

- Nudibranchia), with the description of a new genus and a new family. *Zoologica Scripta* 28:315–360.
- Wägele, H. 1984. Kiemen und Hämolympfkreislauf von *Phyllidia pulitzeri* (Gastropoda, Opisthobranchia, Doridacea). *Zoomorphology* 104:246–251.
- Wägele, H. 1985. The anatomy and histology of *Phyllidia pulitzeri* Pruvot-Fol, 1962, with remarks on the three Mediterranean species of *Phyllidia* (Nudibranchia, Doridacea). *Veliger* 28:63–79.
- Wägele, H. 1989. A revision of the Antarctic species of *Bathydoris* Bergh, 1884 and comparison with other known bathydorids (Opisthobranchia, Nudibranchia). *Journal of Molluscan Studies* 55:343–364.
- Wägele, H., and G. Johnson. 2001. Observations on the histology and photosynthetic performance of “solar-powered” opisthobranchs (Mollusca, Gastropoda, Opisthobranchia) containing symbiotic chloroplasts or zooxanthellae. *Organisms, Diversity and Evolution* 1:193–210.
- Wägele, H., and Willan, R. C. 2000. On the phylogeny of the Nudibranchia. *Zoological Journal of the Linnean Society* 130:83–18.
- Wägele, J. W. 2000. *Grundlagen der Phylogenetischen Systematik*. Verlag Dr. Friedrich Pfeil Munich, Germany. 315pp.
- Wenzel, J. W., and M. E. Sidall. 1999. *Noise*. *Cladistics* 15:51–64.
- Willan, R. C. 1987. Phylogenetic systematics of the Notaspidea (Opisthobranchia) with reappraisal of families and genera. *American Malacological Bulletin* 5:215–241.
- Winnepeninckx, B., G. Steiner, T. Backeljau, and R. DeWachter. 1998. Details of gastropod phylogeny inferred from 18S rRNA sequences. *Molecular Phylogenetics and Evolution* 9:55–63.
- Wollscheid, E., and H. Wägele. 1999. Initial results on the molecular phylogeny of the Nudibranchia (Gastropoda, Opisthobranchia) based on 18S rDNA data. *Molecular Phylogenetics and Evolution* 13:215–226.
- Wollscheid-Lengeling, E., J. Boore, W. Brown, and H. Wägele. 2001. The phylogeny of Nudibranchia (Opisthobranchia, Gastropoda, Mollusca) reconstructed by three molecular markers. *Organisms, Diversity and Evolution* 1:241–256.
- Wu, C.-I., and W.-H. Li. 1985. Evidence for higher rates of nucleotide substitution in rodents than in man. *Proceedings of the National Academy of Sciences U.S.A.* 82:1741–1745.

Molecular Systematics and
Phylogeography of Mollusks
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2003

PHYLOGEOGRAPHY AND DIVERSIFICATION IN AQUATIC MOLLUSKS

A fundamental goal of ecology and evolutionary biology is to establish the factors that determine species distributions. These factors are both intrinsic to a species, such as traits that determine limits to physiological tolerance or reproductive capacity, and extrinsic, such as events that fragment continuously distributed species or populations. Direct analysis of the interactions among these forces is typically not possible because of the broad evolutionary time scale involved. However, the field of phylogeography (Avice 2000) provides a framework for inferring the relative importance of these factors in determining present-day species distributions. An inherent assumption in phylogeographic studies is that intraspecific descriptions of genetic and phenotypic variation can illuminate the same determinant factors that have shaped biotic diversity at higher levels of organization (Burton 1998; Wares et al. 2001; Wares 2002; Meyer and Paulay, in review).

The field of phylogeography, together with related population genetic methods, has been extensively reviewed elsewhere (e.g., Avice 2000, Grosberg and Cunningham 2001). These methods are used primarily to qualitatively discriminate among patterns of genealogical and geographic structuring (e.g., Avice 1992; Templeton et al. 1995), as well as to analyze the boundaries between recently diverged species (Knowlton 2000). New techniques allow hypothesis testing to be more quantitative, focusing on the resolution of temporal hypotheses (e.g., Edwards and Beerli 2000; Nielsen and Wakeley 2001). Comparative phylogeography applies these same techniques to a set of distributed species. When phylogeographic patterns are concordant among a set of species, this implies the uniform action of extrinsic forces in shaping genetic diversity (Avice 1992; Bermingham and Moritz 1998; Wares 2002).

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Understanding the broad interactions among intrinsic traits and extrinsic forces acting on species requires the comparison of a large number of taxa with variation in the traits that may influence the phylogeographic patterns for that species or species group. Aquatic mollusks are an exemplary taxon for this purpose. Nearly 100,000 molluscan species exist (Barnes et al. 2001), with broad variation in dispersal mode, development, physiological tolerances, sexual systems, and metabolic needs. We also have a detailed fossil record for mollusks, particularly among marine species, that can be used to clarify the temporal concordance among competing historical hypotheses (Cunningham and Collins 1994; Marko 2002). In this chapter, we review how phylogeographers use these attributes of mollusks in marine and freshwater environments to illuminate the evolutionary processes responsible for the diversification and survival of species in the face of climatic and environmental change. This is not intended to be an exhaustive review of the literature, but rather an exhibition of the promise that molluscan models hold for generating truly integrative studies of phylogeography and speciation.

FROM GENES TO SPECIES

Our review of the phylogeography of freshwater and marine mollusks is limited primarily to studies that use data that can be explicitly ordered into a genealogy using standard phylogenetic methods (e.g., DNA sequences). These data allow the simultaneous evaluation of spatial and temporal genetic variation. Placing phylogeographic studies in a temporal context is crucial (Cunningham and Collins 1994; Templeton et al. 1995; Avise 2000; Turner et al. 2000), and studies that rely on more traditional analysis of unordered gene frequencies (e.g., F -statistics based on allozyme data) do not offer this temporal context (see Grosberg and Cunningham 2001).

Many inferences made in phylogeographic studies are based on an elegant connection between the statistical expectation of genealogical patterns and the demography and ecology of particular organisms (coalescent theory; reviewed in Hudson 1990). Given a randomly mating population with genetic effective population size N_e , the genetic divergence between any pair or group of alleles sampled from this population is proportional to N_e . Any process that affects N_e (including mating system, variance in reproductive success, life span, abundance, and dispersal mechanisms) can alter the overall shape of a gene tree.

Thus, a number of particular features of the species themselves must be considered when performing phylogeographic analyses. These features contribute to the range of responses a species may have when faced with environmental

change. Intrinsic features, such as mating system or body size, constrain the effects of extrinsic forces, such as glaciation or fragmentation events. In this chapter, we review the different patterns predicted by these extrinsic and intrinsic forces and conclude with a discussion of the genealogical signals generated by interactions between the two.

EXTRINSIC FORCES IN MARINE MOLLUSCAN PHYLOGEOGRAPHY

From our review of the literature, it is evident that marine species respond to very different forces than freshwater molluscan species. Extrinsic events, such as oceanographic or geological forces, have rarely led to vicariant speciation in marine species (Palumbi 1992, 1994), whereas vicariant forces (the isolation of aquatic habitats) dominate the discussion of phylogeographic patterns in freshwater species. In essence, marine species experience a geographically homogeneous landscape, whereas that of freshwater species is more fractal-like. The difference between these two environments has led researchers to look for different forces to play a role.

Geographic range expansion is one important phylogeographic process that may be captured in marine populations. The range fluctuations experienced by molluscan species during Pleistocene climatic changes are clearly important for genetic and phenotypic diversification of populations. A genetic analysis of populations of the marine gastropod *Acanthinucella spirata* to the north and south of Point Conception, California, indicate a northward range expansion from refugial populations south of Point Conception (Figure 9.1; Hellberg et al. 2001). However, although it is typical for expansion populations to exhibit lower genetic diversity, it is also possible for such expansion populations to experience a significant "founder effect." In the case of *Acanthinucella*, the expansion from refugial populations was accompanied by dramatic evolution of shell shape and size. Pleistocene populations of *Acanthinucella*, as evidenced by fossil data, do not differ significantly from modern populations of *A. spirata* in the refugial range; but the genetically depauperate expansion populations contain morphotypes not found in either ancestral populations or modern refugial populations. This suggests that the altered shell morphology is in some way favored in the northern populations and has become newly evolved or increased in frequency after range expansion.

These range expansion events typically generate patterns of lower genetic diversity in the expansion populations; the inference of such an event is stronger when multiple species share this pattern (Dillon and Manzi 1992; Marko 1998;

influence whether phylogeographic patterns among a number of species are concordant.

The correspondence between phylogeographic discontinuities and known areas of biogeographic transition is of particular importance. Studies that have used phylogeographic methods to directly test for the mechanisms responsible for faunal transition (Awise 1992; Burton 1998; Hare and Awise 1998; Wares et al. 2001; Wares 2002) indicate a need to distinguish among transition zones that have been caused by divergent forces of natural selection, historical vicariant events, or other environmental processes that could act as a partial barrier to gene flow.

Another well-known transition zone involves a number of marine taxa that have divergent genetic lineages in the Gulf of Mexico and Atlantic (Awise 1992), including molluscan taxa *Geukensia demissa* (ribbed mussel, Sarver et al. 1992), *Stramonia haemostoma* (southern oyster drill, Liu et al. 1991), the clam *Mercenaria mercenaria* (Ó Foighil et al. 1996), the squid *Loligo pealei* (Herke and Foltz 2002), and the oyster *Crassostrea virginica* (Awise 1992; Hare and Awise 1998; and references therein). Because of the broad range of taxa that appear to be phylogeographically discordant between Gulf and Atlantic populations, there is strong rationale for supporting a late Pleistocene vicariance event as the cause for this common pattern (Awise 1992). Between glacial maxima, sea level was much higher than it is today, and it is believed that many coastal populations that are currently disjunct owing to the projection of the Florida peninsula into tropical waters were continuously distributed at that time. Subsequent isolation of these lineages may be responsible for the common pattern, but the mechanisms that *maintain* this phylogeographic break, which tends to localize to the east coast of Florida near Cape Canaveral (Awise 1992), are less well understood.

The oyster *Crassostrea* has been well studied in this regard. A combination of nuclear and mitochondrial gene trees, and analyses of allele frequency variation in allozymes and nuclear restriction site polymorphisms, have been used to distinguish among the hypotheses that this phylogeographic break represents secondary contact with introgression among the two formerly separate lineages, or that there is an oceanographic or other environmental barrier to dispersal between the two lineages. Because Gulf and Atlantic populations are reproductively compatible but completely distinct at mitochondrial loci and in some nuclear restriction fragment-length polymorphism (RFLP) assays (Karl and Awise 1992), the use of data from additional, independent nuclear loci can be used to illustrate the rate of genetic exchange between these two lineages. In *Crassostrea*, Hare and Awise (1998) show that the combination of data from multiple mitochondrial and nuclear loci are consistent with the idea that barriers to gene

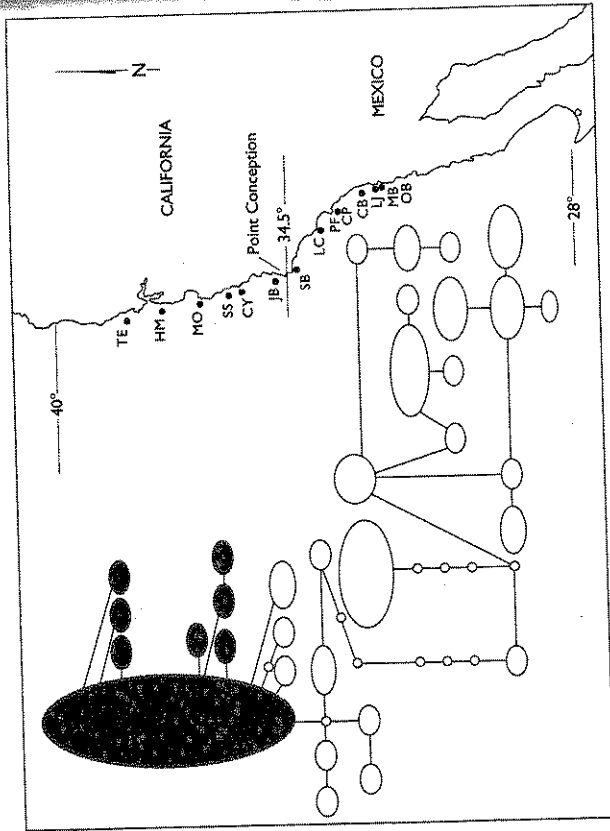


Figure 9.1. Phylogeographic data suggesting a Holocene range expansion in the intertidal snail *Acanthinucella spirata*. Significant differences in measures of allelic diversity for populations north of (shaded) and south of (open) Point Conception, California, are just one measure that indicates a disequilibrium between gene flow and the geographic range of *A. spirata*. Similar patterns have been noted in other species at Point Conception (see text; adapted from Hellberg et al. 2001).

