Ecological and evolutionary consequences of coastal invasions

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Although coastal estuarine and marine systems are among the most heavily invaded systems in the world, the study of nonindigenous species in these systems has, historically, lagged behind that of terrestrial and freshwater systems. However, in the past decade, a rapid increase in studies of coastal invasions has provided important insight into the invasion process in these systems and how these invasions might differ qualitatively from invasions elsewhere. Based on new evidence for cryptic species invasions, hybridization among invaders and native species, impacts on multiple species and ecosystems, and the rapid and extensive geographical spread of invaders, it is clear that the ecological and evolutionary consequences of invasions in heavily invaded coastal habitats might be more extensive than previously realized. Although these studies have produced important new advances, many other areas remain relatively unexplored and are ripe for future investigation.

Coastal marine habitats are among the most heavily invaded systems on Earth, stemming, in part, from human-mediated transport of non-native species in the ballast of ships and from intentional introductions for aquaculture and fisheries enhancement [1,2]. Given the large number of nonindigenous species that occupy coastal estuarine and marine habitats (hereafter coastal systems or habitats), it is paradoxical that the study of invasions in coastal systems has, historically, lagged behind similar studies in terrestrial and aquatic systems. Whereas our understanding of non-native species invasions dates back to Elton [3], and general concern about invasions dates back several centuries [4], the study of invasions in coastal systems and habitats only really began a little more than two decades ago [5,6] (J.T. Carlton, PhD thesis, University of California, Davis, 1985). The near absence of studies of coastal invasions in earlier edited volumes on invasions also highlights the lack of our understanding of invasions in these habitats [7,8]. In the past ten years, however, there has been increased interest in the invasion biology of coastal systems fueled, in part, by the highly publicized impacts of the zebra mussels *Dreissena* spp. in the North American Great Lakes [9]. This interest has translated into a rapidly accumulating literature that addresses both the ecological and evolutionary consequences of invasions, and has significantly contributed to closing the gap in our understanding of invasions in coastal systems relative to terrestrial and aquatic ones.

Previous reviews of coastal invasion studies have comprehensively analysed invasion pathways [5,6,10–12] or specific categories of ecological effects, such as single species impacts on native species [13,14], or documented specific evolutionary transitions of invaders [15]. Here, I highlight current progress in the study of coastal invasions, primarily those involving marine and estuarine invertebrates, on a range of subjects dealing with ecological and evolutionary consequences, discuss the gaps that remain in our understanding, and highlight future directions for research.

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Ecological consequences of invasion

The conceptual framework and methodology employed by most invasion biologists in coastal habitats are derived from benthic community ecology, with most studies focusing on the direct impacts of the invader on adjacent trophic levels. Recent studies have begun to examine indirect effects of invaders, their impacts on species at different trophic levels, and impacts on food-web properties and ecosystem processes. Current work has also investigated features of the native community that might influence invasion, rather than focusing only on the impacts of the invader on native species in the recipient community. Together, these new studies represent substantial progress towards developing a more complete understanding of invasions in coastal systems (Table 1).

Species-level consequences

Several studies have quantified the impacts of an invading species on the demography of a single native species. Both Race [16], working on the introduced snail *Ilyanassa obsoleta* in San Francisco Bay (CA, USA), and Brenchley and Carlton [17], working on another introduced snail *Littorina littorea* in Cape Cod Bay (MA, USA) demonstrated the negative impacts of the invaders on populations of native snails.

The impacts of the introduced snail *Batillaria attramentaria* on specific demographic parameters, including survival, growth and reproduction, of the native snail *Cerithidea californica* in central California [18,19] have been quantified using manipulative field experiments and demographic models. The invader was significantly more efficient in translating food resources into offspring than was the native. Experimental data and modeling projections of future population sizes were used to show that the *B. attramentaria* is slowly replacing *C. californica* and that declines in the reproductive output of *C. californica* can be used as a sensitive predictor of population decline.

