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7 Parasites and Genetics in Marine Invertebrate Introductions: Signatures of Diversity Declines across Systems

7.1 Introduction

Over the last several decades, non-indigenous species (NIS) have become a global concern due to intentional and unintentional translocation of species around the world across large geographic distances and natural migratory barriers; this in turn has resulted in considerable evolutionary, ecological, and environmental impacts on native communities and habitats (Ruiz *et al.*, 2000; Simberloff *et al.*, 2013). In fact, species invasions have been ranked second only to habitat loss as a major force of ecological disturbance worldwide (Crowl *et al.*, 2008; Vitousek *et al.*, 1997). Across the biosphere, numerous species have become successful in non-native regions, including notorious aquatic examples like the zebra mussel (*Dreissena polymorpha*) in the Great Lakes (Carlton, 2008); the Eurasian reed (*Phragmites australis*) in freshwater and estuarine systems of North America (Saltonstall, 2002); the Asian carp (several cyprinid fish species) in river systems of the South and Midwest United States (Kolar *et al.*, 2005); the lionfish (*Pterois volitans*) in Western Atlantic and Caribbean waters (Albins & Hixon, 2013); and the European green crab (*Carcinus maenas*) in numerous coastal populations across North America, Asia, Australia, and South America (Carlton & Cohen, 2003).

Some alien species, like the ones listed above, may demonstrate massive population explosions and strong negative interactions with native organisms in their new environments even without prior co-evolutionary history with their novel communities and habitats (Simberloff *et al.*, 2013). While there are numerous hypotheses as to why this seemingly counter-intuitive pattern has been shown to occur over and over again across ecosystems, two prominent ecological and evolutionary explanations for a non-native species' success in unfamiliar territory include: 1) *a loss of natural enemies* (e.g., predators, competitors, parasites, disease) in non-native versus native populations (e.g., Keane and Crawley, 2002; Torchin *et al.*, 2001, 2002, 2003; Liu & Stiling, 2006; Blakeslee *et al.*, 2013) and 2) *a genetic bottleneck* in non-native versus native populations. While this latter consequence could result in deleterious effects, especially in small founding populations, the invasion process may actually enhance success in some species by selecting for the "hardiest" individuals in the founding population and eliminating the more sensitive ones—similar to the phenomenon observed in bacterial communities that show antibiotic resistance as a result of inadvertent selection for resistant alleles that become dominant in gene pools (Lavergne

and Molofsky, 2007; Saltonstall, 2002; Simberloff, 2009). Interestingly, these two commonly observed signatures of biological invasion—enemy release and genetic bottlenecks—can also serve as lines of evidence or tools to better understand invasions or even resolve uncertain invasion histories (e.g., Blakeslee *et al.*, 2008).

7.1.1 Multiple Lines of Evidence in Marine NIS

Regardless of the reasons for NIS success, the reality is that questions surrounding biological invasions are typically the norm, making it challenging to predict their impacts or determine how to manage them. Because NIS may go undetected for years or even decades before they are recognized or pose any environmental, ecological, or economic impacts (Carlton, 1996a), understanding the how, when, and what of an invasion can be difficult, considering little historical, ecological, or evolutionary knowledge may exist, leading to numerous uncertainties and questions. Though not all-inclusive, these questions (Figure 7.1) may include: (1) *Introduction Vector*: the human-mediated mechanism of NIS establishment in new regions (e.g., shipping, agriculture/aquaculture, bait, biocontrol, canals, etc.), which is strongly associated with 'propagule pressure' (the number of individuals entrained within a vector and the number of introduction events; Kolar & Lodge, 2001); (2) *Source*: the region from which the NIS originated and specific source populations; (3) *Timing of Introduction*: when a NIS first became established in a non-native region; (4) *Genetic diversity of founding populations*: NIS may only introduce a subset of their source genetic diversity, which will be strongly influenced by propagule pressure (Roman & Darling, 2007; see Fig. 2-A); (5) *Associated biota*: NIS may carry with them free-living and/or symbiotic hitchhiking organisms (Torchin & Mitchell, 2004; see Figure 7.2-B); (6) *Influence on natives*: NIS may influence native biota and habitats, e.g., competitive and predatory interactions (e.g., Byers, 2009; Rilov, 2009); (7) *Geographic spread*: the ability of NIS to expand ranges beyond original sites of introduction may be aided or impeded by natural dispersal processes and/or multiple introductions; (8) *Cryptogenic species*: species that cannot be demonstrably classified as native or non-native (Carlton, 1996b), a particularly troublesome issue from a management perspective.

As a result of these many uncertainties, multiple lines of evidence may be required. Moreover, these uncertainties may be more pronounced in marine versus terrestrial or freshwater systems since marine biota are inherently more difficult to study and track, and historical information regarding their movements may be non-existent or poor. Therefore, piecing together the evidence necessary to resolve invasion histories in marine systems may require innovative tools (e.g., parasites and genetics—see below). Fortunately, NIS can demonstrate discernible ecological, geographical, and evolutionary signatures, and these can be used as "clues" to resolve uncertainties, such as distinguishing among the native and non-native species in a marine community. For example, Chapman & Carlton (1991) compiled a list of ten criteria that could be used

to resolve ambiguous invasion histories and tested their criteria using a cryptogenic (=origin uncertain; Carlton, 1996b) species of isopod crustacean, *Synidotea laticauda*, in San Francisco Bay, California. Assembling substantial local and global data on the species for these ten criteria, Chapman & Carlton (1991) determined that the isopod was a non-native species, probably having arrived a century earlier on the hulls of ships from Pacific Asia to Pacific North America. Over the years, Chapman & Carlton's criteria (1991) have been cited and used to help resolve questionable invasion histories for numerous other marine species (e.g., Coles *et al.*, 1999; Willis *et al.*, 2004; Glasby *et al.*, 2006) and for other species considered cryptogenic (Carlton, 1996b).

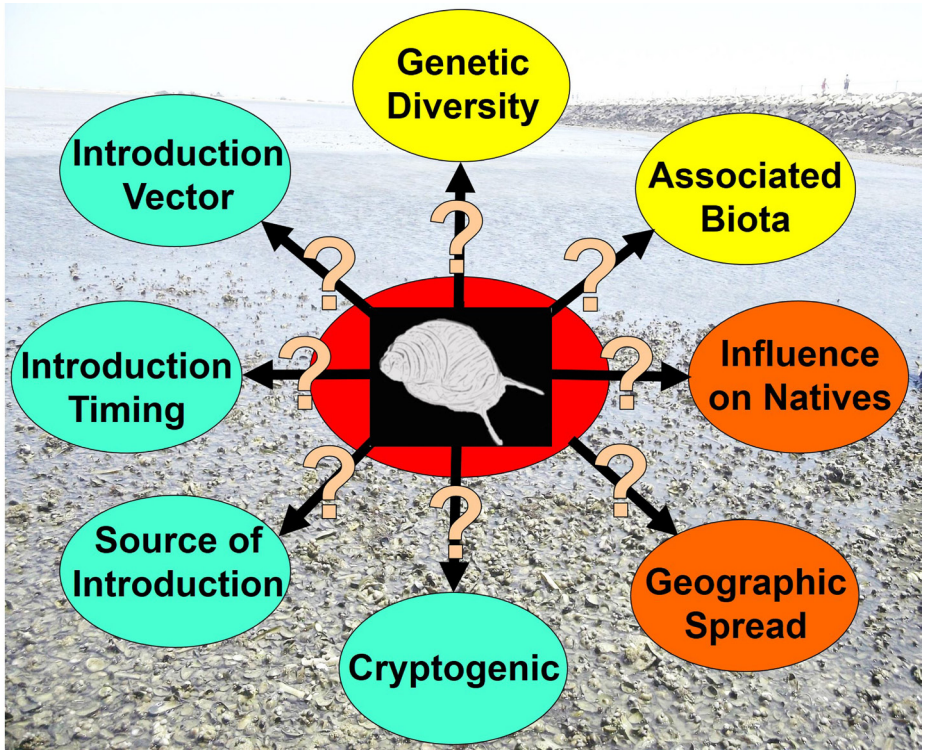

Fig. 7.1: Some of the numerous questions that may surround a newly discovered species in a marine population.

7.1.2 Genetics and Parasites in Marine NIS

Chapman & Carlton's study (1991) provides a very valuable set of criteria for helping resolve uncertain invasion histories, like cryptogenic status; yet, in some cases, additional lines of evidence are needed when available information is conflicting, vague, or poor (Blakeslee, 2007). Over the past couple of decades, molecular genetics has

been a valuable tool for resolving ecological and evolutionary questions across biological disciplines, including marine invasions (e.g., Geller *et al.*, 2010). Additionally, parasites can impart important evidence of a host's ecological history and may sometimes provide more information regarding a host's distribution than the host itself (e.g., Criscione *et al.*, 2006). Thus, studies of parasite and genetic diversity can be important synergistic tools for understanding invasion histories; yet few studies have explored them together to look for emerging patterns.

A recent example of a problematic species where both parasites and genetics were used to resolve an ambiguous invasion history is the common periwinkle, *Littorina littorea*, a highly abundant marine snail found on both Atlantic coasts. A known native of Europe, the snail's status as native or non-native in northeastern North America was debated for over 100 years as a result of conflicting historical, genetic, ecological, and paleontological evidence, even though *L. littorea* is one of the most well-studied marine intertidal snails globally, and its native or non-native status had been examined in over a dozen publications from the late 1800s to 2000s (Blakeslee, 2007). Using novel parasite and genetic evidence, Blakeslee & Byers (2008) and Blakeslee *et al.* (2008) explored two common signatures of an invasion (parasite escape and genetic founder effects in the host and its most common parasite) and found significant reductions in diversity in snail and parasite populations in eastern North America compared to Europe. A further study by Brawley *et al.* (2009) found congruent molecular and shipping evidence for connections between North American populations and the British Isles, representing a potential source region for the snail's introduction.

Thus, when used together, parasite and genetic data can help resolve long-term ambiguities in a species' ecological history and can also provide powerful evidence for numerous other questions in biological invasion studies. Below, I further explore these two signatures (genetic bottlenecks and parasite escape) and the work that has been done independently on each. I then examine these two signatures *together* to look for emerging patterns, as well as what they can offer to our understanding of marine invasions.

7.1.3 Genetic Diversity and Founder Effects

Genetic data has been used in numerous studies to reveal species' invasive tracks, including source populations, introduction timing, and likely vectors (see Table 7.1 for numerous citations). Moreover, species introductions are often associated with 'founder effects', whereby founding populations demonstrate significant genetic bottlenecks compared to source populations (Grossberg & Cunningham, 2000). While this is a strong signature in many marine invasions, there remain some successful invaders that do not conform to this expectation, instead exhibiting little indication of a bottleneck, possibly due to multiple introductions and/or high propagule pressure (Roman & Darling, 2007). Depending on the type of introduction vector and invasion pathway, there could

be multiple abiotic and/or biotic factors affecting NIS during the invasion process, and these divergent vectors and pathways may impact resulting genetic diversity in non-native populations (Figure 7.2A). While such a "genetic paradox" has been demonstrated in many free-living organisms, how these signatures manifest in parasites is much less clear. In fact, parasites may be more prone to genetic founder effects and genetically depauperate founding populations than hosts because of inherently smaller founding populations, lower genetic diversity, and complex life cycles (Figure 7.2B).

