Pattern, Process, and Prediction in Marine Invasion Ecology

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ABSTRACT
Invasions frequently continue long after dispersal corridors have been well established. Six interrelated processes (changes in donor regions, new donor regions, changes in recipient region, invasion windows, stochastic inoculation events, and dispersal vector changes) are examined to explain this phenomenon. The combination of these processes makes it difficult to forge a list of species from potential donor regions that will never become successful invaders and, by extension, to thus define the characteristics of species that have failed to invade. Predictions relative to which species will invade and when they will invade can be improved by more detailed attention to these six categories of interrelated processes that mediate invasion success. Copyright © 1996 Elsevier Science Limited

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INTRODUCTION
Introductions (human-mediated invasions, as opposed to natural range expansions) appear to be occurring with increased frequency at the close of the 20th century in coastal regions of the world (Carlton, 1989; Chapman & Carlton, 1991; Baldwin, 1992; Berman et al., 1992; Hutchings, 1992; Carlton & Geller, 1993; Buttermore et al., 1994). This is due, in large part, to the successful transport and release of species in ships' ballast water and sediments (Carlton, 1985; Carlton & Geller, 1993). It has been estimated, for example, that on any one day more than 3000 species may be in motion around the world in the ballast of ocean-going vessels (Carlton & Geller, 1993, note 12). Given that the diversity of this assemblage is kaleidoscopic in time and space, it is clear that on an annual basis tens of 1000s of species of marine bacteria, viruses, protists, plants, and animals are being transported within and between oceans, irrespective of any natural spatial and temporal barriers.

It is not difficult to predict that more invasions will continue to occur in coastal environments around the world as long as ballast water is transported and released. However, which species will invade and when they will appear have proven to be more elusive targets. Explored here are challenges and questions associated with (1) the processes that mediate when invasions will occur, using marine and freshwater systems as examples; (2) the ability to predict the identity of potential invaders; and (3) determining the number of successful invasions against the background pool of inoculants. This discussion will focus on shallow (less than 100 m depth) North American systems, with an emphasis upon estuarine habitats.

THE PROCESSES THAT MEDIATE WHEN INVASIONS WILL OCCUR
Why do marine and freshwater invasions occur when they do? Dramatic global invasions in the 1980s and 1990s have sparked a good deal of informal discussion as to why such invasions appear to be
increasing - that they are, and that it is not an artifact of increased attention to the phenomenon, appears to be the case (Carlton et al., 1995). Why, if a corridor is in place for a given period of time (for example, 100 years), would a species newly appear at the end of that corridor in year 101? Do most of the transportable species become transported immediately, with 'straggler invasions' following decades or centuries behind? Why do the Eurasian zebra mussels Dreissena polymorpha and Dreissena bugensis, transported by ballast water, colonize North America in the 1980s, and not the 1960s? Why does the native western European fouling sea squirt (ascidian) Ascidella aspersa, transportable by ships' hulls, successfully colonize New England in the 1980s and not the 1780s?

Vermeij (this issue) has noted that it would be of no small interest to determine how species that successfully invade differ from those in the donor biota that do not invade. Carried further to an inoculation stage, Vermeij notes that it would be similarly important to establish how species that do colonize after arrival differ from arrivals that do not maintain reproducing populations.

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Table 1. When invasions will occur in aquatic ecosystems: summary of six scenarios

DR  Donor Region (dispersal hub within which a species interfaces with a transport mechanism)
RR  Recipient Region (endpoint of dispersal spoke at which a species is released (initial point of inoculation))

A problem in the recognition and selection of candidate 'failures' in such analyses is the assumption that those species that have failed to succeed as invaders have had a reasonable amount of opportunity to do so, and, having failed, may possess characteristics that distinguish them from successful invaders (here meaning more than simple weedy vs non-weedy attributes (Baker & Stebbins, 1965)).

Invasion ecology has generally lacked a framework by which to approach an understanding of when invasions occur, an understanding that would permit us to make the assumption that the failure of a species successfully to leave a donor region is a potentially fixed attribute. Six scenarios (Table 1), which are not mutually exclusive, suggest that there is risk in such an assumption. I review these here.