It is not only introduced snails that have been

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Table 1. Examples of studies of ecological and evolutionary consequences of invasions in coastal systems

Category	Area of study	Invading taxa	Refs
Ecological consequences	Single-species impacts	*Ilyanassa obsoleta* (snail)	16
		Littorina littorea (snail)	17,26,27
		Batillaria attramentaria (snail)	18,19
		Membranipora membranacea (bryozoan)	20
	Multiple-species impacts	*Musculista senhousia* (mussel)	21,22
		Carcinus maenas (crab)	23–25
	Multiple trophic-level impacts	*Carcinus maenas*	25,29
	Ecosystem-level impacts	*Potamocorbula amurensis* (clam)	30,31
		Pseudodiaptomus inopinus (copepod)	54
	Recipient community impacts	*Musculista senhousia*	32,33
		Codium fragile (alga)	34
		Various	35
	Geographical spread	Various	37
	Pathogens and disease spread	*Vibrio cholerae*, others	38
Evolutionary consequences	Invasion pathways	*Carcinus maenas*	39
		Eurytemora affinis	15,51
	Cryptic species	*Carcinus aestuarii* (crab)	40
		Mytilus galloprovincialis (mussel)	41,42
		Botrylloides sp. (tunicate)	56
	Hybridization with natives	*Spartina alterniflora* (marsh grass)	45,46
	Plasticity in native species	*Carcinus maenas*	47,48
	Population differentiation	*Botrylloides* sp.	49,56
		Potamocorbula amurensis	50
		Eurytemora affinis (copepod)	52
	Physiological adaptation	*Eurytemora affinis*	15,51

found to have negative impacts at the species level. Lambert *et al.* [20] examined the impact of an introduced bryozoan *Membranipora membranacea* on native kelps *Laminaria* spp. in subtidal rocky reefs in the Gulf of Maine (ME, USA) [20]. They found that the bryozoans caused the kelp that they were growing on to become brittle and prematurely senesce and break off, with potentially serious implications for other organisms in these kelp-dominated systems.

Community-level consequences

As suggested by the work of Lambert *et al.*, invaders can impact not only on single species, but also on an entire community. Two studies [21,22] on the impact of the exotic Asian mussel *Musculista senhousia* on the abundance and diversity of native species in mudflat communities in Mission Bay, San Diego (CA, USA) illustrated how important a single species can be in changing the makeup of an entire community. Crooks *et al.* found that mats of byssal threads produced by the mussel created a habitat that was not present in the otherwise largely unstructured mudflats and which, as a result, encouraged the development of a unique community assemblage. Using experimental manipulations of mussel densities, they found that the novel assemblage inside clumps of the exotic mussel had higher diversity and abundance of organisms than did the adjacent unstructured mudflat.

Although rarely mentioned as an invader in the eastern USA, the European green crab *Carcinus maenas*, which became established in the eastern USA in the early 1800s, has been shown to be important in structuring rocky shore communities, especially in Maine and Massachusetts (USA). Green crabs can substantially alter surrounding habitats through predation on mussels in areas of lower water flow [23–25], thus altering community structure in those areas. In higher flow areas, where green crabs were unable to forage, communities were dominated by mussels and their associated fauna.

Previous studies of rocky shores in the northeastern USA also documented how introduced species have important impacts on rocky shore communities, although the non-native status of the focal species was rarely mentioned. Lubchenco showed the importance of herbivory by the introduced periwinkle *Littorina littorea* in determining patterns of algal diversity on rocky shores of Massachusetts [26]. On protected rocky shores of Rhode Island (USA), Bertness [27] showed that intense grazing by *L. littorea* influences sediment accumulation and actually changes the local environment from one of largely soft sediment to one that is dominated by hard substrate.

However, it might take some time before changes at one trophic level or to one functional group are reflected by changes at higher trophic levels or by higher functional groups. For example, green crabs in central California were found to be responsible for dramatic declines in the abundances of native clams *Nutricola* spp. and shore crabs *Hemigrapsus oregonensis* in the mudflat habitat within two years of the invasion [28,29]. However, declines at these lower trophic levels have yet to translate into declines in wintering populations of migratory shorebirds that depend on the invertebrates for food. Such studies suggest that several factors contribute to these results and emphasize that changes at higher trophic levels might substantially lag behind those at lower trophic levels.

Ecosystem-level consequences

Coastal invasions can also cause changes that are quantifiable at the ecosystem level. Notable examples are the studies by Cloern *et al.* [30,31] of the ecosystem-level impacts of the estuarine Asian clam *Potamocorbula amurensis* in San Francisco Bay. The Asian clam invasion is closely correlated with the shutdown of the spring phytoplankton bloom in the bay, which usually fuels much of the pelagic ecosystem of the bay, which is dominated by zooplankton and larval fish. Most of this primary production is transferred to the benthic food webs, which are dominated by benthic invertebrates and bottom-feeding fishes.

