

## Global Invasions of Marine and Estuarine Habitats by Non-Indigenous Species: Mechanisms, Extent, and Consequences<sup>1</sup>

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**SYNOPSIS.** Non-indigenous species (NIS) are increasingly conspicuous in marine and estuarine habitats throughout the world, as the number, variety, and effects of these species continue to accrue. Most of these NIS invasions result from anthropogenic dispersal. Although the relative importance of different dispersal mechanisms varies both spatially and temporally, the global movement of ballast water by ships appears to be the largest single vector for NIS transfer today, and many recent invasions have resulted from this transfer. The rate of new invasions may have increased in recent decades, perhaps due to changes in ballast water transport. Estuaries have been especially common sites of invasions, accumulating from tens to hundreds of NIS per estuary that include most major taxonomic and trophic groups. We now know of approximately 400 NIS along the Pacific, Atlantic and Gulf coasts of the U.S., and hundreds of marine and estuarine NIS are reported from other regions of the world. Although available information about invasions is limited to a few regions and underestimates the actual number of NIS invasions, there are apparent differences in the frequency of NIS among sites. Mechanisms responsible for observed patterns among sites likely include variation in supply of NIS, and perhaps variation in properties of recipient or donor communities, but the role of these mechanisms has not been tested. Although our present knowledge about the extent, patterns and mechanisms of marine invasions is still in its infancy, it is clear that NIS are a significant force of change in marine and especially estuarine communities globally. Taxonomically diverse NIS are having significant effects on many, if not most, estuaries that fundamentally alter population, community, and ecosystems processes. The impacts of most NIS remain unknown, and the predictability of their direct and indirect effects remains uncertain. Nonetheless, based upon the documented extent of NIS invasions and scope of their effects, studies of marine communities that do not include NIS are increasingly incomplete.

### INTRODUCTION

Human-mediated invasions of terrestrial, freshwater, and marine habitats by non-indigenous species (NIS) are occurring throughout the world, and the extent and cumulative impact of these invasions have been enormous (*e.g.*, Elton, 1958; Mooney and Drake, 1986; Carlton, 1989). For example, a 1993 report by the U.S. Congressional Office of Tech-

nology Assessment (OTA) estimates that there are a minimum of 4,500 NIS known to be established in the United States, representing 2–8% of the taxonomic groups examined. Approximately 15% of these NIS are thought to be nuisance species that have significant ecological and/or economic impact (OTA, 1993). The scope of this phenomenon has been recognized most frequently for terrestrial environments, where invasions have diminished the size of native populations, sometimes causing extinctions, and significantly altered community structure and ecosystem function (*e.g.*, Mooney and Drake, 1986; OTA, 1993).

<sup>1</sup> From the Symposium *Molecules to Mudflats* presented at the Annual Meeting of the Society for Integrative and Comparative Biology, 26–30 December 1995, at Washington, D.C.

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The significance of NIS in marine environments (including bays, estuaries, and open coasts) has received relatively little attention compared to terrestrial and freshwater habitats (*e.g.*, Carlton, 1989; OTA, 1993). This disparity has changed in recent years. With increased scrutiny, it has become clear that NIS are common in marine communities and are a potent force of ecological change on local, regional, and global scales (*e.g.*, Por, 1978; Carlton, 1979*a, b*, 1987, 1989, 1992*a*; Pollard and Hutchings, 1990; Hutchings, 1992; Cohen and Carlton, 1996; also see below).

Although some marine invasions result from natural dispersal mechanisms, human-mediated invasions appear to be much more prevalent now. The relative contribution of anthropogenic dispersal to marine invasions has increased over the past few centuries and may be increasing still (*e.g.*, Carlton, 1985; Vermeij, 1991; Carlton and Geller, 1993; Cohen and Carlton, 1996). This increase has modified the patterns of dispersal and invasions in two significant ways. First, the overall rate of invasions has increased, because the results of natural and anthropogenic dispersal are additive. Second, many natural barriers to dispersal such as distance or currents have been breached, increasing the potential pool of species that can invade a region and the number of donor regions from which invasions can occur.