Two scenarios focus on the donor (source) regions and two on the recipient region. In these scenarios, the donor region is the specific site (the hub) at which a given species interfaces with a transport mecha-
nism, while the recipient region is the specific site (the end-point of the hub's spoke) where a species is initially released. In the broader senses discussed above a 'donor' region may be taken as all of western Europe, and the 'recipient' region as all of New England. The fifth scenario considers stochastic inoculation events. A sixth scenario focuses on the mechanism of dispersal. All assume that the successful establishment of a species - that is, whether a species will invade in addition to when - is rarely related to any one environmental parameter ( Crawley, 1989). The life history stage of the colonizer and its reproductive repertoire, the size of the inoculant population (minimum propagule size: Crowell, 1973; Roughgarden, 1986), and the metabolic fitness and genetic variability of the colonists, the chemical and physical nature of the environment, trophic resources, resident species diversity, competitors, predators, parasites, the scales and ranges of biological and physical disturbance, minimum habitat size (Roughgarden, 1986) and a host of other variables may mediate most invasion events, and, indeed, may often be species-specific.

Aspects of the following scenarios are applicable not only to initial invasions but also to subsequent post-invasion spread. Required are experimental data that establish cause and effect within the framework of these and other scenarios.

1. Changes in the donor region

The donor region may change environmentally, which can lead to (a) population increases of pre-existing (resident) species, such that more individuals would be available to interface with a transport mechanism (such as ballast water) or (b) regional species not present in the donor region (local species) may expand their ranges into the donor area to interface with the transport mechanism. Of course, both resident and local species may be native or introduced. Extensive efforts to reduce pollution, for example, may improve harbor, river, or port water quality to the point that certain species may expand their range to now-cleaner harbor waters; alternatively, increased pollution may enhance local populations. Carlton (1992) noted the correlation between the increase of the bay-dwelling clam Theora lubrica in polluted environments in the Inland Sea of Japan in 1978-79 and its appearance in the early 1980s in San Francisco Bay, which receives a good deal of ballast water from the Inland Sea.

Alternatively, the environment may not change, but a new species may invade a region, and interface (for the first time) with an existing transport mechanism. This is, in essence, a 'hub and spoke' model, where an invader enters a high-intensity transport hub (the center of a potential dispersal wheel) potentially to be carried along a corridor (one or more of the spokes radiating out from that hub) to another transport hub, which lies at the end of the spoke—which in turn is another hub, and from which radiate out new corridors. A species entering one major port system is thus likely quickly to interface with multiple global transportation ballast water conveyor belts.

An example is the history of the dispersal of the southern Californian spider crab Pyromai a tuberculata which, once it became established and abundant in San Francisco Bay in the 1960s (Carlton, 1979a), was transported by shipping to Japan (Sakai, 1976) shortly thereafter, from where it was then transported to Korea (Kim, 1985), and thence from Asia to New Zealand (Dromgoole & Foster, 1983). Each 'jump' was contingent upon pre-establishment in a prior port system: Pyromai a may not have previously invaded New Zealand because it was not previously available in donor Asian ports. Similar broad 'jumps' may be more common than have been reported; it appears probable that the Asian seasquirt Styela clava and the Asian green alga Codium fragile tomentosoides arrived on the Atlantic North American coast via western Europe, rather than directly from Japan (Carlton & Scanlon, 1985; Carlton, 1989).

All sites that receive new invasions thus become new potential donor regions. The Laurentian Great Lakes are now thus exporters of the Eurasian zebra mussel Dreissena, the Rhine River (as discussed below) is now an exporter of the Eurasian tubicolous amphipod Corophium curvispinum, and Long Island Sound is now an exporter of the Japanese crab Hemigrapsus sanguineus. An analysis of in-ballast vessel traffic patterns departing these regions could provide insight into where these species may next appear.

