search effort, since number of species detected clearly increases with both temporal and spatial components of effort (113). However, this is not possible because the effort is so uneven among the various information sources and is poorly documented (115; but see 31). Furthermore, with the advent of new molecular approaches, we are now detecting invasions that previously could not be discerned (3, 57, 115). For example, the recent discovery of two bivalves, *Macoma petulum* and *Mytilus galloprovincialis*, along the West Coast reflects use of molecular tools to identify NIS that clearly arrived many decades earlier (Appendix 1). Although few marine NIS in North America have been identified with such molecular techniques, this underscores the general issue of increasing search effort.

If we examine the temporal pattern for molluscs, following the rationale above, the rate of reported marine NIS known for North America increased significantly over time (Figure 5; $y = 0.1417x - 1.6$, $r^2 = 0.956$; where y is number of new invasions and x is time in 30 year intervals, indicated as the first year of each interval). However, the increase is linear in contrast to the exponential function observed for all taxonomic groups combined (Figure 5). Although we suggest that molluscs provide a good proxy measure to remove temporal bias, the extent to which they represent other taxonomic groups with respect to invasion rates has not been tested.

We hypothesize that the rate of marine invasions is increasing over time, driven by the combination of increasing propagule supply and decreasing invasion resistance. However, we also predict that the apparent rates of invasion are inflated, due to the prevalence of undetected early invasions and increasing search effort over time. Lag times in population increase of invaders may also serve to inflate the apparent rate of invasion, as detection probably depends upon both density and search effort (36, 65, 113). This could be especially important if the population dynamics of invaders has changed over time, perhaps in response to anthropogenic

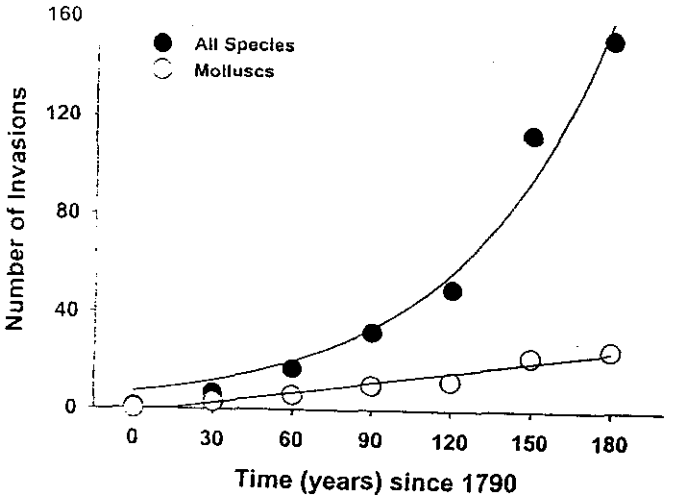

Figure 5 Rate of reported marine invasions of North America since 1790 for (a) molluscs and (b) all species of invertebrates and algae. *Open circles* indicate the number of new invasions for molluscs; *filled circles* indicate those for all taxa. Data are plotted for 30 y intervals as in Figure 1.

changes to estuarine habitats. These hypotheses remain to be tested and are best examined with temporally replicated, standardized measures that we now lack.

Taxonomic Patterns of Invasion

We hypothesize that strong bias also exists for the taxonomic distribution of invasions, and that the prevalence of small invading organisms is grossly underrepresented by current measures. In general, the quality of systematic and biogeographic information diminishes with organism size, and the available baseline information for small organisms and microorganisms is poor relative to large invertebrates (49). With the exception of a few dinoflagellates (61), there is a conspicuous lack of surveys or baseline studies to evaluate the extent of marine microorganism invasions. If invasions were occurring, even at a high rate, how would we know? Furthermore, invasion biology in these groups is even more complicated than for other taxa, due to the occurrence of gene transfer that is reported in the field (74). At present, invasion by microorganisms, including parasites and pathogens that cause disease (62), is a fundamental gap in our understanding of patterns and consequences of marine invasions.

Salinity and Habitat Patterns of Invasion

Sites vary significantly in the relative size of salinity zones and habitats that may strongly influence some of the spatial, temporal, taxonomic, and salinity patterns observed. Perhaps most striking is the extent of variable freshwater and oligohaline zones in estuaries. As noted previously, several bays have only small areas of low salinity, restricting the opportunity for colonization by species of freshwater origin. This is especially so for Puget Sound and Port Philip Bay in our analyses. Consequently, the search effort for low salinity taxa is uneven among bays. If we remove the freshwater and oligohaline species from our analysis (Appendix 1 and Table 1), many of the same patterns are evident: (*a*) more NIS are known for the West Coast (217) compared to the East Coast (95) and Gulf Coast (30), and (*b*) more NIS are known for San Francisco Bay compared to other bays. However, attempting to standardize for salinity generally reduces the observed spatial variation in the extent of invasions.