Box1. Tracing invasion pathways using microsatellite DNA

Tracing the history of introduced species using molecular techniques can help to identify the source of an invasion, which, in turn, can aid predictions about the impacts of the invasion, the prevention of further invasions, as well as permitting the estimation of the size of the founding population and providing information about post-invasion population dynamics. Several methods, including the use of microsatellite DNA (mtDNA), have been developed that can provide the necessary information. mtDNA is hypervariable, and is therefore particularly suitable for tracing invasion pathways, because useful levels of allelic variation can persist through the severe bottlenecks that often accompany invasions.

Using five microsatellite loci, Bagley and Geller [a] examined European green crabs *Carcinus maenas* collected from populations in the native range of the crab in western and southern Europe as well as from introduced populations in six independent invasions: Japan, South Africa, eastern North America, western North America, Australia and Tasmania. They found no significant differences in allelic frequencies among European populations, although there were substantial differences between Atlantic and Mediterranean populations, further verifying earlier results from using mtDNA that Atlantic and Mediterranean populations are actually sibling species [b]. Bagley and Geller were able to use these differences to distinguish the Atlantic and Mediterranean sources for several green crab invasions. When they compared heterozygosity between native and introduced populations, they found that, on average, introduced populations had a 7–31% reduction in heterozygosity and diminished allele counts. This founder effect gives each invasion a distinct signature, and allowed Bagley and Geller to determine that eastern North America was the source population for the invasion of western North America in 1989 and that mainland Australia was the source population for the invasion of Tasmania in 1993.

The stepping stone invasion that the work of Bagley and Geller [a] has uncovered sheds new light on the process of invasion in coastal areas, and demonstrates the utility of using multilocus genotyping methods, such as mtDNA, to determine pathways of invasion.

References

a Bagley, M.J. and Geller, J.B. (2000) Microsatellite DNA analysis of native and invading populations of European green crabs. In *Marine Bioinvasions: Proceedings of the First National Conference* (Pederson, J., ed.), pp. 241–243, MIT Sea Grant College Program

b Geller, J.B. *et al.* (1997) Cryptic invasion of *Carcinus* detected by molecular phylogeography. *Mol. Ecol.* 6, 901–906

Consequences for invading species

Although much of the focus of recent studies has been on the effect of invasive species on the invaded community or environment, some studies have considered how characteristics of native communities influence the success of invading species. For example, in estuaries in San Diego, the invasive Asian mussel *Musculista senhousia* experienced higher predation in the presence of native benthic invertebrates, particularly predatory gastropods, than it did in its native environment [32,33]. Reusch and Williams found that native eelgrass *Zostera marina* was also significant in limiting the growth and spread of the mussel. Therefore, native species might be able to resist exotics under certain conditions. However, this is not always the case, as shown by Trowbridge [34], who examined the preferences of native herbivores for the exotic alga *Codium fragile* ssp. *tomentosoides* in New Zealand, as well as their ability to limit its distribution. In this case, native species were not effective in limiting the distribution of this rapidly spreading alga.

Diversity of the recipient community *per se* has recently been shown to influence invasion success in a study of fouling communities in southern New England, USA [35]. Stachowicz *et al.* constructed experimental assemblages of resident invertebrates and followed the invasion success of exotic species. They found that increasing diversity of the recipient assemblage was associated with a lower recruitment of non-native species. They concluded that the more diverse communities in their system were less easily invaded because, as the number of native species increased, fluctuations in the amount of open space available for invasion decreased. However, the relationship between species diversity and susceptibility to invasion remains hotly debated [36].

Geographical spread

Given that both biological and physical characteristics of native communities influence the establishment of invaders, these same characteristics could also affect the rate and extent of geographical spread of invasive species. When the rate of geographical range expansion for introduced coastal species was compared with similar rates for terrestrial species [37], coastal invasions showed greater variation in the rate of spread, and frequently experienced explosive and extensive range expansion over a very short period. The mean interannual rate of range expansion for coastal invaders, however, was similar to that for terrestrial species.

Consequences for pathogens and diseases

There is now increasing evidence that not only are free-living species being introduced into coastal systems, but that pathogens and parasites are also being transported more frequently, and in much larger numbers, than had been previously realized [38]. New work by Ruiz and colleagues has shown that diseases, such as cholera *Vibrio cholerae* and others, are being transported in extremely high densities into major USA harbors by ballast water and other vectors. The consequences of these exotic pathogens for native species, aquaculture, fisheries and human health are potentially enormous.