Wares and Cunningham 2001). Comparisons of the population structure in the partially sympatric species *Nucella ostrina* and *N. emarginata* (also distributed around Point Conception) show that, although these species currently inhabit adjacent zoogeographic provinces, they partially overlap in geographic range because of a recent northward range expansion by *N. emarginata* (Marko 1998). The concordance of both mitochondrial sequence data and nuclear allozyme markers is evidence that the lower genetic diversity in the region of overlap is due to the effects of this historical event.

Even this fairly typical response to climatic change may be modified by the intrinsic traits of particular species. Fossil evidence shows that, in general, large-bodied molluscan species in the eastern Pacific were more able to shift their geographic ranges during Pleistocene climatic change than smaller species (Roy et al. 2001). This suggests that the range limits of certain taxa will be more un-stable during climatic change than those of other species. This effect alone may

flow exist between the two lineages, despite high capacity for gene flow due to planktonic larval dispersal. In contrast to the mitochondrial gene trees that show reciprocal monophyly between Atlantic and Gulf lineages, sequence data from three nuclear loci illustrate a pattern more consistent with incomplete lineage sorting than with partial introgression. This is expected when the isolation event is evolutionarily recent (Awise 1994 2000; Palumbi et al. 2001).

Regional environmental and oceanographic data support the compelling arguments for local ocean currents acting as partial or complete barriers to gene flow at Cape Canaveral (Hare and Awise 1998; but see Engle and Summers 1999). The Gulf Stream diverges from the North American coast at this point, potentially carrying larvae and juveniles from southern populations out to sea, and limiting the spread of northern types southward. In other regions of upwelling or strong oceanographic forces, such patterns have been inferred through phylogeographic analysis (e.g., Rocha-Olivares and Vetter 1999; Wares et al. 2001).

The influence of ocean currents on gene flow is illustrated particularly well in the Australian muricid snail *Bedevia hanleyi*. Populations of *Bedevia* are characterized by low gene flow because their larvae are direct developing; most genetic exchange is accomplished by rafting, although not often enough to overcome the divergent effects of genetic drift (Hoskin 2000). The East Australian Current transports water southward along the outer continental shelf of Australia, impinging on the coast itself from about latitude 26 to 33 degrees South. Where this current separates from the coast, there is also cold coastal upwelling, and so nearshore surface water south of this region is transported offshore. The metapopulation of *B. hanleyi* thus consists of two adjacent regions with very different gene-flow characteristics (Hoskin 2000); in the northern region, relatively higher gene flow occurs among local populations than in the southern region. For marine mollusks, ocean currents appear to be an important influence on the overall population structure of a species and the phylogeographic history of a region.

EXTRINSIC FORCES IN FRESHWATER MOLLUSCAN PHYLOGEOGRAPHY

Freshwaters comprise less than 1% of the total water on earth, yet there is a remarkable diversity of freshwater aquatic forms. Approximately 8% of mollusks occur in freshwater (Pechenik 1995)—more than would be predicted based on a simple species-area relationship alone. The distribution of freshwater habitats is patchy and widely interspersed across a largely terrestrial landscape.

Freshwater habitats are typically connected in a hierarchical, fractal geometric fashion with low-order streams draining into larger streams and rivers. Unlike marine systems, this hierarchical organization permits formulation of a very clear hypothesis of current migration routes, and increases the effective distance separating populations. Freshwater habitats often bear the mark of historical events that have shaped the distribution of organisms. For example, river courses in North America are known to have been dramatically altered by repeated glaciation events (Mayden 1988). Thus, both contemporary and historical extrinsic forces shape the distribution of freshwater mollusks and should strongly affect phylogeographic structure. The patchy nature of freshwater habitats may in some respects account for the high species diversity encountered there because the opportunity for geographic isolation (and presumably allopatric speciation) is greater than in marine habitats.

The phylogeographic approach is expected to be especially fruitful for the study of distributional changes and speciation processes in freshwater mollusks. In turn, an awareness of these distributional patterns will help illuminate and refine our understanding of the timing and scale of extrinsic forces that are likely to affect all freshwater organisms. The reasons are twofold: (1) freshwater mollusks on the whole are poor dispersers (Dillon 2000), and (2) the dynamic and patchy distribution of freshwater environments offers a complex geographic landscape where geographic isolation of populations at small spatial scales is probable.

Nine families of bivalve mollusks and 16 families of gastropods have successfully colonized freshwaters. Phylogeographic history in most of these species remains unstudied. For those already studied, the focus has been the role of geological forces in shaping genetic diversity under an allopatric speciation model. However, many codistributed species differ in intrinsic features that should affect gene flow and response to environmental change, offering enormous potential for uncovering the interactions between intrinsic and extrinsic forces in shaping genetic diversity within and among closely related species. Our review highlights some of these features and indicates where comparative phylogeography is likely to provide insight into the roles of these different factors.

Of the bivalves that have successfully invaded freshwaters, most phylogeographic studies have focused on three families: Unionidae, Corbiculidae, and Dreissenidae. The latter two families have representative species (*Corbicula fluminea*-Asian clam, *Dreissena polymorpha*-zebra mussel, and *Dreissena bugensis*-quagga mussel) that are invasive in western Europe and North America and have rapidly expanded their geographic ranges and regional abundances (McMahon 1983; Strayer 1991). As a result of their potential economic and biotic impact, the life history and ecology of these invasive species is fairly well

known (Dillon 2000). Moreover, genetic and distributional data gathered after invasion events have contributed substantial knowledge about the mechanisms of dispersal (Wilson et al. 1999; Muller et al. 2001; Lewis et al. 2000) and extrinsic factors that can limit dispersal or successful colonization in these species (e.g., Allen and Ramcharan 2001). To our knowledge, no detailed phylogeographic studies have been made of these taxa in their native ranges, but several studies have evaluated phylogeography in introduced ranges, seeking to discern the source population(s) of the colonists (Stepien et al. 1999; Renard et al. 2000).

The main focus of freshwater molluscan phylogeographic studies has been the bivalve family Unionidae. Although cosmopolitan, unionids attain highest species diversity in North America. Despite this richness, freshwater bivalves in North America are imperiled. Of roughly 280 described unionid species in the United States, more than 70 species are listed as federally threatened or endangered (Williams et al. 1993). Several authors have recognized that much of the biodiversity of this fauna may be lost before it is fully known (Williams et al. 1993; Lydeard and Mayden 1995; Lydeard and Roe 1998; Neves 1999). This conservation crisis has motivated phylogeographic studies to document genetically distinct lineages within and among closely related species (Mulvey et al. 1997; Lydeard and Roe 1998; Roe and Lydeard 1998; King et al. 1999). Two general observations have arisen: (1) there is often a poor relationship between conchological variation and genetic variation among closely related species (e.g., Mulvey et al. 1997), and (2) over broad spatial scales, genetic divergences appear to conform to expectations based on geological evidence and phylogeographic patterns established in other organisms (e.g., Mulvey et al. 1997; Roe et al. 2001). Attempts to study phylogeography at finer spatial scales have revealed previously unknown population fragmentation events in Atlantic slope drainages in the eastern United States (King et al. 1999) and the Ouachita drainage of southwestern Arkansas (Turner et al. 2000).

Geological processes and climate fluctuations over time have also altered drainage connections in the Colorado River and Rio Grande basins of the American Southwest. Timing and extent of drainage alteration have been hypothesized largely on the basis of zoogeographic trends in fishes coupled with an analysis of the geological histories of the respective basins (Minckley et al. 1986). Hershler et al. (1999) sought to evaluate the concordance of speciation events in the genus *Tryonia* (family Hydrobiidae) with the hypothesized zoogeographic history of the region. They argued that this genus was particularly well suited for studying zoogeography because most species are locally endemic to patchy aquatic habitats and exhibit limited dispersal capability.

Phylogenetic relationships derived from nucleotide sequence variation in the mitochondrial cytochrome *c* oxidase subunit I (COI) gene were consistent with

(1) a freshwater, southeastern United States origin for southwestern *Tryonia*, consistent with well-known vicariant separation of coastal drainages in the Gulf of Mexico (Bermingham and Avise 1986; Avise 1992), and (2) a sequence of speciation events that were largely consistent with geological events that separated drainage basins in the Southwest. Interestingly, two areas of local endemism were identified within a single drainage basin (Amargosa Basin), which is concordant with the hypothesis that this region is a biotic and geological composite attributable to late Miocene and Pliocene tectonic events that rerouted the drainages, with subsequent incursions of the Gulf of California, to separate local fauna (Taylor 1985). The composite nature of the Amargosa drainage is not evident in the phylogeography of similarly distributed desert pupfish species (Echelle and Dowling 1992), suggesting the importance of studying many groups for a biogeographic synthesis of aquatic habitats in the desert southwest.

Two important points emerge from this study. First, the only parthenogenetic southwestern spring snail, *Tryonia protea*, was identified as the most widely distributed species and was characterized by low genetic diversity among populations. Vicariant events apparently had little effect on spatial phylogeographic discontinuities in this species. These results support the idea that mating system (in this case, parthenogenesis) is crucial for determining the distribution of species and genetic diversity on the landscape. Second, shell features could not be distinguished among the relevant clades, rendering the biogeographic interpretation of morphological variation equivocal. There is often poor correspondence of shell features and genetic divergence in freshwater mollusks (e.g., Lydeard et al. 2000). However, a combination of molecular data and shell characteristics may help uncover sources of variation in shell features, whether environmental or a product of local selection on heritable conchological traits (DeWitt et al. 1998).

Vicariant processes can also play an important role in the formation of new parthenogenetic species. The caenogastropod genus *Campeloma* forms a species complex of parthenogenetic and sexual forms in Atlantic and Gulf coastal drainages of the southeastern United States. The distributions of three sexual species, *C. decisum* (west of the Mobile River), *C. geniculum* (between the Mobile and Appalachian rivers), and *C. limum* (occurs east of the Appalachian River) are consistent with well-established zoogeographic boundaries (Bermingham and Avise 1986; Wooten et al. 1988; Avise 1992). Phylogeographic analysis of parthenogenetic species, including both spontaneous and allotriplloid forms, indicated that the sexual *C. limum* is the maternal ancestor of all parthenogenetic lineages (at least four independent spontaneous parthenogenetic *C. limum* lineages and one allotriplloid species, *C. parithenum*; Johnson and Bragg 1999). The male ancestor of the allotriplloid form was *C. genicu-*

lum, which suggests that spontaneously parthenogenetic *C. limum* colonized west of the Appalachian River and hybridized with the local sexual species. Spontaneous and allotriploid parthenogens were more widely distributed than their sexual relatives and were able to transcend zoogeographic boundaries. Johnson and Bragg (1999) speculated that increased probability of successful colonization, coupled with local competition with sexual forms, facilitated the spread of parthenogenetic lineages.

The phylogeography of the pulmonate snail genus *Biomphalaria* provides an important example of the power of a well-documented (and independently derived) vicariance hypothesis coupled with phylogeographic analysis to infer forces that shape genetic diversity within and among closely related species. *Biomphalaria* species, which are the only intermediate hosts for the intensely studied trematode *Schistosoma mansoni*, are widely distributed across South America and Africa. This distributional pattern led early researchers to propose a Gondwanan origin for the genus (Pilsbry 1911; Davis 1980). If correct, then South American and African species should be reciprocally monophyletic with a long branch (indicating a large number of evolutionary changes) separating them. Phylogeographic analysis of the genus indicated an alternative scenario. DeJong et al. (2001) showed that African species were indeed monophyletic, but were the sister group to *Biomphalaria glabrata*, a widespread (and phylogenetically derived) South American endemic. African species were derived, with South American species at the base of the tree (DeJong et al. 2001). The phylogenetic tree topology supported very strongly the conclusion that *Biomphalaria* originated in South America, and that African species of this genus arose many millions of years after continental separation when colonized by a *B. glabrata*-like ancestor. A probable mechanism for colonization was passive dispersal by birds (see general discussion of passive dispersal by birds in Wesselingh et al. 1999).

INTRINSIC FORCES IN MARINE MOLLUSCAN PHYLOGEOGRAPHY

Phylogeography, at the most fundamental level, considers the interactions between intrinsic effects on both the genetic effective population size and migration. Effective population size may be altered by a number of intrinsic life-history traits of a species, but perhaps most strongly by mating system. Migration ability is also an intrinsic property of species or populations (Peterson and Denno 1997; Collin 2001) and is the basis for gene flow among populations. Acknowledging the importance of these traits permits phylogeographers to go beyond documenting the historical changes in species to establish predictive

hypotheses. In each case, generalizations about the effects of mating system or migratory ability are possible, although violations of these expectations are not infrequent. Nevertheless, by generating predictive hypotheses using these traits, the exceptional species will be able to lead us toward identification of other important deterministic traits.

Mating systems in aquatic mollusks are important determinants on genetic effective population size. In marine species, the determinant factors affecting mating system and development and, in turn the genetic effective size of specific populations, include body size, vagility, and latitude (reviewed in Bertness 1999). In general, free-spawning reproduction is common among marine bivalves. This mating system requires a large gametic output and usually results in high prereproductive mortality (type III survivorship) and/or high variance in reproductive success, either of which can reduce the genetic effective population size in marine species (Hedgecock 1994; Grosberg and Cunningham 2001; Turner et al. 2002).