It would be instructive to standardize all data for salinity, habitat, and area. Each of these attributes should have a strong influence on both the taxonomic distribution and number, and perhaps rate, of successful invasions. Effects of habitat type and area on species richness have been well documented (84, 113). We surmise that such species-area relationships cannot explain the overall patterns observed (*e.g.*, East Coast and West Coast are roughly similar in size. Chesapeake Bay and Prince William Sound are larger than San Francisco Bay), but it would be informative to examine invasion patterns with a multivariate approach to control for size, habitat, and salinity characteristics. This approach should be especially valuable as data become available from a broader array of sites, increasing overall sample size and statistical power.

Although it is possible to control for the size and habitat/salinity composition of sites, the uneven nature of existing data remains a problem due to the difficulty in assessing variation in search effort. As a first step toward standardizing the present data, it is possible to document the distribution and types of existing information sources (by habitat, salinity zone, area, and taxonomic group), which can serve to identify studies with the most similar methods as well as to identify conspicuous gaps. It may even be possible to find similar studies for comparisons among bays. Although such approaches can provide useful insights, interpreting the data gathered from non-standardized methods is often an insurmountable problem, which is inherent to studies that were not designed for direct comparison.

CONCLUSIONS AND FUTURE DIRECTIONS

In the past decade, the ecology of marine invasions has come into focus, as knowledge of extent and history of NIS invasions has expanded rapidly for coastal ecosystems of North America and elsewhere. The existing literature for North American coasts shows that scores to hundreds of exotic species have invaded each coast. We have summarized for the first time many of the apparent patterns that emerge from a comprehensive analysis of these North American data. Some patterns are clear, particularly that shipping has been the most important vector of introduction historically and at present, although an array of other vectors have

also operated to introduce many marine and estuarine species into North American waters. Limitations of the present data confound interpretation of other patterns, especially spatial variation in both the extent of invasion and taxonomic distribution of NIS. Geographic variation in the number of invasions is particularly difficult to sort out. Whereas San Francisco Bay clearly is more invaded than Prince William Sound and many other West Coast sites, the greater number of NIS reported in San Francisco Bay than Chesapeake Bay may be an artifact of the Chesapeake's longer history of active vectors (and relative paucity of early biotic surveys coincident with the onset of European trade and colonization), resulting in a greater number of unrecognized invasions. The observed exponential rate of increase for invasions may also be an artifact of data biases. Although we remain uncertain about the actual rate, we are more confident that a striking increase is not artifact, because it holds for subsets of better quality data, including (a) molluscs, a large and well-studied taxon and (b) San Francisco Bay, a site at which early biological studies were nearly contemporaneous with the operation of major vectors.

Despite the value of the existing data for marine invasions of North America, as elsewhere, it is important to recognize their limitations. Most data are derived from literature-based analyses, rather than direct field surveys designed to detect NIS. In fact, contemporary field surveys are lacking for many taxonomic groups and habitats at each site, where the most recent assessments may be decades old, and the quantity and quality of data on marine invasions is highly variable among sites. As a result, this "by-catch" approach to data collection has resulted in inherent biases that confound the interpretation of invasion patterns and processes.

Thus, modifying Lonsdale (82), we consider that the observed patterns of marine invasions reflect the interactive effects of propagule supply (PS), invasion resistance (R) of the recipient system, and bias (B) of the data, such that

$$I = \sum_{i=1}^{n} (PS_i)\,(R_i)\,(B_i)$$

where I is the number of established NIS summed across species from $i = 1$ to n at a location and time. Each component may vary spatially and temporally within a single bay. Rigorous interpretation of invasion patterns is confounded in most ecosystems, because fluctuations of the independent variables of PS and R are not controlled, and because B creates so many interaction terms (PS*B, R*B, PS*R*B) that the main effects are obscured. Clearly, priorities for invasion research include the collection of quantitative and experimental data that allow controlled analysis of the independent variables and elimination of data bias.

Testing many of the invasion hypotheses about propagule supply and invasion resistance requires standardized, quantitative measures of community composition in space and time (75, 115). At present, no program or framework exists to implement such quantitative measures of NIS invasions in North America. We therefore underscore the need to establish standardized ecological surveys of NIS across major regions of the North American shoreline and elsewhere (115; see also 67 for discussion of such a program). Furthermore, we advocate repeated quantitative measures at multiple sites, as well as across taxa and habitats, to avoid conclusions based upon a single site (taxa or habitat) that may not be broadly representative. Indeed, it is measures of variation in space and time that are necessary to test hypotheses about supply and resistance. Although a proposition for long-term temporal data, only this approach can provide data free of many potential biases that presently confound our interpretation of invasion patterns and processes.

Spatial and temporal measures of propagule supply are also fundamental to understanding of invasion mechanisms. To a large extent, we presently lack standardized measures of propagule supply. Despite existing measures of propagule supply, the data derive from a diverse variety of methods and often only focus on a single vector for a short (1–2 y) time period. As with ecological surveys, we must establish quantitative measures of propagule supply (or vector strength) that are collected in a standard fashion in space and time, if we are to test many key hypotheses about supply and invasion resistance.

