We are IntechOpen,
the world's leading publisher of
Open Access books
Built by scientists, for scientists

4,400
Open access books available

118,000
International authors and editors

130M
Downloads

Our authors are among the

154
Countries delivered to

TOP 1%
most cited scientists

12.2%
Contributors from top 500 universities

CLARIVATE ANALYTICS
BOOK CITATION INDEX
INDEXED

WEB OF SCIENCE™

Selection of our books indexed in the Book Citation Index
in Web of Science™ Core Collection (BKCI)

Interested in publishing with us?
Contact book.department@intechopen.com

Aquatic Introductions and Genetic Founder Effects: How do Parasites Compare to Hosts?

April M. H. Blakeslee and Amy E. Fowler
Long Island University, CW Post Campus
Smithsonian Environmental Research Center
USA

1. Introduction

Aquatic parasites have intrigued researchers over the past several decades due to their often unique and complex life cycles, which can require multiple hosts to progress from larval to adult reproductive stages (Shoop, 1998). Parasites are also integral in community and ecosystem functioning and have the potential to impact community structure through direct (e.g., affecting host growth, reproduction, and survivorship) or indirect (e.g., influencing host predation and/or competition) means (Lafferty & Morris, 1996; Torchin et al., 2002; Blakeslee et al., 2009). Recently, parasites have become recognized not only as interesting biological/model species, but also as useful indicator species and biological tools for resolving ecological questions. For example, parasites can be indicators of ecosystem health (Huspeni & Lafferty, 2004) or even utilized to more accurately resolve questions surrounding cryptic species invasions (Blakeslee et al., 2008) or biogeographic movements of hosts (Criscione et al., 2006). Even with these recent developments in aquatic parasite research, and although parasites are known to represent a fundamental component of aquatic systems worldwide (Kuris et al., 2008), genetic diversity patterns of aquatic parasites are much less understood than they are for free-living species. This is especially true for hosts/parasites with broad habitat ranges across bioregions and those introduced to new locations through anthropogenic transport. We believe these knowledge gaps exist for two major reasons: 1) parasites are less visible than free-living species and 2) parasites are logistically more challenging to study (i.e., often requiring destructive sampling, knowledge of parasite taxonomy, and parasite specific genetic markers). Even still, parasites have numerous interesting and important ecological, evolutionary, and conservation implications, including those related to their population genetics in introduced versus native regions. Aquatic parasites thereby represent an important, but overlooked, ecological group. In addition, aquatic invasions are on the rise in recent years (Carlton & Geller, 1993; Ruiz et al., 2000); yet the importance of parasites in those invasions (which have increased both in frequency and in distribution) is often less understood and/or tracked. Therefore, for this chapter, we focus on aquatic parasites, closely exploring how species introductions may affect genetic diversity patterns differently in parasites versus their free-living hosts.

Theoretically, anthropogenic introductions are believed to result in apparent founder effect signatures, whereby the introduced population(s) are subjected to an extreme genetic

bottleneck, resulting in significantly lower genetic diversity in the introduced population(s) compared to native populations (Grosberg & Cunningham 2000). Moreover, in some systems, genetic bottlenecks have been correlated with detrimental fitness effects in individuals in the non-native population (Reed & Frankham 2003). However, a recent review by Roman & Darling (2007) found that many introduced populations retained high levels of genetic diversity (i.e., no genetic bottleneck or apparent founder effect signatures), which was counter to theoretical expectations for known introduced populations. The authors suggested that this 'genetic paradox' was likely due to the inherent complexity and individuality of each invasion pathway, which is strongly affected by the number of introduced individuals and the frequency of introduction events (i.e., propagule pressure), as well as invasion timing, effective population size, and the type of introduction vector (Voisin et al., 2005, Roman & Darling, 2007, Darling et al., 2008). Thus, population genetics signatures will be strongly influenced by each species' particular invasion pathway (Roman, 2006; Roman & Darling 2007; Geller et al., 2010).

Not included in the review by Roman & Darling (2007), however, were parasites which, as discussed above, are integral members of aquatic communities. Thus, it remains unclear how genetic diversity patterns across parasite groups could be affected by their hosts' individual invasion pathways. In particular, one important factor to consider is that only a subset of all hosts introduced to a new location will harbor parasites. In addition, parasite life cycles can be highly complex, often requiring multiple hosts (Shoop, 1988). As such, parasite founding populations will be small and subject to evolutionary forces that tend to reduce genetic variability in small populations (i.e., genetic drift). In addition, Allee effects may serve to further reduce variability in newly formed parasite populations if individuals cannot successfully mate and pass on their genes (Chang et al., 2011). In fact, a parasite's complex life cycle could serve to heighten Allee effects since successful reproduction in many aquatic parasite species requires transmission through multiple hosts, and at some stages in the life cycle, host species can be highly specific, if not obligate. This, in turn, may result in inherent challenges for a parasite's successful establishment in a new region (especially if gene flow is limited), which could potentially further reduce genetic diversity and influence its ability to find and infect appropriate hosts vital to its life cycle. In fact, introduced parasite species with complex life stages are expected to show divergent evolutionary patterns at local versus geographic scales (for example, native versus introduced ranges) due their distinct life histories as well as due to the mobility of their hosts (Jarne & Theron, 2003; Prugnolle et al., 2005). For example, highly mobile definitive hosts can play an important role in reducing the genetic variation within populations of parasites by disseminating eggs over long distances (Blouin et al., 1995; Kennedy, 1998; McCoy et al., 2003; Gittenberger et al., 2006; Louhi et al., 2010), potentially outside the area where the parasite's other hosts are present.

As a result of the important evolutionary and ecological distinctions of parasite life cycles compared to their free-living hosts (briefly summarized above), we were curious how genetic diversity patterns may differ between introduced parasites and hosts, and whether parasites would be more likely to exhibit theoretical genetic founder effect signatures than their hosts. Therefore, we ask the following questions: will aquatic parasites exhibit different genetic diversity signatures than their hosts in introduced versus native ranges? And more specifically, will they be more likely to conform to genetic bottlenecks and apparent founder effect signatures than their hosts? Here, we present both a review of the literature and a

specific case study to explore these questions, and determine whether general patterns may be observed across systems.

2. Literature review

Below, we present a review of freshwater and marine studies that explores genetic diversity patterns in native and introduced populations in parasite-host systems. We searched for studies using multiple databases and the following keywords: "parasite" "genetic diversity" "introduction/invasion" "host" and "marine" OR "freshwater". Our goal was to compile data and information that could provide insight into our questions above, as well as a general understanding of what is currently known about source and founding population genetics of marine and freshwater hosts and parasites.

2.1 Freshwater systems

While numerous freshwater parasites have rapidly expanded their ranges due to introduced hosts (Taraschewski 2006), studies explicitly focused on the patterns of freshwater parasite and host genetic diversity in native and introduced populations are rare. Those studies that do exist appear to support reductions in genetic diversity in introduced parasite populations, possibly due to single introduction events of host species and subsequent genetic drift in isolated and small populations (e.g., as observed in the Japanese eel swim bladder nematode, *Anguillicola crassus*; Wielgloss et al., 2007, 2008). In some cases, phylogeographic patterns may be affected by mobile definitive hosts which prevent genetic isolation of freshwater parasite populations on a local scale, but at the global scale, parasite populations are genetically isolated and strong genetic differentiation exists among populations (as observed in a tapeworm (*Ligula intestinalis*) introduced to Australia, New Zealand, and North Africa (Bouzid et al., 2008)). However, such a scenario for isolation and genetic differentiation is not always apparent; for example, populations of the introduced eel parasite, *Gyrodactylus anguillae*, in three separate continents exhibit similar genetic structures and identities, hinting at the existence of multiple independently introduced populations from one source population (Hayward et al., 2001). This particular species is unusual, however, in that it has a direct life cycle, increasing their potential to establish new populations with few propagules (Hayward et al., 2001).

The introduction of exotic parasite species in freshwater systems are mainly known from fish species that have been traditionally used for human consumption (e.g., infections in commercial fish by the cestode, *Bothriocephalus acheilognathi* (Font, 1998); monogeneans of the fish genera, *Pseudodactylogyrus* and *Cichlidogyrus* and *Gyrodactylus*; the nematode *Anguillicola crassus* (Ashworth & Blanc, 1997); the tapeworm *Ligula intestinalis* (Bouzid et al., 2008); the leech *Myzobdella lugubris* (Font, 1998), and the heterophyid trematode *Centrocestus formosanus* (Martin, 1958)). However, relatively little is understood about parasite genetic population structure in these parasites compared to that of their hosts (but see Dybdahl & Lively 1996; Criscione & Blouin 2004; Stohler et al., 2004; Rauch et al., 2005; Keeney et al., 2007) and even less is known about how genetic diversity patterns are modified when introductions occur. Several studies have suggested the existence of strong genetic bottlenecks in introduced freshwater parasite populations (e.g. Weekes & Penlington, 1986; Dove, 2000; Tompkins & Poulin, 2006), but these remain to be empirically tested. However, a recent study has found no evidence for genetic bottlenecks during the Ponto-Caspian invasion of the amphipod

crustacean *Dikerogammarus villosus* or its associated microparasites (Wattier et al., 2007). An even more complicated parasite system is that of the amphipod, *Crangonyx pseudogracilis*, which exhibits a reduction in post-invasion genetic diversity while its associated microparasites do not (Slothouber-Galbreath et al. 2010). Our review therefore suggests that much remains to be understood regarding post-invasion freshwater parasite systems, and there is great potential for comparable global studies in native and introduced freshwater populations that would help resolve questions regarding host versus parasite genetic diversity patterns. In particular, further understanding of how parasite "spillover" (i.e., when an introduced host transmits its parasites to susceptible native hosts) and parasite "spillback" (i.e., when introduced species are susceptible to endemic parasites in the invaded range) affect host versus parasite genetic diversity patterns would be highly informative, given the effects it would have on parasite reproduction and life cycle transmission, especially in small, isolated populations (Dieguez-Uribeonodo & Soderhall, 1993; Barton, 1997; Dunn & Dick, 1998; Rauque et al. 2003; Torchin et al., 2003; Prenter et al., 2004; Münderle et al., 2006; Kelly et al., 2009).