Evolutionary consequences of invasion

Invasion pathways

Studies of coastal marine and estuarine invasions have begun to consider the evolutionary consequences of invasions (Table 1). One example of the many new approaches taken is the use of molecular systematics to determine pathways of invasion. Phylogeography can be used to evaluate the geographical origin of particular invasions, such as the multiple invasions by the European green crab, as recently determined by Bagley and Geller (Box 1) [39].

Cryptic invasions

Cryptic invasions (i.e. where it is unclear whether there is a single invasive species) are another example of invasions with profound evolutionary significance. Geller and colleagues examined the multiple invasions of the European green crab using mitochondrial genes [40] and concluded that the worldwide invasion of the crab actually includes a second crab species, the Mediterranean green crab *Carcinus aestuarii*.

Geller *et al.* examined invasions of exotic mussels in the western USA and found a cryptic invasion of the mussel *Mytilus galloprovincialis*, which, together with the native *Mytilus trossulus*, had long been misidentified as *Mytilus edulis* [41,42]. Evidence from molecular studies of museum specimens suggests that *M. galloprovincialis* displaced *M. trossulus* in southern California within the last century [43]. Given the recent recognition of the frequency of cryptic species in marine systems [44], other cryptic invasions might have also gone undetected.

Hybridization

As well as cryptic invasions, there is also the possibility of loss of native genotypes through hybridization and introgression of the genes of the invaders into native gene pools, as has occurred in the case of the estuarine cordgrass *Spartina alterniflora*, which defines salt-marsh habitat in the eastern USA. In San Francisco Bay, where this species is invasive and has become established since its intentional introduction in 1975, there is extensive hybridization between the exotic *S. alterniflora* and the native cordgrass *Spartina foliosa* [45,46]. The hybrid is extremely invasive (more so than *S. alterniflora*) and native genotypes are becoming locally extinct in invaded marshes within a few years of invasion, largely as a result of pollen swamping by the hybrid.

Phenotypic plasticity

New studies have investigated differentiation among populations of native species as a function of the distribution of the invader. Trussell and Smith [47,48] examined the degree of phenotypic plasticity in New England populations of the native periwinkle *Littorina obtusata* in response to the presence of introduced European green crabs. Chemical cues from crushed snails produced by the activities of predatory crabs induced shell thickening in remaining snails, which presumably helps the snails to avoid predation. Snail populations varied in the degree of plasticity that they showed in response to predator exposure, largely as a result of their previous history of exposure to the crabs.

Population structure

Differentiation among populations of invading species themselves has also been considered, for example, among populations of an introduced compound tunicate *Botrylloides* sp., which was introduced to the Gulf of Maine region <30 years ago [49]. Using replicate clones from individuals collected from sites <50 km apart, substantial differentiation in survival was found in response to an anomalous cold-water upwelling event.

A study by Duda [50] investigated differentiation within populations of the introduced clam *Potamocorbula amurensis* in the San Francisco Bay region, by examining genetic differentiation using allozyme loci. Although there was great variation within subpopulations, there was no evidence for genetic differentiation among subpopulations. Uncovering the scale at which population differentiation occurs will help to guide evolutionary as well as ecological investigations of invading populations.

Physiological adaptation

Lee [51,52] used sequence data from mitochondrial genes encoding cytochrome oxidase I to quantify genetic differentiation among invading populations of the copepod *Eurytemora affinis* in Asia, North America and Europe. Phylogeographic information about the history of invasion was used to infer pathways of invasions and patterns of physiological adaptation in the new habitat. Lee demonstrated that repeated invasions of freshwater by estuarine and marine populations of *Eurytemora* are the result of multiple independent evolutionary events by genetically distinct populations [15,51]. This work underlines the importance of understanding the role of selection and physiological evolution in influencing the success of invading populations.

Conclusions and future directions

The rapidly increasing number of study of invasions in marine and estuarine systems is providing exciting new insights into their ecological and evolutionary consequences. There is a growing understanding that humans are amplifying the natural process of range expansion by many orders of magnitude, the pace and geographical extent of which have no historic precedent. Much can be learned about the structure of coastal ecosystems from the study of invasions; however, several improved approaches are required, if what has been achieved from the more complete work on terrestrial and freshwater invasions is any guide.