Multiple approaches are clearly required to understand the patterns and underlying processes of marine invasions. Standardized measures of variation in vector strength and invasion success (as above) will allow us describe extant patterns and test invasion mechanisms, particularly at large spatial and temporal scales. Although this approach is necessary to understand invasions, it is not sufficient. For example, it will be difficult to control for all of the differences in propagule supply characteristics to different sites (e.g., source region, taxonomic composition, density and tempo of delivery, and capacity of different organisms to invade; for further discussion see Propagule Supply Hypotheses). However, manipulative laboratory and field experiments can provide an effective and unambiguous approach to address such a complex suite of variables at smaller scales, and show a great deal of promise for invasion ecology (70, 79, 125, 129). Thus, a combined strategy of mensurative and experimental approaches to invasion ecology is both complementary and most desirable, given their respective strengths and weaknesses, particularly in addressing issues of scale and complexity (44, 144).

Using these approaches, measures of invasion resistance are urgently needed. Resistance, the independent variable that defines propagule survivorship (the dependent variable), remains vague and poorly measured, especially in marine communities. When propagule supply is known, resistance can be estimated as a relative trait by comparing survivorship (or number of invasions) among locations, habitats, or time periods (82, 144). Comparing estimates of propagule supply and the resulting invasions can be used both to estimate resistance and to test for correlation to particular environmental or biological attributes of the recipient community. Thus, we advocate use of these estimates to advance and test predictions about specific attributes that underlie resistance and mediate the patterns of invasion.

Finally, we emphasize the dual value of these approaches, providing information that is key to both basic and applied areas of invasion ecology. Our emphasis throughout has been on the fundamental science, and we have argued for rigorous,

quantitative and experimental data to test relationships between propagule supply and invasion patterns. However, there are many management and policy initiatives now underway at regional, national and international levels of government to reduce the risk and impacts of coastal invasions (23, 92, 131, 139). The success of fundamental science to guide and evaluate invasion management actions also depends on accurate measures of the basic relationship between propagule supply and invasions.

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LITERATURE CITED

Allee WC. 1931. *Animal Aggregations: A Study in General Sociology*. Chicago: Univ. Chicago Press. 431 pp.

Asakura A. 1992. Recent introductions of marine benthos into Tokyo Bay (review): process of invasion into an urban ecosystem with discussion on the factors inducing their successful introduction. *J. Nat. Hist. Mus. Inst., Chiba* 2(1):1–14

Bagley M, Geller JB. 2000. Sources for worldwide invasions of the European shore crab: Inferences from microsatellite DNA variation. *Proceedings of the First Marine Bioinvasions Conference*. In press.

Baltz DM, Moyle PB. 1993. Invasion resistance to introduced species by a native assemblage of California stream fishes. *Ecol. Appl.* 3(2):246–55

Barrett SCH, Richardson BJ. 1986. Genetic attributes of invading species. *In Ecology of Biological Invasions*, ed. RH Groves, JJ Burdon, pp. 21–33 Cambridge: Cambridge University Press