2.2 Marine systems

Like freshwater systems, studies empirically focused on the differences in genetic diversity of both parasites and their hosts in native versus introduced regions in marine environments remain scarce. Recent studies have focused on resolving the cryptic status of many introduced parasites. For example, Kruse & Hare (2007) utilized molecular techniques to test for genetic homogeneity between native (Gulf of Mexico) and introduced (western Atlantic coast) populations of *Loxothylacus panopaei*, a rhizocephalan parasite of mud crabs. Their results demonstrated a high rate of southward expansion of this introduced parasite species on a scale of tens of kilometers per generation, and they were able to more accurately pinpoint the location of the source population to the western Gulf of Mexico. Parasites have also been used to explain unresolved or cryptic statuses of their hosts in introduced populations to unravel invasion histories. For example, Burreson et al. (2000) resolved the identity of a parasite (*Haplosporidium nelsoni*) in introduced Californian populations of the oyster *Crassostrea gigas*, and were able to show that this parasite species was introduced into Californian and Atlantic waters with native *C. gigas* populations from Japan. Burreson et al. (2000) also demonstrated an example of host-switching in that *H. nelsonii* imported with *C. gigas* to the mid-Atlantic have successfully parasitized previously uninfected populations of native *Crassostrea virginica*. Finally, Blakeslee et al. (2008) explored host and parasite genetics to resolve the cryptogenic (=origin uncertain) status of a highly abundant marine intertidal snail, determining that host and parasite invaded the east coast of North America together.

Studies empirically comparing the genetic structure of native and introduced populations of parasite-host associations in marine systems are also rare, but those few studies that have studied this question provide some support for reductions in genetic diversity in introduced habitats, for both parasites and hosts. For example, Muira et al. (2006) compared the genetic structure of native and introduced populations of the Asian horn snail *Batillaria attramentaria* and its associated parasites and observed reductions in genetic diversity in introduced populations for the snail and one lineage of a cryptic trematode parasite (*C. batillariae*) with the other lineage showing no reductions. Blakeslee et al. (2008) also observed reductions in genetic diversity in the introduced range for a snail host (*Littorina littorea*) and its most common trematode parasite (*Cryptocotyle lingua*); however, the magnitude of these

reductions was not explored. Another ecologically important invader, the European green crab (*Carcinus maenas*) has shown reductions in some of its globally invasive populations, but in others, diversity is not significantly reduced (Darling et al., 2008). At the present time, nothing is known about the genetic structure of its most common trematode parasite, *Microphallus similis*, which infects *C. maenas* in both its native and introduced ranges (Torchin et al., 2001; Blakeslee et al., 2009). It would be interesting to see how genetic diversity in this trematode (which uses the crab as its second-intermediate host) compares to its crab host, considering its moderately high prevalence across native and introduced populations. *Microphallus similis* also uses native snails, *Littorina obtusata* and *L. saxatilis*, as first-intermediate hosts; thus in eastern North America, it is completing its life cycle through native (*L. obtusata*, *L. saxatilis*) and non-native (*C. maenas*) hosts, which may potentially affect its genetic diversity patterns in the introduced region.

2.3 Literature review discussion

Our review of the freshwater and marine literature suggests extensive knowledge gaps in studies of host and parasite genetic diversity in introduced populations. In many cases, hosts and parasites have been explored independently and comparisons between them are not always made, thus it is difficult to determine general patterns from the literature review with the present paucity of appropriate studies. However, those studies that do compare host and parasite genetic diversity in introduced and native ranges tend to suggest reductions in both hosts and their parasites in introduced populations; however, the extent of these reductions is not always clear. In some cases, hosts showed little to no reductions in genetic diversity (as was observed in numerous free-living examples in Roman & Darling (2007)), while in other cases the reductions were more extensive. Many of the parasite examples we found suggested extensive reductions in diversity; however, in a few cases they did not. Our review also found studies from numerous parasite groups, but no trends according to group were apparent, except perhaps for the note regarding direct life cycles versus complex life cycles – the former transmitting through one host versus the latter through multiple hosts. It might be expected that hosts with more complex life cycles could show greater reductions in genetic diversity in introduced populations due to inherent difficulties in completing life cycles; e.g., appropriate hosts may be in low abundance or lacking. Further insight into patterns across parasite groups will require more extensive research of introduced populations (the literature for which is presently sparse), focusing on introduced versus native populations of hosts and parasites, in order to understand whether parasite groups in general are more likely to exhibit theoretical signatures of genetic founder effects than their hosts, or whether certain types of parasites (e.g., multi-host) could be more likely to exhibit significant reductions.

3. Case study

Here, we present a case study to provide further insight into understanding whether founder effect signatures would be more apparent in introduced aquatic parasites than their hosts. Our case study focuses extensively on a prominent North American intertidal species, *Ilyanassa obsoleta*, and its trematode parasites (see Figure 1 for a typical trematode life cycle) in native and introduced regions, as well as comparisons with two *Littorina* sp. snails and parasites in native and introduced populations.
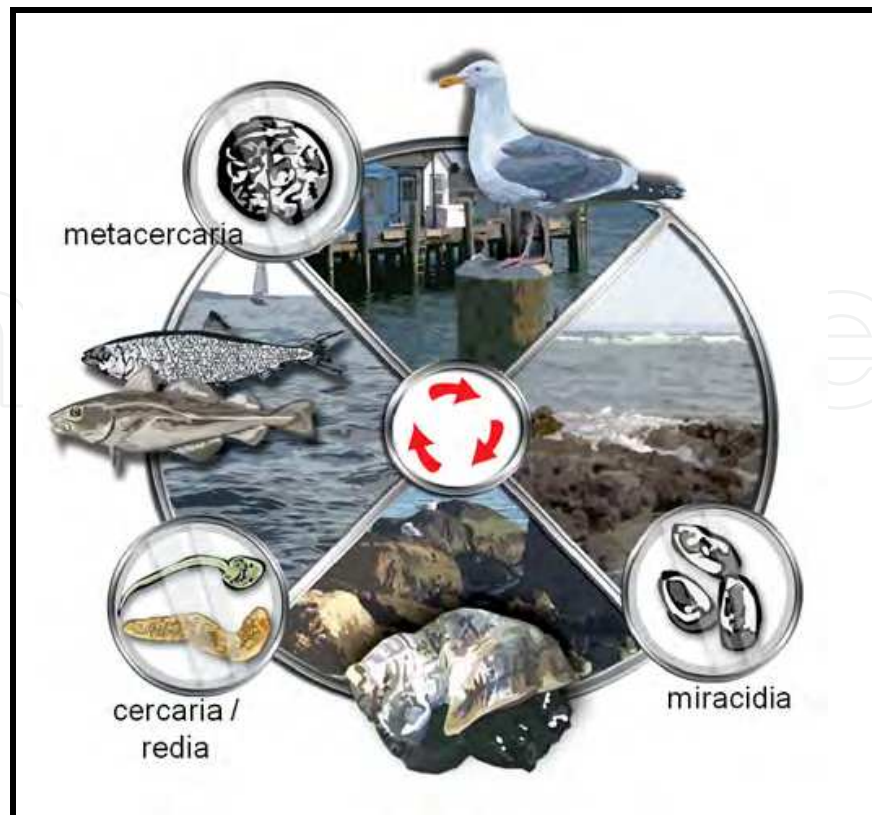
Fig. 1. A typical three-host infection cycle for a trematode parasite. Trematodes asexually reproduce in their first-intermediate snail hosts; then seek out and encyst within a second-intermediate host (e.g., fish); and sexually reproduce within their definitive host (e.g., seabird). This figure represents a typical life cycle of a prevalent trematode species, *Cryptocotyle lingua*, which infects *Littorina littorea* (common periwinkle snail) as its first-intermediate snail host.

3.1 Background information

Ilyanassa obsoleta is native to the east coast of North America, and its range extends from the Gulf of St Lawrence, Canada to northern Florida, USA (Bousfield, 1960; Abbott, 1974). The snail inhabits soft sediment, estuarine, and marine environments and often reaches extremely high abundances in both native and introduced populations (Scheltema, 1961; Brown, 1969; Curtis & Hurd, 1981; Blakeslee et al., 2011; A.M.H.B., pers. obs.). *Ilyanassa obsoleta* was accidentally introduced to the North American west coast in the early 1900's from the mid-Atlantic region of the east coast with commercial shipments of the eastern oyster, *Crassostrea virginica,* for aquacultural purposes (Carlton, 1992). While the intentional introduction of the eastern oyster failed, numerous organisms associated with the oyster successfully established in San Francisco Bay and other areas along the west coast (Carlton, 1979; Carlton, 1992; Miller, 2000), including *I. obsoleta* and several of its parasites (Blakeslee et al., 2011). Presently, *I. obsoleta* is found in three major populations on the west coast: San Francisco Bay (SFB), California, USA (first noted in 1907); Willapa Bay (WB), Washington, USA (first noted in 1945); and Boundary Bay (BB), Washington, USA and British Columbia, Canada (first noted in 1952) (Demond, 1952; Carlton, 1992). Nine trematode parasites infect *I. obsoleta* in its native east coast range (Curtis, 1997), and recent work (Blakeslee et al., 2011) has discovered a total of five

trematodes infecting the snail in its introduced populations on the west coast (all five in San Francisco Bay; three in Willapa Bay; and two in Boundary Bay). This recent work also found a significant reduction in trematode parasite diversity and abundance in numerous populations on the west coast compared to native east coast populations. This observation of *parasite escape* is a signature that has been noted in numerous introductions worldwide (Torchin et al., 2003), and is another consequence of species invasions that could potentially abet introduced hosts in becoming highly successful in their new habitats (Keane & Crawley, 2002; Torchin & Mitchell, 2004; Liu & Stiling, 2006). The resulting reduction of parasite species richness and abundance as a result of parasite escape may affect both host and parasite population genetics, but as of yet, such evolutionary effects of the host-parasite invasion have not been investigated. Here, we present new, unpublished genetic data for the snail and four of its trematode parasites in native and introduced regions to understand the effects of the invasion on genetic diversity in the snail and its trematode parasites.