However, many mobile marine species, particularly gastropods, have internal sexual fertilization accompanied by less variation in reproductive success. Genetic effective size will be less directly influenced by this mating system, although the effects of male competition may play an indirect role. Other mating systems exist, of course, including sequential protandry in the slipper limpet (*Crepidula fornicata*). In this species, fertilization is internal, but socially controlled sexual expression reduces the number of individuals that are permitted to reproduce. Larvae settle as males, but in social clusters only the bottom individual is a female and only the largest male is able to reproduce. As the older female dies, the oldest male takes her place as the reproductive female. In this case, the genetic effective population size is not reduced because the generations overlap; eventually each limpet in a social cluster should have the opportunity to reproduce.

Developmental mode in mollusks is strongly related to latitude and the size of the organism (Bertness 1999). Those species that disperse via planktonic larvae are known to have more fluctuations in population densities than organisms with direct development or short-distance dispersal (Thorson 1950), emphasizing the relationship between a number of phylogenetic and other intrinsic factors and the overall genetic effective population size of a species. Because of the importance of the genetic effective population size for the strength of natural selection and localized adaptation within populations (as well as divergence caused by genetic drift among populations), these factors should be considered in phylogeographic studies.

A good example of intrinsic demographic patterns apparently influencing phylogeographic reconstruction is found in the clam *Lasaea* (Park and Ó Foighil

2000a). In comparisons of populations in Florida and Bermuda, levels of allelic diversity and the general polarity of the mitochondrial gene tree suggest an improbable counter-current colonization of eastern Florida from Bermuda. Park and Ó Foighil (2000a) used reconstructions of temporal changes in genetic effective population size, inferred from genealogical data (Kuhner et al. 1998), in both populations to argue that historical population dynamics in this minute direct-developing bivalve are more likely to be the cause of this pattern than actual historical relationships between the two populations.

INTRINSIC FORCES IN FRESHWATER MOLLUSCAN PHYLOGEOGRAPHY

For freshwater bivalves, much of the variation in traits expected to determine demography and effective size is partitioned at the level of family. Table 9.1 shows how these traits are partitioned among four well-studied families that colonized freshwater environments independently (Park and Ó Foighil 2000b). Mating system differences among families may strongly affect phylogeographic differences by affecting genetic effective population sizes. Members of Dreissenidae and Unionidae are mostly gonochoristic (i.e., dioecious), whereas Corbiculidae and Sphaeriidae have a high incidence of self-compatible hermaphroditism (Heard 1965). Mating system differences lead to two predictions: (1) the ratio of genetic effective population size (N_e) to breeding adult census size (N) will be higher in gonochoristic than in hermaphroditic species because overall genetic diversity is expected to be lowered as a result of self-fertilization; and (2) more colonists are necessary to successfully colonize a new population in gonochoristic species than in hermaphroditic species (which require a minimum of one individual colonist to found a new population). Interestingly, the frequency of hermaphroditism is higher in introduced populations of *Corbicula* than in its native range. Plasticity in the mating system of *Corbicula* may be shaped by a trade-off between fitness costs of selfing in the native range, countered by prodigious colonization ability in the introduced range.

Life span also affects the potential for different phylogeographic histories to arise. Longer life span is predicted to increase the ratio of N_e to N , because long-lived species are able to spread their reproductive effort over several years and thus decrease the variance in reproductive success among individuals (Hill 1979). It is important to note that in our discussion, genetic effective size is standardized by adult breeding census size for purposes of comparison among taxa. However, differences in absolute abundance among taxa may counteract any differences arising from mating system or life span. Local abundances vary greatly among freshwater bivalves. For example, Neves and Widlak (1987)

Table 9.1

Life history and demographic variation among four families of freshwater bivalve mollusks, ranked in descending order of predicted levels of gene flow

Taxon	Mating System	Life Span (years)	Sex Ratio Male:Female	Larval Form	Maximum Offspring Size (mm)
Dreissenidae	Gonochoristic ^a	>3	1:1	Veliger	0.2
Unionidae	Gonochoristic ^a	>10 ^b	1:1	Glochidia/ectoparasite	0.5
Corbiculidae	Simultaneous hermaphroditic ^c	2-4	Variable	Brooding/reduced veliger	0.3
Sphaeriidae	Simultaneous hermaphroditic	2-4	—	Brooding/veliger/juvenile	7.0

Note: Life history information is summarized from accounts in Dillon (2001).

^aHermaphroditic individuals occur at low frequency (usually <5% from population surveys).

^bHeller 1990.

^cA wide range of sexuality is present, see text.

noted that sphaeriid clams were at least an order of magnitude more abundant than unionids in Big Moccasin Creek, Virginia, and *Corbicula* and *Dreissena* can achieve local densities higher than 1,000/m² (Graney et al. 1980). Comparative phylogeographic studies may uncover very different patterns of genetic diversity because of differences in abundance, rather than historical effects.

As in freshwater bivalves, in gastropods, mating system differences are extremely important for predicting differences in phylogeographic history, and variation in mating systems of freshwater gastropods is largely partitioned among higher taxonomic groups. Members of the subclass Pulmonata are best described as simultaneous hermaphrodites with the capability to self-fertilize (although spermatogenesis precedes oogenesis in many species; Dillon 2000). Genetic data suggest that the incidence of self-fertilization is high in the pulmonates *Biomphalaria*, *Physa*, and *Bulinus* (Viard et al. 1997; Monsutti and Perrin 1999; Charbonnel et al. 2000; Mavarez et al. 2000). Conversely, most members of the subclass Caenogastropoda are gonochoristic. Apomictic parthenogenesis (eggs produced by mitosis) occurs in three caenogastropod families: Hydrobiidae, Thiariidae, and Viviparidae. Selfing or parthenogenetic species are typically more widely distributed than their sexual relatives, presumably because of increased likelihood of successful colonization. However, mating system has a profound effect on the distribution of genetic diversity on the spatial landscape, as it does in freshwater bivalves. For parthenogenetic species, rapid geographic range expansion usually stems from the introduction of very few clonal genetic lines, resulting in genetic homogeneity over very

broad geographic scales (e.g., Jacobsen et al. 1996; Samadi et al. 1999; but see Dybdahl and Lively 1995).

DISPERSAL AND GENE FLOW

We emphasize the relationship between phylogeographic history and diverse life history traits because too much trust is placed in the utility of larval dispersal in marine systems and landscape processes of vicariance in freshwaters to accurately predict gene flow. In general, the idea that larval dispersal is a primary determinant of population structure is not often tested in systems where other factors, such as geographic range and other life history traits, do not vary (but see Emlet 1995; Peterson and Denno 1997; and Collin 2001). The counterexamples to this prediction are abundant enough (reviewed in Grosberg and Cunningham 2001) that it is worth focusing our attention on a broader array of traits.

The relationship between dispersal type and gene flow may be inconsistent because of the influence of historical events and other interactions between the intrinsic traits of a species and its environment. Dispersal is essentially passive in most mollusks, suggesting that these interactions (including, although not exclusively, larval and juvenile dispersal) are worth consideration. Here, we consider a group of studies that describe the relationship between gene flow patterns and the environment of a particular species. Although some generalizations may be made, it should be clear that there are enough idiosyncratic results to direct us toward more refined hypotheses.

Collin (2001) presents a good example of codistributed, closely related species of limpets that vary in dispersal ability. These limpets (*Crepidula*) exhibit not only variation in the extent of larval dispersal among species, but also along the Atlantic and Gulf coasts of North America produce results consistent with typical expectations: high gene flow and spatial genetic homogeneity are associated with species that have planktonic dispersal. However, it is difficult to determine whether population structure in poorly dispersing species of *Crepidula* is due to equilibrium isolation by distance (see Grosberg and Cunningham 2001) or other historical effects; divergent clades separated by large geographic distances can represent either pattern, and further sampling may be necessary to discriminate these two hypotheses for many datasets (Templeton et al. 1995; Wares 2002).

In cases where the geographic range of a species has been disrupted or altered in recent geological history, more examples appear to support historical discontinuities in gene flow as playing a stronger role than ongoing migration in generating phylogeographic signal. For example, the periwinkle *Littorina littorea* has planktonic dispersal, but the direct-developing congener *L. saxatilis*

has a broader geographic range in the North Atlantic (Johannesson 1988). Phylogeographic comparisons of the planktonic *L. littorea* (Wares et al. 2002) with the direct-developing *L. obtusata* in the North Atlantic (Wares and Cunningham 2001) show that the difference in larval dispersal is not reflected in differences between the ability of the species to colonize distant lands and, in fact, more phylogeographic differentiation is seen in *L. littorea*. Similarly, the direct-developing dogwhelk *Nucella lapillus* has apparently expanded its range across the North Atlantic since the most recent glacial maximum (Wares and Cunningham 2001), whereas genetic data for the planktonically dispersing mussel *Mytilus edulis* suggests only an ancestral connection between the two coasts (Riginos et al., in review). However, the effects of metapopulation structure can lead to greater broad-scale homogeneity in poorly dispersing species such as *Nucella* (Day et al. 1993), whereas those species that are more demographically stable in the face of rapidly changing environments may be genetically more variable (Wares and McCauley 1988; McCauley 1991).

Some species may maintain intrinsic mechanisms that restrict gene flow and promote diversification in marine settings. Littorimid snails of the subgenus *Neritima* (Reid et al. 1996), the descendants of an invasion of *Littorina* from the Pacific into the North Atlantic, exhibit such intertidal diversification in a number of independent regions and lineages. The species pair *L. obtusata* and *L. fabalis* diverged during the Pleistocene (Reid et al. 1996; Wares 2000), and speciation was facilitated by differences in habitat and feeding preferences (Watson and Norton 1987; Vermeij 1992). The specialization of *L. obtusata* on fucoid algae is a recent adaptation (Vermeij 1992) and floating populations of *L. obtusata* are commonly observed on drifting algae mats (Ingólfsson 1995). This trait could have been important in the postglacial colonization of North America by European populations of *L. obtusata* (Wares and Cunningham 2001) not accompanied by *L. fabalis*.

This recent, apparently sympatric speciation event would be of interest by itself. Yet it is now apparent that phylogeographic divergence of direct-developing *Littorina* species into high- and low-intertidal forms is common throughout the Atlantic and Pacific. In preliminary stages, this is evidenced by single monomorphic populations of *L. brevicula* that separate into high- and low-intertidal populations during breeding (Takada and Rolán-Alvarez 2000). A more advanced pattern of reproductive isolation has formed between sympatric morphs of *L. saxatilis* on the shores of the Iberian peninsula (Johannesson et al. 1995; Rolán-Alvarez et al. 1997; Erlandsson et al. 1998), with only limited gene flow between high- and low-intertidal morphs. Similar differentiation in this species complex plays out among sheltered versus exposed habitats (Johannesson and Johannesson 1996; Tataronkov and Johannesson 1998; but see Tataronkov and Johannesson 1999; Small and Gosling 2000b). Some of this dif-

ferentiation may be due to isolation in distinct glacial refugia during the Pleistocene (Small and Gosling 2000a; Wilding et al. 2000).

In freshwater systems, an obvious constraint to dispersal is the landscape and other geographic barriers to gene flow. If gene flow is a function of dispersal and the probability of successful mating of a migrant with a member of the recipient population, then any trait that affects dispersal ability should affect phylogeographic patterning on the geographic landscape. For creatures that are mobile as adults, such as freshwater and marine gastropods, dispersal can occur over the life of the organism; thus, dispersal capability can be measured by characteristics of larval, juvenile, and adult life history stages. For species with sedentary adult life stages, adult traits such as body size may play an indirect but crucial role in dispersal capability of larval and juvenile life stages (Dillon 2000).

Important differences in dispersal capability exist among families of freshwater bivalves. Variation in early life history (larval size, behavior, and abundance) should determine dispersal capability because adults are sedentary. Movement of genes across the landscape occurs when sperm is released and transported, and when larvae are released. Juvenile and adult movement is only sporadic and opportunistic, although the passive dispersal of adult forms may be important for explaining the rapid invasions of nonnative freshwater mollusks (Counts 1986; Isom 1986; Strayer 1991).

Dreissenidae, with planktonic veliger larvae (unique among freshwater bivalves), is predicted to have the highest potential for gene flow. Larvae are suspended in the water column for up to three weeks before settling (Dillon 2000). Unionids are predicted to have the next highest potential for gene flow, as glochidial larvae become encysted in vagile fish hosts (Williams et al. 1993). Finally, because corbiculids and sphaeriids often brood their larvae to advanced juvenile stages, they have the lowest potential for gene flow via dispersal of propagules. Juvenile size at birth among and within families is variable (Table 9.1) and appears to co-vary with phylogeny at least in sphaeriids (Cooley and Ó Foighil 2000). Larger, more fully developed juveniles may be more apt to settle on substrates close to their parents, whereas moving water may displace smaller juveniles.