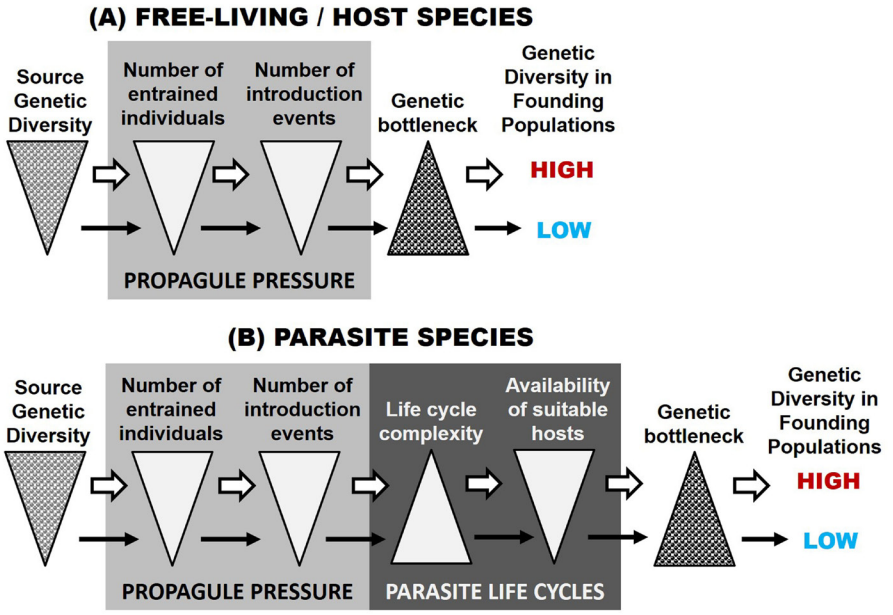

Fig. 7.2: Theoretical schematic for how source diversity and propagule pressure may influence genetic bottlenecks in free-living or host species (A) and parasite species (B) in non-native regions. For hosts (A), if source genetic diversity and propagule pressure are high, the extent of a genetic bottleneck is expected to be low and genetic diversity may then be high. For parasites (B), source genetic diversity and propagule pressure are still major factors influencing genetic bottlenecks in founding regions. However, parasites are dependent on hosts for life cycle completion; thus greater life cycle complexity (e.g., multi-host parasites) and lower host availability to complete life cycles could result in stronger genetic bottlenecks in parasite species. This figure has been adapted from Figure 1 in Roman & Darling (2007) with permission from the authors.

7.1.4 Enemy Release Hypothesis: Parasite Escape

Another well-studied hypothesis explaining why NIS may succeed in novel habitats is the enemy release hypothesis, which can occur when NIS leave behind natural enemies (competitors, predators, parasites) during the invasion process. This results

in fewer enemies in the non-native range compared to the native range (Keane & Crawley, 2002; Torchin *et al.*, 2001, 2002, 2003). Specific to parasites, introductions can serve as a screening-out process, leading to lower parasite burdens (i.e., *parasite escape*) in the non-native region and the potential for ecological and physiological benefits in non-indigenous host populations (Torchin *et al.*, 2003). For example, a recent review of parasite escape in marine and estuarine systems spanning the last 2+ decades and 31 host-parasite systems (= 24 unique host species, 6 host *Classes*, and 20 parasite taxa) found parasite escape to continue to be a significant signature of marine invasions worldwide (Blakeslee *et al.*, 2013). On average, invading hosts carried with them approximately half the number of parasites in their native ranges, although some parasite groups contributed to that escape more than others. Thus, parasite escape has consistently been shown (via seminal works by Torchin *et al.* 2002, 2003, and the update by Blakeslee *et al.*, 2013) to be a strong signature of marine invasions worldwide. Similarly, a recent investigation (Jeschke *et al.*, 2012) exploring six prominent theories in invasion biology, including enemy release, found some invasion theories to demonstrate a "decline effect" with time and evidence, but enemy release has continued to show strong support with time, especially in marine systems. As such, parasite escape is a well-supported signature of invasion, and when compared to evidence from native systems, it could be a helpful line of evidence for resolving questionable invasion histories.

7.1.5 Study Questions

In this review, I searched the literature for marine investigations that included genetic diversity, parasite diversity, or both in native and non-native locations around the world. I explored parasite escape and genetic bottlenecks across studies and compared them to look for emerging patterns in both signatures of invasion, and I also focused on a subset of studies where more precise source areas were known. Finally, I explored a subset of data where hosts and parasites have both been investigated in native and non-native regions to determine if dissimilarities in propagule pressure and life history may have differentially influenced host versus parasite genetic diversities. Specifically, I addressed the following questions:

1. Do parasite escape and genetic bottlenecks show convergent patterns when averaged across marine NIS?
2. Is there a 'source effect', whereby parasite escape and genetic bottleneck signatures are less pronounced than in regional comparisons?
3. Are parasite escape and genetic bottlenecks influenced by vector type, NIS taxa, geography, and/or time since introduction?
4. Do parasites demonstrate more pronounced genetic bottlenecks in non-native regions than their hosts?

Tab. 7.1: The 61 study systems (40 unique species) included in this review of genetic and parasite diversity data in marine invertebrate species from native and non-native regions worldwide.

Species are listed alphabetically by Latin name. Class = the Class of the marine invertebrate species; F/P = free-living versus parasitic species; Vector = vector (mechanism) of introduction; Timing = timing of introduction; Native range (region) = the region where the species is native; Non-native range = the region where the species is non-native; Distance = the direct line distance (km) between the native and non-native region; Marker = the molecular marker the genetic data are based on; Genetic Bottleneck Index = the extent of the bottleneck; Non-native/Native Haplotype Diversity = the ratio of the non-native to the native haplotype diversity; Parasite Taxa = the parasite taxa in native and/or non-native regions; Parasite Escape Index = the extent of the parasite escape; Citations = the references for the genetic and parasite data.

Species: ***Latin name*** (Common name)	***Class***	**F/P**	**Vector**	**Timing**	**Native range (region)**	**Non-native range (region)**	**Distance**	**Marker**	**Genetic Bottleneck Index** $[(N_h - I_h)/N_h]$	**Non-native / Native Haplotype Diversity**	**Parasite Taxa**	**Parasite Escape Index** $[(N_p - I_p)/N_p]$	**Citations**	**Notes**
Asterias amurensis (Northern Pacific seastar)	Asteroidea	F	BWF	1990	Asia (Japan; Russia; North China; Korea: 60N-31N); Lat median: 46N; Lon @ median: 137E	Southern coast of Australia (37S-43S); Lat median: 40S; Lon @ median: 146E	3598	n/a	n/a	n/a	Ciliophora (N), Copepoda (N)	1.000	Torchin *et al.* (2002)	
Austrobilharzia variglandis	Trematoda	P	HOST (*Ilyanassa obsoleta*)	1900	Eastern N. America (Canada to Georgia) (48N to 29N); Lat median: 39N; Lon @ median: 74W	Western N. America (SFB, WB and BB) (49N to 37N); Lat median: 46N; Lon @ median: 123W	4024	COI	0.652	0.717	n/a	n/a	Blakeslee & Fowler (2011); Blakeslee *et al.* (in prep)	Haplotype richness in native and non-native regions represent rarefied values
Batillaria attramentaria (=*cumingi*) (Asian hornsnail)	Gastropoda	F	OYS	1920	Asia (Japan, Hong Kong, other areas of Asia from 40N to equator); Lat median: 20N; Lon @ median: 110E	Western N. America (British Columbia, Washington, Elkhorn Slough, CA: 50N to 36N); Lat median: 43N; Lon @ median: 124W	11093	COI	0.667	0.122	Trematoda (N, I)	0.800	Byers (2000); Torchin *et al.* (2002); Torchin *et al.* (2005); Miura *et al.* (2006); Hechinger (2007); Lafferty & Kuris (2009)	Haplotype diversity represents the rarefied regional values in Figure 7.3

continued **Tab. 7.1:** The 61 study systems (40 unique species) included in this review of genetic and parasite diversity data in marine invertebrate species from native and non-native regions worldwide.

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Batillaria australis	Gastropoda	F	BWF	1950	Southeastern Australia (Whitsunday Islands, Queensland; southwards to Victoria and Tasmania: 20S-43S); Lat median: 32S; Lon @ median: 152E	West Australia (Swan River estuary and Cockburn Sound: 31S-32S); Lat median: 32S; Lon @ median: 115E	3469	n/a	n/a	n/a	Trematoda (N, I)	0.625	Thomsen *et al.* (2010)	
Botrylloides violaceus (violet tunicate)	Tunicata	F	OYS/ BWF	1973	Northwest Pacific (Japan, southern China, Korea) (45N to 21N); Lat median: 33N; Lon @ median: 129E	Eastern N. America (Newfoundland to Chesapeake Bay) (51N to 36N); Lat median: 43N; Lon @ median: 69W	11360	COI	0.800	0.000	n/a	n/a	Lejeusne *et al.* (2011)	
Botryllus schlosseri (golden star tunicate)	Tunicata	F	AQC/ OYS/ BWF	1947	Mediterranean Sea? (45N to 30N; 5W to 36E); Lat median: 37N; Lon median: 16E	Western N. America (Alaska to Mexico) (57N to 30N); Lat median: 44N; Lon @ median: 123W	10100	COI	0.750	0.462	n/a	n/a	Lejeusne *et al.* (2011)	
Botryllus schlosseri (golden star tunicate)	Tunicata	F	AQC/ OYS/ BWF/ DBF	1838	Mediterranean Sea? (45N to 30N; 5W to 36E); Lat median: 37N; Lon median: 16E	Eastern N. America (Newfoundland to Florida) (51N to 28N); Lat median: 40N; Lon @ median: 74W	7472	COI	0.625	0.573	n/a	n/a	Lejeusne *et al.* (2011)	
Caprella mutica (Japanese skeleton shrimp)	Crustacea	F	BWF	1995	Asia (Russia, Japan) (53N to 30N); Lat median: 42N; Lon @ median: 139E	Europe (Scandinavia to British Isles) (71N to 47N); Lat median: 59N; Lon @ median: 5E	8010	COI	0.871	0.264	n/a	n/a	Ashton *et al.* (2008)	

continued **Tab. 7.1:** The 61 study systems (40 unique species) included in this review of genetic and parasite diversity data in marine invertebrate species from native and non-native regions worldwide.

Species: *Latin name* (Common name)	*Class*	F/P	Vector	Timing	Native range (region)	Non-native range (region)	Distance	Marker	Genetic Bottleneck Index $[(N_h - I_h)/N_h]$	Non-native / Native Haplotype Diversity	Parasite Taxa	Parasite Escape Index $[(N_p - I_p)/N_p]$	Citations	Notes
Carcinus maenas (European green crab)	Crustacea	F	DBF/BWF	1810	Europe (Norway to Portugal: 70N-37N); Lat median: 54N; Lon @ median: 5E	Eastern North America (Newfoundland to North Carolina: 49N-34N); Lat median: 42N; Lon @ median: 70W	5459	COI	0.800	0.332	Acanthocepha (N, I), Cestoda (N), Copepoda (N), Fecampida (N), Isopoda (N), Nematoda (N, I), Nemertea (N), Rhizocephala (N), Trematoda (N, I)	0.700	Torchin *et al.* (2001); Torchin *et al.* (2002); Roman (2006); Darling *et al.* (2008); Blakeslee *et al.* (2009); Pringle *et al.* (2011)	
Carcinus maenas (European green crab)	Crustacea	F	APM	1990	Europe (Norway to Portugal: 70N-37N); Lat median: 54N; Lon @ median: 5E	Western North America (British Columbia to San Francisco Bay, California: 50N-37N); Lat median: 44N; Lon @ median: 123W	8050	COI	0.980	0.000	Acantho-cepha (N), Cestoda (N, I), Copepoda (N), Fecampida (N), Isopoda (N), Nematoda (N), Nemertea (N, I), Rhizocephala (N), Trematoda (N)	0.800	Torchin *et al.* (2001); Torchin *et al.* (2002); Darling *et al.* (2008)	
Carcinus maenas (European green crab)	Crustacea	F	BWF	1980	Europe (Norway to Mediterranean Sea: 70N-35N); Lat median: 54N; Lon @ median: 5E	South Africa (Cape Peninsula, Cape Town, S. Africa: 33S-34S); Lat median: 34S; Lon @ median: 18E	9749	COI	0.800	1.064	Acanthocepha (N), Cestoda (N), Copepoda (N), Fecampida (N), Isopoda (N), Nematoda (N), Nemertea (N), Rhizocephala (N), Trematoda (N)	1.000	Torchin *et al.* (2001); Darling *et al.* (2008); Zetlmeisl *et al.* (2010);	

continued **Tab. 7.1:** The 61 study systems (40 unique species) included in this review of genetic and parasite diversity data in marine invertebrate species from native and non-native regions worldwide.