Another prominent marine intertidal snail on the North American east coast is *Littorina littorea* (common periwinkle), which is found from Labrador to Delaware Bay (Steneck & Carlton, 2001), its introduced region. The snail's native range is in Europe, where it inhabits coastlines from the White Sea to Portugal (Reid, 1996). Recent empirical work has suggested the snail was accidentally introduced to the North American east coast in the 1800s when vessel traffic between the British Isles (its purported source area) and North America was high. In fact, a study by Brawley et al. (2010) found congruence between *shipping records* from the British Isles to the Canadian harbor, Pictou, where the snail was first noted in the mid-1800s (Steneck & Carlton, 2001), and *genetic data* that also pinpointed the snail's likely origin of introduction to the British Isles. Rock ballast, prominently used at the time, was suggested as the likely introduction vector for the snail's North American invasion (Brawley et al., 2011). Furthermore, *Littorina littorea* also demonstrated characteristic signatures of parasite escape, in that it showed a significant reduction in parasite diversity in North America versus Europe (Blakeslee & Byers, 2008) when compared to two of its congeners, *Littorina saxatilis* (rough periwinkle) and *Littorina obtusata* (smooth periwinkle), both of which are native throughout the North Atlantic. Moreover, Blakeslee et al. (2008) discovered congruent patterns of genetic diversity reductions in introduced versus native regions for *L. littorea*, as well as its most common trematode parasite, *Cryptocotyle lingua* (Figure 1), finding both the snail and its associated parasite to show a genetic bottleneck in eastern North America and also suggesting a joint introduction of the snail and its parasite to North America. However, the study did not explore the comparative magnitude of these reductions and whether the reduction was more profound for the parasite than the snail. Therefore, we use the data from this study to compare genetic diversity in *L. littorea* and *Cr. lingua*, and additionally include (previously unpublished) diversity data for another common trematode species that infects the snail in its native and non-native ranges, *Cercaria parvicaudata*.

The third snail species we include in our case study is the rough periwinkle, *Littorina saxatilis*, which has a cosmopolitan native range across the North Atlantic (including populations throughout Europe and eastern North America) and an introduced population on the US West Coast in San Francisco Bay. The snail was first noted in SFB in 1993, and it is believed to have been introduced through the live trade vector, specifically baitworms (blood and sand worms) and live lobsters (*Homarus americanus*) from Maine and other areas

of New England, which are packed in intertidal seaweed and shipped to locations around the globe (Carlton & Cohen, 1998). Since 1993, the snail has spread rapidly throughout the Bay and is highly abundant in numerous populations (Blakeslee et al., 2011). The snail is infected by fourteen trematode parasites in its native East Coast range (Blakeslee & Byers, 2008) but only three (from a single population) are found in SFB (Blakeslee et al., 2011), again representing a significant reduction in parasite diversity and abundance in the introduced range. While genetic data exists for the snail's native and introduced populations (Brown, 2007; Brown, Geller, Blakeslee, unpublished), there is no available genetic data for its introduced parasites because of the extremely low abundance and richness of trematodes infecting *L. saxatilis* in SFB (<0.5% throughout the Bay; Blakeslee et al., 2011). However, because the snail is a prominent host to trematode parasites in its native range, and because extensive genetic data exists for the snail in both its native and introduced regions, we include *L. saxatilis* here to complement the data we have for the other two snails in order to provide a better understanding of genetic diversity patterns in general for native versus introduced first-intermediate gastropod hosts. Continued sampling of the snail in its introduced range may reveal sufficient parasite data in the future (especially because the snail's introduction vector remains active), which could further support the results we present here based on three snail hosts and six trematode parasites.

3.2 Methodology

Included in our comparative study are three first-intermediate snail hosts, *Ilyanassa obsoleta*, *Littorina littorea*, and *Littorina saxatilis*, and six trematode parasites from native and introduced regions. The genetic data used in this case study are from previously published and unpublished data, and all are from mitochondrial markers (cytochrome b and cytochrome oxidase I genes). The information for genes, primers, sample sizes, and published studies can be found in Table 1.

We used the genetic data to obtain haplotype (=genetic) diversity values in both native and introduced regions for each snail and parasite individually, and then collectively. We also focused on *I. obsoleta* and its four parasites in a more extensive exploration of haplotype identities, frequencies, and connections across populations and within subregions and regions. For the latter, we obtained frequency data for each individual population and then also combined populations into larger subregions, which included: "North" – those populations found in Maine, New Hampshire, and Massachusetts; "Long Island Sound (LIS)" – those populations located along Long Island Sound; "DELMARVA" – those populations located along the Delaware, Maryland, Virginia (DELMARVA) peninsula; "South" – those populations from North Carolina, South Carolina, and Georgia; "BB" – those populations found in Boundary Bay, British Columbia; "WB" – those populations found in Willapa Bay, Washington; and "SFB" – those populations found in San Francisco Bay, California. The LIS and DELMARVA subregions are both known to be areas where oysters were collected for shipments west (Miller, 2000) and thus are likely source areas for *I. obsoleta's* and its parasites' introductions to the North American west coast (Blakeslee et al., 2011).

Because sampling effort was not equal across populations and regions, we also employed rarefaction techniques to find expected total haplotype richness for each species. This was especially important for the trematode parasites, where sampling was impacted by locating

Species	Mitochondrial Gene(s)	Total base-pairs	Primers	# Samples Native region	# Samples Introduced region	# Sites Native reg
Snails						
Ilyanassa obsoleta	COI	546	1) TCGTGCTGAACTTGGACAAC 2) CCCCAGCTAATACAGGCAAA	250	173	15
Littorina littorea	Cytb & COI	1197	1) CCTTCCCGCACCTTCAAATC 2) ATGAGAAATTTTCAGGGTC 3) CTCTCCTGGGAGATGACCAG 4) TTCTGGGTGACCGAAGAATC	187	183	22
Littorina saxatilis	COI	757	1) GGGGGAGGAGACCCTATTCT 2) GCTCCTGTTTCAGGTGCATT	322	326	23
ALL SNAILS -- TOTAL				**759**	**682**	
Trematode Parasites						
Austrobilharzia variglandis (IO)	COI	571	1) CGCCTCTGTCTGTTGTTGAA 2) AAACCCCAACACTCACCAAA	11	19	3
Himasthla quissetensis (IO)	COI	522	1) CTGCGTCGGTTTGTTTAGGT 2) TCCCCAAACACACAATAGCC	46	30	7
Lepocreadium setiferoides (IO)	COI	514	1) CCCCCTTGTCGAGTGGGGAT 2) TGCAGTATGCACATCCAAACCCACC	62	8	11
Zoogonus rubellus (IO)	COI	535	1) CCGCCTTTATCTTCTGTGGA 2) TATGCACATCCAAACCAACC	109	9	12
Cryptocotyle lingua (LL)	COI	450	1) TTTTTTGGGCATCCTGAGGTTTAT 2) TAAAGAAAGAACATAATGAAAATG	98	98	16
Cercaria parvicaudata (LL)	COI	450	1) TTTTTTGGGCATCCTGAGGTTTAT 2) TAAAGAAAGAACATAATGAAAATG	36	29	9
ALL TREMATODES -- TOTAL				**362**	**193**	

Table 1. Genetic data used in the case study of three snail hosts (*Ilyanassa obsoleta, Littorina littorea, an* trematode parasites (*Austrobilharzia variglandis, Himasthla quissetensis, Lepocreadium setiferoides, Zoogo lingua*, and *Cercaria parvicaudata*). First-intermediate hosts of the six trematode parasites are identifie *Ilyanassa obsoleta and* 'LL' for those infecting *Littorina littorea*. The second column describes the mitoc species (COI = cytochrome oxidase I; cytb = cytochrome b). The third column lists the total number mitochondrial gene fragment. The fourth column lists the forward and reverse primers used in PCR through eight describe the number of sequences sampled in native and introduced regions, as well a in each region. The last column lists the published study for the genetic data or whether the data are

infected snails among all snails (which can only be determined through destructive sampling). Thus, species-specific prevalence can be very heterogeneous (see Blakeslee et al., 2011). As a result, particular trematode species may have been sufficiently prevalent, in low abundance, or completely absent from a site, making it challenging to control for sampling abundance at each site, especially in introduced populations where prevalence was already lower than in native populations (Blakeslee et al., 2011). However, the rarefaction techniques allowed us to obtain *estimates* of expected haplotype richness at each site for native and introduced regions. We could then analyze data using both observed and expected values. We performed these rarefaction analyses using ESTIMATES 8.2 (Colwell, 2009) and selected the non-parametric estimator, Jack2, for calculating expected richness values because this estimator has been shown to perform well in numerous richness studies in terms of bias, precision, and accuracy (e.g., Canning-Clode et al., 2008).