6. Baskin Y. 1998. Winners and losers in a changing world: global changes may promote invasions and alter the fate of invasive species. *BioScience* 48(10):788–92
7. Boesch DF. 1977. A new look at zonation of benthos along the estuarine gradient. In *Ecology of Marine Benthos*, ed. BC Coull, pp. 245–66. Columbia, SC: Univ. S. C. Press
8. Briggs JC. 1974. *Marine Zoogeography*. New York: McGraw-Hill
9. Brock TD, Madigan MT, Matinko JM, Parker J. 1993. *Biology of Microorganisms*. Englewood Cliffs, NJ: Prentice Hall
10. Bryan RT. 1999. Alien species and emerging infectious diseases: past lessons and future implications. In *Invasive Species and Biodiversity Management*, ed. OT Sandlund, PJ Schei, Å Viken, pp. 163–75. Dordrecht, The Netherlands: Kluwer Academic
11. Carlton JT. 1979. *History, biogeography, and ecology of the introduced marine and estuarine invertebrates of the Pacific Coast of North America*. PhD thesis. Univ. Calif., Davis
12. Carlton JT. 1985. Transoceanic and interoceanic dispersal of coastal marine organisms: the biology of ballast water. *Oceanogr. Mar. Biol., Ann. Rev.* 23:313–71
13. Carlton JT. 1989. Man's role in changing the face of the ocean: biological invasions and implications for conservation of near-shore environments. *Conserv. Biol.* 3(3):265–73
14. Carlton JT. 1992. Dispersal of living organisms into aquatic ecosystems as mediated by aquaculture and fisheries activities. In *Dispersal of Living Organisms into Aquatic Ecosystems*, ed. A Rosenfield, R Mann, pp. 13–45. College Park, MD.: MD. Sea Grant
15. Carlton JT. 1993. Introduced marine and estuarine mollusks of North America: an end-of-the-20th-century perspective, part 2. *J. ShellFish Res.* 11:489–505
16. Carlton JT. 1996. Biological invasions and cryptogenic species. *Ecology* 77(6):1653–55
17. Carlton JT. 1996. Patterns, process, and prediction in marine invasion ecology. *Biol. Cons.* 78:97–106
18. Carlton JT. 1999. The scale and ecological consequences of biological invasions in the World's oceans. In *Invasive Species and Biodiversity Management*, ed. OT Sandlund, PJ Schei, Å Viken, pp. 195–212. Dordrecht, The Netherlands: Kluwer Academic
19. Carlton JT. 2000. Global change and biological invasions in the oceans. In *The Impact of Global Change on Invasive Species*, ed. HL Mooney, R Hobbs. Covelo, CA: Island Press
20. Carlton JT, Eldredge L. *Marine Bioinvasions of the Hawaiian Archipelago*. Honolulu, HI: Bernice P. Bishop Museum Press. In press
21. Carlton JT, Geller JB. 1993. Ecological roulette: the global transport of nonindigenous marine organisms. *Science* 261:78–82
22. Carlton JT, Hodder J. 1995. Biogeography and dispersal of coastal marine organisms: experimental studies of a replica of a 16th century sailing vessel. *Mar. Biol.* 121:721–30
23. Carlton JT, Kelly J. 1998. Foreword. In *Ballast Water: Ecological and Fisheries Implications*. 1–4. Int. Counc. Explor. Sea (ICES), Denmark
24. Carlton JT, Reid DM, van Leeuwen H. 1995. *The role of shipping in the introduction of nonindigenous aquatic organisms to the coastal waters of the United States (other than the Great Lakes) and an analysis of control options*. Report to U. S. Coast Guard, Washington D.C.
25. Case TJ. 1990. Invasion resistance arises in strongly interacting species-rich model competition communities. *Proc. Natl. Acad. Sci. USA* 87:9610–14
26. Chapman JW, Carlton JT. 1991. A test of the criteria for introduced species: the global invasion by the isopod *Synidotea laevidorsalis* (Miers, 1881). *J. Crustac. Biol.* 11(3):386–400
27. Chapman JW, Carlton JT. 1994. Predicted discoveries of the introduced isopod *Synidotea laevidorsalis*. *J. Crustac. Biol* 14(4):700–14
28. Chu KH, Tam PF, Fung CH, Chen QC. 1997. A biological survey of ballast water in container ships entering Hong Kong. *Hydrobiologia* 352:201–6
29. Cohen A, Mills C, Berry H, Wonham M, Bingham B, et al. 1998. *Puget Sound Expedition: A Rapid Assessment Survey of Non-Indigenous Species in the Shallow Waters of Puget Sound*. Olympia, WA: Wash. State Dept. Nat. Resour.

Cohen AN, Carlton JT. 1995. *Nonindigenous 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)

Cohen AN, Carlton JT. 1998. Accelerating invasion rate in a highly invaded estuary. *Science* 279:555–58

Coles SL, DeFelice RC, Eldredge LG, Carlton JT. 1999. Historical and recent introductions of non-indigenous marine species into Pearl Harbor, Oahu, Hawaiian Islands. *Mar. Biol.* 135:147–58

Cranfield HJ, Gordon DP, Willan RC, Marshall BA, Battershill CN, et al. 1998. *Adventive Marine Species in New Zealand, 48 pp*, The National Institute of Water and Atmospheric Research, New Zealand

Crawley MJ. 1987. What makes a community invasible? In *Colonization, Succession and Stability*, ed. AJ Gray, MJ Crawley, PJ Edwards, pp. 424–53. Oxford: Blackwell Scientific Publications

Crooks JA. 1998. *Effects of the introduced mussel, Musculista senhousia, and other anthropogenic agents on benthic ecosystems of Mission Bay, San Diego*. PhD thesis. Univ. Calif., San Diego

Crooks JA, Soulé ME. 1999. Lag times in population explosions of invasive species: causes and implications. In *Invasive Species and Biodiversity Management*, ed. OT Sandlund, PJ Schei, Å Viken, pp. 103–25. The Netherlands: Kluwer Academic Publishers

Crosby AW. 1986. Weeds. *Ecological Imperialism: The Biological Expansion of Europe, 900–1900*, pp. 145–336. London: Cambridge University Press

D'Antonio CM, Vitousek PM. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Ann. Rev. Ecol. Syst.* 23:63–87

Daehler CC, Strong DR. 1997. Hybridization between introduced smooth cordgrass (*Spartina alterniflora*; Poaceae) and native California cordgrass (*S. foliosa*) in San Francisco Bay (California). *Am. J. Bot.* 84(5):607–11