2. New donor regions

New commodities from different ports, or newly available ports (earlier restricted from international commerce due to political forces), create opportunities for the transportation of species that previously
have not been dispersed by one or more human-mediated mechanisms. In addition, new ports may make available different genetic stocks (which could possess greater invasive capabilities) of species that have been transported from other regions previously. Both situations may lead to the appearance of novel species. The opening of direct international trade between mainland China and North America in the 1970s thus may be one of the reasons for the appearance of Asian copepods and the clam *Potamocorbula amurenensis* in Pacific North American estuaries.

3. Changes in the recipient region

As with donor regions, recipient regions may change environmentally. In the broadest sense, any environmental change—biological, chemical, physical, or ecological—in the recipient region that changes its susceptibility to invasions comes under consideration here. Physical changes, for example, may lead to changes in minimum habitat size, or to changes in disturbance states. The latter, in turn, may result from natural processes (natural flooding/drying episodes, natural warming/cooling cycles) or from human-mediated causes. In urbanized aquatic ecosystems, this scenario has been frequently posed in terms of changes in water quality due to the increase or amelioration of pollution. A variety of arguments may pertain here: a region may become less polluted, thus being more susceptible to invasions by species previously excluded, or a region may become more polluted, thus being susceptible to invasions by pollution-tolerant species, particularly as previously-present species decline.

Cordell *et al.* (1992) have suggested that the recent establishment of the Asian calanoid copepod *Pseudodiaptomus inopinus* in the Columbia River estuary 'may have been encouraged by a synergism between increased ballast dumping [see scenario 6, below], decrease in maximum flows due to regulation of the river, and the attenuation of extreme low temperatures in the estuary during the last decade'. Nichols *et al.* (1990) have suggested that the success of the Asian clam *Potamocorbula amurenensis* in invading San Francisco Bay may be related in part to the depression of the native biota as a result of a major flooding episode. Van den Brink *et al.* (1993) have argued that the increased salinity and increased water temperatures (resulting from industrial discharges) of the Rhine River in The Netherlands contributed to the invasion of the brackish-water, southern-originating amphipod *Corophium curvispinum*. 'Global warming' could cause changes in mean temperatures; Mandrak (1989) has related such changes to the potential invasion of the Great Lakes by southern freshwater fish species.

Microscale habitat alteration or expansion, particularly related to human activities, could further facilitate successful colonization episodes of substrate-specific species. Thus, for example, expanded use of styrene plastic ('styrofoam') as float supports in cool to warm temperate harbors and marinas would concomitantly provide expanded habitat for the boring isopod *Sphaeroma quoyanum* in regions where its natural substrate, waterlogged and decayed wood, may be limited.

4. Invasion windows in the recipient region

Invasions may occur when the 'proper' combination of physical, chemical, biological, or ecological variables occur, creating an 'opening' within a «-dimensional matrix for a species to enter a new region successfully. Thus Johnstone (1986) framed the concept of 'invasion windows', wherein one or more 'barriers' to invasion are removed. Bump (1963) earlier concluded, in an analysis of the failure to introduce European grouse *Tetrao tetrix* and *Lagopus lagopus* to America, that a set of conditions (of unknown number) must be 'in productive conjunction.' Ehrlich (1989) modified Bump's conclusion into an 'invasion law of the minimum,' where success may depend upon the interaction of multiple factors that is in the least favorable state at the place and time of the introduction.

Crawley (1989) incorporated these concepts under the general maxim that 'good timing is vital in all invasions,' where 'clearly defined windows of time' exist that, for example, match an invader with the proper phenology of recruitment site availability, trophic resources, or dips in the abundance of predators and competitors (the depressions being natural cyclic valleys, distinguishing this concept from scenario 3). Crawley emphasized that it 'is not that chance or timing are all-important, but that the interaction between chance and timing is the vital ingredient.' Indeed, the community assembly (including 'successional') processes that operate in marine fouling habitats to produce strikingly different adjacent species
assemblages (often within 1 or 2 m of each other) under seemingly similar environmental conditions, speak eloquently toward the stochastic vagaries that permit invasion windows to open and close.