In this paper, we provide an overview of our current understanding of marine and especially estuarine invasions by NIS. In particular, we focus on invasions resulting from anthropogenic causes and review mechanisms of species transfer as well as the rate, extent, and consequences of invasions. Although we consider primarily marine to tidal fresh water of coastal habitats, we also include some information about the Great Lakes of North America, because they are functionally considered an estuary and are open to international shipping traffic similar to other coastal estuaries.

#### MECHANISMS OF SPECIES TRANSFER

The transfer and introduction of NIS to coastal regions has been occurring on a global scale for centuries as a result of

many human activities (Elton, 1958; Carlton, 1979*a, b*; 1987, 1989, 1992*a*). The most common mechanisms for species transfer among nearshore waters have included (1) movement of fouling communities on the bottom of ships, (2) movement and/or intentional release of aquaculture, fishery, and bait species along with their assemblages of associated (free-living and parasitic) organisms, (3) connection of waterways through canals, (4) release of species associated with pet industries or management practices, and (5) release of organisms in ballast materials of ships.

The relative importance of particular transfer mechanisms and source regions of NIS exhibits both spatial and temporal variation. For example, the invasions of San Francisco Bay, California (USA) have resulted from a temporal sequence of transfer mechanisms (Carlton, 1979*a*). Prior to 1870, most invaders arrived as fouling organisms on the bottoms of transoceanic ships, primarily from eastern North America. Relatively few organisms now appear to arrive on the bottoms of ships compared to the past, due to current widespread use of metal versus wooden hulls and anti-fouling paints as well as relatively low port residency times and fast ship speeds—changes that all serve to limit colonization of hulls and retention of organisms during voyages. From 1870 to the early 20th century, the Atlantic oyster *Crassostrea virginica* was brought from eastern North America by railroad and planted into San Francisco Bay, along with a large number of associated NIS. Although the oyster did not persist locally, many NIS associated with the oysters became established. The Pacific oyster *Crassostrea gigas* was introduced from Japan between 1930–60 to establish a fishery in San Francisco Bay. As with Atlantic oysters, the transfer of Pacific oysters brought many NIS that successfully invaded this region. Today, most new invasions in San Francisco Bay are thought to result from the transfer and release of ships' ballast water from foreign ports, especially in Asia (Carlton, 1990; Carlton and Geller, 1993; Carlton *et al.*, 1995). However, other vectors for NIS transfer are still active in San Francisco Bay, including transfer on

ship hulls which is difficult to distinguish from ballast water as the cause of some recent invasions (see Cohen and Carlton, 1996, for recent comprehensive analysis).

The total supply of NIS, as well as the relative contribution and specific details of individual transfer mechanisms to this supply, varies among coastal regions. A recent analysis of foreign ballast water released in U.S. ports during 1991 underscores this variation (Carlton *et al.*, 1995). At one extreme, the port system of Chesapeake Bay received over 10,000,000 metric tons of ballast water, originating primarily from Europe and the Mediterranean. In contrast, San Francisco Bay and other Pacific port systems received volumes of one to two orders of magnitude less, and most of this ballast water arrived from Asia. Similar levels of variation among ports undoubtedly exist in the supply of NIS from other transfer mechanisms. Such variation in NIS supply may influence differences in invasion rates among regions (see below), and sites of frequent invasion can themselves become sources for subsequent invasion through passive range expansion or by a "leap-frog effect" of further human transfer (*e.g.*, Grosholz and Ruiz, 1995; Smith *et al.*, 1996).