We analyzed snails and trematode parasites in terms of proportional genetic diversity for native and introduced regions. We also explored haplotype richness for each individual species, as well as collectively ('snails' versus 'trematodes'), to determine whether general differences existed among hosts and their parasites. Finally, we used a single-factor ANOVA to look for significant differences between regions for hosts and parasites, using both observed and expected values (based on rarefaction analysis described above).

3.3 Results and discussion

Overall, we believe our study is suggestive that founder effect signatures are more apparent in the introduced parasites we featured here than their hosts. This is because we found trends for greater reductions in genetic diversity among introduced parasites at both the individual level and collectively than their snail hosts, which we describe in detail below.

Focusing first on our exploration of *Ilyanassa obsoleta* and its four parasites, we found genetic diversity to be reduced in the introduced region for both the snail and its parasites, but this reduction was much greater among the parasites than for the snail. Figure 2 explores haplotype frequencies as a series of pie charts at a biogeographic scale: within populations (smaller pies) and within subregions (larger pies). *Ilyanassa obsoleta* displayed much greater levels of diversity in terms of both shared (colored pie slices) and unshared (gray pie slices) haplotypes in its introduced region than did its trematode parasites. On average ($\pm$SE), native east coast *I. obsoleta* populations had about 17 ($\pm$0.6) haplotypes per site compared to 16 ($\pm$0.2) haplotypes per site in the introduced west coast. In contrast, the snail's trematodes had on average about 17 ($\pm$4.4) haplotypes per site from east coast populations versus only 8 ($\pm$3.5) haplotypes per site from introduced populations. At the subregional level, east coast *I. obsoleta* had on average about 63 ($\pm$6.1) haplotypes per subregion compared to 58 ($\pm$25) haplotypes per subregion on the west coast. In contrast, east coast trematodes had on average 57 ($\pm$12) haplotypes per subregion compared to 22 ($\pm$12) haplotypes per subregion on the west coast. Altogether, these analyses suggest that introduced populations of *I. obsoleta* trematodes tended to have about one-half to one-third the haplotype diversity of native populations/subregions, while the differences for the snail in native versus introduced populations and subregions were nearly nonexistent.

This trend for substantial differences in comparative genetic diversity between *I. obsoleta* and its parasites was also found in our exploration of diversity at the regional level. While *I.*
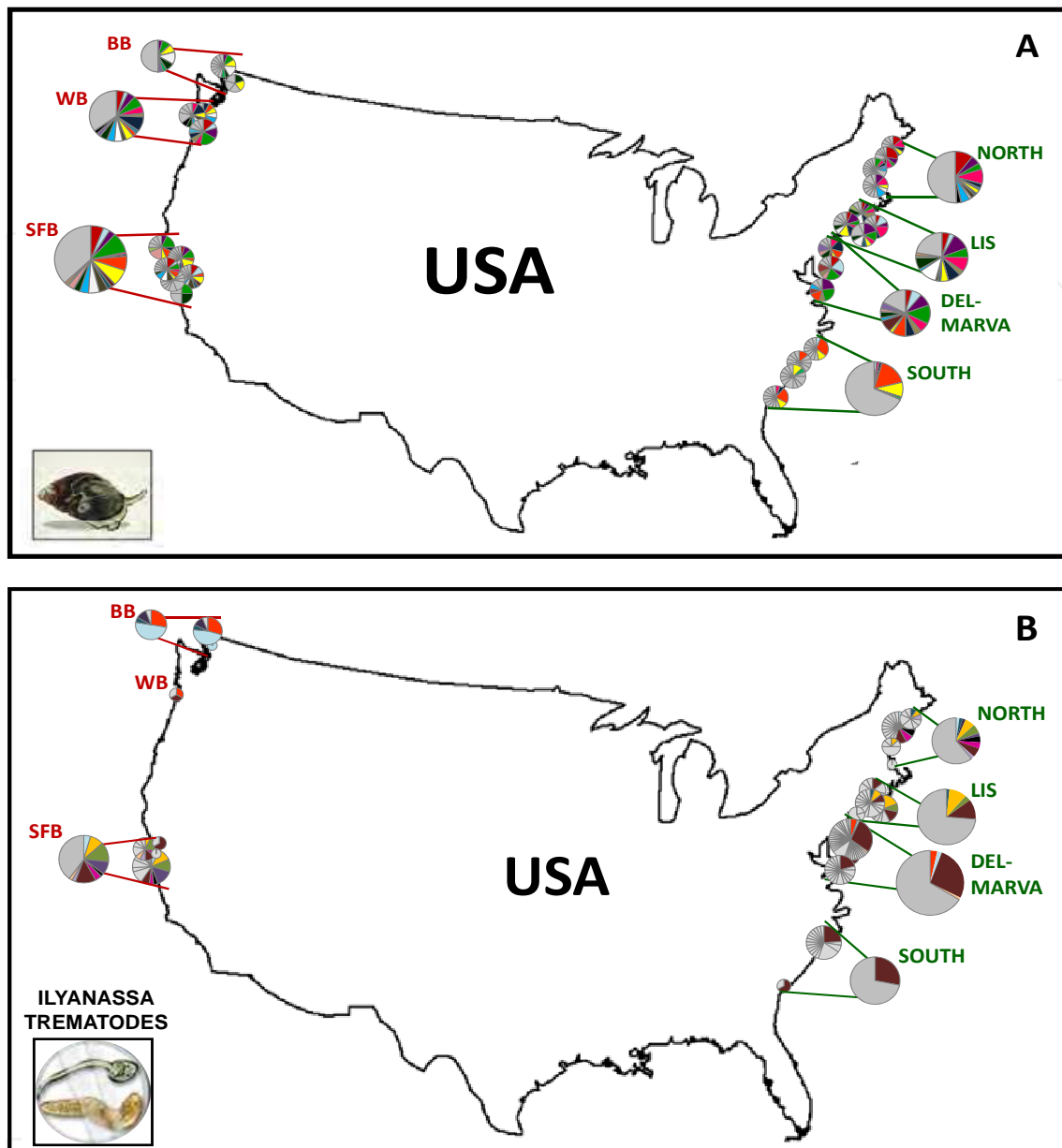
Fig. 2. Haplotype frequencies in native and introduced populations (small pies) and subregions (large pies) on the east and west coasts of North America for *Ilyanassa obsoleta* (A) and its trematode parasites (B). Larger subregions are as follows: "North" – those populations found in Maine, New Hampshire, and Massachusetts; "Long Island Sound (LIS)" – those populations located along Long Island Sound; "DELMARVA" – those populations located along the Delaware, Maryland, Virginia (DELMARVA) peninsula; "South" – those populations from North Carolina, South Carolina, and Georgia; "BB" – those populations found in Boundary Bay, British Columbia; "WB" – those populations found in Willapa Bay, Washington; and "SFB" – those populations found in San Francisco Bay, California. Colored pie pieces represent shared haplotypes between the native east coast and introduced west coast. Gray pie pieces represent unshared haplotypes. Pie charts are relatively sized based on sample size at a site or subregion. *Ilyanassa obsoleta* demonstrates a substantial amount of genetic diversity in its introduced west coast populations, while its trematodes show declines in diversity in introduced west coast populations compared to native east coast populations.
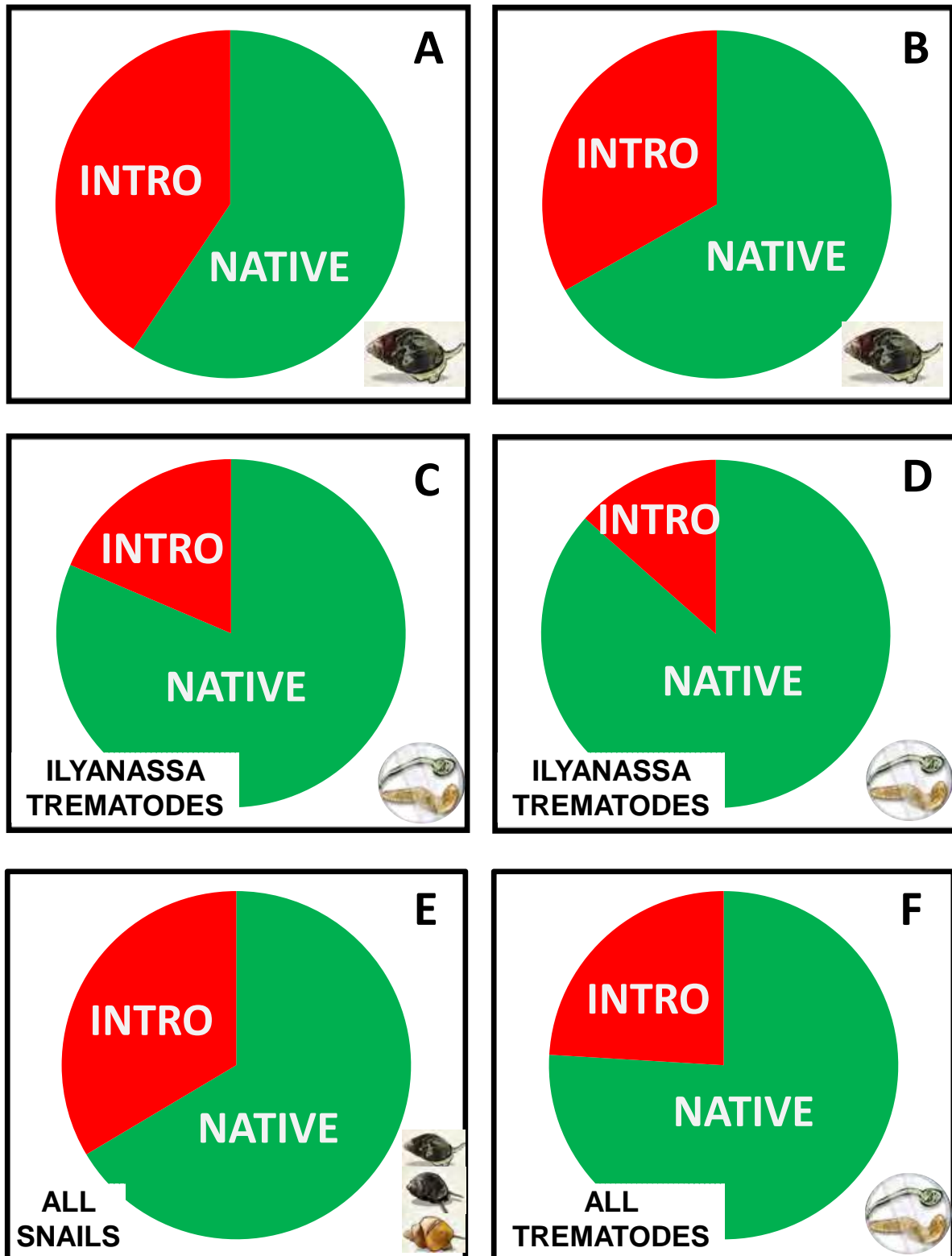
Fig. 3. Measures of regional genetic diversity in *Ilyanassa obsoleta* (A-B), its trematode parasites (C-D), all snail hosts (E), and all trematode parasites (F) for observed (A,C,E,F) and expected (B&D) total diversity in native and introduced (INTRO) regions. In general, snails tended to show a greater proportion of their overall genetic diversity to be 'Introduced' than did parasites.