5. Stochastic inoculation events

Potentially independent of other scenarios, stochastic rare events may occur wherein very large numbers of a species are transported and subsequently released— that is, minimum propagule size (Roughgarden, 1986) is no longer an issue. Clearly, the larger the inoculant pool, the greater the probability of individual colonists physically locating each other, or of the free-spawned gametes of colonists encountering each other.

Thus, a single vessel may have ballasted up hundreds of millions of zebra mussel *Dreissena* larvae or tychoplanktonic juveniles in the Black Sea, and released most of these in Lake St Clair, a small basin in the Laurentian Great Lakes located between Lakes Huron and Erie. Inoculation of the larvae into this semi-enclosed lake may have facilitated successful establishment (Johnson & Padilla, this issue).

6. Dispersal vector and thus inoculation frequency changes

This scenario invokes changes in the dispersal vector to explain novel invasions. Using ships and shipping patterns as an example, three potential phenomena could change inoculation conditions; similar reasoning could be applied to any transport vector:

*Increase in vector size* (for example, more ballast water (due to more ships or larger ships))

As a result of an increase in the signal strength of a vector, inoculant species diversity and abundance of individual inoculants increase. Thus Hutchings (1992) has noted that the volume of ballast water discharged into Australia ‘increased dramatically’ since the late 1960s with the advent of bulk cargo carriers. Couper (1983) also noted that since the 1960s a revolution in merchant shipping occurred as containerization reduced time in ports from weeks to days and as bulk carriers and tankers increased vastly in size. Intense new pulses of shipping activity appear on occasion to have led to new introductions.

Examples include the intensification of pre-established shipping routes due to changing social or political forces. Thus the California Gold Rush of 1848-1850 brought many more ships to the northeastern Pacific Ocean than ever before, and as a result a number of new invasions occurred in San Francisco Bay (Carlton, 19796). Wars can impose upon older routes much higher levels of transport activity. It is thus not surprising to find that a number of marine organisms are thought to have been newly introduced coincidental to world wars (Carlton in Norse, 1993). The Australian barnacle *Elminius modestus* appeared in England during World War II (Crisp, 1958). Two species of Philippine jellyfishes (Doty, 1961), the Californian sphaeromatid isopod *Paracerceis sculptra* (Miller, 1968) and several Indo-Pacific crabs (Edmondson, 1951, 1962) were carried to Hawaii during World War II. The Californian salt water fly *Ephydra gracilis* became established at Hickam Field, Honolulu, at the end of the war in 1946, an occurrence Wirth (1947) related to the proximity of seaplane bases. Cooke (1975) speculated that the presence of cosmopolitan hydroids at Enewetak Atoll may be due to the 'many hundreds of ships and barges that visited in the later part of World War II and during the period of atomic bomb testing.' These examples likely reflect what may have been hundreds of introductions throughout the Pacific Rim during the war. The Korean-Japanese shrimp *Palaemon macrodactylus* appeared in San Francisco Bay shortly after the Korean War (Newman, 1963). A number of western and southwestern Pacific Ocean invertebrates appeared in California harbors during the Vietnam War (Carlton, 1979a). Among these were the fouling isopod *Sphaeroma walkeri* which added to its world voyages by arriving in San Diego Bay, the largest naval port in the western hemisphere, by 1973 (Carlton & Iverson, 1979). Chapman (1988) described the new amphipod species *Corophium alienense* from San Francisco Bay, where it was first collected in 1973, and concluded (based upon morphological similarities to its nearest relatives) that it was a Vietnamese species. Morton (1980) proposed that the fouling dreissenid mussel *Mytilopsis sallei* was transported to Hong Kong on boats of Vietnamese refugees (Morton, 1980).

It may be further noted that a consequence of an increased vector may be increased gene flow between donor and recipient regions, dampening the tendency of allopatric peripheral populations to become genetically distinct over time.
Increase in vector speed (for example, faster ships) Length of transit decreases, and therefore more species and more individuals survive the transport episode, leading, potentially, to an increased number of post-transport individuals that are less metabolically-stressed. Increased vessel speeds could further mean that more ports could be visited in lesser time, meaning that more species could be spread faster to more sites. Roos (1979) has proposed that the apparently relatively recent range expansion of the freshwater and oligohaline hydroid *Cordylophora caspia* may be due to increased ship speeds, shortening the length of immersion of this fouling hydroid in fully marine waters between ports.