Despite considerable spatial variation in supply patterns, the movement of ballast water appears to be the single largest source of NIS transfer throughout the world (Carlton, 1985; Carlton *et al.*, 1995). Most known marine invasions are occurring in or near ports with international shipping traffic and appear linked to ballast water as the most plausible source (*e.g.*, Carlton and Geller, 1993). Today, Australian and U.S. ports each receive >79 million metric tons of ballast water from foreign ports per year (>9 million liters/hour; Kerr, 1994; Carlton *et al.*, 1995), exemplifying the scale of ballast release occurring at international ports generally. A single ship can carry >150,000 metric tons of ballast water that is used to maintain trim and stability. Because ballast is usually taken from bays and estuaries, with waters rich in plankton and nekton, most ships carry a diverse assemblage of organisms in their ballast water (*e.g.*, Medcoff, 1975; Carlton, 1985; Williams *et al.*,

1988; Carlton and Geller, 1993) and sediments that accumulate in ballast tanks (Hallegraeff and Bolch, 1991, 1992; Kelly, 1993). Many species present in ballast tanks, from bacteria and dinoflagellates to crabs and fish, are viable upon arrival to a new port and are capable of invasion when released (*e.g.*, Carlton and Geller, 1993; Smith *et al.*, 1996; unpublished data, GMR *et al.*). Thus, the extensive worldwide use of ballast water sustains a large scale dispersal process by which exotic species can invade new territories.

#### RATE OF INVASIONS

Although invasions resulting from human transfer have been widespread (see below), new invasions continue to occur, and the rate of invasions may be increasing. For example, Carlton and Geller (1993) list 46 recent examples of ballast-mediated invasions that have occurred around the world since the late 1970s, and invasion rates for San Francisco Bay and the Great Lakes appear to have increased in the past 20–30 years (Mills *et al.*, 1993; Cohen and Carlton, 1996). For these and other estuaries, invasions appear to occur in pulses that correspond to changes in the variety and characteristics of transfer mechanisms (*e.g.*, Carlton, 1979a; Cohen and Carlton, 1996; Ruiz *et al.*, 1997). The increase in invasions noted above has been attributed largely to changes in ballast water transport over the past few decades: More ships with larger volumes of ballast water arriving from more regions in less time (due to faster speeds) than ever before, increasing the overall abundance, density and survival of species entrained and transferred in ballast water (Carlton, 1996a). Some of these changes in shipping traffic may also increase the opportunities for transport of organisms on ships' hulls and within seachests (Rainer, 1995; C. Hewitt, personal communication).

It is clear that the rate of invasions has increased recently at a few sites (above), but such detailed analysis is not available for most regions to evaluate the widespread nature of this phenomenon. There appears to be an increase of reported invasions throughout the world, suggesting a general

TABLE 1. *Number of non-indigenous species (NIS) known for estuaries in the United States.*

Estuary	NIS known	Source
Chesapeake Bay (Maryland & Virginia)	116	Ruiz <i>et al.</i> , 1997, unpublished
Coos Bay (Oregon)	60	Carlton, unpublished
Great Lakes (New York to Minnesota)	137	Mills <i>et al.</i> , 1993
San Francisco Bay (California)	212	Cohen and Carlton, 1996

increase in invasion rate among many regions. Certainly new invasions are occurring on a global basis. But any increase in rate of reported invasions may reflect increasing awareness and search effort as much as actual invasion rate. We predict the latter is true in most cases. Sufficient data and analysis are available for San Francisco Bay and the Great Lakes to distinguish among these possibilities, but this is not yet so for other sites.

Interestingly, some heavily invaded estuaries continue to accrue new invasions at relatively high rates (above). Although competition between invading and resident species does occur (*e.g.*, Race, 1982; Brenchley and Carlton, 1983), niche limitation that either limits invasions or eliminates resident species has not been demonstrated or adequately tested to date. In fact, there may actually be a positive feedback whereby initial invasions make a community more susceptible to subsequent invasion (C. Hewitt, personal communication; see also following section for further discussion of variation among sites).

It is also interesting that some invasions occur only after years to decades of dispersal opportunities from source to recipient region (*e.g.*, Carlton, 1996a). Successful establishment (if it occurs) often requires many inoculations, and success will depend partly upon inoculant size as well as physiological condition of individuals and local conditions at time of arrival (Roughgarden, 1986; Simberloff, 1986; Williamson, 1989). Although we can identify additional factors that mediate the rate of marine invasions (*e.g.*, Carlton, 1996a), and we know invasions will continue to occur from new and old transfer mechanisms alike, the prediction of when a species will invade upon arrival remains elusive.