40. Darwin C. 1854. *A Monograph on the Sub-Class Cirripedia*. London: The Bay Society
41. Darwin C. 1859. *The Origin of Species*. London: J. Murray
42. Deaton LE, Greenberg MJ. 1986. There is no horohalinicum. *Estuaries* 9:20–30
43. di Castri F. 1989. History of biological invasions with special emphasis on the old world. In *Biological Invasions: a Global Perspective*, ed. JA Drake, HA Mooney, F di Castri, RH Groves, FJ Kruger, M Rejmánek, M Williamson, pp. 1–30. Chichester, UK: John Wiley & Sons, Ltd.
44. Diamond J. 1986. Overview: laboratory experiments, field experiments, and natural experiments. In *Community Ecology*, ed. J Diamond, TJ Case, pp. 3–23. New York: Harper & Row
45. Dickerson JE Jr, Robinson JV. 1986. The controlled assembly of microcosmic communities: the selective extinction hypothesis. *Oecologia* 71:12–17
46. Drake JA, Huxel GR, Hewitt CL. 1996. Microcosms as models for generating and testing community theory. *Ecology* 77(3):670–77
47. Drake LA, Dobbs FC, Choi KH, Ruiz GM, McCann LD, Mullady TL. 1999. *Inventory of microbes in ballast water of ships arriving in Chesapeake Bay*. Presented at Natl. Conf. Mar. Bioinvasions, 1st, Mass. Inst. Technol., Cambridge, Mass.
48. Ekman S. 1953. *Zoogeography of the Sea*. London: Sidgwick & Jackson, Ltd.
49. Elbrächter M. 1999. Exotic flagellates of coastal North Sea waters. *Helgoländer Meeresunters.* 52:235–42
50. Elton CS. 1958. *The Ecology of Invasions by Animals and Plants*. London: Methuen & Co. Ltd
51. Eno NC. 1996. Non-native marine species in British waters: effects and controls. *Aquat. Cons.: Mar. Freshwater Ecosyst.* 6:215–28
52. Erlich PR. 1986. Which animal will invade? In *Ecology of Biological Invasions of North America and Hawaii*, ed. HA Mooney, JA Drake, pp. 79–95. New York: Springer-Verlag
53. Fofonoff P, Ruiz GM, Hines AH, Carlton JT. 2000. *Assessing the importance of cryptogenic species in estuaries*. American Society of Limnology and Oceanography, Aquatic Sciences Meeting. Copenhagen: Abstract SS21-23
54. Fox MD, Fox BJ. 1986. The susceptibility of natural communities to invasion. In *Ecology of Biological Invasions*, ed. RH Groves, JJ Burdon, pp. 57–66. Cambridge: Cambridge University Press
55. Fuller PM, Nico LG, Williams JD. 1999. *Nonindigenous Fishes Introduced into Inland Waters of the United States*. Bethesda, MD: American Fisheries Society
56. Galil BS, Hulsmann N. 1997. Protist transport via ballast water—biological classification of ballast tanks by food web interactions. *Europ. J. Protis.* 33:244–53
57. Geller, JB. 1996. Molecular approaches to the study of marine biological invasions. In *Molecular Zoology: Advances, Strategies and Protocols*, ed. J Ferraris, S Palumbi, pp. 119–32. New York: Wiley-Liss
58. Gollasch S, Dammer M, Lenz J, Andres HG. 1998. Non-indigenous organisms introduced via ships into German waters. In *Ballast Water: Ecological and Fisheries Implications 50–64*, Int. Counc. Explor. Sea (ICES), Denmark
59. Gollasch S, Leppäkoski E. 1999. *Initial Risk Assessment of Alien Species in Nordic Coastal Waters*. Copenhagen, Denmark: Nordic Council of Ministers
60. Grimes DJ. 1991. Ecology of estuarine bacteria capable of causing human disease: a review. *Estuaries* 14(4):345–60
61. Hallegraeff GM. 1998. Transport of toxic dinoflagellates via ships' ballast water: bioeconomic risk assessment and efficacy of possible ballast water management strategies. *Mar. Ecol. Prog. Ser.* 168:297–309
62. Harvell CD, Kim K, Burkholder JM, Colwell RR, Epstein PR, et al. 1999. Emerging marine diseases—climate links and anthropogenic factors. *Science* 285:1505–10
63. Harvey M, Gilbert M, Gauthier D, Reid D. 1999. *A preliminary assessment of risks for the ballast water–mediated introduction of nonindigenous marine organisms in the estuary and Gulf of St. Lawrence*. Canadian Technical Report of Fisheries and Aquatic Sciences
64. Hay C, Handley S, Dodgshun T, Taylor M, Gibbs W. 1997. *Cawthron's Ballast Water Research Programme Final Report 1996-1997*, Cawthron Institute, Nelson, New Zealand
65. Hayek L-AC, Buzas MA. 1997. *Surveying Natural Populations*. New York: Columbia University Press
66. Hengeveld R. 1988. Mechanisms of biological invasions. *J. Biogeogr.* 15:819–28
67. Hewitt CL, Campbell ML, Thresher RE, Martin RB, ed. 1999. *Marine Biological Invasions of Port Phillip Bay, Victoria*, Technical Report No.20. Centre for Research on Introduced Marine Pests, Hobart
68. Hillman SP, ed. 1999. The ballast water problem–where to from here? *Proceedings of a Workshop Held 5-6 May 1999. Brisbane, Australia*. EcoPorts Monograph Series No. 19. Brisbane, Australia
69. Hines AH, Ruiz GM. 2000. *Biological invasions at cold-water coastal ecosystems: ballast- mediated introductions in Port Valdez/Prince William Sound*. Final Report to Regional Citizens Advisory Council of Prince William Sound
70. Hobbs RJ. 1989. The nature and effects of disturbance relative to invasions. In *Biological Invasions: a Global Perspective*, ed. JA Drake, HA Mooney, F Di Castri, RH Groves, FJ Kruger, M Rejmánek, M