Improvement in vector quality (for example, an increase, as a result of new international and national laws, in the number of 'segregated' or 'dedicated' tanks that hold only ballast water, no longer mixed with petroleum products)

As a result, an increased number of species and of individuals survive a transport episode, and, as with (2) there may be an increased number of less metabolically-stressed individuals.

In summary, if more species, and greater numbers of individuals, are being released at greater rates, there is a greater chance of interfacing with specific changes in the environment (scenario 3) or moving through invasion windows (scenario 4).

Independent of these vector changes, of course, would be the emergence of a new vector from the ‘same’ donor region. This existence of the new vector may or may not be obvious or at least known to regional biologists until one or more new species begin to appear. Examples could include private entrepreneurial efforts, the arrival of semisubmersible self-propelled exploratory platforms, or the release of species newly involved in the bait industry.

PREDICTING THE IDENTITY AND TIMING OF INVASIONS

The continual appearance of new species via a long-established route from donor to recipient region argues against the exhaustion of the potential pool of invaders, and makes the identification of species as non-colonizers from a given donor region problematic, as discussed below. The ‘appearance of failure’ may be transient for many species, with a successful transport and colonization event awaiting the proper combination of conditions and circumstances. Alternatively, some species may be so rigidly locked into a fundamental niche as to prevent them permanently from being successful colonists outside of their native region. Given these considerations, is it possible to predict the identity and timing of invasions? While various workers have successfully predicted certain marine invasions (Carlton *et al.*, 1996), predicting when invasions will occur is extraordinarily difficult. Rigorous attention to changing conditions and phenomena specifically associated with the above six scenarios should, however, critically improve temporal predictions, and should thus reduce the element of surprise.

A simple example would be changes in donor area species composition—such as the appearance of a novel phytoplankton bloom in the donor region—coupled with precise knowledge of active transport vectors (such as ballast water) and their trajectories. Despite the prevalence of such blooms globally, most new occurrences appear to be treated as unexpected (and unpredictable) events, although many lie along predictable dispersal routes (J. Chapman, pers. comm.). More complex examples would be an understanding of how changes in the recipient region (scenario 3) may interface with the minimum survival conditions of potential new invaders (scenario 4, in part)—in essence asking what changes in the recipient environment would be necessary to accommodate a specific new invader.

WHICH SPECIES WILL INVADE?

Mills *et al.* (1993) identified two species of potential Eurasian invaders of eastern North America by examining those taxa with a clear pattern of invasion history in Europe that have the potential to interface with a transoceanic dispersal mechanism. This, of course, is perhaps the simplest predictive technique, applying one aspect of weed theory: invasive species are likely to continue to invade elsewhere if corridors are available and conditions permit. Temporal prediction here, however, is also elusive. With any one or more of the processes operating in the six scenarios discussed above, a successful colonization event could occur any time over one, two, or more centuries (such timing giving little satisfaction to those making predictions). A more focused prediction arises out of scenario (1), above, by
paying close attention to the species that enter new hubs and thus are transportable on new dispersal spokes.

While these two simple approaches may permit the identification of likely candidate invaders, there are very large suites of species whose future role as invaders cannot easily be known. We had no means, for example, to predict the arrival of the Asian shore crab *Hemigrapsus sanguineus* in Atlantic North America (McDermott, 1991)—unless perhaps ballast biota studies had been in place, and the larvae of this particular species had been discovered moving along this transport corridor. Similarly, we had no means to predict the arrival of the Asian euryhaline clam *Potamocorbula amurensis* in California (Carlton et al., 1990).