Gaps in our knowledge

First, at increasingly larger spatial scales, our understanding of the dynamics of introduced coastal species breaks down, because studies on the scale of entire landscapes are almost entirely missing. Species, such as the introduced cordgrass *S. alterniflora* and the introduced sea grass *Zostera japonica* in western USA, can be studied with remote sensing and geographical information systems, and, because the plants create entirely new habitats, such studies will be extremely valuable for understanding broad-scale change at the landscape level.

Second, there are few long-term studies of invasions in coastal systems and most examine ecological change over periods of ten years or less. It is known from other systems that the nature of species interactions changes quickly, for both the invading and the native species, within the first few years of the invasion. Understanding how changes in the first few years of an invasion translate into more permanent changes in coastal systems will be an important addition to our present understanding.

A third important gap in our understanding of coastal invasions is the consideration of more than one invading species. This omission becomes particularly glaring with respect to invaded estuaries, such as San Francisco Bay, where the rates of invasion are so high that as many as three to four species are being detected in the same year [2]. Although there are obvious logistical issues involved with studying multiple invading species, it seems imperative that the impacts of suites of introduced species, rather than species individually, are studied. There are theoretical grounds for suspecting that as a given system becomes increasingly invaded, it becomes more susceptible to further introductions, thus, producing an 'invasional meltdown' [53], although currently there is only minimal evidence for this at present [12].

Finally, we need to investigate how invasions are affected by, and, in turn, affect the cycling of energy, biomass and nutrients in their recipient systems. For example, just as zebra mussels are effective in transferring pelagic primary production in the form of phytoplankton into benthic detritus, the Asian clam is doing the same on a large scale in San Francisco Bay. Beyond these studies, however, there are few other data for coastal systems regarding the impacts of invaders on ecosystem processes. For example, the introduced Asian copepod *Pseudodiaptomus inopinus* has invaded many estuaries in the Pacific Northwest (USA) and is the dominant zooplankton in many of these [54]. Although its ecological impact on primary production is likely to be significant, this impact has yet to be quantified.

Future directions

The degree to which hybridization is occurring with invading species is an important issue that needs to be addressed immediately. Quantifying the degree of hybridization among native and invasive species is crucial given that hybridization with invaders is an effective and rapid means of losing native genotypes [55]. There is also a need for better systematics to distinguish cryptic species groups as well as to distinguish native species from non-native species. Perhaps the largest obstacle to understanding broader patterns of invasion is the uncertainty about which species are native and which are exotic [56]. For less well-understood groups, such as marine and estuarine invertebrates, it is a daunting task to even determine species identity, and species lists are not adequate to delineate the native fauna. A better understanding of species identity and whether they are native is crucial for further advances in invasion studies in coastal systems.

New methods for determining the source population for invasions are also required. Molecular methods of multilocus genotyping include the use of microsatellite DNA, internally transcribed spacers (ITS), restriction fragment length polymorphisms (RFLP) and amplified fragment length polymorphism (AFLP), and others that are being developed and refined, as are the statistical methods that are necessary for their application [57]. Specific application of multilocus methods for defining phylogenetic relationships for coastal marine and estuarine organisms is needed desperately.

Another area for future investigation is the spatial and temporal scale of genetic change in coastal populations. Within-generation dispersal distances are, on average, likely to be longer in marine invaders with planktotrophic larvae than in terrestrial or freshwater species [37] and represent an important contrast with these other systems. Although not all coastal species have the potential for long-distance dispersal, it will be very informative to understand the roles of gene flow and local selection in shaping genetic change in populations of recently introduced species. This interplay between gene flow and selection could influence the response of invading populations to selection pressures posed by the new environment [15,51] and influence their success.

Prospects

In the final analysis of the new work on coastal invasions, several points emerge that suggest the ecological and evolutionary consequences of invasions are greater than were previously realized. There is now convincing evidence of incipient global extinctions, rapid and extensive geographical spread of invaders, impacts on multiple species and ecosystems, transport of pathogens and disease, undetected cryptic invasions, and rapid and extensive hybridization between invaders and native species. As additional studies are directed towards a broad range of ecological and evolutionary consequences of invasions, investigators should find that many of these processes are more common than is currently appreciated. Just as recent studies of highly invaded coastal systems are changing our understanding of the degree to which invaders have altered these habitats, these studies also suggest that what is now known about the ecological and evolutionary changes brought about by non-native coastal species might just be the tip of a very large, human-created, iceberg.

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