iamson. pp 389–405. Chichester, UK:
i Wiley & Sons, Ltd.
vitz CC. 1997. The impact of natural
arbances. In *Strangers in Paradise: Im-
and Management of Nonindigenous
ies in Florida*, ed. D Simberloff, DC
mitz, TC Brown, pp. 63–74. Washing-
D. C.: Island Press
onski D. 1998. Geographic variation
ne molluscan recovery from the end-
aceous extinction. *Science* 279:1327–

ison K. 1994. *Alien Species in the
ine Environment—Introductions to the
ic Sea and the Swedish West Coast
p.*, Swedish Environmental Protection
ncy, Sweden
g SC, Paul JH. 1998. Gene transfer
ansduction in the marine environment.
l. Environ. Microbiol. 64(8):2780–87
eiva P. 1996. Developing a predictive
ogy for non-indigenous species and
ogical invasions. *Ecology* 77:1651–52
y JM. 1993. Ballast water and sedi-
ts as mechanisms for unwanted species
oductions into Washington State. *J.
lfish Res.* 12(2):405–10
oie DM, Smith LD, Ruiz GM. 1999.
potential for intracoastal transfer of
-indigenous species in the ballast wa-
of ships. *Estuarine Coast. Shelf Sci.*
51–64
R, Weatherby AJ, Warren PH. 2000.
the invasibility of persistent protist
munities. *Oikos* 88:319–26
ine JM. 2000. Species diversity and bi-
ical invasions: relating local process to
mmunity pattern. *Science* 288:852–54
ine JM, D'Antonio CM. 1999. Elton
sited: a review of evidence linking di-
ity and invasibility. *Oikos* 87:15–26
ge DM. 1993. Biological invasions:
ons for ecology. *Trends Ecol. Evol.*
:133–36
sdale WM. 1999. Global patterns of
t invasions and the concept of invasi-
y. *Ecology* 80(5):1522–36