obsoleta showed less diversity in its introduced (38-40%) compared to its native (60-62%) range (for both the observed and expected analyses; Figure 3A-B), its trematodes showed substantially less diversity in the introduced (13-19%) compared to native (81-87%) ranges (for both the observed and expected analyses; Figure 3C-D). This suggests that the differential between native and introduced genetic diversity is much lower for *I. obsoleta* than for its trematode parasites.

In our analyses where we included all three snails (*I. obsoleta*, *Littorina littorea*, and *L. saxatilis*) and all six trematode parasites, we found similar patterns as those described above for just *I. obsoleta*. In particular, the snails showed less of a reduction in genetic diversity in their introduced (33-34%) versus native (66-67%) regions [for both observed and expected analyses; Figure 3E (because observed and expected results are so similar, only observed values are shown in the figure)], compared to their trematode parasites, where the decline in genetic diversity was more substantial in the introduced (21-24%) versus native (76-79%) region (for both the observed and expected analyses; Figure 3F).

These differences were also observed at the individual species level. Snail hosts tended to show less reduction in diversity in their introduced versus native regions than their trematode parasites (Figure 4A-B), though variability between and among species was very apparent. This variability is not unexpected, however, given the different life histories (reproduction, life span, dispersal ability, etc.) of each species, as well as their different invasion histories, which would affect the number, identity, and frequency of haplotypes being carried over, as well as the likelihood of becoming established and maintained in the population. Even still, it is interesting that when we explored snail hosts and trematodes collectively, we found some general patterns, especially in regards to diversity reductions in introduced versus native regions in snails versus parasites. For example, when grouped, we found that the introduced snails had on average about half the genetic diversity of their native region (this difference was non-significant; p=0.30); whereas for trematodes, introduced diversity was about one-third that of native diversity (Figure 4C), and the reduction in introduced versus native diversity was marginally significant (p=0.07) [note: an analysis using expected haplotype diversity revealed similar p-values: 0.06 for trematodes and 0.27 for snails].

Altogether, these results continue to support a more profound reduction in genetic diversity for the introduced trematode parasites than their hosts and also are suggestive of general patterns (at least for the three snails and six trematodes from which we collected genetic data) – in that the snails (especially *I. obsoleta*) appear to conform to the "genetic paradox" observed in numerous species in the Roman & Darling (2007) study (where a significant reduction in genetic diversity was not apparent in the introduced region). In contrast, the parasites do show significant reductions in haplotype diversity in the introduced versus native regions, and thus appear to demonstrate founder effect signatures. However, sampling for trematodes was challenging because they are more difficult to locate than their snail hosts (given the logistic nature of having to destructively sample enough snails to obtain an adequate amount of parasite DNA), especially in introduced populations where parasite abundance is already lower (Blakeslee et al., 2011). As a result, we attempted to control for some of the sampling variation in our study (through rarefaction analyses); in addition, we explored collective parasite data in many cases to enhance sample and effect sizes. Therefore, we believe the patterns we observed have merit and suggest that inherent
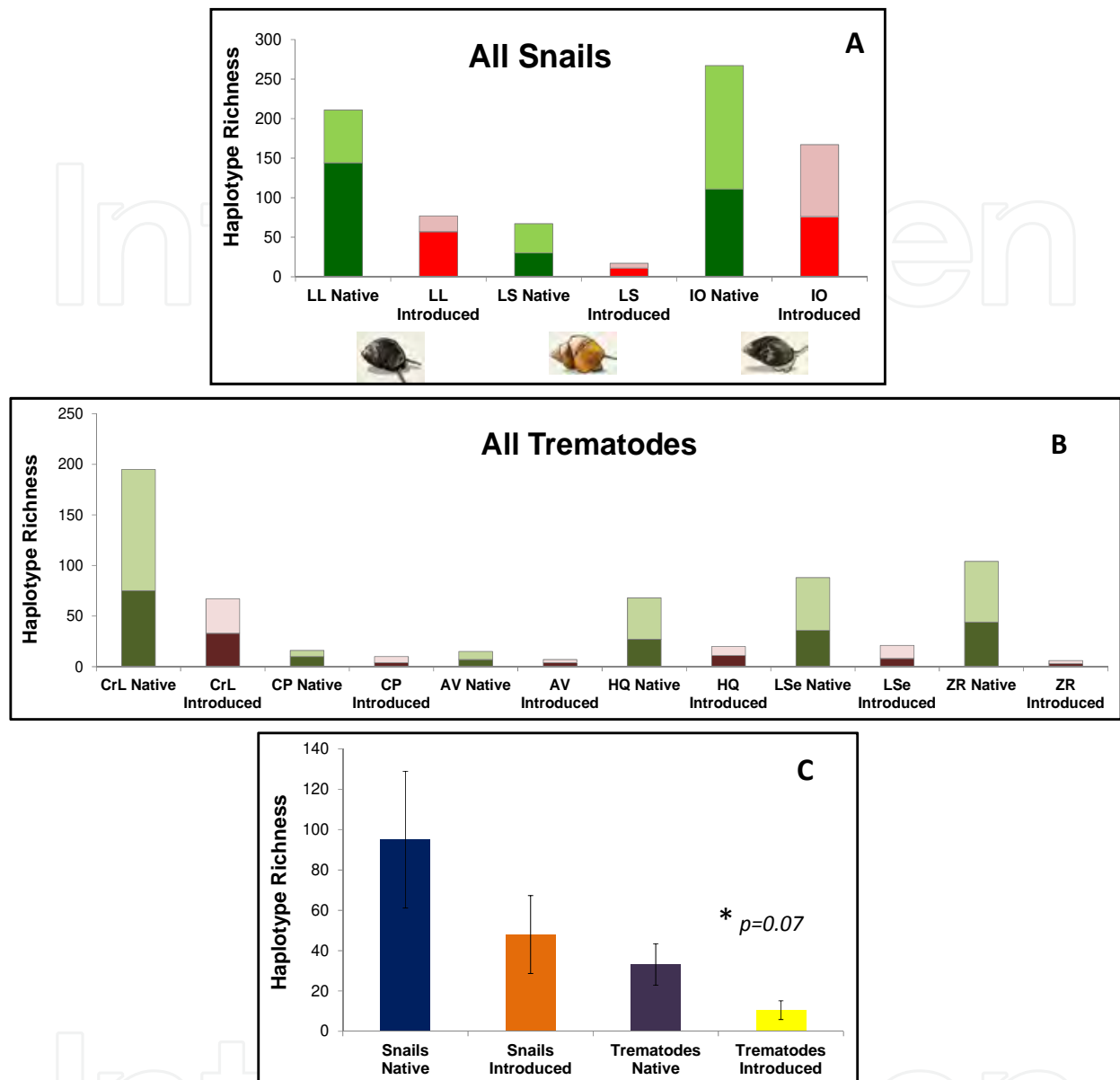
Fig. 4. Native and introduced haplotype richness in the: (A) three snail hosts, *Littorina littorea* (LL), *Littorina saxatilis* (LS), and *Ilyanassa obsoleta* (IO); (B) trematode parasites infecting *Littorina littorea* and *Ilyanassa obsoleta*; (C) snails combined and trematodes combined. While all three snails (individually and collectively) showed some level of genetic diversity reductions in introduced versus native regions, the magnitude of the reduction was less than that of their parasites both individually and combined. In the combined treatment (C), the reduction for the parasites was marginally significant (p=0.07) using a single-factor ANOVA compared to a non-significant reduction (p=0.30) in the snails. Lighter shading in bar graphs of (A) and (B) represent the differential between expected haplotype richness and observed haplotype richness (i.e., observed richness is represented by darker shading and the light shading represents haplotypes that were estimated to have been missed in the sampling). CrL=*Cryptocotyle lingua*; CP=*Cercaria parvicaudata*; AV=*Austrobilharzia variglandis*; HQ=*Himasthla quissetensis*; LSe=*Lepocreadium setiferoides*; ZR=*Zoogonus rubellus*.

differences in invasion pathways and life histories of snail hosts and their parasites affects the likelihood for observing founder effect signatures.