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Carcinus maenas (European green crab)	Crustacea	F	DBF/BWF	1900	Europe (Norway to Portugal: 70N-37N); Lat median: 54N; Lon @ median: 5E	Australia (Victoria; Tasmania: 43S-33S); Lat median: 38S; Lon @ median: 145E	16504	COI	0.900	0.720	Acanthocepha (N), Cestoda (N, I), Copepoda (N), Fecampida (N), Isopoda (N), Nematoda (N, I), Nemertea (N), Rhizocephala (N), Trematoda (N)	0.800	Torchin *et al.* (2001); Darling *et al.* (2008); Zetlmeisl *et al.* (2010);	
Carcinus maenas (European green crab)	Crustacea	F	BWF	1980	Europe (Norway to Mediterranean Sea: 70N-35N); Lat median: 54N; Lon @ median: 5E	Japan (45N-30N); Tokyo Lat/Lon: 35N/139E	9263	COI	0.960	0.438	Acanthocepha (N), Cestoda (N), Copepoda (N), Fecampida (N), Isopoda (N), Nematoda (N), Nemertea (N), Rhizocephala (N), Trematoda (N)	1.000	Torchin *et al.* (2002); Darling *et al.* (2008)	
Carcinus maenas (European green crab)	Crustacea	F	BWF	1999	Europe (Norway to Mediterranean Sea: 70N-35N); Lat median: 54N; Lon @ median: 5E	Eastern Argentina (46S to 43S)	12830	COI	0.980	0.000	n/a	n/a	Darling *et al.* (2008)	
Ceratostoma inornatum (=Ocinebrellus inornatus) (Japanese oyster drill)	Gastropoda	F	OYS	1924	Asia (Japan, Korea) (45N to 31N); Lat median: 38N; Lon @ median: 139E	Western N. America (British Columbia to California (49N to 37N); Lat median: 43N; Lon @ median: 124W	7727	COI	0.667	n/a	n/a	n/a	Martel *et al.* (2004)	

continued **Tab. 7.1:** The 61 study systems (40 unique species) included in this review of genetic and parasite diversity data in marine invertebrate species from native and non-native regions worldwide.

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Ceratostoma inornatum (=Ocinebrellus inornatus) (Japanese oyster drill)	Gastropoda	F	OYS	1995	Asia (Japan, Korea) (45N to 31N); Lat median: 38N; Lon @ median: 139E	Europe (France) (50N to 43N); Lat median: 47N; Lon @ median: 2W	9793	COI	0.583	n/a	n/a	n/a	Martel *et al.* (2004)	
Cercaria batillaria (HL1)	Trematoda	P	HOST (*Batillaria attramentaria*)	1920	Asia (Japan, Hong Kong, other areas of Asia from 40N to equator); Lat median: 20N; Lon @ median: 110E	Western N. America (British Columbia, Washington, Elkhorn Slough, CA: 50N to 36N); Lat median: 43N; Lon @ median: 124W	11093	COI	0.125	0.989	n/a	n/a	Miura *et al.* (2006)	Haplotype diversity represents the rarefied regional values in Figure 3
Cercaria batillaria (HL6)	Trematoda	P	HOST (*Batillaria attramentaria*)	1920	Asia (Japan, Hong Kong, other areas of Asia from 40N to equator); Lat median: 20N; Lon @ median: 110E	Western N. America (British Columbia, Washington, Elkhorn Slough, CA: 50N to 36N); Lat median: 43N; Lon @ median: 124W	11093	COI	0.727	0.632	n/a	n/a	Miura *et al.* (2006)	Haplotype diversity represents the rarefied regional values in Figure 3
Cercaria parvicaudata	Trematoda	P	HOST (*Littorina littorea*)	1840	Europe (White Sea to Portgual) (70N to 40N); Lat median: 55N; Lon @ median: 8E	Northeastern N. America (Labrador to Delaware Bay) (51N to 38N); Lat median: 45N; Lon @ median: 66W	5144	COI	0.375	0.470	n/a	n/a	Blakeslee & Fowler (2011); Blakeslee (unpublished)	Haplotype richness in native and non-native regions represent rarefied values

continued **Tab. 7.1:** The 61 study systems (40 unique species) included in this review of genetic and parasite diversity data in marine invertebrate species from native and non-native regions worldwide.

Species: *Latin name* (Common name)	*Class*	F/P	Vector	Timing	Native range (region)	Non-native range (region)	Distance	Marker	Genetic Bottleneck Index $[(N_h - I_h)/N_h]$	Non-native / Native Haplotype Diversity	Parasite Taxa	Parasite Escape Index $[(N_p - I_p)/N_p]$	Citations	Notes
Cercopagis pengoi (Fishook waterflea)	Crustacea	F	BWF	1198	Ponto-Caspian (Black, Azov, Caspian, and Aral Seas): Lat median: 41N; Lon median: 41E	Great Lakes; St. Lawrence River/Seaway (48N to 41N; 92W to 76W); Lat median: 44N; Lon @ median: 82W	8977	COI	0.857	n/a	n/a	n/a	Critescu *et al.* (2001)	
Chtlalamus proteus Caribbean barnacle)	Crustacea	F	BWF	1995	Gulf of Mexico; Caribbean Sea; South Atlantic (29N to 23S); Lat median: 3N; Lon @ median: 51W	Hawaiian islands (21N to 18N); Lat median: 20N; Lon @ median: 156W	11446	COI	0.111	n/a	n/a	n/a	Zardus & Hadfield (2005)	
Crassostrea angulata (Portuguese oyster)	Bivalvia	F	DEL	1500s	Portugal, Spain, France (48N to 36N); Lat median: 42N; Lon @ median: 8W	Taiwan (25N to 21N); Lat median: 23N; Lon @ median: 120E	11022	COI	0.556	n/a	n/a	n/a	Boudry *et al.* (1998); Foighil *et al.* (1998); Huvet *et al.* (2000)	
Crassostrea gigas (Pacific oyster)	Bivalvia	F	OYS	1900	Asia (Russia; east coast of China; Korea; Japan: 59N-22N); Lat median: 41N; Lon @ median: 129E	Western North America (southern Alaska to Humboldt Bay, California: 40N-60N); Lat median: 50N; Lon @ median: 125W	7596	ALLOZYME	-0.056	1.197	Copepoda (N, I), Nematoda (N), Trematoda (N), Turbellaria (N)	0.750	Mann *et al.* (1991); English *et al.* (2000)	**Mitochondrial data not available, so also including allozyme data here; i.e., data based upon mean alleles and observed heterozygosities from table 6 in English *et al.* (2000)

continued **Tab. 7.1:** The 61 study systems (40 unique species) included in this review of genetic and parasite diversity data in marine invertebrate species from native and non-native regions worldwide.

Species: *Latin name* (Common name)	*Class*	F/P	Vector	Timing	Native range (region)	Non-native range (region)	Distance	Marker	Genetic Bottleneck Index $[(N_h - I_h)/N_h]$	Non-native / Native Haplotype Diversity	Parasite Taxa	Parasite Escape Index $[(N_p - I_p)/N_p]$	Citations	Notes
Crassostrea gigas (Pacific oyster)	Bivalvia	F	OYS	1960	Asia (Russia; east coast of China; Korea; Japan: 59N-22N); Lat median: 41N; Lon @ median: 129E	Western Europe (Exe Estuary, Great Britain; Wadden Sea; France; Netherlands; Belgium; Germany; Denmark; Sweden; Norway: 65N-44N); Lat median: 55N; Lon @ median: 8E	7964	MNR	0.094	0.769	Copepoda (N, I), Nematoda (N), Polychaeta (I), Trematoda (N, I), Turbellaria (N, I)	-0.500	Mann *et al.* (1991); Aguiere-Macedo and Kennedy (1999); English *et al.* (2000); Krakau *et al.* (2006); Troost (2010); Elsner *et al.* (2011); Moeller *et al.* (2011); Thieltges *et al.* (2013)	**Only mitochondrial data in the non-native region (Moeller *et al.*, 2011), so also including allozyme data here; i.e., data based upon mean alleles and observed heterozygosities from table 6 in English *et al.* (2000)
Crassostrea gigas (Pacific oyster)	Bivalvia	F	BWF	1950	Asia (Russia; east coast of China; Korea; Japan: 59N-22N); Lat median: 41N; Lon @ median: 129E	New Zealand (46S-34S); Lat median: 40S; Lon @ median: 175E	10129	ALLOZYME	-0.007	0.875	Copepoda (N, I), Nematoda (N, I), Trematoda (N), Turbellaria (N, I)	0.000	Dinamami (1986); English *et al.* (2000)	**Mitochondrial data not available, so also including allozyme data here; i.e., data based upon mean alleles and observed heterozygosities from table 6 in English *et al.* (2000)
Cryptocotyle lingua	Trematoda	P	HOST (*Littorina littorea*)	1840	Europe (White Sea to Portgual) (70N to 40N); Lat median: 55N; Lon @ median: 8E	Northeastern N. America (Labrador to Delaware Bay) (51N to 38N); Lat median: 45N; Lon @ median: 66W	5144	COI	0.851	0.902	n/a	n/a	Blakeslee *et al.* (2008)	Haplotype richness in native and non-native regions represent rarefied values

continued **Tab. 7.1:** The 61 study systems (40 unique species) included in this review of genetic and parasite diversity data in marine invertebrate species from native and non-native regions worldwide.

Species: *Latin name* (Common name)	*Class*	F/P	Vector	Timing	Native range (region)	Non-native range (region)	Distance	Marker	Genetic Bottleneck Index $[(N_h - I_h)/N_h]$	Non-native / Native Haplotype Diversity	Parasite Taxa	Parasite Escape Index $[(N_p - I_p)/N_p]$	Citations	Notes
Cyclope nerite	Gastropoda	F	OYS	1976	Mediterranean Sea; Black Sea; Morocco; southern Portugal; southern Spain (46N to 27N); Lat median: 37N; Lon @ median: 16E	France (48N to 43N); Lat median: 46N; Lon @ median: 1W	1727	COI	-3.167	1.809	Trematoda (N, I)	0.500	Simon-Bouhet *et al.* (2006); Couceiro *et al.* (2012)	
Didemnum vexillum / sp. A (Didemnum tunicate)	Tunicata	F	BWF	1993	Asia (Japan) (45N to 30N); Lat median: 38N; Lon @ median: 139E	Western N. Amerca (Alaska to Mexico) (57N to 30N); Lat median: 44N; Lon @ median: 123W	7733	COI	0.375	n/a	n/a	n/a	Stefaniak *et al.* (2009)	
Didemnum vexillum / sp. A (Didemnum tunicate)	Tunicata	F	BWF	1982	Asia (Japan) (45N to 30N); Lat median: 38N; Lon @ median: 139E	Eastern N. America (Maine to Long Island) (45N to 40N); Lat median: 43N; Lon @ median: 70W	10537	COI	0.625	n/a	n/a	n/a	Stefaniak *et al.* (2009)	
Didemnum vexillum / sp. A (Didemnum tunicate)	Tunicata	F	BWF	1991	Asia (Japan) (45N to 30N); Lat median: 38N; Lon @ median: 139E	Europe (North Sea to Spain) (58N to 36N); Lat median: 43N; Lon @ median: 3W	10219	COI	0.625	n/a	n/a	n/a	Stefaniak *et al.* (2009)	
Echinogammarus ischnus (Scud)	Crustacea	F	BWF	1995	Ponto-Caspian (Black, Azov, Caspian, and Aral Seas): Lat median: 41N; Lon median: 41E	Great Lakes; St. Lawrence River/ Seaway (50N to 41N; 92W to 64W); Lat median: 45N; Lon @ median: 81W	8841	COI	0.818	0.000	n/a	n/a	Critescu *et al.* (2004)	

continued **Tab. 7.1:** The 61 study systems (40 unique species) included in this review of genetic and parasite diversity data in marine invertebrate species from native and non-native regions worldwide.