83. Loope LL, Mueller-Dombois D. 1989. Characteristics of invaded islands, with special reference to Hawaii. In *Biological Invasions: a Global Perspective*, ed. JA Drake, F DiCastri, RH Groves, FJ Kruger, HA Mooney, M Rejmánek, MH Williamson, pp. 257–80. Chichester, UK: John Wiley & Sons, Ltd.
84. MacArthur R, Wilson E. 1967. *The Theory of Island Biogeography*, Princeton: Princeton University Press
85. Mayr E. 1963. *Animal Species and Evolution*. Cambridge, MA: The Belknap Press of Harvard University Press
86. Medcof JC. 1975. Living marine animals in a ship's ballast water. *Proc. Natl. Shellfish. Ass.* 65:11–12
87. Mills EL, Leach JH, Carlton JT, Secor CL. 1993. Exotic species in the Great Lakes: a history of biotic crises and anthropogenic introductions. *J. Great Lakes Res.* 19(1):1–54
88. Mills EL, Scheuerell MD, Carlton JT, Strayer D. 1997. Biological invasions in the Hudson River: an inventory and historical analysis. *New York State Mus. Circ.* 57:1–51
89. Mooney HA, Hobbs R, ed. 2000. *The Impact of Global Change on Invasive Species*. Covelo, CA: Island Press
90. Mooney HA, Hofgaard A. 1999. Biological invasions and global change. In *Invasive Species and Biodiversity Management*, ed. OT Sandlund, PJ Schei, Å Viken, pp. 139–48. The Netherlands: Kluwer Academic Publishers
91. Moulton MP, Pimm SL. 1986. Species introductions to Hawaii. In *Ecology of Biological Invasions in North America and Hawaii*, ed. HA Mooney, JA Drake, pp. 231–49. New York: Springer-Verlag
92. National Research Council. 1996. *Stemming the Tide: Controlling Introductions of Nonindigenous Species by Ships' Ballast Water*, ed. Marine Board Commission on Engineering and Technical Systems. Washington, D.C.: National Academy Press
93. Newsome AE, Noble IR. 1986. Ecological and physiological characters of invading species. In *Ecology of Biological Invasions*, ed. RH Groves, JJ Burdon, pp. 1–20. Cambridge: Cambridge University Press
94. Olenin S, Leppäkoski E. 2000. *Inventory of Baltic Sea alien species*. http://www.ku.lt/nemo/species.htm
95. Patz JA, Epstein PR, Burke TA, Balbus JM. 1996. Global climate change and emerging infectious diseases. *J. Am. Med. Ass.* 275(3):217–23
96. Pechenik JA. 1990. Delayed metamorphosis by larvae of benthic marine invertebrates: Does it occur? Is there a price to pay? *Ophelia* 32:63–94
97. Pechenik JA, Wendt DE, Jarrett JN. 1998. Metamorphosis is not a new beginning—larval experience influences juvenile performance. *BioScience* 11:901–10
98. Pickett STA, White PS. 1985. *The Ecology of Natural Disturbance and Patch Dynamics*. New York: Academic Press
99. Pierce RW, Carlton JT, Carlton DA, Geller JB. 1997. Ballast water as a vector for tintinnid transport. *Mar. Ecol. Prog. Ser.* 149:295–97
100. Pimm SL. 1989. Theories of predicting success and impact of introduced species. In *Biological Invasions: a Global Perspective*, ed. JA Drake, F. Di Castri, RH Groves, FJ Kruger, HA Mooney, M Rejmánek, MH Williamson, pp. 351–67. Chichester, UK: John Wiley & Sons, Ltd.
101. Pimm SL 1991. *The Balance of Nature?* Chicago, Illinois: University of Chicago Press
102. Por FD. 1978. *Lessepsian Migration: The Influx of Red Sea Biota into the Mediterranean by Way of the Suez Canal*. Heidelberg: Springer-Verlag
103. Por FD. 1990. Lessepsian migration. An appraisal and new data. *Bull. Inst. Océanogr. Monaco Spec. Vol.* 7:1–10
104. Pysek P. 1995. On the terminology used in plant invasion studies. In *Plant Invasions - General Aspects and Special Problems*, ed. P Pysek, K Prach, M Rejmánek, M Wade, pp. 71–81. Amsterdam: SPB Academic
105. Reise K, Gollasch S, Wolff WJ. 1999. Introduced marine species of the North Sea coasts. *Helgoländer Meeresunters.* 52:219–34
106. Rejmánek M. 1989. Invasibility of plant communities. In *Biological Invasions: a Global Perspective*, ed. JA Drake, F DiCastri, RH Groves, FJ Kruger, HA Mooney, M Rejmánek, MH Williamson, pp. 369–88. Chichester, UK: John Wiley & Sons, Ltd.
107. Rejmánek M. 1996. Theory of seed plant invasiveness: The first sketch. *Biol. Conserv.* 78:171–81
108. Rejmánek M, Richardson DM. 1996. What attributes make some plant species more invasive? *Ecology* 77(6):1655–61
109. Ribera MA, Boudouresque C-F. 1995. Introduced marine plants, with special reference to macroalgae: mechanisms and impact. *Prog. Phycol. Res.* 11:187–268
110. Robinson GR, Quinn JF, Stanton ML. 1995. Invasibility of experimental habitat islands in a California winter annual grassland. *Ecology* 76:786–94
111. Robinson JV, Dickerson JE Jr. 1984. Testing the invulnerability of laboratory island communities to invasion. *Oecologia* 61:169–74
112. Robinson JV, Edgemon MA. 1988. An experimental evaluation of the effect of invasion history on community structure. *Ecology* 69(5):1410–17
113. Rosenzweig ML. 1995. *Species Diversity in Space and Time*. Cambridge: Cambridge University Press
114. Roughgarden J. 1986. Predicting invasions and rates of spread. In *Ecology of Biological Invasions of North America and Hawaii*, ed. HA Mooney, JA Drake, pp. 179–90. New York: Springer-Verlag
115. Ruiz GM, Carlton JT, Fofonoff P, Strayer D, Mills E, et al. 2000. *Interpreting*