Recent invasions of corbiculoids and dreissenids into Europe and North America offer an opportunity to evaluate how mating system and high-dispersal strategies can lead to the same kinds of geographic distributions but very different genealogical data. *Corbicula fluminea* was introduced into the United States in 1938 in western Washington (Isom 1986). Presently, the species is found in nearly all major drainages of the contiguous 48 states. The primary mechanism of dispersal in *Corbicula* is thought to be human-facilitated introduction of adults into new drainages. Despite their abundance and vast geo-

graphic range, there is little genetic variation in the introduced range of *Corbicula* except for a genetic divergence between two widely distributed groups that probably reflect separate colonization events from different source populations (Hillis and Patton 1982; McLeod 1986; Siripattawan et al. 2000). An identical pattern is observed in Europe (Renard et al. 2000). In *Corbicula* there appears to be a high probability of successful introduction followed by rapid expansion of geographic range, even when very few individuals related to the population. Prodigious colonization ability is undoubtedly related to the ability to self-fertilize. However, this mating system has important consequences for genetic diversity in the introduced range, resulting in virtually no genetic diversity within groups, and spatial partitioning of genetic diversity among groups that reflects colonization history.

Dreissena polymorpha, introduced to the Great Lakes region in 1988, has rapidly expanded its range to encompass much of the lower Mississippi River drainage (USGS nonindigenous mollusk web site, <http://nas.er.usgs.gov/images/currezmm00.gif>). Genetic diversity of the colonizing populations is high and appears to reflect the diversity in the native range (Marsden et al. 1996). This suggests that a large number of colonists were present in initial introductions. Once established, the high dispersal ability of *D. polymorpha* (perhaps aided by human-facilitated movements of large numbers of individuals attached to boat hulls) has resulted in its rapid spread. To our knowledge, no population genetic studies have been conducted over the current range of *Dreissena*. If larval dispersal is the primary mechanism for the spread of the species, then we predict comparable levels of heterozygosity and gene diversity over the entire range and little spatial population structure. However, if local introduction by humans is the primary mechanism, then within-population heterozygosity should be reduced and among-population divergence increased. Genealogical-based analytical methods are well suited to partition the effects of migration and local genetic drift for explaining spatial genetic patterns (Turner et al. 2000; Beerli and Felsenstein 2001).

Perhaps the most fruitful avenue for comparative phylogeography of freshwater bivalves is comparisons within and among sphaeriids and unionids because their distributions often overlap at local and regional scales. Phylogenetic relationships and evolutionary history of demographic and life history characters that should influence phylogeography are well understood within each group (Lydeard et al. 1996; Graf and Ó Foighil 1999; Park and Ó Foighil 2000b) and taxa can be selected that vary in key traits predicted to influence phylogeographic relationships within and among families. Roe et al. (2001) illustrate this in *Lampsilis*, a group that disperses glochidial larvae via fish hosts. There is a strong phylogenetic component to the analysis of this group, as all of the

superconglutinate lampshells form a monophyletic clade. However, designated species are not all reciprocally monophyletic, and neither are distinct river drainages (Roe et al. 2001), suggesting both the recent isolation of these lineages and the need to focus on their interactions with historical events (e.g., Pleistocene changes in sea level) and with other species (their fish hosts; discussed below). Unfortunately, we know of no phylogeographic studies of sphaeriid clams with which to compare these results.

Euryhaline gastropod species have been examined for differences in genetic structure related to dispersal capability and habitat selection. Wilke and Davis (2000) studied two species of gonochoristic mud snails, *Hydrobia ulvae* and *H. ventrosa*, that are codistributed across the Atlantic, Baltic, and North Sea coasts of Europe. Microhabitats differ between the two species. *H. ulvae* is found along shorelines where it is directly exposed to waves and high salinities. *H. ventrosa* is restricted to lower salinity and less energetically stressful backwater environments. These two species also differ in larval characters that can influence dispersal; *H. ulvae* produces free-swimming veliger larvae with planktonic development, and *H. ventrosa* produces offspring that develop directly into juveniles. Based on these differences, Wilke and Davis (2000) predicted that genetic divergence among sample localities would be lower (and gene flow higher) for *H. ulvae* than for *H. ventrosa*.

Indeed, when compared side by side, *H. ulvae* displayed higher gene flow in a pattern consistent with Wright's (1977) island model. Under this model, the probability of migrant exchange is equal among spatially structured populations. Conversely, *H. ventrosa* exhibited lower gene flow and higher divergence across the study area, with population structure consistent with an isolation by distance (IBD) model of gene exchange. Under IBD, the probability of gene flow decreases with increasing geographic distances separating populations (Hellberg 1994; Grosberg and Cunningham 2001). Observed measures of gene flow are consistent with predictions based on dispersal differences among species. Planktonic larvae are known to travel long distances and gene flow from larval movement has been hypothesized to homogenize allele frequencies among geographically distant populations (Scheltema 1986).

Wilke and Davis (2000) noted that this interpretation is confounded by interspecific differences in adult habitat preference, which may relate to probabilities of adult movement. Ecological studies of development and larval behavior of *H. ulvae* suggest that veliger larvae have a rather short life in the plankton (less than three days) stage. In some *H. ulvae* populations, the veliger larval stage was bypassed entirely and offspring developed directly. These observations suggested a diminished role for larval dispersal and implicated adult movement as the most important factor for determining genetic diversity dif-

ferences between the two species. Adult movement was hypothesized to be more likely for *H. ulvae* because of its proximity to open ocean.

Is it plausible for adult movement to account for differences in genetic patterns observed in these species? A series of studies on *Bembicium vittatum* (a littorinid snail) occurring on the Houtman Abrolhos Islands in Western Australia indicated that the answer is yes, but the magnitude of movement depends on extrinsic environmental factors related to barriers to migration (Johnson and Black 1991, 1998). *Bembicium* populations are distributed on the shoreline of the eastern and western sides of the islands. On eastern shores, the species is also found in isolated tidal pools. Comparison across tidal pool localities on the eastern side of the islands indicated IBD, as did a separate analysis of adjacent shoreline localities. Only the magnitude of the relationships differed and, in general, genetic divergences were pronounced across tidal pool and shoreline localities (Johnson and Black 1998). Conversely, western shoreline localities showed no obvious IBD (based on our examination of the data), and overall levels of genetic divergence were very low across localities (Johnson and Black 1991). Because they face open reefs, western shores are subject to greater flow of water, which increased dispersal among these localities when compared with shore and tidal pool localities on eastern shores.

Passive dispersal by birds (Wesselingh et al. 1999) appears to enhance gene flow in a variety of freshwater gastropod species. For two codistributed *Hydrobia* species, gene flow was greatly increased and of similar magnitude among populations located within a migratory bird flyway across the North Sea (Wilke and Davis 2000), despite differences in larval dispersal and adult microhabitat preferences that had consequences for gene flow in other parts of their range. Wesselingh et al. (1999) showed that species distributions of *Tryonia* and *Planorbartius* in the Caribbean Sea and continental Europe, respectively, were consistent with migratory waterfowl flyways. These authors suggested that the probability of successful colonization depends on intrinsic factors related to mating system, body size, brooding characteristics, and environmental preferences. Hermaphroditic or parthenogenetic mating systems permit a single colonist to give rise to a new population. Sexual species that brood eggs can colonize a new area with a single gravid female.

INTEGRATING THE INTRINSIC AND EXTRINSIC: COMPARATIVE MOLLUSCAN PHYLOGEOGRAPHY

Biogeographic trends are made clear by the concordant distribution patterns of many species (Briggs 1974). By the same reasoning, finding concordance

among phylogeographic histories, whether caused by vicariance, range expansion, or similar processes, in a number of species, strengthens the inference for a common mechanism that broadly acted on species dynamics. The trans-Arctic interchange, discussed below, was inferred from the distributional changes in hundreds of molluscan species (Vermeij 1991). Similarly, explicit hypothesis testing of the spatial and temporal concordance of phylogeographic patterns with well-studied geological events ensures a direct link between landscape-level changes and population genetic responses within and among species.

An exemplary study comparing biogeographic and phylogeographic boundaries in the Indo-West Pacific uses most of the extant species of cowries (cypræid gastropods) to examine the major hypotheses describing the formation of biodiversity (Meyer and Paulay, in review). The isolation patterns of numerous cowrie lineages in this region are concordant with other regional phylogeographic and biogeographic divisions. Meyer and Paulay (in review) illustrate the importance of allopatry-forming mechanisms in producing general distributions of faunal change, although often these are current ecological mechanisms rather than geological or vicariant. The hypothesis that Plio-Pleistocene climatic and oceanographic changes were responsible for diversification across a number of distinct biota is also tested using cowrie phylogeographic data. By carefully establishing the substitution rate for their mitochondrial dataset using a detailed fossil record, Meyer and Paulay were able to reject this hypothesis, instead suggesting that many of the phylogeographic discontinuities in this dataset were not representative of a single set of historical events.

Fossils are one of the few independent means of dating the establishment of new populations or the divergence of older populations. The development of molluscan shells is believed to have promoted the diversification of molluscan species because of protection from predators and desiccation (Vermeij 1987), and shells account for much of the available fossil record. These fossils can be correlated with specific geological events (e.g., Bowen and Sykes 1988), and by comparing this date with the divergence in genes sampled from involved populations or species, we can calculate the rate of substitution for a particular gene. Knowing this substitution rate then allows the estimation of the timing of other events with respect to a phylogeny or genealogy constructed with that gene. Studies that have generated lineage-specific genetic substitution rates have primarily focused on two well-documented historical events: the trans-Arctic interchange and the closure of the Isthmus of Panama.

In fossil beds of Iceland, northern Europe, and the Canadian Maritimes, hundreds of molluscan taxa appear for the first time around 3.5 million years ago (Vermeij 1991; Reid et al. 1996). These species are either found in the Pacific or are closely related to Pacific fauna and arrived after a massive asymmetric exchange of species from the Pacific to the Atlantic when sea levels rose above

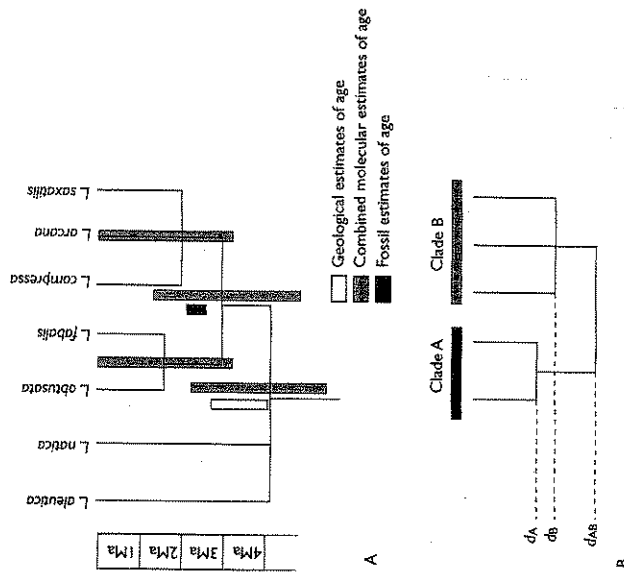


Figure 9.2. (A) Fossil data and geological events used to calibrate the substitution rate for genes used in phylogeographic studies. The intertidal periwinkle genus *Littorina* invaded the North Atlantic via the trans-Arctic Interchange twice; one of the invading lineages has undergone a subsequent radiation, with at least five species found in the North Atlantic. Fossil data for the arrival of *Littorina* and hundreds of other molluscan species in the Atlantic, along with geological evidence regarding the opening of the Bering Strait, have been used to calibrate the substitution rates for a number of mitochondrial genes. (From Reid et al. 1996) (B) Appropriate measures of divergence rates also require estimates of within-population divergence. Measures of d , the molecular divergence between two populations or taxa, are modified by the mean divergence within each group. This mean within-group divergence is a correlate of the diversity expected given the effective population size, and must be subtracted from the overall divergence estimate because of the within-population differentiation expected in the ancestral population. This adjusted estimate is usually expressed as $d = d_{AB} - (d_A + d_B)/2$ (Nei and Li 1979; Edwards and Beerli 2000).

the Bering land bridge (Vermeij 1991). Among these invading species were two lineages of the northern hemisphere periwinkle *Littorina*. An excellent fossil record and knowledge of the timing of this trans-Arctic interchange event allowed Reid et al. (1996) to generate robust estimates of the substitution rate at three mitochondrial genes (Figure 9.2), consistent with other widely applied rates.

Collins et al. (1996) followed a similar path in establishing the rate of molecular evolution for the intertidal gastropod *Nucella*. Although a combination of geological and paleontological evidence showed that the North Atlantic populations of trans-Arctic interchange participants could be no older than 3.5 to 5 million years (Vermeij 1991; Collins et al. 1996; Marinovitch and Gladenkov 1999), the volcanic activity that formed the Isthmus of Panama ended gene flow between populations in the eastern Pacific and Caribbean. This final closure of the Panamanian isthmus about 3 million years ago (Keigwin 1978; Knowlton and Weigt 1998) indicates a constraint on marine species to have diverged at the same time or before this event. Rate calibrations for *Nucella* using closely related taxa with good fossil records that were separated by each of these geological events are not entirely consistent (Collins et al. 1996), suggesting that rate variation among even closely related lineages has the potential to bias tests of specific phylogeographic hypotheses.