Species: ***Latin name*** (Common name)	***Class***	**F/P**	**Vector**	**Timing**	**Native range (region)**	**Non-native range (region)**	**Distance**	**Marker**	**Genetic Bottleneck Index** $[(N_h - I_h)/N_h]$	**Non-native / Native Haplotype Diversity**	**Parasite Taxa**	**Parasite Escape Index** $[(N_p - I_p)/N_p]$	**Citations**	**Notes**
Ensis directus (=americanus) (razor shell)	Bivalvia	F	BWF	1978	Eastern N. America (Labrador to Florida) (59N to 25N); Lat median: 42N; Lon median: 70W	Europe (Southern Norway to Normandy; North Sea; British Isles) (59 N to 48N); Lat median: 54N; Lon median: 8E	5644	COI	-0.385	1.086	Trematoda (N, I)	n/a	Armonies and Reise (1999); Krakau *et al.* (2006); Thieltges *et al.* (2006); Vierna *et al.* (2012)	4 parasites in non-native range but native range is undersampled - suggestion that more exist but only one (*Himasthla quissitensis*) detected.
Gammarus tigrinus	Crustacea	F	OTHER	1931	Eastern N. America (Gulf of St Lawrence, Quebec to N. Florida) (49N to 29N); Lat median: 39N; Lon @ median: 74W	Europe (Baltic to Rhine; also British Isles) (60N to 49N); Lat median: 55N; Lon @ median: 12E	6319	COI	0.903	0.615	n/a	n/a	Kelly *et al.* (2006)	Averaged from Table 3
Gammarus tigrinus	Crustacea	F	OTHER	1931	Eastern N. America (Gulf of St Lawrence, Quebec to N. Florida) (49N to 29N); Lat median: 39N; Lon @ median: 74W	Great Lakes (48N to 41N; 91W to 76W); Lat median: 45N; Lon @ median: 83W	997	COI	0.968	n/a	n/a	n/a	Kelly *et al.* (2006)	
Gemma gemma (Gem clam)	Bivalvia	F	OYS	1880	Eastern N. America (Labrador to Florida; Gulf of Mexico) (53N to 25N); Lat median: 39N; Lon median: 74W	Western N. America (Puget Sound, WA to San Diego, CA) (47N to 32N); Lat median: 40N; Lon median: 124W	4231	COI	0.476	0.925	n/a	n/a	Hoos *et al.* (2010)	

continued **Tab. 7.1:** The 61 study systems (40 unique species) included in this review of genetic and parasite diversity data in marine invertebrate species from native and non-native regions worldwide.

Species: ***Latin name*** (Common name)	***Class***	**F/P**	**Vector**	**Timing**	**Native range (region)**	**Non-native range (region)**	**Distance**	**Marker**	**Genetic Bottleneck Index** $[(N_h - I_h)/N_h]$	**Non-native / Native Haplotype Diversity**	**Parasite Taxa**	**Parasite Escape Index** $[(N_p - I_p)/N_p]$	**Citations**	**Notes**
Haminoea japonica (Japanese bubble snail)	Gastropoda	F	OYS	1966	Asia (Japan; Korea; Thailand: 45N-13N); Lat median: 29N; Lon @ median: 122E	Wesern N. America (Boundary Bay, Washington, San Francisco Bay, Tomales Bay, California) (49N to 37N); Lat median: 43N; Lon @ median: 124W	9552	COI	0.909	0.544	Trematoda (I)	n/a	Brant *et al.* (2010); Hanson *et al.* (2013)	1 schistosome trematode found in San Francisco Bay, but not found in other locations on the west coast. No schistosome parasites observed in Japanese snails.
Haminoea japonica (Japanese bubble snail)	Gastropoda	F	OYS	1992	Asia (Japan; Korea; Thailand: 45N-13N); Lat median: 29N; Lon @ median: 122E	Europe (France, Italy, Spain, Mediterranean) (48N to 38N); Lat median: 43N; Lon @ median: 7E	9617	COI	0.909	0.333	n/a	n/a	Hanson *et al.* (2013)	No schistosome parasites observed in Japanese snails, nor European snails.
Hemigrapsus sanguineus (Asian shorecrab)	Crustacea	F	BWF	1988	Asia (Russia, Japan, Hong Kong) (52N to 22N); Lat median: 37N; Lon @ median: 141E	Eastern N. America (southern Maine to North Carolina) (43N to 35N); Lat median: 39N; Lon @ median: 74W	10829	COI	0.885	0.866	Acanthocephala (I), Nematoda (I), Microspora (N), Rhizocephala (N), Trematoda (N)	0.750	Blakeslee *et al.* (2009); Epifanio (2013); McDermott (2011); Blakeslee *et al.* (in prep)	Haplotype richness in native and non-native regions represent rarefied values
Himasthla quissitensis	Trematoda	P	HOST (*Ilyanassa obsoleta*)	1900	Eastern N. America (Canada to Georgia) (48N to 29N); Lat median: 39N; Lon @ median: 74W	Western N. America (SFB, WB and BB) (49N to 37N); Lat median: 46N; Lon @ median: 123W	4024	COI	0.839	0.805	n/a	n/a	Blakeslee & Fowler (2011); Blakeslee *et al.* (in prep)	Haplotype richness in native and non-native regions represent rarefied values

continued **Tab. 7.1:** The 61 study systems (40 unique species) included in this review of genetic and parasite diversity data in marine invertebrate species from native and non-native regions worldwide.

Species: *Latin name* (Common name)	*Class*	F/P	Vector	Timing	Native range (region)	Non-native range (region)	Distance	Marker	Genetic Bottleneck Index $[(N_h - I_h)/N_h]$	Non-native / Native Haplotype Diversity	Parasite Taxa	Parasite Escape Index $[(N_p - I_p)/N_p]$	Citations	Notes
Ilyanassa obsoleta (eastern mud snail)	Gastropoda	F	OYS	1900	Eastern N. America (Canada to Georgia) (48N to 29N); Lat median: 39N; Lon @ median: 74W	Western N. America (SFB, WB and BB) (49N to 37N); Lat median: 46N; Lon @ median: 123W	4024	COI	0.481	1.025	Trematoda (N, I)	0.444	Curtis (1997); Blakeslee & Fowler (2011); Blakeslee *et al.* (2012); Blakeslee *et al.* (in prep)	Haplotype richness in native and non-native regions represent rarefied values
Lepocreadium setiferoides	Trematoda	P	HOST (*Ilyanasaa obsoleta*)	1900	Eastern N. America (Canada to Georgia) (48N to 29N); Lat median: 39N; Lon @ median: 74W	Western N. America (SFB, WB and BB) (49N to 37N); Lat median: 46N; Lon @ median: 123W	4024	COI	0.793	1.146	n/a	n/a	Blakeslee & Fowler (2011); Blakeslee *et al.* (in prep)	Haplotype richness in native and non-native regions represent rarefied values
Littorina littorea (common periwinkle snail)	Gastropoda	F	DBF	1840	Europe (White Sea, Russia to Portgual: 70N to 40N); Lat median: 55N; Lon @ median: 8E	Eastern North America (Labrador to Delaware Bay: 51N to 38N); Lat median: 45N; Lon @ median: 66W	5144	CYTB	0.873	1.096	Trematoda (N, I)	0.545	Blakeslee *et al.* (2008); Blakeslee & Byers (2008)	Haplotype richness in native and non-native regions represent rarefied values
Littorina littorea (common periwinkle snail)	Gastropoda	F	DEL	1960	Europe (White Sea, Russia to Portgual: 70N to 40N); Lat median: 55N; Lon @ median: 8E	Western North America (San Francisco Bay, California); Lat median: 37N; Lon @ median: 122W	8728	CYTB	0.938	1.092	Trematoda (N, I)	0.909	Chang *et al.* (2011); Blakeslee (unpublished)	Haplotype richness in native and non-native regions represent rarefied values

continued **Tab. 7.1:** The 61 study systems (40 unique species) included in this review of genetic and parasite diversity data in marine invertebrate species from native and non-native regions worldwide.

Species: ***Latin name*** (Common name)	***Class***	**F/P**	**Vector**	**Timing**	**Native range (region)**	**Non-native range (region)**	**Distance**	**Marker**	**Genetic Bottleneck Index** $[(N_h - I_h)/N_h]$	**Non-native / Native Haplotype Diversity**	**Parasite Taxa**	**Parasite Escape Index** $[(N_p - I_p)/N_p]$	**Citations**	**Notes**
Littorina saxatilis (rough periwinkle snail)	Gastropoda	F	APM	1990	Northeastern N. America (Labrador to Long Island, New York; 64N-40N); Lat median: 52N; Lon @ median: 65W	Western North America (San Francisco Bay, California: 37N); Lat median: 37N; Lon @ median: 122W	4678	COI	0.746	0.791	Trematoda (N, I)	0.786	Blakeslee & Fowler (2011); Blakeslee *et al.* (2012); Blakeslee *et al.* (unpublished)	Haplotype richness in native and non-native regions represent rarefied values
Littorina saxatilis (rough periwinkle snail)	Gastropoda	F	DBF	1792	Europe (Barents Sea to Portugal) (71N to36N); Lat median: 54N; Lon @ median: 8E	Mediterranean (Venice: 45N; 12E); Lat median: 45N; Lon @ median: 12E	1040	COI	0.987	0.000	n/a	n/a	Panova *et al.* (2011)	Haplotype richness in native and non-native regions represent rarefied values
Loxothylacus panopaei	Crustacea	P	HOST (*Rhithropanopeus harrisii*)	1964	Gulf of Mexico to southeast Florida; Caribbean (29N to 8N); Lat median: 19N; Lon @ median: 96W	Eastern N. America (Long Island Sound to central Florida) (40N to 28N); Lat median: 34N; Lon @ median: 77W	2511	COI	0.700	n/a	n/a	n/a	Kruse *et al.* (2007); Kruse *et al.* (2011)	
Mnemiopsis leidyi (Atlantic ctenophore)	Tentaculata	F	BWF	1980	Eastern North America (New York to Florida: 40N to 26N); Lat median: 33N; Lon @ median: 78W	Black Sea; Mediterranean Sea; Baltic Sea; North Sea (57N-31N); Lat median: 44N; Lon @ median: 34E	9027	ITS	-0.222	1.245	Amphipoda (N), Cnidaria (N, I), Nematoda (N, I), Trematoda (N)	0.500	Torchin *et al.* (2002); Selandar *et al.* (2010); Ghabooli *et al.* (2010)	*represents allelic diversity
Musculista senhousia (Asian date mussel)	Bivalvia	F	OYS	1980	Asia (Russia; Korea; Japan; China; Singapore: 60N to 1N); Lat median: 31N; Lon @ median: 121E	New Zealand (46S-34S); Lat median: 40S; Lon @ median: 175E	9651	COI	0.538	0.942	Copepoda (N, I)	0.667	Miller *et al.* (2008); Asif & Krug (2012)	

continued **Tab. 7.1:** The 61 study systems (40 unique species) included in this review of genetic and parasite diversity data in marine invertebrate species from native and non-native regions worldwide.

Species: *Latin name* (Common name)	*Class*	F/P	Vector	Timing	Native range (region)	Non-native range (region)	Distance	Marker	Genetic Bottleneck Index $[(N_h - I_h)/N_h]$	Non-native / Native Haplotype Diversity	Parasite Taxa	Parasite Escape Index $[(N_p - I_p)/N_p]$	Citations	Notes
Musculista senhousia (Asian date mussel)	Bivalvia	F	OYS	1924	Asia (Russia; Korea; Japan; China; Singapore: 60N to 1N); Lat median: 31N; Lon @ median: 121E	Western N. America (Puget Sound, WA to San Diego, CA) (47N to 32N); Lat median: 40N; Lon median: 124W	9660	COI	0.590	0.675	n/a	n/a	Asif & Krug (2012)	
Mya arenaria (Soft shell clam)	Bivalvia	F	DEL	1600s	Eastern North America (Labrador to South Carolina: 54N-32N); Lat median: 43N; Lon @ median: 70W	Europe (northern Wadden Sea: 57N-53N); Lat median: 55N; Lon @ median: 8E	5530	COI	0.400	1.361	Copepoda (N), Nematoda (I), Trematoda (N, I), Turbellaria (I)	0.000	Thieltges *et al.* (2006); Petersen *et al.* (1992)	
Mytella charruana (Charru mussel)	Bivalvia	F	BWF	1986	Southeastern Pacific and southernwestern Atlantic (Mexico to Ecuador, Columbia to Argentina) (25N to 38S); Lat median: 7S; Lon @ median: 34W	Southeast N. America (South Carolina to Florida) (33N to 25N); Lat median: 29N; Lon @ median: 81W	6422	COI	0.400	0.836	n/a	n/a	Gillis *et al.* (2009)	
Mytilus galloprovincialis (Mediterranean mussel)	Bivalvia	F	BWF	1970	Mediterranean Sea, Black Sea, and Adriatic Sea (47N to 30N; 5W to 41E); Lat median: 39N; Lon median: 18E	Cape of Good Hope in South Africa to Lüderitz in southern Namibia (26S to 34S); Lat median: 30S; Lon @ median: 17E	7668	COI	0.400	n/a	Copepoda (N), Microspora (N), Trematoda (N), Turbellaria (N)	1.000	Villalba *et al.* (2007); Gerard *et al.* (2008)	

continued **Tab. 7.1:** The 61 study systems (40 unique species) included in this review of genetic and parasite diversity data in marine invertebrate species from native and non-native regions worldwide.