ision patterns from ecological sur-
s, Report to the U.S. Fish and Wildlife
vice
z GM, Carlton JT, Grosholz ED, Hines
I. 1997. Global invasions of marine
l estuarine habitats by non-indigenous
cies: mechanisms, extent, and conse-
ences. *Am. Zool.* 37:621–32
iz GM, Fofonoff P, Carlton JT, Hines
H. 2000. *Invasion History of Chesa-*
ake Bay, Report to U.S. Fish and
ildlife Service Washington, D.C.
iz GM, Fofonoff P, Hines AH. 1999.
on-indigenous species as stressors in
stuarine and marine communities: as-
ssing invasion impacts and interactions.
imnol. Oceanogr. 44(3, part 2):950–72
choener TW, Spiller DA. 1995. Ef-
ect of predators and area invasion: An
xperiment with island spiders. *Science*
67:1811–13
Simberloff D. 1986. Introduced insects:
biogeographic and systematic perspec-
ive. In *Ecology of Biological Invasions*
of North America and Hawaii, ed. HA
Mooney, JA Drake, pp. 3–26. New York:
Springer-Verlag
Simberloff D. 1989. Which insect intro-
ductions succeed and which fail? In *Bio-*
logical Invasions: a Global Perspective,
ed. JA Drake, F DiCastri, RH Groves, FJ
Kruger, HA Mooney, M Rejmánek, MH
Williamson, pp. 61–75. Chichester, UK:
John Wiley & Sons, Ltd.
Simberloff D, Von Holle B. 1999. Positive
interactions of nonindigenous species:
invasional meltdown? *Biol. Invasions* 1:
21–32
Smith LD, Wonham MJ, McCann LD,
Ruiz GM, Hines AH, Carlton JT. 1999.
Invasion pressure to a ballast-flooded es-
tuary and an assessment of inoculant sur-
vival. *Biol. Invasions* 1:67–87
Sousa WP. 1984. The role of disturbance
in natural communities. *Ann. Rev. Ecol.*
Syst. 15:353–91
Stachowicz JJ, Whitlach RB, Osman RW.
1999. Species diversity and invasion re-
sistance in a marine ecosystem. *Science*
286:1577–79
Stohlgren TJ, Binkley D, Chong GW,
Kalkhan MA, Schell LD, et al. 1999.
Exotic plant species invade hot spots
of native plant diversity. *Ecol. Monogr.*
69(1):25–46
Subba Rao DV, Sprules WG, Locke A,
Carlton JT. 1994. *Exotic phytoplankton*
from ships' ballast waters: risk of po-
tential spread to mariculture sites on
Canada's east coast, Canadian Data Re-
port of Fisheries and Aquatic Sciences
Symstad AJ. 2000. A test of the effects
of functional group richness and compo-
sition on grassland invasibility. *Ecology*
81(1):99–109
Tilman D. 1997. Community invasibility,
recruitment limitation, and grassland bio-
diversity. *Ecology* 78(1):81–92
Tilman D. 1999. The ecological conse-
quences of changes in biodiversity: a
search for general principles. *Ecology*
80(5):1455–74
U.S. Congress. 1996. National Invasive
Species Act, Public Law 104–332. In
Congressional Record, 142. Washington,
D.C.: U.S. Government Printing Office
U.S. Congress Office of Technology As-
sessment. 1993. *Harmful Non-Indigenous*
Species in the United States, OTF-F-565,
Washington, D.C.: U.S. Government
Printing Office
Usher MB. 1988. Biological invasions of
nature reserves: a search for generaliza-
tions. *Biol. Conserv.* 44:119–35
Vermeij GJ. 1978. *Biogeography and*
Adaptation: Patterns of Marine Life.
Cambridge: Harvard University Press
Vermeij GJ. 1991. When biotas meet: Un-
derstanding biotic interchange. *Science*
253 (5024):1099–104
Vitousek PM. 1990. Biological invasions
and ecosystem processes: toward an inte-
gration of population biology and ecosys-
tem studies. *Oikos* 57:7–13
Vitousek PM, Walker LR. 1989.
Biological invasion by *Myrica faya* in
Hawai'i: plant demography, nitrogen fix-
ation, ecosystem effects. *Ecol. Monogr.*
59:247–65
Webb DA. 1985. What are the criteria
for presuming native status? *Watsonia*
15:231–365
White House. 1999. *Executive Order:*
Invasive Species. http://www.pub.white-
house.gov/urires/I2R?urn:pdi://oma.eop.
gov.us/1999/2/3/14.text.1
Wilcove DS, Rothstein D, Dubow J,
Phillips A, Losos E. 1998. Quantifying
threats to imperiled species in the United
States. *BioScience* 48(8):607–15
Williams RJ, Griffiths FB, van der Wal
EJ, Kelly J. 1988. Cargo vessel ballast
water as a vector for the transport of
non-indigenous marine species. *Estuar-*
ine Coast. Shelf Sci. 26(4):409–20
Williamson M. 1989. Mathematical mod-
els of invasion. In *Biological Invasions:*
a Global Perspective, ed. JA Drake, HA
Mooney, F di Castri, RH Groves, FJ
Kruger, M Rejmánek, M Williamson, pp.
329–50. Chichester, UK: John Wiley &
Sons, Ltd.
Williamson M. 1996. *Biological Inva-*
sions. London: Chapman & Hall
Williamson M. 1999. Invasions. *Ecogra-*
phy 22:5–12
Wiser SK, Allen RB, Clinton PW, Platt
KH. 1998. Community structure and for-
est invasion by an exotic herb over 23
years. *Ecology* 79:2071–81
Wonham MJ, Carlton JT, Ruiz GM, Smith
LD. 2000. Fish and ships: relating dis-
persal frequency to success in biological
invasions. *Mar. Biol.* 136:1111–21
Wonham MJ, Walton WC, Frese AM,
Ruiz GM. 1996. *Transoceanic transport*
of ballast water: Biological and physical
dynamics of ballasted communities and
the effectiveness of mid-ocean exchange.
Final Report to the U.S. Fish and Wildlife
Service and the Compton Foundation
Wright S. 1978. *Evolution and the Genet-*
ics of Populations Volume 4–Variability
Within and Among Natural Populations.
Chicago: University of Chicago Press
Zhang F, Dickman M. 1999. Mid-ocean
exchange of container vessel ballast wa-
ter. 1: Seasonal factors affecting the trans-
port of harmful diatoms and dinoflagel-
lates. *Mar. Ecol. Prog. Ser.* 176:243–51
Zolotarev V. 1996. Black Sea ecosystem
changes related to the introduction of new
mollusc species. *Mar. Ecol.* 17(1–3):227–
36