#### EXTENT OF INVASIONS

Among marine environments, estuaries have been common sites of invasions. For example, for a few U.S. estuaries in which NIS have been studied intensively, the number of known NIS range from 60 to 212 per estuary (Table 1). These NIS include a broad range of taxonomic and trophic groups (*e.g.*, filter feeders, deposit feeders, parasites) that occupy diverse habitats (*e.g.*, soft-sediment, hard substrata, marsh surface, and water column) and originate from throughout the world, with Asia and Europe being especially common source regions.

Similar invasions have occurred in marine habitats on all continents of the world. However, the extent of invasions have not been estimated for most estuaries or coastal regions. A few invasions are known for many or most geographic regions, consisting of an occasional record, and NIS are only known to be common in a few regions where they have been explicitly surveyed. Among the latter, we now know of approximately 400 NIS along the Pacific, Atlantic, and Gulf coasts of the continental U.S., excluding the Great Lakes and other inland waters (Mills *et al.*, 1996; Cohen and Carlton, 1996; Ruiz *et al.*, 1997; unpublished data, J.T.C. and G.M.R.). Over 240 NIS are known from the Mediterranean Sea, and 75% of these species are attributed to the Lessepsian Migration through the Suez Canal since its opening in 1869 (Por, 1978; Boudouresque, 1994; Ribera, 1994). It is estimated that as many as 500 Lessepsian species may have invaded the eastern Mediterranean from the Red Sea, representing 11% of the fish species and 21% of the decapod crustacean species there (Por, 1978). Seventy NIS are reported in Australian waters (Pollard and Hutchings, 1990a, b; Jones, 1992; Thresher and Martin, 1995),

and recent surveys have added many other species to the total list (C. Hewitt, personal communication). Invasions also appear to be common in marine habitats of Great Britain (52 NIS; Eno, 1996), the Baltic Sea (35 NIS; Leppakoski, 1994), and Japan (15 NIS known from Tokyo Bay alone; Asakura, 1992).

Despite the large number of NIS known from some estuaries and regions, the actual extent of invasions (where studied) is underestimated for two major reasons. First, many species simply are not examined. Most studies focus primarily on "accessible" taxa, or those groups for which historical distribution records and taxonomic identities are well established, excluding many of the small and less conspicuous species for which there are few or no historical and geological records. Second, of those species examined, the native versus non-native status often is not evident and may never be resolved. Thus, species can be classified as native, non-native, or "cryptogenic" (*i.e.*, of unknown origin; Carlton, 1996b), and a large number of species from most regions belong to this last group, that undoubtedly includes many non-native species. Recent use of molecular techniques may help resolve some cryptogenic invasions, especially those involving sibling species complexes (Geller, 1996).

Currently, our ability to compare the extent of invasions among continents, among regions (*e.g.*, temperate versus tropical), among habitats, and between island and mainland is very limited. Such comparisons require comprehensive and high quality data (*i.e.*, a synthesis and documentation of NIS that derives from an adequate review of literature and survey of biota), and an analysis of invasions is simply not available for most regions or habitats. Nevertheless, some interesting patterns are evident in the available data. First, it appears that estuaries and embayments have been invaded more frequently than rocky or sandy shores of the outer coast. This pattern is most striking when comparing the 212 NIS known from San Francisco Bay to the <10 NIS known from the adjacent outer coast, for which the biota is also well known (*e.g.*, see Carlton, 1979a). Although this disparity may be

smaller when scaled to the relative size of resident species pools in each habitat, large differences should still exist in the percentage of total species that are invaders among these habitats. Second, there appears to be relatively large variation in the extent of invasions among estuaries where NIS have been well documented (Table 1).