Species: *Latin name* (Common name)	*Class*	F/P	Vector	Timing	Native range (region)	Non-native range (region)	Distance	Marker	Genetic Bottleneck Index $[(N_h - I_h)/N_h]$	Non-native / Native Haplotype Diversity	Parasite Taxa	Parasite Escape Index $[(N_p - I_p)/N_p]$	Citations	Notes
Paralithoides camtschaticus (red king crab)	Crustacea	F	DEL	1960	North Pacific; Alaska (71N-34N); Lat median: 53N; Lon @ median: 160E	Barents Sea (76N-67N); Lat median: 72N; Lon @ median: 24E	5696	COI	0.400	n/a	Acanthocephala (N, I), Bivalvia (I), Copepoda (N, I), Nemertea (N, I), Isopoda (N), Rhizocephala (N), Turbellaria (I)	0.375	Hawkes *et al.* (1986); Sparks (1987); Kuris *et al.* (1991); Jansen *et al.* (1998); Hemmingsen *et al.* (2005)	
Potamopyrgus antipodarum (New Zealand mud snail)	Gastropoda	F	BWF	1859	New Zealand (36S to 46S); Lat median: 41S; Lon @ median: 173E	Europe (British Isles to Russia to Mediterranean) (70N to 40N); Lat median: 50N; Lon @ median: 11E	18287	16S	0.882	0.570	Trematoda (N, I)	0.714	Jokela & Livey (1995); Morley (2008)	
Rhithropanopeus harrisii (Harris mud crab)	Crustacea	F	OYS	1937	Eastern N. America (Gulf of St Lawrence to Florida) and Gulf of Mexico (Florida to Veracruz, Mexico) (49 N to 19N); Lat median: 34N; Lon @ median: 77W	Western N. America (Oregon and California to San Francisco Bay) (45N to 37N); Lat median: 42N; Lon @ median: 124W	11289	COI	0.864	n/a	n/a	n/a	Petersen (2006)	

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Species: ***Latin name*** (Common name)	***Class***	**F/P**	**Vector**	**Timing**	**Native range (region)**	**Non-native range (region)**	**Distance**	**Marker**	**Genetic Bottleneck Index** $[(N_h - I_h)/N_h]$	**Non-native / Native Haplotype Diversity**	**Parasite Taxa**	**Parasite Escape Index** $[(N_p - I_p)/N_p]$	**Citations**	**Notes**
Rhithropanopeus harrisii (Harris mud crab)	Crustacea	F	DBF/BWF	1874	Eastern N. America (Gulf of St Lawrence to Florida) and Gulf of Mexico (Florida to Veracruz, Mexico) (49 N to 19N); Lat median: 34N; Lon @ median: 77W	Europe (Baltic Sea to Portugal; Caspian and Black Seas; the Mediterranean Sea) (60N to 37N); Lat median: 49N; Lon @ median: 1E	6406	COI	0.727	0.690	Rhizocephala (N)	1.000	Projecto-Garcia *et al.* (2010); Fowler *et al.* (2013)	No parasites in the Baltic (Fowler *et al.*, 2013). *Loxothylacus panopaei* infects the crab in its native range, but no studies could be found that have looked for other parasites in the crab aside from *L. panopaei*.
Rhithropanopeus harrisii (Harris mud crab)	Crustacea	F	AQC	1988	Eastern N. America (Gulf of St Lawrence to Florida) and Gulf of Mexico (Florida to Veracruz, Mexico) (49 N to 19N); Lat median: 34N; Lon @ median: 77W	Texas Lakes (33N; 98W)	1946	COI	0.773	n/a	Rhizocephala (N)	1.000	Boyle *et al.* (2010)	No parasites have been found in inland lakes, and there is just one described parasite in the native range, Loxothylacus panopaei, but no studies have looked for other parasites in the crab.

continued **Tab. 7.1:** The 61 study systems (40 unique species) included in this review of genetic and parasite diversity data in marine invertebrate species from native and non-native regions worldwide.

Species: *Latin name* (Common name)	*Class*	F/P	Vector	Timing	Native range (region)	Non-native range (region)	Distance	Marker	Genetic Bottleneck Index $[(N_h - I_h)/N_h]$	Non-native / Native Haplotype Diversity	Parasite Taxa	Parasite Escape Index $[(N_p - I_p)/N_p]$	Citations	Notes
Ruditapes philippinarum *(Manila clam)*	Bivalvia	F	OYS	1970	Indo-Pacific (40N-1N); Lat median: 21N; Lon @ median: 110E	Europe (France: 48N-43N); Lat median: 45N; Lon @ median: 1W	9894	n/a	n/a	n/a	Trematodes (N, I)	0.600	Rybakov *et al.* (1983); Rybakov (1987); Hua (1989); Mei (1994); Lee *et al.* (2001); Lasalle *et al.* (2007); Park *et al.* (2008); Dang *et al.* (2009); Yanagida *et al.* (2009)	
Styela clava (club sea squirt)	Tunicata	F	OYS / BWF	1933	Northwest Pacific (Shanghai to the Sea of Okhotsk and southeastern Bering Sea) (61N to 31N); Lat median: 46N; Lon @ median: 138E	Western N. America (British Columbia to San Diego Bay, California) (50N to 32N); Lat median: 41N; Lon @ median: 124W	7388	COI	0.375	n/a	n/a	n/a	Goldstein *et al.* (2011)	
Styela clava (club sea squirt)	Tunicata	F	OYS / BWF	1970	Northwest Pacific (Shanghai to the Sea of Okhotsk and southeastern Bering Sea) (61N to 31N); Lat median: 46N; Lon @ median: 138E	Eastern N. America (Prince Edward Island to Virginia) (46N to 37N); Lat median: 42N; Lon @ median: 70W	9838	COI	0.375	n/a	n/a	n/a	Goldstein *et al.* (2011)	

continued **Tab. 7.1:** The 61 study systems (40 unique species) included in this review of genetic and parasite diversity data in marine invertebrate species from native and non-native regions worldwide.

Species: ***Latin name*** (Common name)	***Class***	**F/P**	**Vector**	**Timing**	**Native range (region)**	**Non-native range (region)**	**Distance**	**Marker**	**Genetic Bottleneck Index** $[(N_h - I_h)/N_h]$	**Non-native / Native Haplotype Diversity**	**Parasite Taxa**	**Parasite Escape Index** $[(N_p - I_p)/N_p]$	**Citations**	**Notes**
Styela clava (club sea squirt)	Tunicata	F	OYS / BWF	1953	Northwest Pacific (Shanghai to the Sea of Okhotsk and southeastern Bering Sea) (61N to 31N); Lat median: 46N; Lon @ median: 138E	Europe (Denmark to Portugal) (57N to 36N); Lat median: 46N; Lon @ median: 2W	9056	COI	0.438	n/a	n/a	n/a	Goldstein *et al.* (2011)	
Zoogonus rubellus	Trematoda	P	HOST (*Ilyanasaa obsoleta*)	1900	Eastern N. America (Canada to Georgia) (48N to 29N); Lat median: 39N; Lon @ median: 74W	Western N. America (SFB, WB and BB) (49N to 37N); Lat median: 46N; Lon @ median: 123W	4024	COI	0.936	0.933	n/a	n/a	Blakeslee & Fowler (2011); Blakeslee *et al.* (in prep)	Haplotype richness in native and non-native regions represent rarefied values

7.2 Methods

7.2.1 Data Sources

I gathered genetic and/or parasite data from studies of NIS marine or estuarine invertebrate species across populations in native and non-native regions. I focused on marine invertebrates because they are some of the most commonly introduced species globally (Cohen & Carlton, 1995; Ruiz *et al.*, 2000) and, additionally, they often serve as hosts to marine parasites (e.g. Lauckner, 1987a,b; Marcogliese, 2002; Torchin *et al.*, 2002). Although I attempted to include as many studies as possible, the data presented here are likely not exhaustive.

7.2.1.1 Genetic Diversity

To assess genetic diversity in marine and estuarine hosts in native and non-native regions, I used the list of species in Table 1 of Blakeslee *et al.* (2013) and in Table 1 of Roman & Darling (2007) as a first filter, and from there, I searched the literature for additional studies of NIS marine and estuarine invertebrates, concentrating on studies with mitochondrial (mt) DNA markers. I focused on mtDNA because mitochondrial markers (e.g., cytochrome oxidase I) have been used in numerous population genetics and bar-coding studies over the past couple of decades, resulting in ample available data for comparison and also allowing for the inclusion of introductions investigated in the recent past (Ratnasingham & Hebert, 2007). In a couple cases, mtDNA data was not available, and I instead reported nuclear markers.

7.2.1.2 Parasite Diversity

To assess parasite diversity and subsequent parasite escape in non-native versus native estuarine and marine regions, I primarily used the studies from Table 7.1 in Blakeslee *et al.* (2013) but also searched for any additional studies including parasite species richness in native and non-native regions in marine systems worldwide.

7.2.2 Data Extraction

For both genetic and parasite diversity, I extracted the following data from publications, online databases (e.g. Encyclopedia of Life, the USGS Nonindigenous Aquatic Species database, the Global Invasive Species Database, the National Exotic Marine and Estuarine Species Information System), regional websites reporting biogeographic information, or information in Table 7.1 of Blakeslee *et al.* (2013):

- *NIS Identification* to lowest taxonomic level as identified in publications.
- *NIS Taxa (including parasites)*: this included larger taxonomic groups. For free-living NIS, I used the *Class* level of classification; for parasites, I used the classi-

fication (often to *Class* or *Order* level) provided in published works. I ensured that this taxonomic classification was consistent across comparisons.
- *Free-living (F) or Parasitic (P)*: whether the species is free-living or parasitic. Many free-living species in this investigation also serve as hosts to marine parasites.
- *Introduction Vector*: as in Blakeslee *et al.* (2013), marine and estuarine hosts were categorized into the following bins based on their vector type:
  - APM—association with algal packing materials for live bait and trade
  - AQC—introductions associated with non-oyster aquaculture
  - BWF—ballast water and/or hull fouling associated with ballast-water-carrying vessels
  - CANAL—introductions following the creation of a canal, connecting two previously unconnected bodies of water
  - DEL—deliberate introductions not associated with aquaculture (e.g., research or bio-control).
  - DBF—dry ballast and/or fouling associated with solid-ballast-carrying vessels
  - HOST—a parasite that has been introduced with its host
  - OTHER—other accidental introductions
  - OYS—introductions associated with oyster transplantation
- *Timing of Introduction*: If multiple dates were listed, we used the earliest recorded date for timing of introduction; in addition, I assumed that the host introduction date was equivalent to the parasite introduction date. While in many cases this may not be correct (i.e., in cases of multiple introductions), introduction dates for parasites are typically not available or known; thus the host's introduction date was used as the best possible understanding of introduction timing for the parasite.
- *Native and Non-native Regions, and Native and Non-native Latitude and Longitude*: median whole number latitude was calculated from the most northern and southern extents of the host's native and invasive ranges, and longitude was classified at the median latitude point or, if within an enclosed sea, the median longitude point within that sea. Ranges for latitude and longitude were based upon reports from various databases and/or the literature and represented an approximation in order to calculate a relative direct line distance between the native and non-native regions (see below).
- *Distance (km) between Native and Non-native Regions*: using median whole number latitude and longitude values, I calculated distance between source and recipient ranges using NOAA's latitude/longitude distance calculator (http://www.nhc.noaa.gov/gccalc.shtml).
- *Molecular Marker*: the molecular marker used in the studies (with a focus on mitochondrial markers).
- *Genetic Bottleneck Index*: in order to directly compare with parasite escape, the genetic bottleneck index employed here uses the same formula as for parasite escape (Torchin *et al.*, 2003, see below) taking into account genetic richness

(i.e., haplotype richness for mitochondrial markers). It includes the total haplotype richness of a species' native range and the total haplotype richness of its non-native range as reported in publications and was calculated using the following formula: $[(N_h—I_h) / N_h]$, where N_h is haplotype richness in the native region and I_h is the haplotype richness in the introduced region. The index ranges from 0 to 1, where 0 would signify no bottleneck and values close to 1 would be a very strong bottleneck. Because these totals are influenced by sampling effort, rarefaction techniques were used in as many cases as possible to predict haplotype richness in native and non-native regions.