Interestingly, we found consistent patterns across parasites even with differences in host invasion histories – which (depending on the particular introduction vector) may result in a greater or lesser likelihood for parasite and genetic transfer to introduced populations. For example, *I. obsoleta's* particular introduction vector would have likely provided numerous opportunities for gene flow and parasite transfer between native east coast populations and those areas on the west coast (in particular San Francisco Bay) receiving shipments of eastern oysters and associated biota (including *I. obsoleta*) (Blakeslee et al., 2011). This is likely for several reasons. First, shipments of oysters to the west coast occurred on a massive scale sustained over numerous years and resulting in billions of oysters being transported across the country (Miller, 2000), increasing the likelihood for associated organisms like *I. obsoleta* to be transferred with the oysters. This would have also resulted in multiple introductions of the snail, enhancing genetic diversity in the introduced region. In addition, the main harvesting method for oyster extraction – dredging – was very unselective (Ingersoll, 1881; Carlton, 1992), thus numerous individuals from numerous source populations could have been captured in the process, resulting in a greater diversity of alleles being transferred. Finally, commercial oysters were packaged for transcontinental shipping in a manner that ensured their survival, also benefiting the survival of hitchhiking organisms (including parasites) (Carlton, 1979); as such, the loss of alleles and parasites due to mortality during the transfer process would have been reduced. Altogether, this information suggests that *I. obsoleta* could have transferred a substantial amount of the genetic diversity of its source populations (which span a large area, from Virginia to Connecticut; Blakeslee et al., 2011) to its introduced populations. Additionally, this introduction vector would have allowed for some level of parasite gene flow between native and introduced populations as well. However, due to the inherently lower number of parasites being transferred (since only a subset of invading snails would be infected) and the trematode's complex life history requiring multiple hosts (e.g., Figure 1), the movement of trematode genes to the introduced populations would have automatically been lower and more subject to forces reducing diversity, like genetic drift (given the smaller introduced population) and Allee effects. Altogether, this would have resulted in much greater reductions in genetic diversity in the introduced populations of the parasites than their snail host.

Our genetic data appear to support these theories. In particular, genetic diversity in introduced *I. obsoleta* populations was not significantly depressed, and in some west coast populations (especially in San Francisco Bay), genetic diversity was similar if not larger than native east coast populations. We also observed that a substantial amount of the snail's introduced diversity originated from putative source populations along Long Island Sound and the Delmarva peninsula (Figure 2A). For parasites, on the other hand, all of *I. obsoleta's* trematodes showed signatures of genetic founder effects. This was also the case for *Littorina littorea* and its trematode parasites, though the latter snail showed a greater reduction in diversity in its introduced population than *I. obsoleta*. This difference between the snail hosts could be because of major distinctions between their invasion pathways. In particular, *L. littorea's* introduction vector (purportedly rock ballast in ships; Brawley et al., 2009) probably did not allow for as much gene flow between source and founding populations as did *I. obsoleta's* introduction vector due to longer transit times and harsher transfer

conditions for *L. littorea* versus *I. obsoleta*. Even still, we found parasites of both snails to exhibit more apparent founder effect signatures than their snail hosts.

Altogether, these snails may benefit from the lack of a considerable genetic bottleneck in their introduced populations, especially for *I. obsoleta*, which exhibited substantial amounts of genetic diversity in many of its introduced populations. This is because small, genetically depauperate populations can be subject to detrimental fitness effects often associated with extreme bottlenecks, including inbreeding depression and loss of diversity through genetic drift (Roman & Darling, 2007). Avoiding such impacts may have assisted *I. obsoleta* in its successful establishment and spread throughout San Francisco Bay and other west coast bays, where it is presently highly abundant (A.M.H.B., pers. obs.).

4. Conclusion

As we have seen throughout the chapter, characteristics associated with a specific introduction vector strongly affect the likelihood for a species' successful introduction to a new location, and its likelihood for transferring a substantial subset of the genetic diversity of its native range. In particular, the number of host individuals transported, frequency of transport events, and transport conditions are important characteristics that will affect the entrainment, transfer, and ultimate success of a species and its ability to establish and maintain a significant level of genetic diversity in its new environment (Miller & Ruiz, 2009; Roman & Darling, 2007). In particular, for successful establishment and spread, invasive species must be able to survive and reproduce in their novel environment, and for a multi-host parasite, this depends on the presence and abundance of suitable hosts, which serve as their biological habitats (Blakeslee et al., 2011). Thus, hosts and parasites are likely to be impacted differently by the invasion process, ultimately affecting their genetic diversity patterns. This is supported by our case study results, which suggest that, for the most part, invasive parasites will be more likely to exhibit genetic bottleneck and founder effect signatures (in terms of genetic diversity loss) in introduced ranges than their hosts, and this is likely a result of the inherent differences in their propagule pressures, life histories, and invasion pathways.

Furthermore, it is important to note that because parasites and hosts are fundamentally intertwined, they will also greatly impact one another's evolutionary processes. For example, parasites may affect host genetic structure if there is differential reproductive success of infected versus uninfected host genotypes. Thus, if parasites reduce host reproduction or survival and if host genotypes differ in their susceptibility to parasitic infection, then parasite-mediated changes in gene frequencies can occur. As a result, co-evolutionary processes will be highly important to the genetic structure of both groups; i.e. the Red Queen hypothesis (Haldane 1949; Jaenike 1978; Hamilton 1980; Bell 1982), which states that parasites and hosts are both under strong selection pressures as a result of one another – the parasite to adapt to infect locally common host genotypes, and the host to adapt to be genetically unique (e.g., possessing rare genotypes) to avoid fitness-reducing infections. As hosts and parasites are constantly co-evolving, this can generate a time-lag in selection of both parasite and host genotypes and produce oscillations in gene frequencies (Clarke 1976; Hutson and Law 1981; Nee 1989, Dybdahl and Lively 1998; Jokela et al. 2009; Wolinska and Spaak 2009) all over a relatively short evolutionary time period (Koskella and Lively 2009; Morran et al. 2009; Paterson et al. 2010, Schulte et al. 2010). Parasites may also differ from their hosts in being genetically structured over relatively small spatial scales due

to their complex life histories that depend on hosts for habitat and successful reproduction (Prugnolle et al., 2005). Thus, there are many ecological and evolutionary bases for strong differences in genetic diversity and genetic structure between parasites and hosts in natural situations; anthropogenic movements of species and genes complicates understanding further and has resulted in many unanswered questions regarding the effects of invasion on host and parasite population genetics. Our study has explored some of these questions, though much still needs to be investigated and resolved.

Our chapter has therefore provided important preliminary clues regarding the differences between host and parasite genetic structure and diversity patterns in aquatic systems as a result of anthropogenic introductions. Continued research in these areas will further our understanding of the roles of each and how they may impact one another and affect evolutionary change, especially in recently introduced founding populations. Furthermore, detailed invasion history information is required to understand the effects of the invasion process on hosts and parasites, especially considering the impact of the invasion pathway on the transfer of propagules and alleles across geographic barriers. Genetic diversity data is also important in understanding parasite contributions to aquatic communities, especially for those parasites with human health effects (such as schistosome trematodes). Moreover, at the conservation level, detailed genetic information can help track the movements of genotypes locally and also at the global scale, providing managers with important information on source, timing, and introduction vector which can aid in prevention or mitigation measures. Finally, we have identified significant knowledge gaps in parasite research for aquatic introductions in this chapter through our literature review, where very few studies existed comparing host and parasite genetic diversities in founding populations; therefore, our chapter also provides impetus for continued research on comparative host-parasite studies to determine whether patterns could be found across systems and across parasite groups.

5. Acknowledgments

6. References

Abbott, R.T. (1974) *American seashells: the marine Mollusca of the Atlantic and Pacific coasts of North America.* Van Nostrand Reinhold, New York.

Ashworth, S. T., and Blanc, G., (1997) *Anguillicola crassus*, a recently introduced aggressive colonizer of European eel stocks. *Bulletin Francais de la Peche et de la Pisciculture,* 344/ 345, 335-342.

Barton, D.P. (1997) Introduced animals and their parasites: the cane toad, *Bufo marinus,* in Australia. *Australian Journal of Ecology,* 22: 316–24.

Bell, G. (1982) The masterpiece of nature: the evolution and genetics of sexuality. Univ. of California Press, Berkeley, CA.

Blakeslee, A.M.H., Altman, I., Miller, A.W., Byers, J.E., Hamer, C.E. & Ruiz, G.M. (2011) Parasites and invasions: a biogeographic examination of parasites and hosts in native and introduced ranges. *Journal of Biogeography*. DOI: 10.1111/j.1365-2699.2011.02631.x

Blakeslee, A.M.H., Keogh, C.L., Byers, J.E., Kuris, A.M., Lafferty, K.D. & Torchin, M.E. (2009) Differential escape from parasites by two competing introduced crabs. *Marine Ecology Progress Series*, 393, 83–96.

Blakeslee, A.M.H., Byers, J.E. & Lesser, M.P. (2008) Resolving cryptogenic histories using host and parasite genetics: the resolution of *Littorina littorea's* North American origin. *Molecular Ecology*, 17, 3684-3696.