In fact, fossil data suggest that many species separated by the Isthmus of Panama may have diverged long before the final proposed cessation of gene flow through this region. Separation of arctic bivalve geminate pairs may predate the formation of this geological barrier by 10 million years (Marko and Jackson 2001; Marko 2002). Although the appearance of distinct taxa in the fossil record is known to underestimate the true divergence time of two species, the assumption that vicariance among geminate sister species around the Isthmus of Panama occurred at the final closure of this seaway is a potentially much stronger bias in the estimation of substitution rates. Nevertheless, there is generally a strong relationship between phylogenetic evidence, fossil data, and the inferred rates of molecular evolution across a number of studies of different molluscan taxa (e.g., Cunningham and Collins 1994; Rawson and Hilbish 1995; Collins et al. 1996; Reid et al. 1996; Hellberg 1998; Wares and Cunningham 2001; Meyer and Paulay, in review).

The issue of establishing accurate estimates of substitution rates in molecular markers is important for a number of reasons. It is not sufficient for a phylogeography study to show congruence between the topology of genealogical lineages and their geographic origins. If the events causing the separation of genetic lineages and those causing geographic changes do not occur contemporaneously, we may be misled into believing that there is a common geological cause for a phylogeographic event when in fact it is a case of "pseudo-congruence" (Cunningham and Collins 1994). The field of phylogeography is rapidly becoming one based on greater statistical rigor, and the accurate dating of events and their correspondence with competing phylogeographic hypotheses is crucial (Meyer and Paulay, in review).

Direct comparisons between fossil evidence and phylogeographic evidence

illustrate the importance of these rate estimates for interpreting the evolutionary processes acting on ancestral populations. In *Acanthinucella spirata*, the combination of fossil evidence for a range expansion in the late Pleistocene, accompanied by genetic data that are spatially and temporally concordant with this hypothesis, confirms the predictions typically cited for genetic data given a range expansion (Hewitt 1996). Additionally, the rate estimates used for the mitochondrial genes in this study were used to reconstruct changes in effective population size (N_e) in the ancestral population, and again the results of this analysis coincided with a late Pleistocene population expansion (Hellberg et al. 2001).

These comparisons among genetic and fossil data illustrate the importance of independent lines of support for a hypothesis. In phylogeography, this is typically achieved by comparing the results from multiple genes or loci (Hare and Avise 1998; Wollenberg and Avise 1998). It may also include the use of other physiological or genetic characteristics for a species. We know that speciation involves more than simply neutral processes, and the analysis of the traits involved in speciation is an important line of investigation. The phylogeography of the marine bivalve *Mytilus* has revealed the mechanics of speciation and the dynamics of hybridization among populations and species of the northern hemisphere *M. edulis* group (including *M. edulis*, *M. trossulus*, and *M. galloprovincialis*). The history of *Mytilus* in the Atlantic Ocean can be described by a number of partly independent evolutionary lineages that have been separated for only a brief time (Figure 9.3).

Mytilus offers a unique system for studying adaptive diversification because it is an osmoconformer found in habitats with a broad salinity range. Much early work on *Mytilus* indicated strong clinal variation in some allozyme loci that apparently corresponds to osmolarity gradients in their habitat. For instance, allele frequencies at the *Lap* locus strongly conform to patterns consistent with natural selection (reviewed in Hilbish 1996). Similar allele frequency differences at this locus and other allozyme loci between populations of *M. trossulus* in the Baltic Sea and the North Atlantic *M. edulis* were believed to represent historical differentiation of these populations, but recent work by Riginos et al. (2002) suggests otherwise.

Hybridization between the Baltic populations of *M. trossulus* and *M. edulis* was initially described using data from the mitochondrial genome (Quesada et al. 1995; Rawson et al. 1996a; Rawson and Hilbish 1998). Because the diagnostic allozyme loci for *M. trossulus* were stable in frequency, but the *M. edulis* mitochondrial type is now found throughout the Baltic, it appeared that mitochondrial introgression was more rapid than for nuclear markers. However, Riginos et al. (2002) used a number of additional nuclear genes to test this hy-

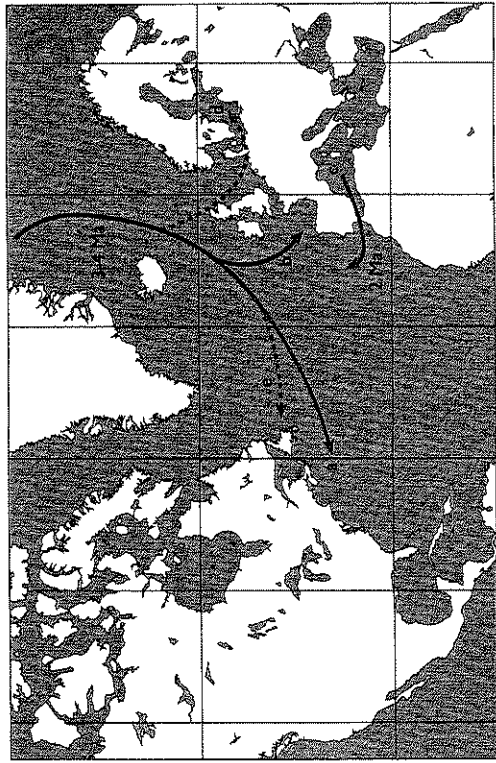


Figure 9.3. The history of *Mytilus* in the North Atlantic. This bivalve genus was not present in the Atlantic before its arrival in the late Pliocene, a range expansion event that involved the ancestral population of the Pacific species *M. trossulus* (Rawson and Hilbish 1995; Beynon and Skibinski 1996). The North Atlantic species *M. edulis* is a direct descendant of this event (a and b), and the combination of Pleistocene vicariance events (c, the brief separation of populations that formed *M. galloprovincialis*; Barsotti and Meluzzi 1968; Rawson and Hilbish 1995) and late Pleistocene or Holocene secondary invasions (d and e, the secondary introduction of *M. trossulus* to the Atlantic during a warm interglacial period; Riginos et al. in review; T. J. Hilbish, personal communication; J. P. Wares, unpublished data) have produced a patchwork of secondary contact zones between putative species of *Mytilus* in the North Atlantic. The distribution of the Mediterranean and eastern Atlantic species *M. galloprovincialis* overlaps with *M. edulis* in and around the British Isles, while recently arrived populations of *M. trossulus* hybridize with *M. edulis* in the Baltic Sea and along the east coast of Canada. Because this system has been intensively studied, it may be useful for comparisons with other molluscan phylogeographic studies for species that have similar geographic distributions.

pothesis. Data from the ribosomal internal transcribed spacer (ITS) region, two protein-coding genes that are responsible for the adhesion of byssal strands (Glu-5'; Rawson et al. 1996a) and sperm packaging (PL-II-a; Heath et al. 1995), and an anonymous nuclear marker (MAL-1; Rawson et al. 1996b) were sampled from Baltic populations of *M. trossulus*. In each case, *M. edulis* alleles are found in high frequency throughout these populations of *M. trossulus*, evidence of

strong introgression as well as an indication that the allozyme loci represent an ancestral coadapted gene complex that improves the fitness of *Mytilus* individuals in the low-salinity Baltic (Hilbish 1996; Riginos et al. 2002). The maintenance of such coadapted gene complexes in the face of introgression is probably a general issue in molluscan diversification (e.g., the intertidal whelk *Nucella*; see Kirby 2000). The use of additional genes helps resolve two very different phylogeographic histories involving introgression.

Attempts to elucidate the phylogeographic history of *Mytilus* have illuminated other unique genetic processes that play a role in diversification of this genus. The phenomenon of doubly uniparental inheritance (DUI) of the mitochondrial genome (reviewed in Zouros 2000) complicates our interpretation of the divergence of populations and species of *Mytilus*. Separate male and female mitochondrial genomes that evolve independently at different rates apparently predate the genus itself (Rawson and Hilbish 1995) and may play a role in sex determination in *Mytilus* (Saavedra et al. 1997). The effect that this sexual system has on the reconstruction of phylogeographic history in mussels is unclear, but the two mitochondrial genomes described very different histories. The isolation of European and North American populations of *M. edulis*, for example, is quite ancient in the male mitochondrial lineage, but female lineages are only recently diverged (Wares and Cunningham 2001; Riginos et al., in review). DUI of mtDNA has also been noted in the freshwater unionid bivalve *Anodonta* (Hoeh et al. 1996; Liu et al. 1996a).

In other taxa, phylogeographic patterns may be better explained when additional genetic mechanisms are explored. One good example involves the intertidal snail *Tegula*. Interspecific gene trees using the mitochondrial 12S and COI genes (Hellberg 1998) showed a surprising number of sister species to *Tegula* in sympatry, a relationship that is unexpected if allopatry is believed to be responsible for most speciation. Earlier work using abalone (*Haliotis*) as a model system for reproductive isolation involving gametic interactions (Lee et al. 1995) had shown that gametic recognition proteins might be under strong diversifying selection. Comparisons of these same genes in *Tegula* found that, indeed, the sperm-related lysin protein evolves at a rate that is an order of magnitude faster than the fastest reported mammalian genes (Hellberg and Vacquier 1999). If gametic recognition proteins evolve extremely rapidly, then even short periods of isolation or allopatry among populations could produce lineages and populations that are reproductively incompatible. Clearly, such interactions have strong implications for the generation of diverse lineages in marine settings, which often contain a surprising amount of cryptic species diversity given the lack of obvious geographic barriers to gene flow (Palumbi 1994).

COMPARATIVE BIOGEOGRAPHY

Other comparisons may be made with other marine biogeographic and phylogeographic studies. As detailed above, a tremendous amount of work has been done on the diversification and phylogeographic relationships among different populations of the bivalve *Mytilus* (Figure 9.3). Patterns in other taxa may be due to other mechanisms (e.g., the trans-Atlantic relationships in the ocean quahog, *Arctica islandica*, are indicative of a recent range expansion rather than an equilibrium history; Dahlgren et al. 2000). They may also represent a weaker phylogeographic signal than *Mytilus* (e.g., the pattern of isolation by distance in the cuttlefish *Sepia* that is geographically concordant with the initial isolation of *M. galloprovincialis*; Perez-Losada et al. 1999). Nevertheless, such comparisons should be used when possible. This allows us to find the most general mechanisms that may be responsible for regional diversification, whether they are intrinsic or extrinsic forces.

In the freshwater milieu, little comparative work has been done in phylogeography. However, the potential is great for comparisons among taxa that use different modes of reproduction, dispersal, or other means of interacting with the extrinsic environment. The remarkable reproductive biology of unionid bivalves, featuring an obligate parasitic (glochidial) phase on fish hosts (Coker et al. 1921), could serve as the basis for productive research in comparative phylogeography evaluating coevolutionary relationships of mussels and their fish hosts. We propose a very basic hypothesis for the expected relationship between the spatial distribution of genetic variation in freshwater unionid mussels and their fish hosts based on the following premises: (1) Fish and mussel species richness is positively related, suggesting that dispersal limitation is an important factor structuring freshwater mussel communities (Vaughn and Taylor 2000). (2) Fish and mussel species richness increases with stream order (Sheldon 1968; Gelwick 1990; Kingsolving and Bain 1993; Strayer and Ralley 1993). (3) Maximum body size usually increases as fish communities become more species-rich (Smith 1978). (4) Vagility and gene flow increase in fishes as a function of body size (Roff 1988, 1991; Turner and Trexler 1998).

These premises lead to the hypothesis that unionid mussels with distributions that are limited to low-order streams (e.g., creeks, small tributaries) should exhibit lower gene flow between populations and greater divergence among populations than those found in a broad range of stream orders, or those limited to larger rivers (Berg et al. 1997) if host selection is random. This is because fish hosts, on average, are expected to exhibit lower vagility (as a result of smaller body size) in low-order streams. A compilation of phylogeographic studies of

freshwater mussels lends some very weak support to this hypothesis (Table 9.2). Species limited to creeks and small rivers exhibit higher intraspecific genetic distance values and limited dispersion of shared haplotypes (with respect to the maximum distance separating sampling localities) compared with generalist or large-river species. Refinement of this hypothesis will certainly be necessary. If a particular mussel species requires a specific fish host (or a subset of available fish hosts), then the spatial distribution of genetic variation should reflect dispersal dynamics of that particular host, or subset of hosts. Differences among species should be reflected in mean body size differences (weighted by abundance) of available hosts.

Brooding characteristics and the timing of glochidial release may also affect unionid mussel dispersal. Four broad categories describe brooding characteristics in unionids (Dillon 2000): (1) summer tachytictic (short brooding time, release with rising temperatures; (2) winter tachytictic (short brooding time, release with falling temperatures; (3) summer bradytictic (overwinter brooding, release with rising temperatures; and (4) winter bradytictic (overwinter brooding, release with falling temperatures). Adult life cycle differences are expected to influence dispersal of glochidia in at least two ways. First, temperature at release is expected to correspond to developmental rates of glochidia within the fish host (Gillooly et al. 2001), and perhaps net movement of glochidia may increase with time encysted on a fish host. Second, dispersal behavior may differ seasonally in fish hosts (e.g., migration associated with spring reproduction), or local fish assemblage structure may fluctuate seasonally (Gelwick 1990). Brooding characters and other glochidial characteristics (presence/absence of hooks, etc.) are widely studied across unionids and appear to be strongly related to phylogenetic history in the group (Lydeard et al. 1996; Graf and Ó Foighil 1999). This information should permit careful selection of taxa for comparative phylogeographic study.