- *Ratio of Non-native to Native Genetic Diversity*: this is the ratio of the averaged haplotype diversity for all reported populations in the non-native region to the averaged haplotype diversity for all reported populations in the non-native region. The higher the ratio value (i.e., closer to 1.0), the more similar the two regions are in their haplotype diversity.
- *Parasite Escape Index*: this index includes the total taxonomic richness of parasites in a host's native range and the total taxonomic richness of parasites in its introduced range. The index is calculated as in Torchin *et al.* (2003): $[(N_p—I_p) / N_p]$, where N_p is the parasite taxonomic richness in the native region and I_p is the parasite taxonomic richness in the introduced region. The index ranges from 0 to 1, where 0 would signify no parasite escape and 1 would signify a complete escape from parasites. In non-native regions, parasite taxonomic richness in a host can include parasites introduced with the host, or those the host has newly acquired in its non-native range (Torchin & Mitchell, 2004).

7.2.3 Data Analysis

Three measures were used as response variables in analyses exploring patterns across the global dataset: the genetic bottleneck index, the ratio of non-native to native genetic diversity, and the parasite escape index. These indexes were compared across the various species represented in Table 1, and they were also analyzed for possible influences of vector type, NIS taxa, distance, and time since introduction using ANOVAs and post-hoc Tukey's tests. Pearson's correlations of the response variables were also performed for some analyses.

Where possible, I also explored these data using the known source area of an introduction rather than the whole native range; i.e., I calculated the genetic bottleneck and parasite escape indexes using data from the source area and the non-native region, and then compared it to the regional analysis (Table 7.1). This was to determine whether there would be differences in source versus whole region analyses since parasite escape might be overstated if the entire native range is included rather than the specific source populations from which the introduction originated (Colautti *et al.*, 2004; Colautti *et al.*, 2006).

Finally, I compared genetic data in hosts versus parasites to determine whether parasites are more likely to demonstrate stronger genetic bottleneck signatures and lower genetic diversity ratios than their hosts (Figure 7.2B). To date, few studies have investigated the genetic diversities of both host and parasite; thus, this analysis represents a preliminary exploration.

7.3 Results and Discussion

7.3.1 Trends in NIS Species Classification and Source/Recipient Regions

In this global review, I found 61 systems (Table 7.1) that included genetic diversity (focused on mtDNA), parasite diversity, or both in native and non-native regions. This yielded 40 unique marine invertebrate species, 31 of which were free-living and 9 of which were parasite species. Altogether, these species represented 7 invertebrate *Classes: Asteroidea*, *Bivalvia*, *Crustacea*, *Gastropoda*, *Tentaculata*, *Trematoda*, and *Tunicata*. Bivalves, crustaceans, and gastropods made up the majority of the species represented in the study systems (Figure 7.3), similar to several prior investigations (e.g., Cohen & Carlton, 1995; Ruiz *et al.*, 2000; Blakeslee *et al.*, 2013) demonstrating the dominance of these three *Classes* in marine invasions worldwide.

The native (source) regions *from which* the 61 systems originated included five continents: Asia, Australia, Europe, North America, and South America. Non-native (founding) regions where species were *introduced to* included the same five continents and additionally Africa (Figure 7.4). However, proportions of species introductions differed between founding and source regions. For example, Asia was the continent *from which* most introductions originated, followed by North America and Europe (Figure 7.4A), but

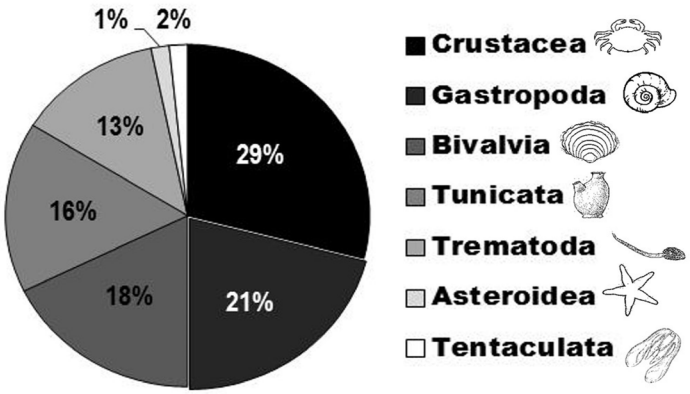

Fig. 7.3: The proportion of species in Table 7.1 that were the following seven Classes: Asteroidea, Bivalvia, Crustacea, Gastropoda, Tentaculata, Trematoda, and Tunicata. Crustaceans, gastropods, and bivalves made up two-thirds of all species introduced to new locations worldwide based on the studies in this investigation.

Asia had one of lowest proportions of species *introduced to* it (i.e., Asia was an important source but not recipient region). Instead, North America had the largest proportion of species introduced to it (>50% of all introductions; Figure 7.4B), while Europe was second highest, and collectively, North America and Europe made up over two-thirds of all the introductions *to* and *from* these regions. Several mechanisms may explain these patterns, including: *Global shipping*—in recent years, shipping has been dominated by Asian, North American and European ports, enhancing the likelihood of species transfer among these regions (Carlton, 1992; Ruiz *et al.*, 2000); *Oyster translocations*—this prominent global vector has been responsible for the accidental introduction of numerous hitchhiking species associated with oysters (e.g., bivalves, gastropods, crustaceans, and tunicates), and oysters in this vector primarily originate from two major regions: eastern North America, where *Crassostrea virginica* is native, and Asia, where *Crassostrea gigas* (Pacific oyster) is native (Ruesink *et al.*, 2005); and *Sampling bias*—many more studies published in English have been conducted in North America and Europe, and as such, reports of non-native species may be biased towards these two regions; for example,

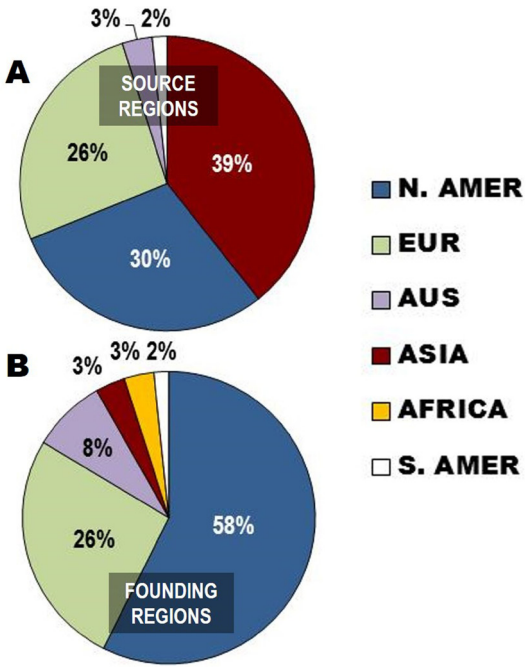

Fig. 7.4: The proportion of species in Table 7.1 that (A) came from (source regions) and were (B) introduced to (founding regions) the six continents listed above. Collectively, Asia, North America (N. AMER) and Europe (EUR) made up the largest proportion (95%) of the source regions, while Australia (AUS) and South America (S. AMER) made up the remaining 5%. In contrast, North America had the largest proportion (57%) of founding species introduced to the region, representing more than half the number of introductions for the species in Table 7.1, while Asia had one of the lowest proportions (3%).

Pysek *et al.* (2008) found clear sampling biases in invasion ecology research across continents, whereby the regions that were the most well studied were: North America > Europe > Australia > South America > Asia > Africa. With the exception of South America, these trends mirror our own data in terms of the founding/recipient regions (Figure 7.4B), where North America > Europe > Australia > Asia > Africa > South America.

7.3.2 Comparisons of Parasite Escape, Genetic Bottlenecks, and Haplotype Diversity across Studies

In general, the genetic bottleneck and parasite escape indexes showed fairly similar patterns, demonstrating about a 50% loss of haplotypes compared to a 66% loss of parasites in non-native regions compared to native regions (Figure 7.5). In fact, there was a significant positive correlation between parasite and genetic diversity losses in non-native versus native regions (Figure 7.6). This may suggest that the invasion process operates in a similar fashion for both parasite escape and genetic bottlenecks in influencing the number (and potentially types) of alleles and parasites that "survive" the process and are introduced (or not) to the new region.

While the two indexes appear to congruently support signatures of enemy release and genetic founder effects, the non-native to native haplotype diversity analysis provides seemingly contradictory results. In particular, non-native haplotype diversity represented about 75% of native haplotype diversity (Figure 7.5), suggesting less diversity loss at the population level in non-native regions rather than collectively across the region. Such a pattern for limited reductions in genetic diversity in

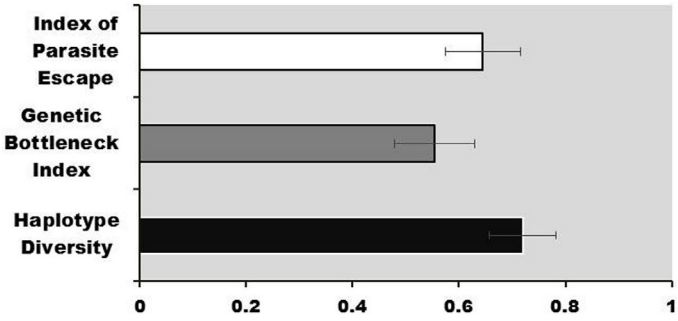

Fig. 7.5: The two indexes based on native and non-native diversity (see Methods and Table 7.1 for formulae) and the ratio of non-native to native haplotype diversity. Both indexes and the ratio represent averages (± SE) across all studies in the investigation. Both indexes demonstrate substantial levels of parasite escape and genetic bottlenecks (i.e., there has been a loss of more than 50% of the parasites and haplotypes in non-native regions). In contrast, haplotype diversity demonstrates a less substantial decline in average population-level genetic diversity in non-native versus native regions.

non-native versus native populations was the subject of the Roman & Darling (2007) paper, "Paradox lost: genetic diversity and the success of aquatic invasions". Roman & Darling (2007) hypothesized that this genetic 'paradox' – higher levels of genetic diversity than might be expected in recent founding events – could be due to multiple introductions and high levels of propagule pressure, which would result in a lessened bottleneck (see adapted Figure 7.2A). While this 'paradox' is likely playing a role here, especially for some groups (see below), another possible reason for this pattern could be because introduced populations may have been better sampled for genetic diversity than native populations, possibly limiting the ability to detect differences in average population diversity between native and non-native regions.