Observed patterns of invasion among sites may be largely a function of NIS supply. Supply is not only a necessity for invasion, but the frequency and intensity (or size) of inoculation are critical components in colonization success (*e.g.*, MacArthur and Wilson, 1967; Roughgarden, 1986; Robinson and Edgemon, 1988; Williamson, 1989; Schoener and Spiller, 1995). This alone may explain any difference in the extent of invasions between estuaries and outer coastal habitats, as most human activities associated with NIS transfer (as above) are localized in estuaries and bays. In addition, these organisms usually originate from an estuarine environment and are perhaps most likely to survive and colonize other estuarine (versus outer coastal) habitats.

The extent of invasion may also be influenced by differences in susceptibility to invasion among recipient habitats or regions. Specifically, some communities are thought to have a relatively high susceptibility to invasion compared to others, because of differences in disturbance regime, diversity, or other attributes (*e.g.*, Fox and Fox, 1986; Case, 1990; Vermeij, 1991). This may interact with variation in capacity to invade that is thought to exist among donor regions, suggesting that some communities are comprised of inherently better invaders than others (*e.g.*, Vermeij, 1991). However, it is not clear how much variation in either quality of recipient and donor communities influence invasion success (*e.g.*, Simberloff, 1986; but see also Schoener and Spiller, 1995).

We predict that further study will indicate NIS are common in most estuarine environments throughout the world. Although we know of only a few NIS for many regions, these are invariably regions for which an analysis of invasions is lacking. Because the transfer mechanisms responsible for invasions are operating globally, we surmise

that frequent invasions are the rule, which is supported by analyses to date (Table 1 and above). Undoubtedly, variation and patterns in the extent of invasions (among habitats and regions) will become evident through further analysis. While indicating that some recipient communities are more heavily invaded, it will remain difficult to interpret the susceptibility of communities without controlling for supply of NIS (which is nearly unique to each region). This is a major challenge in the study of invasion biology.

#### CONSEQUENCES OF INVASIONS

Ecological impacts of NIS have been documented in marine, and especially estuarine, habitats throughout the world, from New Zealand and Europe to North America and Asia, that result from invasions by diverse taxa such as molluscs, bryozoans, crabs, ctenophores, and vascular plants (Table 2). These effects are most striking, and best measured, where NIS have become numerical or aspect dominants in a community. For example, the recent invasions of North America by the Asian clam *Potamocorbula amurensis* in San Francisco Bay and the Eurasian zebra mussel *Dreissena polymorpha* in the Great Lakes have fundamentally altered community structure and function. In both cases, the bivalves have become numerically dominant in the invaded communities, achieving densities >10,000 per m<sup>2</sup>, replacing other benthic organisms, and clearing plankton communities from overlying waters (e.g., Carlton *et al.*, 1990; Nichols *et al.*, 1990; Hebert *et al.*, 1991; Wu and Culver, 1991; Alpine and Cloern, 1992; Cloern, 1996; McIssac, 1996). Furthermore, these direct effects appear to have many indirect effects on ecosystem characteristics, from food web structure to nutrient dynamics and sedimentation rates.

Some invasions can have significant economic impacts as well as serious health risks. For example, the recent zebra mussel invasion is expected to cost U.S.\$1.8–3.4 billion in control measures in the U.S. by the year 2,000, and the North American ctenophore *Mnemiopsis ledyi* is associated with the loss of a \$250 million (U.S.) fish-

ery in the Azov and Black Seas, although cause-effect relationships are less certain in this latter example (OTA, 1993; Harbison and Volovick, 1994). The recent collapse of Chesapeake Bay's oyster fishery is due largely to two pathogens, one of which may be introduced (e.g., Andrews, 1980; Sindermann, 1990; Chesapeake Bay Commission, 1995). The European green crab *Carcinus maenas* appears to have a significant impact on commercial bivalve fisheries along the northeastern U.S., and some townships have implemented green crab control programs that include bounties for removal (Tettlebach, 1986; W. Walton and R. Karney, personal communication). Conversely, some intentional and unintentional introductions are considered beneficial, mostly through creating commercial and recreational fisheries (e.g., Courtney and Williams, 1992; Neushal *et al.*, 1992; OTA, 1993; Galil, 1994).