SUMMARY AND CONCLUSIONS

Molluscan diversification is rapid, especially in the tropics (Flessa and Jablon-ski 1996). The tremendous amount of diversity found in aquatic mollusks is nevertheless enigmatic. In the oceans, few obvious physical barriers separate populations—a mechanism for allopatric speciation (Mayr 1942)—yet there is a surprising amount of species (and phylogeographic) diversity (Palumbi 1994). In freshwater ecosystems, dispersal from one body of water to the next or even within a drainage is a limiting step that tends to generate increased diversity,

but there are predictable ways in which genetic and species diversity will be modified by the life history traits of different molluscan groups. In short, the intrinsic mechanisms used by molluscan species for recognition, development, and dispersal are crucial for producing and maintaining cohesive species groups.

The interactions of these intrinsic features with the extrinsic environment generate the phylogeographic history and patterns of interest. In some cases, we have only begun to realize the potential of molluscan systems for illuminating primary mechanisms of diversification. The marine gastropod *Tegula*, for instance, has undergone a tremendous species radiation in the past 4 million years (Hellberg 1998). Although speciation is typically thought to occur when populations are allopatric, many sister species to *Tegula* in the tropical eastern Pacific are currently sympatric and probably have been for most of their independent evolutionary histories. Landscape processes, including the dimensionality of the habitat, may play a role in species diversification (Hellberg 1998). If different processes are responsible for the divergence of populations and species when they are distributed along one-dimensional habitats (e.g., rivers or coastlines) than when distributed in two-dimensional habitats (e.g., nearby lakes or islands), then comparing these processes will help illustrate how much a species' response to environmental change depends on intrinsic qualities (which affect the genetic effective population size and migration ability of a species), and how much the response depends on extrinsic forces (including geographic forces, oceanography or hydrology, climate, and substrate type).

Essentially, the time has come when we can integrate a broader amount of information about species and their habitat into phylogeographic analysis. A number of life history traits, beyond larval development and dispersal, will contribute to a species' response to changes in the environment. We can go beyond these phenotypic traits to a diverse set of genetic markers that are informative about both the historical and adaptive milieu for diversification. Thanks to the excellent fossil record available for most molluscan taxa, there are few limits on the amount of resolution that can be obtained for phylogeographic studies, including ancestral population dynamics that may be crucial in establishing which of two hypotheses is more accurate. More thorough sampling, including the use of GIS systems to explicitly map genetic variation onto the landscape, will enable discrimination between subtly different but biologically relevant competing histories.

Although our understanding of coevolution in phylogeography is minimal, it is clear that even a single species has the capability to dramatically change the habitat it lives in and these changes may influence the genetic structure of co-occurring taxa. The intertidal snail *Littorina littorea* is a perfect example.

Table 9.2 A compilation of phylogeographic studies of freshwater unionid mussels

Species	Reference	Individuals / Localities	Genetic Marker(s)	<i>P</i>	Distance Between Samples (km) ^b	Haplotype Distance (km) ^c	Habitat Type ^d
<i>Lampsilis ornata</i>	Roe et al. 2001	5/5	16S RNA + COI	1.01	170	75	1
<i>Lampsilis australis</i>	Roe et al. 2001	5/5	16S RNA + COI	1.89	130	0	1
<i>Lampsilis subangulata</i>	Roe et al. 2001	3/3	16S RNA + COI	0.95	80	0	1
<i>Lampsilis perovialis</i>	Roe et al. 2001	5/5	16S RNA + COI	1.15	140	0	1
<i>Lasmigona subviridis</i>	King et al. 1999	37/9	COI	0.23	840	840	1
<i>Lasmigona subviridis</i>	King et al. 1999	40/9	ITS-1	0.49	840	375	1
<i>Megalobolus nervosa</i>	King et al. 1999	7/6	16S RNA	0.2	1,100	600	2
<i>Lampsilis hydana</i>	Turner et al. 2000	240/14	16S RNA	0.76	500	500	2
<i>Pyganodon (Anodonta) grandis</i>	Liu et al. 1996	72/5	RFLP	0.11	335	335	2
Whole mtDNA							
<i>Amblyema ellioti</i>	Mulvey et al. 1996	11/2	16S RNA	0	80	80	3
<i>Amblyema plicata</i>	Mulvey et al. 1996	5/2	16S RNA	0	115	115	3
<i>Megalobolus nervosa boykhamana</i>	Mulvey et al. 1996	17/11	16S RNA	0.5	1,130	1,130	3

^a*p* = average pairwise genetic distance between (female) haplotypes identified in each species.

^bEstimate of the maximum linear distance separating sampling localities.

^cEstimate of the distance separating populations with a shared haplotype.

^dHabitat type: 1 = creeks and small rivers, 2 = generalist, 3 = large rivers. Habitat preferences, when not described by the authors of the study, were from descriptions in Cummings et al. (1992), and Illinois Natural History Survey and Florida Museum of Natural History mollusk databases.

Studied for more than a century as an example of a species that may have been introduced by humans from Europe to North America (Ganong 1886), this snail has had a dramatic impact on the abundance and distribution of other intertidal species (Bertness 1984), including other molluscan species. Examining how this species arrived in North America is an important facet in the study of this system. Recent analysis of *L. littorea* indicates that this species has in fact maintained a limited (and paradoxical) geographic distribution on both the New England and European coasts of the Atlantic (Wares et al., unpublished data). Although *L. littorea* has clearly been extant in Europe for a much longer time (Vermeij 1991), populations in North America were founded long before European colonization of North America (by humans). Phylogeographic exposure of the extraordinary history of trans-Atlantic range expansion, followed by geographic isolation in the Canadian Maritimes until recent times, indicates that we must be cautious in speculating on the sources of diversity in natural populations and that interactions among species in forming phylogeographic patterns may be crucial (Wares 2002; Sotka et al., in press).

The interaction of molluscan species with their community is a vital interaction that must be better understood for precise phylogeographic hypothesis testing to be carried out. Whether the association is based on diet or substrate (Ingólfsson 1992, 1995), parasites, hosts, or commensal interactions, or more general geographic or landscape patterns (e.g., Hellberg 1998), more attention must be paid to these interactions. Furthermore, the appropriate use of null models (Haydon et al. 1994) and comparative studies (Cunningham and Collins 1998; Avise 2000; Wares and Cunningham 2001) must be examined to accurately determine the mechanisms involved. These mechanisms, both extrinsic to the species and part of their natural traits of reproduction, migration, and development, will lead to a better comprehension of the evolutionary forces acting on these traits (Collins et al. 1996).

Most importantly, we believe that a new era in phylogeography is arriving that not only informs us about the history of individual species, but will also detail the interactions that have led to broad evolutionary events in the phylogenetic history of mollusks and other organisms. Many of the comparisons suggested in this chapter are at the family level; to what extent are the distinct features of these higher-level groups a phylogenetic accident, and to what extent are these features deterministic of the phylogenetic history of mollusks? Throughout time, diversification in different lineages has accelerated and declined because of the interaction of species with their environment (see Jablon-ski et al. 1996). These interactions have shaped the extant molluscan fauna in ways that cannot always be isolated by a collection of sequence data.

ACKNOWLEDGMENTS

We would like to thank Megan McPhee, Dominique Aló, Cynthia Riginos, Peter Marko, Mike Hellberg, Randy DeFong, Sam Loker, Jess Morgan, and Jerry Hillbush for organizational and editorial help in writing this chapter. J. Wares would also like to thank Cliff Cunningham for his advice and assistance in this process, and Geerat Vermeij for many helpful discussions about molluscan evolution.

REFERENCES

- Allen, Y. C., and C. W. Ramcharan. 2001. *Dreissena* distribution in commercial waterways of the US: Using failed invasions to identify limiting factors. *Canadian Journal of Fisheries and Aquatic Sciences* 58:898–907.
- Avise, J. C. 1992. Molecular population structure and the biogeographic history of a regional fauna: A case history with lessons for conservation biology. *Oikos* 63: 62–76.
- Avise, J. C. 1994. Molecular Markers, Natural History, and Evolution. Chapman and Hall, New York.
- Avise, J. C. 2000. Phylogeography: The History and Formation of Species. Harvard University Press, Cambridge, MA.
- Barnes, R. S. K., P. Calow, P. J. W. Olive, D. W. Golding, and J. I. Spicer. 2001. The Invertebrates: A Synthesis, 3rd ed. Blackwell, Oxford.
- Barsootti, G., and C. Meluzzi. 1968. Osservazioni su *Mytilus edulis* L. e *Mytilus galloprovincialis* Lamarek. *Conchiglia* 4:50–58.
- Beerli, P., and J. Felsenstein. 2001. Maximum likelihood estimation of a migration matrix and effective population size in *n* subpopulations by using a coalescent approach. *Proceedings of the National Academy of Sciences U.S.A.* 98:4563–4568.
- Berg, D., S. I. Gutman, and E. G. Cantonwine. 1997. Micro- and macro-genetic differentiation among mussel populations. P. 284 in *Conservation and Management of Freshwater Mussels II: Initiatives for the Future* (K. S. Cummings, A. C. Buchanan, C. A. Mayer, and T. J. Naimo, eds.). *Proceedings of a UMRCC Symposium*, St. Louis, MO, Illinois Natural History Survey, Champaign, IL.
- Bermingham, E., and J. C. Avise. 1986. Molecular zoogeography of fresh-water fishes in the southeastern United States. *Genetics* 113:939–965.
- Bermingham, E., and C. Moritz. 1998. Comparative phylogeography: Concepts and applications. *Molecular Ecology* 7:367–369.
- Bertness, M. D. 1984. Habitat and community modification by an introduced herbivorous snail. *Ecology* 65:370–381.
- Bertness, M. D. 1999. *The Ecology of Atlantic Shorelines*. Sinauer Associates, Sunderland, MA.
- Beynon, C. M., and D. O. F. Skibinski. 1996. The evolutionary relationships between