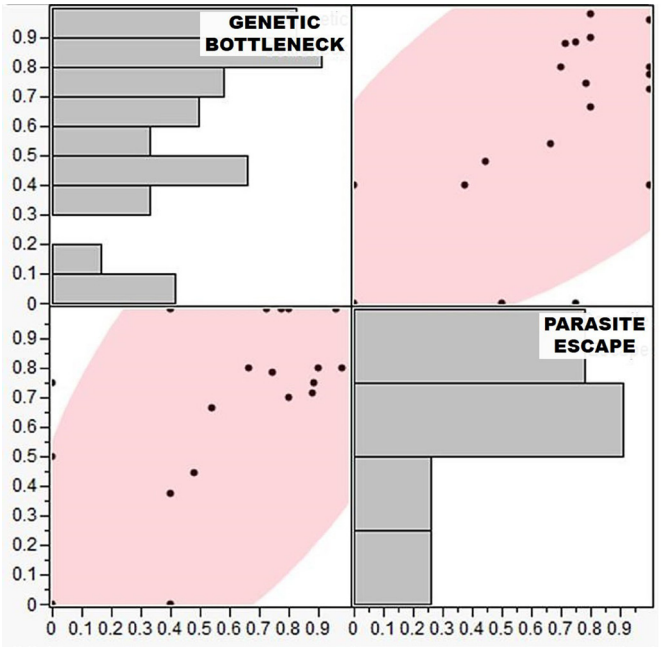

Fig. 7.6: Scatterplot Matrix of genetic bottleneck and parasite escape index correlations. This figure demonstrates correlations between the two indexes and histograms representing frequencies of proportion bins for each variable. Using a Pearson's pairwise correlation analysis, a significant positive correlation was found between the two indexes (Pearson's r = 0.637; p = 0.0025).

7.3.2.1 Source Area Analysis

While the results above suggest a substantial loss in both parasite and genetic diversity in non-native regions, they were based upon multiple native populations averaged across a larger regional exploration, which could overstate diversity losses if more precise source areas for introductions are not used for native versus non-native comparisons (Colautti *et al.*, 2004; Colautti *et al.*, 2005). The reality is that in many cases,

a precise source area is unknown or difficult to pinpoint. Here, I attempted to explore whether I might find a 'source effect' in my data; however, source subregions could only be ascertained in six study species that also had available parasite and genetic diversity data. These six species included: *Batillaria attramentaria* (Asian hornsnail)—introduced from source populations in Japan to Pacific North America; *Carcinus maenas* (European green crab)—originally introduced from source populations in central/southern Europe to northeastern North America; *Ilyanassa obsoleta* (eastern mudsnail)—introduced from source populations in the mid-Atlantic USA to Pacific North America; *Littorina littorea* (common periwinkle)—introduced from the British Isles to northeastern North America; *Littorina saxatilis* (rough periwinkle)—introduced from northeastern USA to San Francisco Bay in Pacific North America; and *Rhithropanopeus harrisii* (Harris mud crab)—introduced from the Gulf of Mexico to inland Texas lakes in the USA. *Littorina littorea*, *L. saxatilis*, and *R. harrisii* have also been introduced to other locations around the world, but I only focused on the introductions described above for this analysis. Moreover, *C. maenas* has had two introduction events to northeastern North America (Roman, 2006), but this analysis focuses on the original 1800s introduction.

Altogether, there was some evidence for a 'source effect' on resulting patterns of parasite escape and genetic bottlenecks, but this was primarily for genetic diversity, where two species (*I. obsoleta* and *R. harrisii*) demonstrated substantial drops in genetic bottlenecks for source versus native regions, while another species demonstrated a modest decline (*B. attramentaria*) (Figure 7.7). In contrast, parasite escape showed much less of an effect, and only two species (*B. attramentaria* and *C. maenas*) demon-

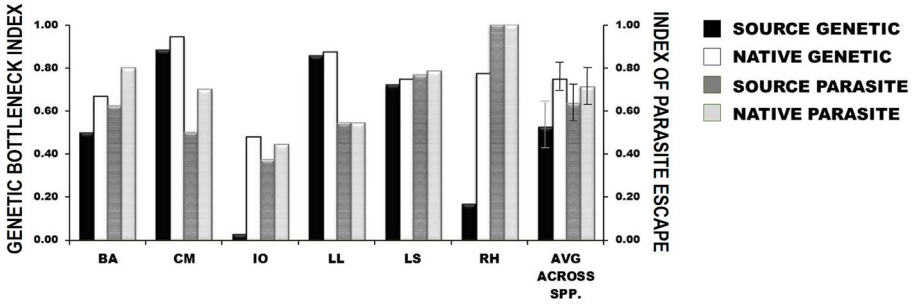

Fig. 7.7: An exploration of 6 study species where parasite and genetic diversity were reported for the native range as a whole and also for a more precise source area. The figure demonstrates the extent of the genetic bottleneck for the source area (black) and the larger native region (white), and the extent of parasite escape for the source area (dark gray) and the larger native region (light gray). Also calculated is the average across all six species. While the focus on source data can provide a more precise understanding of genetic and parasite diversity losses in non-native regions for some individuals, the analysis here of a small subset of the studies in Table 7.1 found no significant difference in parasite escape ($p = 0.64$) and genetic bottlenecks ($p = 0.478$) averaged across the six study species for source versus regional analyses. BA = *Batillaria attramentaria*, CM = *Carcinus maenas*, IO = *Ilyanassa obsoleta*, LL = *Littorina littorea*, LS = *Littorina saxatilis*, RH =*Rhithropanopeus harrisii*.

strated modest reductions in source versus native regions. When averaged across the six species, there was no evidence of a 'source effect' in one-way ANOVAs for genetic bottlenecks ($p = 0.478$) and parasite escape ($p = 0.649$), nor in a two-way ANOVA for both indexes ($p = 0.783$).

On the whole, these data suggest (albeit based on a small sample) that pinpointing precise source regions may help better understand effects on parasite and genetic diversity in non-native regions for some species. However, more data are needed to determine if these results are representative across systems, or if it is species- and/or invasion pathway-dependent. For example, in Figure 7.7, *I. obsoleta* showed evidence of a 'source effect' for genetic diversity; this may be due to its invasion vector—oysters—which are commonly associated with strong entrainment and transfer of propagules to non-native regions. *Ilyanassa obsoleta* was introduced to the west coast as a hitchhiking species with commercial shipments of the eastern oyster (*Crassostrea virginica*) (Carlton, 1992), and these shipments occurred on a massive scale sustained over many years (Miller, 2000); in addition, oysters were packaged for shipping in a manner ensuring their survival, and also enhancing the survival of hitchhiking organisms (Carlton, 1979). Thus, the intentional movement of oysters and associated individuals (including parasitized ones) has likely strongly influenced parasite escape and genetic bottlenecks in this species. In contrast, another intertidal snail species, *L. saxatilis*, demonstrates much greater levels of both parasite escape and genetic bottlenecks in its introduced region on the USA west coast, where there is little difference between source and regional analyses (Figure 7.7). Its introduction vector is much different: *L. saxatilis* was transferred to the west coast as an associate of packing algae in the live baitworm trade (Carlton & Cohen, 1998). In general, the magnitude of algal packing materials and associated individuals transferred with the live bait vector is far less than for commercial oysters, and the vector itself is accidental, which would promote fewer associated individuals than the intentional oyster vector (Blakeslee *et al.*, 2012).

7.3.3 Introduction Vector, NIS Taxa, Distance between Source and Recipient Region, and Time since Introduction

7.3.3.1 Introduction Vector

Because some vectors are associated with higher levels of propagule pressure than others, these vectors may be more likely to introduce parasites and alleles. When I explored this possibility, I found no significant differences ($p = 0.364$) in a two-way ANOVA for the two indexes with vector; however, when vectors were lumped into intentional (e.g., aquaculture/oysters) versus accidental (e.g., wet and dry ship ballast, hull fouling, and hosts) vectors, I found a significant difference between intentional and accidental vectors for both genetic bottlenecks ($p = 0.041$) and parasite escape ($p = 0.049$) in individual one-way ANOVAS and also in a two-way ANOVA

(p = 0.042) (Fig. 8). As discussed in Blakeslee *et al.* (2013), accidental vectors like ballast water may be less likely to introduce parasites than intentional vectors like oysters because ballast water primarily transfers larvae from native to non-native locations and larvae are not typically the infective stages of most marine parasites; moreover, propagule pressure (especially related to introduction of parasites) would be expected to be higher for intentional introductions, like oysters, versus accidental vectors, like ballast water (Torchin & Mitchell, 2004). In fact, Torchin & Lafferty (2009) suggested that "ballast water introduction may be a particularly potent means for marine species to escape parasites." While some of these expectations might also hold true for genetic bottlenecks, introduced larvae via shipping vectors could still contribute to the genetic diversity of a NIS' non-native region, and this may help explain why there was a trend for the ballast water vector to have a higher index of parasite escape than a genetic bottleneck (Figure 7.8). Altogether, these results may also support some of the expectations presented in Figure 7.2A, where certain vectors would be more likely to lead to strong bottlenecks, while others show little difference between native and non-native regions as a result of high propagule pressure and multiple introductions.

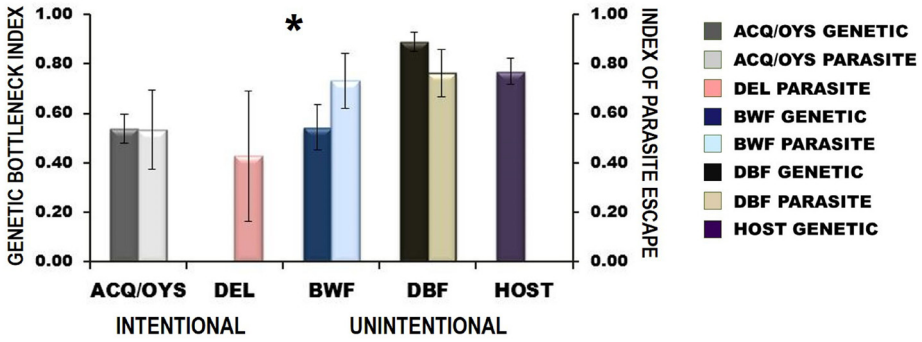

Fig. 7.8: Analysis of vector as a factor influencing the genetic bottleneck index (dark shades) and the parasite escape index (light shades). While there were no significant differences for vector, there was a significant difference between intentional and accidental vectors, whereby intentional vectors demonstrate lower levels of genetic bottlenecks and parasite escape than unintentional vectors (represented by a *). AQC/OYS = aquaculture/oysters; DEL = deliberate, non-aquaculture introduction; DBF = dry ballast & fouling; HOST = parasite introductions with their host.

7.3.3.2 NIS Taxonomy

When I explored the effect of NIS taxonomy (at the *Class* level) in native versus non-native regions in individual one-way ANOVAs, I found a significant effect of *Class* on the genetic bottleneck index ($p < 0.0001$) and the parasite escape index ($p = 0.043$), and also in a two-way ANOVA for both indexes ($p = 0.010$). For para-

site escape, there was only sufficient data for bivalves, crustaceans, and gastropods. Post-hoc analyses demonstrated similar results for bivalves and crustaceans for both indexes, where crustaceans had significantly ($p < 0.05$) greater genetic and parasite diversity losses compared to bivalves. Moreover, for the genetic bottleneck index, two other groups—gastropods and trematodes—also demonstrated significantly ($p < 0.05$) greater diversity losses than bivalves (Figure 7.9). These data suggest the importance of taxonomic groups in influencing the introductions of alleles and associated parasites; e.g., congruent signatures between the two indexes for two *Classes*: crustaceans and bivalves. In both cases, crustaceans demonstrated much greater parasite escape and loss of haplotypes in non-native regions than did bivalves. Another interesting finding was how much lower the two indexes were for bivalves compared to the other investigated *Classes*. A similar result was observed just for parasite escape in the global review by Blakeslee *et al.* (2013). A possible explanation is that one of the most prominent bivalves in our analysis was the Pacific oyster, *Crassostrea gigas*, which is not only a vector for movement of other free-living organisms (including other bivalve species) but also for the transmission of hitchhiking parasites (Ruesink *et al.*, 2005). As a result, propagule pressure is likely much higher for this vector, and correspondingly, greater numbers of associated alleles and parasites could be transferred with the bivalve to introduced regions. Moreover, the results of this analysis further exemplify the expectations in Figure 7.2A; however, in this case, some taxonomic groups (e.g., bivalves) are more associated with higher propagule pressure and introduction of alleles and parasites than others (e.g., crustaceans) that demonstrate strong bottlenecks and parasite escape.