Blakeslee, A.M.H. & Byers, J.E. (2008) Using parasites to inform ecological history: comparisons among three congeneric marine snails. *Ecology*, 89, 1068-1078.

Blouin, M.S., Yowell, C.A., Courtney, C.H., Dame, J.B. (1995) Host movement and the genetic structure of populations of parasitic nematodes. *Genetics*, 141, 1007–1014.

Bouzid, W., Stefka, J., Hypsa, V., Lek, S., Scholz, T., Legal, L., Hassine, O.K.B., Loot, G. (2008) Geography and host specificity: Two forces behind the genetic structure of the freshwater fish parasites *Lingua intestinalis* (Cestoda: Diphyllobothriidae). *International Journal for Parasitology*, 38, 1465-1479.

Brawley, S.H., Coyer, J.A., Blakeslee, A.M.H., Olsen, J.L., Hoarau, G., Johnson, L.E., Byers, J.E. & Stam, W.T. (2009) Historical invasions of the intertidal zone of Atlantic North America associated with distinctive patterns of trade and emigration. *Proceedings of the National Academy of Sciences USA*, 106, 8239-8244.

Brown, C.W. (2007) Genetic variation of the invasive gastropod *Littorina saxatilis* (Olivi) in San Francisco Bay. M.S. Thesis, San Francisco State University, San Francisco, CA.

Brown, S.C. (1969) The structure and function of the digestive system of the mud snail *Nassarius obsoletus* (Say). *Malacologia*, 9, 447-500.

Bousfield, E.L. (1960) *Canadian Atlantic Sea Shells*. Department of Northern Affairs and National Resources, National Museum of Canada, Ottawa, 72 pp.

Burreson, E.M., Stokes, N.A., Friedman, C.S. (2000) Increased Virulence in an Introduced Pathogen: *Haplosporidium nelsoni* (MSX) in the Eastern Oyster *Crassostrea virginica*. *Journal of Aquatic Animal Health* 12, 1–8.

Canning-Clode, J., Valdivia, N., Molis, M., Thomason, J.C. & Wahl, M. (2008) Estimation of regional richness in marine benthic communities: quantifying the error. *Journal of Limnology and Oceanography Methods*, 6, 580– 590.

Carlton, J.T. (1979) *History, biogeography, and ecology of the introduced marine and estuarine invertebrates of the Pacific coast of North America*. PhD Thesis, University of California, Davis, CA.

Carlton, J.T. (1992) Introduced marine and estuarine mollusks of North America: an end-of-the-century perspective. *Journal of Shellfish Research*, 11, 489-505.

Carlton, J.T. & Cohen, A.N. (1998) Periwinkle's progress: the Atlantic snail *Littorina saxatilis* (Mollusca: Gastropoda) establishes a colony on a Pacific shore. *Veliger*, 41, 333-338.

Carlton, J.T. & Geller, J.B. (1993) Ecological roulette: the global transport of nonindigenous marine organisms. *Science*, 261, 78-82.

Chang, A.L., A.M.H. Blakeslee, A.W. Miller & G.M. Ruiz (2011) Why do invasions fail? A case history of *Littorina littorea* in California, USA. *PLOS One,* 6, e16035.

Curtis, L.A. & Hurd, L.E. (1981) Nutrient procurement strategy of a deposit-feeding estuarine neogastropod, *Ilyanassa obsoleta*. *Estuarine Coastal and Shelf Science*, 13, 277-285.

Clarke, B. (1976) The ecological relationships of host-parasite relationships. In A. E. R. Taylor, & R. Muller, eds. *Genetic aspects of host-parasite relationships*. Blackwell, Oxford. Pp. 87–103.

Criscione, C.D. & Blouin, M.S. (2004) Life cycles shape parasite evolution: comparative population genetics of salmon trematodes. *Evolution*, 58, 198–202.

Criscione, C.D., Cooper, B., Blouin, M. (2006) Parasite genotypes identify source populations of migratory fish more accurately than fish genotypes. *Ecology*, 87, 823–826.

Darling, J.A., Bagley, M.J., Roman, J., Tepolt, C.K., Geller, J.B. (2008) Genetic patterns across multiple introductions of the globally invasive crab genus *Carcinus*. *Molecular Ecology*, 17, 4992–5007.

Dieguez-Uribeondo J. & Soderhall, K. (1993) *Procambarus clarkia* (Girard) as a vector for the crayfish plague fungus, *Aphanomyces ascaci* (Schikora). *Aquatic Fisheries Management,* 2,:761–765.

Dove, A.D.M. (2000) Richness patterns in the parasite communities of exotic poeciliid fishes. *Parasitology,* 120, 609–23.

Dunn, A.M. & Dick, J.T.A. (1998) Parasitism and epibiosis in native and non-native gammarids in freshwater in Ireland. *Ecography*, 21, 593–598.

Dybdahl, M.F. & Lively, C.M. (1996) The geography of coevolution:comparative population structures for a snail and its trematode parasite. *Evolution*, 50, 2264–2275.

Dybdahl, M.F. & Lively, C.M. (1998) Host-parasite coevolution: evidence for rare advantage and time-lagged selection in a natural population. *Evolution,* 52, 1057–1066.

Font, W.F. (1998), Parasites in paradise: patterns of helminth distribution among streams and fish hosts in Hawai'i. *Journal of Helminthology,* 72, 307-311.

Geller, J.B., Darling, J.A. & Carlton, J.T. (2010) Genetic Perspectives on marine biological invasions. *Annual Review of Marine Science*, 2, 367–393.

Gittenberger, E., Groenenberg, D.S.J., Kokshoorn, B., Preece, R.C. (2006) Molecular trails from hitch-hiking snails. *Nature*, 439, 409.

Grosberg R, Cunningham CW (2000) Genetic structure in the sea from populations to communities. In: Marine Community Ecology (eds Bertness M, Gaines S, Hay M), pp. 61–84. Sinauer Associates, Sunderland, Massachusetts.

Haldane, J. B. S. (1949) Disease and evolution. *Ricerca Scientifica.* 19, 68–76.

Hamilton, W. D. (1980) Sex versus non-sex versus parasite. *Oikos*, 35, 282-290.

Hayward, C.J., Iwashita, M., Ogawa, K. Ernst I. (2001) Global spread of the eel parasite *Gyrodactylus anguillae* (Monogenea). *Biological Invasions*, 3, 417-424.

Huspeni, T.C. & Lafferty, K.D. (2004) Using larval trematodes that parasitize snails to evaluate a saltmarsh restoration project. *Ecological Applications*, 14, 795-804.

Hutson, V., & Law, R. (1981) Evolution of recombination in populations experiencing frequency-dependent selection with time delay. *Proceedings of the Royal Society of London* B 213, 345–359.

Jaenike, J. (1978) An hypothesis to account for the maintenance of sex within populations. *Evolutionary Theory*, 3, 191–194.

Jarne, P. & Theron, A. (2003) Genetic structure in natural populations of flukes and snails: a practical approach and   review. *Parasitology,* 123, 27–40.

Jokela, J., Dybdahl, M. F., Lively, C. M. (2009) The maintenance of sex, clonal dynamics, and host-parasite coevolution in a mixed population of sexual and asexual snails. *American Naturalist*, 174, S43-S53.

Keane, R.M. & Crawley, M.J. (2002) Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution*, 17, 164-170.

Keeney, D.B., Waters, J.M., Poulin, R. (2007) Diversity of trematode genetic clones within amphipods and the timing of same-clone infections. *International Journal for Parasitology*, 37, 351–357

Kelly, D.W., Paterson, R.A., Townsend, C.R., Poulin, R., Tompkins, D.M. (2009) Parasite spillback: a neglected concept in invasion ecology? *Ecology* 90, 2047–2056.

Kennedy, C.R. (1998) Aquatic birds as agents of parasite dispersal: a field test of the effectiveness of helminth colonisation strategies. *Bulletin of the Scandinavian Society for Parasitology*, 8, 23–28.

Koskella, B. & Lively, C.M. (2009) Evidence for negative frequency-dependent selection during experimental coevolution of a freshwater snail and a sterilizing trematode. *Evolution*, 63, 2213-2221.

Kruse, I. & Hare, M.P. (2007) Genetic diversity and expanding nonindigenous range of the rhizocephalan *Loxothylacus panopaei* parasitizing mud crabs in the western North Atlantic. *Journal of Parasitology*, 93, 575-582.

Kuris, A.M., Hechinger, R.F., Shaw, J.C., Whitney, K.L., Aguirre-Macedo, L., Boch, C.A., Dobson, A.P.,

Dunham, E.J., Fredensborg, B.L., Huspeni, T.C., Lorda, J., Mababa, L., Mancini, F.T., Mora, A.B.,

Pickering, M., Talhouk, N.L., Torchin, M.E. & Lafferty, K.D. (2008) Ecosystem energetic implications of parasite and free-living biomass in three estuaries. *Nature*, 454, 515-518.

Lafferty, K.D. & Morris, A.K. (1996) Altered behavior of parasitized killifish increases susceptibility to predation by bird final hosts. *Ecology*, 77, 1390-1397.

Louhi, K.-R., Karvonen, A., Rellstab, C., Jokela, J. 2010. Is the population genetic structure of complex life cycle parasites determined by the geographic range of the most motile host? *Infection, Genetics and Evolution,* 10, 1271-1277.