- three species of mussel (*Mytilus*) based on anonymous DNA polymorphism. *Journal of Experimental Marine Biology and Ecology* 203:1–10.
- Bowen, D. Q., and G. A. Sykes. 1988. Correlation of marine events and glaciations on the northeast Atlantic margin. *Philosophical Transactions of the Royal Society of London B* 318:619–635.
- Briggs, J. C. 1974. *Marine Zoogeography*. McGraw-Hill, New York.
- Burton, R. S. 1998. Intraspecific phylogeography across the Point Conception biogeographic boundary. *Evolution* 52(3):734–745.
- Charbonnel, N., B. Angers, R. Razafavonjizay, P. Bremond, and P. Jame. 2000. Micro-satellite variation in the freshwater snail *Biomphalaria Pfeifferi*. *Molecular Ecology* 9:1006–1007.
- Coker, R., A. Shira, H. Clark, and A. Howard. 1921. Natural history and propagation of fresh-water mussels. *Bulletin of the United States Bureau of Fisheries* 37:75–181.
- Collin, R. 2001. The effects of mode of development on phylogeography and population structure of North Atlantic *Crepidula* (Gastropoda: Calyptraeidae). *Molecular Ecology* 10:2249–2262.
- Collins, T. M., K. Frazer, A. R. Palmer, G. J. Vermeij, and W. M. Brown. 1996. Evolutionary history of northern hemisphere *Nucella* (Gastropoda, Muricidae): Molecular, morphological, ecological, and paleontological evidence. *Evolution* 50:2287–2304.
- Cooley, L. R., and D. Ó Foighil. 2000. Phylogenetic analysis of the Sphaeriidae (Mollusca: Bivalvia) based on partial mitochondrial 16S rDNA gene sequences. *Invertebrate Biology* 119:299–308.
- Counis, C. L., III. 1986. The zoogeography and history of the invasion of the United States by *Corbicula fluminea* (Bivalvia: Corbiculidae). *American Malacological Bulletin*, Special Edition 2:7–39.
- Cunningham, C. W., and T. M. Collins. 1994. Developing model systems for molecular biogeography: Vicariance and interchange in marine invertebrates. Pp. 405–433 in *Molecular Ecology and Evolution: Approaches and Applications* (B. Schierwater, B. Streit, G. Wagner, and R. DeSalle, eds.). Birkhauser Verlag, Basel.
- Cunningham, C. W., and T. M. Collins. 1998. Beyond area relationships: Extinction and recolonization in molecular marine biogeography. Pp. 297–321 in *Molecular Approaches to Ecology and Evolution* (R. DeSalle and B. Schierwater, eds.). Birkhauser Berlin.
- Dahlgren, T. G., J. R. Weinberg, and K. M. Halanaych. 2000. Phylogeography of the ocean quahog (*Arctica islandica*): Influences of paleoclimate on genetic diversity and species range. *Marine Biology* 137:487–495.
- Davis, G. M. 1980. Snail hosts of Asian Schistosoma infecting man: Evolution and co-evolution. Pp. 195–238 in *The Mekong Schistosoma* (J. Bruce and S. Sornmani, eds.). Malacological Review, MI.
- Day, A. J., H. P. Leinas, and M. Austersrud. 1993. Allozyme differentiation of populations of the dogwhelk *Nucella lapillus*, (L.): The relative effects of geographic distance and variation in chromosome number. *Biological Journal of the Linnean Society* 51:257–277.
- DeLong, R. J., J. A. T. Morgan, W. L. Paransen, J. P. Pointer, M. Amarista, and 24 others. 2001. Evolutionary relationships and biogeography of *Biomphalaria* (Gastropoda: Planorbidae) with implications regarding its role as a host of the human bloodfluke. *Molecular Biology and Evolution* 18:2225–2239.
- DeWitt, T. J., A. Sih, and D. S. Wilson. 1998. Costs and limits of phenotypic plasticity. *Trends in Ecology and Evolution* 13:77–81.
- Dillon, R. T. 2000. *The Ecology of Freshwater Molluscs*. Cambridge University Press, Cambridge.
- Dillon, R. T., and J. J. Manzi. 1992. Population genetics of the hard clam, *Mercenaria mercenaria*, at the northern limit of its range. *Canadian Journal of Fisheries and Aquatic Sciences* 49:2574–2578.
- Dybdahl, M. F., and C. M. Lively. 1995. Diverse, endemic and polytypic clones in mixed populations of a fresh-water snail (*Potamopyrgus antipodarum*). *Journal of Evolutionary Biology* 8:385–398.
- Echelle, A. A., and T. E. Dowling. 1992. Mitochondrial DNA variation and evolution of the death-valley pupfishes (*Cyprinodon*, Cyprinodontidae). *Evolution* 46:193–206.
- Edwards, S. V., and P. Beerli. 2000. Perspective: Gene divergence, population divergence, and the variance in coalescence time in phylogeographic studies. *Evolution* 54:1839–1854.
- Emlet, R. B. 1995. Developmental mode and species geographic range in regular sea urchins (Echinodermata: Echinoidea). *Evolution* 49:476–489.
- Engle, V. D., and J. K. Summers. 1999. Latitudinal gradients in benthic community composition in Western Atlantic estuaries. *Journal of Biogeography* 26:1007–1023.
- Erlandsson, J., E. Rolán-Alvarez, and K. Johannesson. 1998. Migratory differences between ecotypes of the snail *Littorina saxatilis* on Galician rocky shores. *Evolutionary Ecology* 12:913–924.
- Flessa, K., and D. Jablonski. 1996. The geography of evolutionary turnover: A global analysis of extant bivalves. Pp. 376–397 in *Evolutionary Paleobiology* (D. Jablonski, D. H. Erwin, and J. H. Lapps, eds.). University of Chicago Press, Chicago.
- Ganong, W. F. 1886. Is *Littorina littorea* introduced or indigenous? *American Naturalist* 20:931–940.
- Gelwick, F. P. 1990. Longitudinal and temporal comparisons of riffle and pool fish assemblages in a northeastern Oklahoma Ozark stream. *Copeia* 1990:1072–1082.
- Gillooly J. F., J. H. Brown, G. B. West, V. M. Savage, and E. L. Charnov. 2001. Effects of size and temperature on metabolic rate. *Science* 293:2248–2251.
- Graf, D. L., and D. Ó Foighil. 1999. The evolution of brooding characters among the freshwater pearly mussels (Bivalvia: Unionoidea) of North America. *Journal of Molecular Evolution* 49:157–170.
- Graney, R., D. Chery, J. Rogers Jr., and J. Cairns. 1980. The influence of thermal discharge and substrate composition on the population structure of the Asiatic clam, *Corbicula fluminea*, in the New River, Virginia. *Nautilus* 94:130–135.
- Grosberg, R. K., and C. W. Cunningham. 2001. Genetic structure in the sea: From populations to communities. Pp. 61–84 in *Marine Community Ecology* (M. D. Bertness, S. D. Gaines, and M. E. Hay, eds.). Sinauer Associates, Sunderland, MA.

- Hare, M. P., and J. C. Avise. 1998. Population structure in the American Oyster as inferred by nuclear gene genealogies. *Molecular Biology and Evolution* 15:119–128.
- Haydon, D. T., B. I. Crother, and E. R. Pianka. 1994. New directions in biogeography? *Trends in Ecology and Evolution* 9:403–406.
- Heard, W. 1965. Comparative life histories of North American pill clams (Sphaeriidae: Pisidium). *Malacologica* 2:381–411.
- Heath, D. D., P. D. Rawson, and T. J. Hilbish. 1995. PCR-based nuclear markers identify introduced *Mytilus edulis* genotypes in British Columbia. *Aquaculture* 137:51.
- Hedgecock, D. 1994. Does variance in reproductive success limit effective population sizes of marine organisms? Pp. 122–134 in *Genetics and Evolution of Aquatic Organisms* (A. R. Beaumont, ed.). Chapman and Hall, London.
- Hellberg, M. E. 1994. Relationships between inferred levels of gene flow and geographic distance in a philopatric coral, *Balanophyllia elegans*. *Evolution* 48:1829–1854.
- Hellberg, M. E. 1998. Sympatric sea shells along the sea's shore: The geography of speciation in the marine gastropod *Tegula*. *Evolution* 52:1311–1324.
- Hellberg, M. E., and V. D. Vacquier. 1999. Rapid evolution of fertilization selectivity and lysin cDNA sequences in Teguline gastropods. *Molecular Biology and Evolution* 16:839–848.
- Hellberg, M. E., D. P. Balch, and K. Roy. 2001. Climate-driven range expansion and morphological evolution in a marine gastropod. *Science* 292:1707–1710.
- Herke, S. W., and D. L. Foltz. 2002. Phylogeography of two squid (*Loligo pealei* and *L. plei*) in the Gulf of Mexico and northwestern Atlantic Ocean. *Marine Biology* 140:103–115.
- Hershler, R., H. P. Liu, and M. Mulvey. 1999. Phylogenetic relationships within the aquatic snail genus *Tryonia*: Implications for biogeography of the North American Southwest. *Molecular Phylogenetics and Evolution* 13:377–391.
- Hewitt, G. M. 1996. Some genetic consequences of ice ages, and their role in divergence and speciation. *Biological Journal of the Linnean Society* 58:247–276.
- Hilbish, T. J. 1996. Population genetics of marine species: The interaction of natural selection and historically differentiated populations. *Journal of Experimental Marine Biology and Ecology* 200:67–83.
- Hill, W. G. 1979. Note on effective population-size with overlapping generations. *Genetics* 92:317–322.
- Hillis, D. M., and J. C. Patton. 1982. Morphological and electrophoretic evidence for two species of *Corbicula* (Bivalvia: Corbiculidae) in North America. *American Midland Naturalist* 108:74–80.
- Hoeh, W. R., D. T. Stewart, G. W. Sutherland, and E. Zouros. 1996. Multiple origins of gender-associated mitochondrial DNA lineages in bivalves (Mollusca: Bivalvia). *Evolution* 50:2276–2286.
- Hoskin, M. G. 2000. Effects of the East Australian Current on the genetic structure of a direct developing muricid snail (*Bezdova hanleyi*, Angas): Variability within and among local populations. *Biological Journal of the Linnean Society* 69:245–262.
- Hudson, R. R. 1990. Gene genealogies and the coalescent process. Pp. 1–44 in *Oxford Surveys in Evolutionary Biology*, vol. 7 (D. Futuyma and J. Antonovics, eds.). Oxford University Press, Oxford.
- Ingólfsson, A. 1992. The origin of the rocky shore fauna of Iceland and the Canadian Maritimes. *Journal of Biogeography* 19:705–712.
- Ingólfsson, A. 1995. Floating clumps of seaweed around Iceland: Natural microcosms and a means of dispersal for shore fauna. *Marine Biology* 122:13–21.
- Isom, B. G. 1986. Historical review of Asiatic clam (*Corbicula*) invasion and biofouling of waters and industries in the Americas. *American Malacological Bulletin*, sp. ed. 2:1–5.
- Jablonski, D., D. H. Erwin, and J. H. Lipps. 1996. *Evolutionary Paleobiology*. University of Chicago Press, Chicago.
- Jacobsen, R., V. E. Forbes, and O. Skovgaard. 1996. Genetic population structure of the prosobranch snail *Potamopyrgus antipodarum* (Gray) in Denmark using PCR-RAPD fingerprints. *Proceedings of the Royal Society of London B*. 263:1065–1070.
- Johannesson, K. 1988. The paradox of Rockall: Why is a brooding gastropod (*Littorina saxatilis*) more widespread than one having a planktonic larval dispersal stage (*L. littorea*)? *Marine Biology* 99:507–513.
- Johannesson, B., and K. Johannesson. 1996. Population differences in behavior and morphology in the snail *Littorina saxatilis*: Phenotypic plasticity or genetic differentiation? *Journal of Zoology* 240:475–493.
- Johannesson K., E. Rolán-Alvarez, and A. Ekdahl. 1995. Incipient reproductive isolation between two sympatric morphs of the intertidal snail *Littorina saxatilis*. *Evolution* 49:1180–1190.
- Johnson, M. S., and R. Black. 1991. Genetic subdivision of the intertidal snail *Bembicium vittatum* (Gastropoda, Littorinidae) varies with habitat in the Houtman Abrolhos islands, western Australia. *Heredity* 67:205–213.
- Johnson, M. S., and R. Black. 1998. Increased genetic divergence and reduced genetic variation in populations of the snail *Bembicium vittatum* in isolated tidal ponds. *Heredity* 80:163–172.
- Johnson, S. G., and E. Bragg. 1999. Age and polyphyletic origins of hybrid and spontaneous parthenogenetic *Campeloma* (Gastropoda: Viviparidae) from the southeastern United States. *Evolution* 53:1769–1781.
- Karl, S. A., and J. C. Avise. 1992. Balancing selection at allozyme loci in oysters: Implications from nuclear RFLPs. *Science* 256:100–102.
- Keigwin, L. D. 1978. Pliocene closing of the Isthmus of Panama, based on biostratigraphic evidence from nearby Pacific Ocean and Caribbean sea cores. *Geology* 6:630–634.
- King, T. L., M. S. Eackles, B. Gjetvaj, and W. R. Hoeh. 1999. Intraspecific phylogeography of *Lasnigona subviridis* (Bivalvia: Unionidae): Conservation implications of range discontinuity. *Molecular Ecology* 8:S65–S78.
- Kingsolving, A. D., and M. B. Bain. 1993. Fish assemblage recovery along a riverine disturbance gradient. *Ecological Applications* 3:531–544.
- Kirby, R. R. 2000. An ancient transpecific polymorphism shows extreme divergence in