Two types of health risks associated with NIS have received the most attention to date. The increased frequency of toxic red tides, which threaten both public health and marine fisheries, is due partly to the worldwide transfer of dinoflagellates and their cysts in ships' ballast tanks (Hallegraeff *et al.*, 1988; Anderson, 1989; Hallegraeff and Bolch, 1991, 1992; Hallegraeff, 1993; Kelly, 1993). Such ship-mediated transfer is also thought to play a role in the epidemiology of cholera (*Vibrio cholerae*) in human populations, and especially in the recent epidemic of South and Central America that resulted in an estimated 731,312 cases and 6,323 deaths in the first two years (1991–1992; Morbidity and Mortality Weekly Report, 1993). These bacteria are in the ballast tanks of some ships (McCarthy and Khambaty, 1994) and attach to a variety of marine and estuarine organisms (e.g., Huq *et al.*, 1983, 1984; Epstein, 1992). Although we know that bacteria and viruses are common in ballast water (densities of 10<sup>6</sup>/ml are not unusual for each; G.M.R., unpublished data), and include pathogenic forms, the fate and effects of such transfer are virtually unexplored.

Despite the significant impacts recognized for some invasions, effects of most NIS remain unknown. Where considered,

TABLE 2. Examples of non-indigenous species (NIS) that have had significant ecological effects in marine and estuarine habitats.\*

NIS	Source region	Recipient region	Reference
<i>Carcinus maenas</i> (decapod crustacean)	Europe	Western U.S., Australia	1,2
<i>Cyprinus carpio</i> (fish)	Asia	Australia, Europe, Eastern U.S.	3,4
<i>Dreissena polymorpha</i> (bivalve mollusc)	Europe	Eastern U.S.	5
<i>Hydrilla verticillata</i> (vascular plant)	Asia	Eastern U.S.	6
<i>Illyanassa obsoleta</i> (gastropod mollusc)	Eastern U.S.	Western U.S.	7
<i>Littorina littorea</i> (gastropod mollusc)	Europe	Eastern U.S.	8
<i>Membranipora membranacea</i> (bryozoan)	Europe	Eastern U.S.	9
<i>Mnemiopsis leidy</i> (ctenophore)	Western Atlantic	Black Sea	10,11
<i>Potamocorbula amurensis</i> (bivalve mollusc)	Asia	U.S. Pacific	12,13,14
<i>Spartina anglica</i> (vascular plant)	Eastern U.S. (hybrid)	Europe, New Zealand, Asia	15,16,17
<i>Tritonia plebia</i> (nudibranch)	Europe	Eastern U.S.	18
<i>Zostera japonica</i> (vascular plant)	Asia	U.S. Pacific	19

\* References as follows: <sup>1</sup> Grosholz and Ruiz, 1995; <sup>2</sup> unpublished data, GMR & TEG; <sup>3</sup> Crivelli, 1983; <sup>4</sup> Roberts *et al.*, 1995; <sup>5</sup> McLissac, 1996; <sup>6</sup> Posey *et al.*, 1994; <sup>7</sup> Race, 1982; <sup>8</sup> Brenchley and Carlton, 1983; <sup>9</sup> Lambert *et al.*, 1992; <sup>10</sup> Harbison and Volovick, 1994; <sup>11</sup> Vindogradov *et al.*, 1996; <sup>12</sup> Cloern, 1996; <sup>13</sup> Alpine and Cloern, 1992; <sup>14</sup> Kimmerer *et al.*, 1994; <sup>15</sup> Partridge, 1987; <sup>16</sup> Goss-Custard and Moser, 1988; <sup>17</sup> Adam, 1990; <sup>18</sup> Allmon and Sebens, 1988; <sup>19</sup> Posey, 1988.

the ecological impacts of NIS are most often inferred from densities and limited knowledge of an invader's ecology, relying often on observations in the native range. Quantitative studies of ecological effects are rare. Those cases mentioned above and in Table 2 are a subset of the limited exceptions that have (a) measured changes in a population or community correlated to an invasion in space or time and (b) tested hypotheses about the underlying cause-effect relationships involved. These provide important examples of ways to study invasions, and they also underscore the possible significance of marine invasions (see also Schmitt and Osenberg, 1996 for comprehensive discussion of experimental design for impact studies). However, to date, we have not begun to consider the complex interactions, or cumulative impact, of the tens-to-hundreds of NIS that can occur in single communities.