Liu, H. & Stiling, P. (2006) Testing the enemy release hypothesis: a review and meta-analysis. *Biological Invasions*, 8, 1535-1545

Martin, W. E. (1958) The life histories of some Hawaiian heterophyid trematodes. *Journal of Parasitology* 44, 305-323.

McCoy, K.D., Boulinier, T., Tirard, C., Michalakis, Y. (2003) Hostdependent genetic structure of parasite populations: differential dispersal of seabird tick host races. *Evolution*, 57, 288–296.

Miller, A.W. (2000) *Assessing the importance of biological attributes for invasion success: Eastern oyster* (Crossostrea virginica) *introductions and associated molluscan invasions of Pacific and Atlantic coastal systems.* PhD Thesis, University of California Los Angeles, Los Angeles, CA.

Miller, A.W. & Ruiz, G.M. (2009) Differentiating successful and failed invaders: species pools and the importance of defining vector, source and recipient regions. *Biological invasions in marine ecosystems: ecological, management, and geographic perspectives* (ed. by G. Rilov and J. Crooks), pp. 153-170, Springer Verlag, Berlin.

Miura, O., Torchin, M.E., Kuris, A.M., Hechinger, R.F., Chiba, S. (2006) Introduced cryptic species of parasites exhibit different invasion pathways. *Proc Natl Acad Sci USA*, 103, 19818–19823.

Morran, L. T., Parmenter, M. D., Phillips, P. C. (2009) Mutational load and rapid adaptation favour outcrossing over self-fertilization. *Nature,* 462, 350-352.

Münderle, M., Taraschewski, H., Klar, B. Chang, C. W. , Shiao, J. C. , Shen, K. N. , He, J. T. , Lin, S. H. , Tzeng, W. N. (2006) Occurrence of *Anguillicola crassus* (Nematoda: Dracunculoidea) in Japanese eels *Anguilla japonica* from a river and an aquaculture unit in southwest Taiwan. *Diseases of Aquatic Organisms* 71, 101–108.

Nee, S. (1989) Antagonistic coevolution and the evolution of genotypic randomization. *Journal of Theoretical Biology*, 140, 499–518.

Paterson, S., Vogwill, T., Buckling, A. D., Benmayor, R., Spiers, A. J., Thomson, N. R., Quail, M., Smith, F., Walker, D., Libberton, B., Fenton, A., Hall, N., Brockhurst, M. A. (2010) Antagonistic coevolution accelerates molecular evolution. *Nature*, 464, 275-278.

Prenter, J., MacNeil, C., Dick, J.T.A., Dunn, A.M. (2004) Roles of parasites in animal invasions. *Trends in Ecology and   Evolution*, 19, 385–390.

Prugnolle, F., Liu, H., de Meeus, T., Balloux, F. (2005) Population genetics of complex life-cycle parasites: an illustration with trematodes. *International Journal of Parasitology*, 35, 255–263.

Rauch G, Kalbe M, Reusch TBH (2005) How a complex life cycle can improve a parasite's sex life. *Journal of Evolutionary   Biology*, 18, 1069-1075.Rauque, C.A., Viozzi, G.P., Semenas, L.G. (2003) Component population study of *Acanthocephalus tumescens* (Acanthocephala) in fishes from Lake Moreno, Argentina. *Folia Parasitology* 50, 72–78.

Reed, D.H. & Frankham, R. (2003) Correlation between Fitness and Genetic Diversity. *Conservation Biology,* 17, 230-237.

Reid, D.G. (1996) *Systematics and evolution of* Littorina (ed. by D.G. Reid), pp. 278–340. The Ray Society, Andover, UK.

Roman, J. (2006) Diluting the founder effect: cryptic invasions expand a marine invader's range. *Proceedings of the Royal Society B: Biological Sciences*, 273, 2453–2459.

Roman, J. & Darling, J.A. (2007) Paradox lost: genetic diversity and the success of aquatic invasions. *Trends in Ecology and Evolution*, 22, 454–464.

Ruiz, G.M., Fofonoff, P., Carlton, J.T., Wonham, M. & Hines, A.H. (2000) Invasion of coastal marine communities in North America: apparent patterns, process, and biases. *Annual Review of Ecology and Systematics*, 31, 481–531.

Scheltema, R.S. (1961) Metamorphosis of the veliger larvae of *Nassarius obsoletus* (Gastropoda) in response to bottom sediment. *Biological Bulletin*, 120, 92-109.

Schulte, R. D., Makus, C., Hasert, B., Michiels, N. K., Schulenburg, H. (2010) Multiple reciprocal adaptations and rapid genetic change upon experimental coevolution of an animal host and its microbial parasite. *Proceedings of the National Academy of Sciences*, 107, 7359-7364.

Shoop, W.L. 1988. Trematode transmission patterns. *Journal of Parasitology*, 74, 46-59.

Slothouber-Galbreath, J. G. M., Smith, J. E., Becnel, J. J., Butlin, R. K., and Dun, A. M. (2010) Reduction in post-invasion genetic diversity in Crangonyx pseudogracilis; a genetic

bottleneck or the work of hitchhiking, vertically transmitted microparasites? *Biological Invasions*.12 191-209.

Steneck, R. & Carlton J.T. (2001) Human alterations of marine communities: students beware!. In: Marine Community Ecology (eds Bertness M, Gaines S, Hay M), pp. 445–468. Sinauer Associates, Sunderland, Massachusetts.

Stohler, R. A., Curtis, J., Minchella, D. J. (2004) A comparison of microsatellite polymorphism and heterozygosity among field and laboratory populations of *Schistosoma mansoni*. *International Journal of Parasitology,* 34, 595–601.

Taraschewski, H. (2006) Hosts and parasites as aliens. *Journal of Helminthology*, 80, 99-128.

Tompkins, D.M. & Poulin, R. (2006). Parasites and biological invasions. In: *Biological Invasions in New Zealand* (eds Aleen, R.B. & Lee, W.G.). Springer-Verlag, Berlin, pp. 67–82.

Torchin, M.E., Lafferty, K.D., Kuris, A.M. (2001) Release from parasites as natural enemies: increased performance of a globally introduced marine crab. *Biological Invasions* 3, 333–45.

Torchin, M.E., Lafferty, K.D., Dobson, A., McKenzie, V. & Kuris, A.M. (2003) Introduced species and their missing parasites. *Nature*, 421, 628–630.

Torchin, M.E. & Mitchell, C.E. (2004) Parasites, pathogens, and invasions by plants and animals. *Frontiers in Ecology and the Environment*, 2, 183–190.

Voisin, M., Engel, C.R. & Viard, F. (2005) Differential shuffling of native genetic diversity across introduced regions in a brown alga: aquaculture vs. maritime traffic effects. *Proceedings of the National Academy of Sciences USA*, 102, 5432-5437.

Wattier, R. A., Haine, E. R., Beguet, J., Martin, G., Bollache, L., Musko, I. B., Platvoet, D., and Rigaud, T. (2007). No genetic bottleneck or associated microparasite loss in invasive populations of a freshwater amphipod, *Oikos* 116, 1941–1953.

Wielgoss, S., Sanetra, M., Meyer, A., Wirth, T. (2007) Isolation and characterization of short tandem repeats in an invasive swimbladder nematode, parasitic in Atlantic freshwater eels, *Anguillicola crassus*. *Molecular Ecology Notes*, 7, 1051–1053.

Wielgloss, S., Taraschewski H., Meyer, A., Wirth, T. (2008) Population structure of the parasitic nematode *Anguillicola crassus*, an invader of declining North Atlantic eel socks. *Molecular Ecology*, 17, 3478-3495.

Wolinska, J., & Spaak, P. (2009) The cost of being common: evidence from natural *Daphnia* populations. *Evolution*,63, 1893-1901.
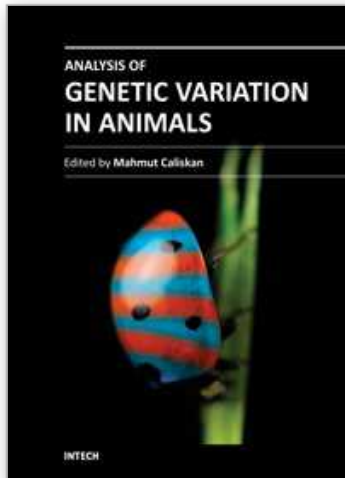
Analysis of Genetic Variation in Animals

Edited by Prof. Mahmut Caliskan

Analysis of Genetic Variation in Animals includes chapters revealing the magnitude of genetic variation existing in animal populations. The genetic diversity between and within populations displayed by molecular markers receive extensive interest due to the usefulness of this information in breeding and conservation programs. In this concept molecular markers give valuable information. The increasing availability of PCR-based molecular markers allows the detailed analyses and evaluation of genetic diversity in animals and also, the detection of genes influencing economically important traits. The purpose of the book is to provide a glimpse into the dynamic process of genetic variation in animals by presenting the thoughts of scientists who are engaged in the generation of new idea and techniques employed for the assessment of genetic diversity, often from very different perspectives. The book should prove useful to students, researchers, and experts in the area of conservation biology, genetic diversity, and molecular biology.

How to reference

In order to correctly reference this scholarly work, feel free to copy and paste the following:

April M. H. Blakeslee and Amy E. Fowler (2012). Aquatic Introductions and Genetic Founder Effects: How do Parasites Compare to Hosts?, Analysis of Genetic Variation in Animals, Prof. Mahmut Caliskan (Ed.), ISBN: 978-953-51-0093-5, InTech, Available from: http://www.intechopen.com/books/analysis-of-genetic-variation-in-animals/security-limitations-of-spectral-amplitude-coding-based-on-modified-quadratic-congruence-code-system

INTECH
open science | open minds