Put in other terms, we would never have examined the Asian biota and 'seen' these species, which have no known invasion histories in their native regions, as potential colonizers. Conversely, their failure to appear outside of Asia until the 1980s could have erroneously placed them in the pool of donor region species to be searched for characteristics that had made them unsuccessful emigrants. This observation, however, leads to the suggestion that there are large numbers of species that remain within donor regions that do not differ in any notable way from species that have become successful invaders. It is perhaps within this species pool that we must dip for a more careful assessment of potential future invaders.

**How many inoculated species result in established invasions?**

There are few data for marine ecosystems that permit an estimate of the number of ‘successful’ invasions relative to the number of species inoculated into a system. That is, if 50 species are released at a given site, how many are likely to become established? A first consideration, it may be argued, is that this imaginary species pool now directly interacts with the processes discussed above in the invasion-timing scenarios. That is, of the 50 species, a certain subset were, *a priori*, removed from the field of candidate colonists upon release because: (1) they cannot survive in the recipient site for physiological reasons, either because of their inherent biology, or (scenario 4) because of release under the ‘wrong’ conditions; (2) they were released in numbers too few (i.e. below minimum propagule size) to permit successful establishment (for example, species that can only reproduce by direct exchange of gametes, with individuals either unable to locate each other or (in organisms such as barnacles) settling at too great a distance to copulate (i.e. scenario 5 was *not* in operation); or (3) some were not viable upon release because of the nature and conditions of the transport episode (i.e. scenario 6 was *not* operating). Other transport and release phenomena will be at play as well.

For these reasons, it is more reasonable to take the ‘total inoculant species pool’ over some set time period within a given geographic region (and, as discussed below, further summed over the total number of transport vectors) as the effective number, rather than any one release event. None of 50 species released at one site at one time might survive; some fraction of the same 50, released over a long period of time at the same site or multiple sites, may be successful invaders.

The resolution of an inoculant:established ratio requires both an accurate estimate of: (1) how many species are released in a given time/space framework; and (2) how many species establish reproducing populations (as measured over a given minimal length of time). Numbers for (1) have been difficult in the past to acquire in marine transport pathways—how many species are transported with commercial oyster shipments from Japan to Mexico, or to British Columbia, or to France?, or how many species are on the bottom of a fouled ship arriving from twelve previous ports-of-call into Hong Kong? And, of course, data are required for multiple oyster shipments, and many ship bottoms.

In recent years, data sets are becoming available for what has now become perhaps the most significant interoceanic and transoceanic human-mediated dispersal vector for marine organisms, ballast water. Multiple ships have now been sampled and the plankton within them analyzed, in part, in Australia (Williams et al., 1988), in the United States (Carlton & Geller, 1993) and in Canada (Locke et al., 1993). Limitations on these data sets are (1) the frequent difficulty (and often impossibility) of identifying meroplankton ('bivalve larvae,' 'polychaete larvae,' and so forth, necessarily usually being lumped together); (2) the non-sampling of microplankton (ciliate protozoans, nematodes, rotifers, gastrotrichs, etc.); (3) the difficulty in securing samples of nektonic organisms that can evade sampling devices; and (4) the difficulty in collecting enough sediment from ballast tanks and ballasted cargo holds for an ade-
quate sample of the 'benthic' ballast biota. All of these factors lead to an underestimate of the number of species arriving in ballast.

In the United States work, Carlton and Geller (1993) estimated a minimum of 367 taxa (distinct morphological types, many not identified to species level, as noted above) of invertebrates, fish, and plants in ballast water released from Japanese ports into one estuary. Coos Bay, Oregon, in 159 ships between 1986 and 1991. This number thus represents a partial picture of the total number of species radiating out from Asia in ballasted ships to other Pacific rim ports. The size of the total species pool remains unknown: vessels departing from different ports other than those sampled, at different times of the year or different times of the day from those ports that were sampled, and ballasting water up from different habitats, would add to the total number of species potentially transportable and transported. Thus, for example, Carlton and Geller's (1993) pool of ships arrived from marine ports of Japan, whereas many vessels depart other Japanese and Asian ports with brackish or fresh water, not represented in Carlton and Geller's samples. The Asian freshwater and oligohaline copepod species that have invaded San Francisco Bay (Orsi et al., 1983; Ferrari & Orsi, 1984; Orsi & Walter, 1991) and the Columbia River (Cordell et al., 1992) were thus not found in the pool of 159 ships reported upon by Carlton and Geller (1993) (J. Cordell, pers. comm.).