Although approximately 10–15% of NIS are thought to be nuisance species, causing undesirable impacts (OTA, 1993; Williamson and Fitter, 1996), these estimates derive almost exclusively from freshwater or terrestrial systems, and there is no comparable estimate available for marine invasions. Such estimates may not yet be possible due to the paucity of data compared to non-ma-

rine habitats. Furthermore, the consequences of an invasion are often not easily predicted based upon knowledge of a species in its native range. For example, the American comb jelly *Mnemiopsis leidy*, which feeds on copepods in its native community along the eastern Atlantic, has unexpectedly contributed to the collapse of fisheries in the Black and Azov Seas (Harbison and Volovick, 1994). The European green crab *Carcinus maenas* achieves a greater size, grows faster, and uses different habitat types in some invading populations compared to the native populations (Grosholz and Ruiz, 1996; E.D.G. and G.M.R., unpublished data). It is not surprising that characteristics of a species in one community can be a poor predictor of performance in a novel community with a unique combination of habitat conditions, food sources, competitors, predators, pathogens and parasites. However, the predictability of invasion characteristics is largely untested (Grosholz and Ruiz, 1996). The uncertainty surrounding which NIS become established and their respective impacts in a novel community has led Carlton and Geller (1993) to consider release of ballast organisms as "ecological roulette".

In addition to the functional effects of NIS above, invasions can have an impact

on biodiversity at many different levels (e.g., National Research Council, 1995). Invasions initially increase local species number, sometimes referred to as species richness or alpha diversity (Peet, 1974). However, through strong direct or indirect effects, this may lead to (1) reduced species richness (extinction) of native species and/or (2) a decrease in the abundance or "evenness" of remaining species (e.g., Macdonald *et al.*, 1989; Drake, 1991). In addition, invasions may have the overall effect of decreasing beta diversity, or variation in species composition among communities, essentially increasing homogeneity through both adding common (exotic) species and removing unique or endemic species (see Harrison, 1993, for discussion). Although invasions may also influence spatial (e.g., landscape) patterns of diversity above the species level, measure of such higher-level diversity is still being debated (Gaston, 1996). Finally, invasions may alter genetic diversity both within and among populations, resulting from increased gene flow and differential success of particular genotypes.

Presently, the effects of NIS invasions on species-level diversity in marine and estuarine communities are poorly understood. The U.S. Fish and Wildlife Service considers NIS a significant contributing factor in the listing of 160 native species as "threatened" or "endangered" (OTA, 1993). Interestingly, these effects are almost exclusively restricted to terrestrial ecosystems on islands and freshwater ecosystems, where extinctions appear to be most common (see also Macdonald *et al.*, 1989). By contrast, there are very few recent extinctions known for marine and estuarine habitats, and none of these appear to be related to invasions (Carlton, 1993). While it is possible that marine extinctions are simply overlooked, as marine habitats receive less scrutiny than terrestrial and freshwater systems (Carlton, 1993), marine populations may be inherently less susceptible to extinction. A partial explanation for this may lie in the open nature and large sizes of many marine populations, having waterborne dispersal that allows recruitment among distant populations and provides resilience from local and regional extinction. While this contrasts

strongly with freshwater and island ecosystems, we would still expect to see marine extinctions on islands with a high degree of endemism (*i.e.*, relatively small, closed populations). We therefore predict that NIS effects on marine biodiversity, as for terrestrial biodiversity, will be greatest on islands. This relationship, and the effect(s) of NIS on all measures of biodiversity in marine and estuarine (continental and island) systems, remains to be tested.