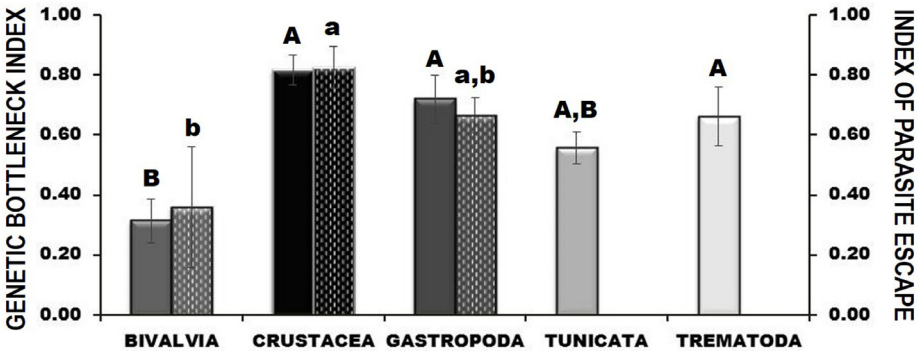

Fig. 7.9: Analysis of taxonomy as a factor influencing the genetic bottleneck index (dark shades) and the parasite escape index (patterned shades) by Class. There was a significant effect of Class on the genetic bottleneck index ($p < 0.001$). Post-hoc Tukey's tests revealed significant differences between crustaceans and bivalves ($p < 0.001$), gastropods and bivalves ($p = 0.007$), and trematodes and bivalves ($p = 0.021$); crustaceans and tunicates showed a nearly significant difference ($p = 0.063$). For parasite escape, the overall analysis was also significant ($p = 0.043$), and there was a significant difference between crustaceans and bivalves ($p = 0.034$). Significance is represented by upper case letters for genetic bottlenecks and lower case letters for parasite escape.

7.3.3.3 Distance between Source and Recipient Regions

Distance between source and recipient regions might be expected to influence parasite and genetic diversity in non-native regions because distance can serve as a proxy for transit time and stress on hitchhiking organisms (Miller & Ruiz, 2009). In other words, if the distance between the source and recipient regions is short, the native and non-native ranges are likely to experience more frequent connectivity, to share more phylogenetically similar taxa, and to allow for a greater proportion of entrained species (and parasites) to survive the journey (e.g. Drake & Lodge, 2004), which may lead to less pronounced bottlenecks and parasite escape. In my analyses, I found little support for this expectation (parasite escape: R = 0.001; p = 0.636; genetic diversity: R = 0.004; p = 0.862; native to non-native ratio: R = 0.084; p = 0.066), except in a couple instances for specific groups: there was a significant positive correlation between the genetic bottleneck index and distance for *Tunicata* ($R^2 = 0.419$; p = 0.043), thus the bottleneck increased with distance, and there was also a significant negative correlation for the non-native to native haplotype diversity ratio and distance for the aquaculture/oyster vector (Figure 7.10); in other words, as distance increased, population-level haplotype diversity was lower in non-native regions compared to native regions. This result is a bit more difficult to explain considering the strong propagule pressure in the oyster vector, thus I would have predicted little effect of distance for this vector type. There were no apparent patterns for parasite escape.

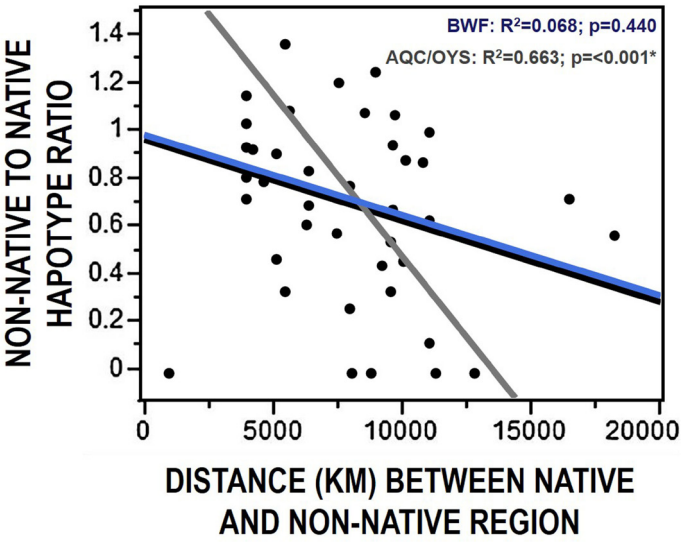

Fig. 7.10: Regression of the ratio of non-native to native haplotype diversity with distance (km) between source and recipient regions, grouped by vector. Altogether, there was a significant negative correlation for the vector, AQC/OYS (gray line), but no correlation for BWF (blue line).

7.3.3.4 Time since Introduction

Finally, I explored the potential effect of time since introduction on genetic or parasite diversity in non-native regions. Time since introduction may be expected to have an effect if older introductions have had more time to accrue more alleles and more parasites than newer introductions (Torchin & Lafferty, 2009). However, I found no effect of introduction timing on either of the two indexes, nor on the ratio of non-native to native haplotype diversity based on the study species in Table 7.1 (data not shown).

7.3.4 Do Parasites Demonstrate Greater Losses of Genetic Diversity in Non-native Regions than their Hosts?

In Figure 7.2B, I proposed that parasites may be more likely to demonstrate genetic bottlenecks compared to their hosts based on their more complex life cycles, which often require multiple suitable hosts. For this analysis, I was only able to compile evidence for four hosts where there was also genetic evidence for their parasites (n = 7). My analysis here based on these four hosts and seven parasites does not appear to support this hypothesis for either response variable (p = 0.616 and p = 0.814, respectively), albeit the sample size is very small (Figure 7.11). While Blakeslee & Fowler (2012) found some support for greater genetic diversity in aquatic systems (freshwater and marine) for non-native hosts compared to parasites, presently there is too little evidence in marine systems to adequately assess this question. More host-parasite systems need to be analyzed in order to determine whether such a pattern is likely to exist across multiple marine communities.

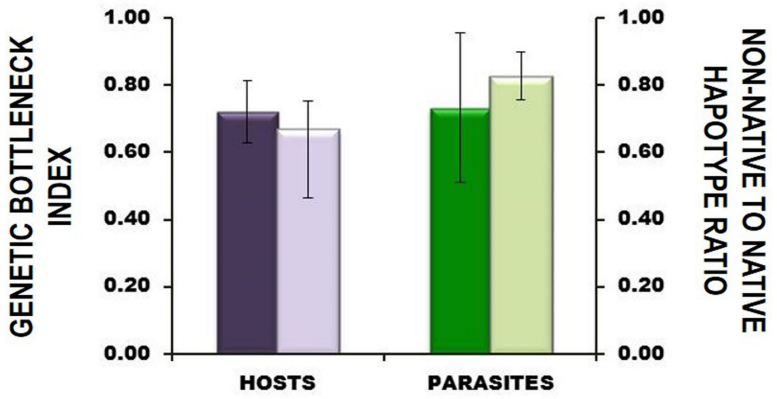

Fig. 7.11: The genetic bottleneck index (dark shades) and the ratio of non-native to native haplotype diversity (light shades) in hosts versus parasites. This analysis includes four hosts (*B. attramentaria*, *I. obsoleta*, *L. littorea*, and *R. harrisii*) and seven parasites (six trematodes and one rhizocephalan). Altogether, there is no difference between hosts and parasites for either analysis.

7.3.5 Conclusions: Parasite and Genetic Analyses—Implications for their Use in Marine Invasions

Altogether, these results demonstrate the complexity of marine introductions and how they are influenced by several variables associated with their invasion pathway, e.g., vector, source area, NIS taxa, and geography. In particular, I found trends for differences in diversity analyses based on the type of vector and propagule pressure; e.g., intentional vectors demonstrated lessened bottlenecks and parasite escape than did accidental vectors. I also found a significant effect of NIS taxa on diversity indexes, particularly for crustaceans and bivalves, which demonstrated higher versus lower losses of diversity, respectively. I also found geographic distance between source and recipient regions to be a factor for a few vector and taxonomic comparisons.

Even with all this complexity, my analysis continues to support conventional expectations for genetic founder effects and parasite escape in non-native regions, in that both haplotype and parasite richness were significantly lower in non-native versus native regions in this global review. In addition, I found a significant, positive correlation between the index of parasite escape and the genetic bottleneck index, showing that reductions in both parasite and genetic diversity can be closely linked and that they represent strong signatures of invasion—albeit, depending on propagule pressure, the signature may be a lot less apparent for some NIS than for others (Figure 7.2A; Roman & Darling, 2007).

On the whole, these results further emphasize the utility of these two signatures, especially when used together and with other lines of evidence for helping to resolve uncertain invasion histories and those species where invasion status remains uncertain (cryptogenic). These signatures can be especially important when historical information about the species is vague or unknown. For example, originally thought to be native to Europe, the Portuguese oyster (*Crassostrea angulata*) was discovered within the last 15 years to have actually been introduced from Asia as a result of intentional transplantation by Portuguese traders in the 16th century. As a result of its misclassified status, management and conservation plans in Europe had been based upon its incorrectly assigned native status, and there was even concern about the possible impact of the Pacific oyster, *C. gigas*, on the abundance and distribution of *C. angulata* in the region (Huvet *et al.*, 2000). The use of genetics, therefore, was very important in resolving this misconception and the oyster's true origin. Moreover, there are numerous other examples for how genetic data can be a highly important tool in marine investigations (reviewed in Geller *et al.*, 2010), and many other investigations on the use of parasite diversity in better understanding host invasions (reviewed in Blakeslee *et al.*, 2013); however, few investigations have explored these two invasion signatures in concert. Such a combination can be an even more powerful approach for resolving uncertainties and better understanding invasion processes in marine invertebrate systems, particularly gastropods, bivalves, and crustaceans, which are the most commonly intro-

duced marine organisms globally (e.g., Ruiz *et al.*, 2000) and also common hosts for marine parasites (e.g., Torchin *et al.*, 2002). For example, via host and parasite genetic analyses, Miura *et al.* (2006) were able to pinpoint the source area within Asia for *B. attramentaria's* introduction to western North America, and they also discovered that what was originally believed to be a single associated parasite species introduced with the snail was, in actuality, three cryptic species.

In conclusion, while genetic evidence has been recognized as a powerful tool in biological investigations for many years, parasites have been an understudied resource. In this review, I have demonstrated how parasites can be highly valuable to studies of global marine invasions, especially in cases where numerous uncertainties exist—a common reality in many NIS studies that go undetected for years following a successful introduction. In turn, there may be a multitude of questions surrounding an invasion; thus, innovative scientific clues may be required. As argued here, a combination of parasite and genetic evidence, along with other sources of evidence, could in fact provide the needed proof to resolve many of these challenging invasion questions. Moreover, for many invasive species, parasite and genetic diversity losses may in fact correlate, providing even more informative evidence for studies of biological invasions.

7.4 Acknowledgements

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In a nutshell

- The movement of marine organisms, especially invertebrate species, has rapidly increased with enhanced human globalization. As a result, accidental or intentional introductions of marine NIS have added numerous new species to marine ecosystems, including parasites—less visible associates of invading species that can have major impacts on native communities.
- Two patterns often emerge in species introductions: significant genetic bottlenecks (i.e., founder effects) and significant reductions in parasite diversity (i.e., parasite escape) in founding populations. While both signatures are apparent in some systems, one or both may be less so in others, especially when there have been multiple introductions. Yet few studies have synergistically examined these signatures to determine potential correlations, or if variables associated with invasion pathways influence the patterns.
- Using a meta-analysis of global marine invertebrate introductions with parasite and/or genetic evidence, this study found haplotype and parasite richness to be significantly lower in non-native versus native regions at large scales; additionally, positive correlations were found between the two diversity indexes. Results also demonstrated the complexity of marine introductions and the influence of invasion pathway variables on genetic and parasite diversity patterns, including vector, source area, NIS taxa, and geography.
- While genetic evidence has long been recognized as a powerful tool across biological disciplines, the role that parasites can play in such investigations is much less recognized. This study demonstrates the importance of both signatures in better understanding biological invasions.

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