For the taxa identified to species level, work is now in progress (Carlton et al., in prep.) comparing the number of inoculated species to the number of established species. Of necessity, this work must take a broad geographic approach. The number of established introduced species in the Coos Bay estuary as a result of these ballast water releases is, unfortunately, incompletely known. Japanese polychaete larvae representing many different families—spionids, polynoids, nereids, capitellids, terebellids, syllids, and others—are regularly released into Coos Bay, but there are no modern surveys of the Bay's polychaetes. Similarly, diatoms and copepods are the most common taxa in sampled ships, but the phytoplankton flora of Coos Bay remains undocumented, and copepod surveys have been limited. However, this limitation only has an effect if the question of the inoculant: established ratio is restricted to Coos Bay. If the species pool (367) identified by Carlton and Geller (1993) is taken as the inoculant number for a larger spatial scale—in this case, the set of all Pacific Rim ports for which invasions data are available and to which Japanese ballast water goes —then the inoculation: established ratio could in theory become clearer. The value in Carlton and Geller's (1993) studies thus lies more in describing one example of the scale of the daily movement of a vast diversity of marine life, rather than in providing a particular picture of the inoculant: established ratio at any one site.

While exact numbers are not yet available, some of the complexities in an inoculant:established ratio analysis can be addressed. The effective 'inoculant species number' for invasion analysis necessarily becomes those taxa that were identified to species level. The bivalve mollusks, one of the best known groups of invertebrates, serve as an example. While Carlton and Geller (1993) noted at least nine species of bivalves, only three of these were successfully cultured and identified. These were the native Asian clams Theora lubrica and Trapezium liratum, and the Mediterranean mussel Mytilus galloprovincialis, introduced to Japan. None are known to have become established in Coos Bay, with molecular genetic analysis confirming the absence of Mytilus galloprovincialis from that bay (Geller et al., 1993), despite its constant inoculation into the system (as discussed above, this may not mean that it will not be a successful future invasion of Coos Bay).

However, all three species are known invaders elsewhere. Theora has become established, presumably by ballast water transport, in San Francisco Bay, the bays of southern California, and various Australasian ports. Trapezium has become established in British Columbia, but apparently as a result of the introduction of Pacific oysters from Japan. Mytilus has colonized many southern and central California ports, but appears to have arrived in the eastern Pacific sometime during or before World War II by ship fouling. Presumably Mytilus galloprovincialis continues to be inoculated and reinoculated around the Pacific rim by ballast water, and there may thus be active gene pool mixing in progress not only within the Pacific Ocean but globally.

These three bivalves have thus been successful invaders, but the complexities of their transport mechanisms and their timing and regions of establishment preclude calculating a simple inoculant: establishment ratio. Indeed, these examples point to the probable 'correct' set of species from which to be able eventually to calculate inoculant: establishment ratios. All species leaving a given donor region (whether in this case on or in commercial oysters, ships' hulls, or ships' ballast water) represent the total invasion
pool—while some species may now all be transported and released by one mechanism, they may have arrived earlier through other mechanisms.

It is worth emphasizing that the number of successful invasions taken against the number of inoculants, while of paleo- and neo-biogeographic and ecological interest, may not be related to the potential or actual ecological consequences of an invasion. The invasion of the zebra mussels *Dreissena polymorpha* and *Dreissena bugensis* in North America may represent only 1% of all European mollusks transported to and released in North America, but this number may provide little comfort to those who are economically impacted by these invaders, and little evolutionary solace to those native North American unionid mussels which may go extinct under the dreissenid wave.