#### CONCLUSIONS

Our current knowledge of human-mediated invasions indicates that this phenomenon is a significant and growing force of global change in marine environments. It is clear that NIS are widespread globally and include most major taxonomic groups. The high species richness and densities of NIS reported for many regions have significantly altered population, community, and ecosystem processes. Importantly, new invasions continue to occur, perhaps at increasing rates. The ecological consequences of these invasions are cumulative over time, as NIS accrue and play an increasing role in communities.

Although we recognize some patterns and consequences of invasions, many aspects of invasion biology remain unpredictable. Perhaps most significant is the uncertainty about (1) which species will invade, (2) when and where it will invade, and (3) what its ecological or economic significance will be. It would be a mistake to consider all NIS as undesirable, because some species are valued additions. However, all newly arriving NIS carry a risk of being undesirable, because predicting the outcome of direct and indirect interactions for intentional or unintentional introductions is elusive. This is underscored by recent impacts of the ctenophore *Mnemiopsis leidyi* in the Azov and Black Sea (as above).

Invasions are undoubtedly influenced by local and regional human activities. Beyond the transfer of species, any change(s) in the physical habitat, prevailing environmental conditions, and resident plant and animal communities that interact with NIS may influence invasion characteristics and community interactions, including colonization success, abundance, persistence, range expan-



sion, and ecological and evolutionary effects (see Karieva *et al.*, 1993 for review). For example, habitats or communities that experience severe and/or frequent disturbances are often thought to be more susceptible to invasion (*e.g.*, Simberloff, 1986). Although the specifics of this relationship are unclear, the concept has some theoretical and empirical support. An extension of this concept suggests that human activities such as habitat alteration and intensive fishing may enhance invasion success for NIS, but the degree to which this occurs is unknown.

On a global scale, predictions for increasing surface temperature (*e.g.*, Schneider, 1993, and references therein) would likely have a strong influence on marine invasions. First, temperature currently prevents some NIS from becoming established at release sites. Strong support for this exists in examining the fauna around thermal plumes of power plants which can differ significantly from, and include NIS not present in, surrounding waters (*e.g.*, Paine, 1993, and references therein). Altered temperature would therefore change the pool of species that could invade. Second, regional changes in temperature would shift the ranges of NIS that are temperature-limited in their present distributions, and, arguably, this is a common determinant of species distributions. Temperature shifts surrounding El Niño events are partly responsible for short-term range extensions of many species in the southern and northern hemispheres (for review see Glynn, 1988). We should therefore expect some shifts in temperature, and perhaps current, barriers to occur and allow range expansions of NIS beyond their current distributions. Third, changes in temperature may affect a suite of population characteristics (*e.g.*, reproductive, growth, and survival rates) as well as interspecific interactions that can influence distribution, abundance and ecological significance of NIS as well as native species.

It is evident that invasions by NIS are a significant force interacting with other aspects of local, regional, and global change to structure our marine ecosystems. It is the challenge of invasion biology and marine ecology to develop a theoretical and empirical understanding of these interactions. Be-

cause of the extent and significance of invasions, our knowledge of marine systems is increasingly incomplete without this perspective. In addition, these species "additions" offer unique opportunities to examine community structure and function through perturbation at unprecedented scales. We find these to be compelling reasons to incorporate invasions into our paradigm and studies of marine communities.

#### ACKNOWLEDGMENTS

We thank P. L. deFur for the opportunity to participate in this symposium. This paper was improved by discussions with R. Everett, P. Fofonoff, S. Godwin, C. Hewitt, L. McCann, L. D. Smith, D. Strong, J. Toft, B. VonHolle, W. C. Walton, and M. Wonham. We also thank J. Crooks, J. Geller, and an anonymous reviewer for constructive comments. Some of the research presented here was supported by Maryland Sea Grant (R/ES-04) and National Science Foundation (OCE-94000706 and DEB-9322797). SERC Invasion Program Contribution No. 11.

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