**CONCLUSIONS: THE ECOLOGICAL CHALLENGES**

I have addressed here only three current challenges in marine invasion ecology—why invasions continue long after corridors are well established, the limited ability to predict the next invasion in time and space, and the vexing issue of determining the number of successful invaders from a given inoculant pool.

Equally important, of course, are the ecological challenges—in systems such as Tasmania and southeastern Australia, San Francisco Bay, and the Mediterranean, invader after invader continues to appear. While there is a frequent concentration upon (and concern for) the interactions between native and introduced species, in regions such as San Francisco Bay the more immediate interactions of interest—indeed, interactions that may influence the outcome of a given invasion—are likely occurring between introduced species rather than between exotic and native species. Where fewer invasions occur, such as regional satellite bays near intensive invasion centers, new introductions may more clearly and directly interact with native biota (Groshoiz & Ruiz, this issue).

These cascading, sequential invasions, perhaps occurring within months of each other, mean that there are extensive non-equilibrium conditions in place. A carnivore appears, becomes abundant, and begins to spread—and then a second carnivore appears, becomes abundant, and begins to spread; in between, a new herbivore (and potential prey species) becomes established. Experimental and genetic studies are critical to keep up with the modern flow of invasions—although this flow is potentially frustrating to those experimenters attempting to capture the ecological effects of one invader as another invader arrives. Similarly, manipulative experimental studies such as those of Race (1982) are imperative if we are to recreate interactions between introduced and native species that may have occurred long before any observations—qualitative or quantitative—are available.

It would be remiss not to comment briefly on intentional introductions in the ocean, a matter of increasing concern in three regards: (1) the increasing interest in the use of novel (non-indigenous) species in open-sea aquaculture and mariculture (DeVoe, 1992); (2) marine biocontrol programs; and (3) the increasing interest in the release of genetically modified organisms (GMOs) in the sea.

In the first case, a central question is whether there are commercially useful species and target release sites for which there is sufficient knowledge to predict confidently ‘minimal’ ecological impacts, or, at least, ecological impacts that would not outweigh the positive economic and social values of a new fisheries resource.

In the second case, increasing global invasions will inevitably lead to a growing interest in the use of additional species (parasites or predators) to control a nuisance invasion. All of the concerns classically associated with biocontrol efforts—such as biocontrol species shifting their attention to native species—are applicable. Thus the invasion of the American comb jellyfish *Mnemiopsis leidyi* in the 1980s into the Black and Azov Seas—and the subsequent demise of the anchovy fisheries in the late 1980s and early 1990s—have led to serious interest in the identification and possible release of an American comb jelly predator (Harbison & Volovik, 1994).

In the third case, the ability genetically to modify commercially-valuable species to increase their growth rate or broaden their environmental tolerances has led to considerable debate about the release of such species in aquatic environments (Hallerman & Kapuscinski, 1990; Kapuscinski & Hallerman, 1990). Concerns range from the development of unexpected adaptations to genetic mixing with wild stocks, to the ecological impact of GMOs if they expand into habitats (because of broader physiological capabilities) not previously occupied. At the moment, the release of GMOs in the coastal ocean, in terms of potential ecological and genetic impacts, remains a largely speculative, but potentially serious, concern.
A frequent and growing lamentation in invasion biology is that we are faced with an increasing catalogue ('lists') of invasions rich with spatial and temporal anecdotes but largely devoid of quantitative, experimental, and genetic data.

While process-oriented studies must be encouraged and financially supported, there remains great potential to search for patterns by creating road maps with these lists—by turning these catalogues into Invasion Atlases. Thus in marine systems, a careful examination of the patterns of invasions across major coastal marine habitats (intertidal rocky shores, estuaries, sand-mud flats, mangroves, sandy beaches, coral reefs, salt marshes, kelp beds, seagrass beds, and so forth) set against broad latitudinal realms (boreal, temperate, tropical), within the further context of continental and maritime climates, would be of extraordinary value. Within such matrices may lie clearer patterns of the tempo and mode of modern marine invasions. Fundamental to such endeavors is the coupling of these patterns with process-oriented work that seeks to determine the causes, and not just the correlations, of successful invasions.

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