- a multitrait cline in an intertidal snail (*Nucella lapillus* (L.)). *Molecular Biology and Evolution* 17:1816–1825.
- Knowlton, N. 2000. Molecular genetic analyses of species boundaries in the sea. *Hydrobiologia* 420:73–90.
- Knowlton, N., and L. A. Weigt. 1998. New dates and new rates for divergence across the Isthmus of Panama. *Proceedings of the Royal Society of London B* 265:2257–2263.
- Kulmer, M. K., J. Yamato, and J. Felsenstein. 1998. Maximum likelihood estimation of population growth rates based on the coalescent. *Genetics* 149:429–434.
- Lee, Y.-H., T. Ota, and V. D. Vacquier. 1995. Positive selection is a general phenomenon in the evolution of abalone sperm lysin. *Molecular Biology and Evolution* 12:231–238.
- Lewis, K. M., J. L. Feder, and G. A. Lamberti. 2000. Population genetics of the zebra mussel, *Dreissena polymorpha* (Pallas): Local allozyme differentiation within midwestern lakes and streams. *Canadian Journal of Fisheries and Aquatic Science* 57:637–643.
- Liu, L. L., D. W. Foltz, and W. B. Stickle. 1991. Genetic population structure of the southern oyster drill *Stramonia* (= *Thais*) *haemostoma*. *Marine Biology* 111:71–79.
- Liu, H. P., J. B. Mitton, and S. K. Wu. 1996a. Paternal mitochondrial DNA differentiation far exceeds maternal mitochondrial DNA and allozyme differentiation in the freshwater mussel, *Anodonta grandis grandis*. *Evolution* 50:952–957.
- Liu, H. P., J. B. Mitton, and S. J. Herrmann. 1996b. Genetic differentiation in and management recommendations for the freshwater mussel, *Pygamodon grandis* (Say, 1829). *American Malacological Bulletin* 13:177–124.
- Lydeard, C., and R. L. Mayden. 1995. A diverse and endangered aquatic ecosystem of the southeast United States. *Conservation Biology* 9:800–805.
- Lydeard, C., R. L. Minton, and J. D. Williams. 2000. Prodigious polyphyly in imperiled freshwater pearly-mussels (Bivalvia: Unionidae): A phylogenetic test of species and generic designations. Pp. 145–158 in *The Evolutionary Biology of the Bivalvia* (E. M. Harper, J. A. Crame, and J. D. Taylor, eds.). Geological Society of London, Special Publication 177.
- Lydeard, C., M. Mulvey, G. M. Davis. 1996. Molecular systematics and evolution of reproductive traits of North American freshwater unionacean mussels (Mollusca: Bivalvia) as inferred from 16S rRNA gene sequences. *Philosophical Transactions of the Royal Society of London B* 351:1593–1603.
- Lydeard, C., and K. J. Roe. 1998. Phylogenetic systematics: The missing ingredient in the conservation of freshwater unionid bivalves. *Fisheries* 23:16–17.
- Marincovich, L., and A. Y. Gladenkov. 1999. Evidence for an early opening of the Bering Strait. *Nature* 397:149–151.
- Marko, P. B. 1998. Historical allopatry and the biogeography of speciation in the Prosobranch snail genus *Nucella*. *Evolution* 52:757–774.
- Marko, P. B. 2002. Fossil calibration of the COI molecular clock reveals ancient divergence times for geminate species pairs separated by the Isthmus of Panama. *Molecular Biology and Evolution* 19:2005–2021.
- Marko, P. B., and J. B. C. Jackson. 2001. Patterns of morphological diversity among and within arcid bivalve species pairs separated by the Isthmus of Panama. *Journal of Paleontology* 75:590–606.
- Marsden, J. E., A. P. Spidle, and B. May. 1996. Review of genetic studies of *Dreissena* spp. *American Zoologist* 36:259–270.
- Mavarez, J., M. Amariasta, J. P. Pointier, and P. Jarne. 2000. Microsatellite variation in the freshwater schistosome transmitting snail *Biomphalaria glabrata*. *Molecular Ecology* 9:1009–1011.
- Mayden, R. L. 1988. Vicariance biogeography, parsimony, and evolution in North American freshwater fishes. *Systematic Zoology* 37:329–355.
- Mayr, E. 1942. *Systematics and the Origin of Species*. New York: Columbia University Press.
- McCaughey, D. E. 1991. Genetic consequences of local population extinction and recolonization. *Trends in Ecology and Evolution* 6:5–8.
- McLeod, M. 1986. Electrophoretic variation in North American *Corbicula*. *Malacological Bulletin*, sp. ed. 2:125–132.
- McMahon, R. 1983. Ecology of an invasive pest bivalve, *Corbicula*. Pp. 505–561 in *The Mollusca*, Vol. 6 (W. Russell-Hunter, ed.). Academic Press, New York.
- Meyer, C., and G. Paulay. In review. Recurrent speciation at biogeographic boundaries drives diversification of reef fauna.
- Minskley, W. L., D. A. Hendrickson, and C. E. Bond. 1986. Geography of western North American freshwater fishes: Descriptions and relationships to intracontinental tectonism. Pp. 519–613 in *The Zoogeography of North American Freshwater Fishes* (C. E. Hocutt and E. O. Wiley, eds.). Wiley, New York.
- Monsutti, A., and N. Perrin. 1999. Dinucleotide microsatellite loci reveal a high selfing rate in the freshwater snail *Physa acuta*. *Molecular Ecology* 8:1076–1078.
- Muller, J., S. Woll, U. Fuchs, A. Seitz. 2001. Genetic interchange of *Dreissena polymorpha* populations across a canal. *Heredity* 86:103–109.
- Mulvey, M., C. Lydeard, D. L. Pyer, K. M. Hicks, J. Brim-Box, J. D. Williams, and R. S. Butler. 1997. Conservation genetics of North American freshwater mussels *Anodonta* and *Megalania*. *Conservation Biology* 11:868–878.
- Nei, M., and W.-H. Li. 1979. Mathematical model for studying genetic variation in terms of restriction endonucleases. *Proceedings of the National Academy of Sciences U.S.A.* 76:5269–5273.
- Neves, R. J. 1999. Conservation and commerce: Management of freshwater mussel (Bivalvia: Unionoidea) resources in the United States. *Malacologia* 41:461–474.
- Neves, R., and J. Widlak. 1987. Habitat ecology of juvenile freshwater mussels (Bivalvia: Unionidae) in a headwater stream in Virginia. *American Malacological Bulletin* 5:1–7.
- Nielsen, R., and J. Wakeley. 2001. Distinguishing migration from isolation: A Markov Chain Monte Carlo approach. *Genetics* 158:885–896.
- Ó Foighil, D., T. J. Hibish, and R. M. Showman. 1996. Mitochondrial gene variation in *Mercenaria* clam sibling species reveals a relict secondary contact zone in the western Gulf of Mexico. *Marine Biology* 126:675–683.

- Palumbi, S. R. 1992. Marine speciation on a small planet. Trends in Ecology and Evolution 7:114-118.
- Palumbi, S. R. 1994. Genetic divergence, reproductive isolation, and marine speciation. Annual Review of Ecology and Systematics 25:547-572.
- Palumbi, S. R., F. Cipriano, and M. P. Hare. 2001. Predicting nuclear gene coalescence from mitochondrial data: The three-times rule. Evolution 55:859-868.
- Park, J.-K., and D. Ó Foighil. 2000a. Genetic diversity of oceanic island *Lasaea* (Mollusca: Bivalvia) lineages exceeds that of continental populations in the northwestern Atlantic. Biological Bulletin 198:396-403.
- Park, J.-K., and D. Ó Foighil. 2000b. Sphaeriid and corbiculid clams represent separate heterodont bivalve radiations into freshwater environments. Molecular Phylogenetics and Evolution 14:75-88.
- Peterson, M. A., and R. F. Demko. 1997. The influence of intraspecific variation in dispersal strategies on the genetic structure of planthopper populations. Evolution 51:1189-1206.
- Perez-Losada, M., A. Guerra, and A. Sanjuan. 1999. Allozyme differentiation in the cuttlefish *Sepia officinalis* (Mollusca: Cephalopoda) from the NE Atlantic and Mediterranean. Heredity 83:280-289.
- Pilsbry, H. A. 1911. Non-marine mollusca of Patagonia. Report of the Princeton University expedition to Patagonia, 1896-1899.
- Quesada, H., R. Wenne, and D. O. F. Skibinski. 1995. Differential introgression of mitochondrial DNA across species boundaries within the marine mussel genus *Mytilus*. Proceedings of the Royal Society of London B 262:51-56.
- Rawson, P. D., and T. J. Hilbish. 1995. Evolutionary relationships among the male and female mitochondrial DNA lineages in the *Mytilus edulis* species complex. Molecular Biology and Evolution 12:893-901.
- Rawson, P. D., and T. J. Hilbish. 1998. Asymmetric introgression of mitochondrial DNA among European populations of blue mussels (*Mytilus* spp.). Evolution 52:100-108.
- Rawson, P. D., K. Joyner, and T. J. Hilbish. 1996a. Evidence for intragenic recombination with a novel genetic marker that distinguishes mussels in the *Mytilus edulis* species complex. Heredity 77:599-607.
- Rawson, P. D., C. L. Secor, and T. J. Hilbish. 1996b. The effects of natural hybridization on the regulation of doubly uniparental mtDNA inheritance in blue mussels (*Mytilus* spp.). Genetics 144:241-248.
- Reid, D. G., E. Rumbak, and R. H. Thomas. 1996. DNA, morphology and fossils: Phylogeny and evolutionary rates of the gastropod genus *Littorina*. Philosophical Transactions of the Royal Society of London B 351:877-895.
- Renard, E., V. Bachmann, M. L. Cariou, and J. C. Moreteau. 2000. Morphological and molecular differentiation of invasive freshwater species of the genus *Corbicula* (Bivalvia, Corbiculidae) suggest the presence of three taxa in French rivers. Molecular Ecology 9:2009-2016.
- Riginos, C., M. J. Hickerson, C. M. Henzler, and C. W. Cunningham. In review. Differential patterns of male and female trans-Atlantic gene flow in the blue mussel, *Mytilus edulis*.
- Riginos, C., K. Sukhdeo, and C. W. Cunningham. 2002. Extreme discordance of allozyme and non-allozyme introgression across a mussel hybrid zone. Molecular Biology and Evolution 19:347-351.
- Rocha-Olivares, A., and R. D. Vetter. 1999. Effects of oceanographic circulation on the gene flow, genetic structure, and phylogeography of the rosethorn rockfish (*Sebastes hebomaculatus*). Canadian Journal of Fisheries and Aquatic Sciences 56:803-813.
- Roe, K. J., P. D. Hartfield, and C. Lydeard. 2001. Phylogeographic analysis of the threatened and endangered superconglutinate-producing mussels of the genus *Lampsilis* (Bivalvia: Unionidae). Molecular Ecology 10:225-2234.
- Roe, K. J., and C. Lydeard. 1998. Molecular systematics of the freshwater mussel genus *Potamilus* (Bivalvia: Unionidae). Malacologia 39:195-205.
- Roff, D. A. 1988. The evolution of migration and some life-history parameters in marine fishes. Environmental Biology of Fishes 22:133-146.
- Roff, D. A. 1991. Life-history consequences of bioenergetic and biomechanical constraints on migration. American Zoologist 31:205-215.
- Rolán-Alvarez, E., K. Johannesson, and J. Erlandsson. 1997. The maintenance of a cline in the marine snail *Littorina saxatilis*: The role of home site advantage and hybrid fitness. Evolution 51:1838-1847.
- Roy, K., D. Jablonski, and J. W. Valentine. 2001. Climate change, species range limits and body size in marine bivalves. Ecology Letters 4:366-370.
- Saavedra, C., M.-I. Reyero, and E. Zouros. 1997. Male-dependent doubly uniparental inheritance of mitochondrial DNA and female-dependent sex-ratio in the mussel *Mytilus galloprovincialis*. Genetics 145:1073-1082.
- Samadi, S., E. Artigebielle, A. Estoup, J. P. Pointier, J. F. Silvain, J. Heller, M. L. Cariou, and P. Jarne. 1999. Density and variability of dinucleotide microsatellites in the parthenogenetic polyploid snail *Melanooides tuberculata*. Molecular Ecology 7:1233-1236.
- Sarver, S. K., M. C. Landrum, and D. W. Foltz. 1992. Genetics and taxonomy of ribbed mussels (*Geukensia* spp.). Marine Biology 113:385-390.
- Scheltema, R. S. 1986. On dispersal and planktonic larvae of benthic invertebrates: An eclectic overview and summary of problems. Bulletin Marine Science 39:290-322.
- Sheldon, A. L., 1968. Species diversity and longitudinal succession in stream fishes. Ecology 49:193-198.
- Siripatrawan, S., J. K. Park, and D. Ó Foighil. 2000. Two lineages of the introduced Asian freshwater clam *Corbicula* occur in North America. Journal of Molluscan Studies 66:423-429.
- Small, M. P., and E. M. Gosling. 2000a. Genetic structure and relationships in the snail species complex *Littorina arcana* Hannaford Ellis, *L. compressa* Jeffreys and *L. saxatilis* (Olivier) in the British Isles using SSCPs of cytochrome-*b* fragments. Heredity 84:692-701.
- Small, M. P., and E. M. Gosling. 2000b. Species relationships and population structure of *Littorina saxatilis* Olivier and *L. tenebrosa* Montagu in Ireland using single-strand conformational polymorphisms. Molecular Ecology 9:39-52.

- Smith, G. R., 1978. Biogeography of intermountain fishes. Pp. 17-42 in Intermountain Biogeography: A Symposium. Great Basin Naturalist Memoirs. Vol. 2. Brigham Young University Press, Salt Lake City, UT.
- Sotka, E. E., J. P. Wares, and M. E. Hay. (in press). Geographic and genetic variation in feeding preference for chemically-defended seaweeds. *Evolution*.
- Stepien, C. A., A. N. Hubers, and J. L. Skidmore. 1999. Diagnostic genetic markers and evolutionary relationships among invasive dreissenoid and corbiculoid bivalves in North America: Phylogenetic signal from mitochondrial 16S rDNA. *Molecular Phylogenetics and Evolution* 13:31-49.
- Strayer, D. L. 1991. Projected distribution of the zebra mussel, *Dreissena polymorpha*, in North America. *Canadian Journal of Fisheries and Aquatic Science* 48:1389-1395.
- Strayer, D. L., and J. Ralley. 1993. Microhabitat use by an assemblage of stream-dwelling unionaceans (Bivalvia), including two rare species of *Alasmidonta*. *Journal of the North American Benthological Society* 12:247-258.
- Takada, Y., and E. Rolán-Alvarez. 2000. Assortative mating between phenotypes of the intertidal snail *Littorina brevicula*: A putative case of incipient speciation? *Ophelia* 52:1-8.
- Taylor, D. W. 1985. Evolution of freshwater drainages and mollusks in western North America. Pp. 256-321 in Late Cenozoic History of the Pacific Northwest (A. E. Levinton, ed.). American Association for the Advancement of Science, San Francisco, CA.
- Tataronkov, A., and K. Johannesson. 1998. Evidence of a reproductive barrier between two forms of the marine periwinkle *Littorina fabalis* (Gastropoda). *Biological Journal of the Linnean Society* 63:349-365.
- Tataronkov, A., and K. Johannesson. 1999. Micro- and macrogeographic allozyme variation in *Littorina fabalis*: Do sheltered and exposed forms hybridize? *Biological Journal of the Linnean Society* 67:199-212.
- Templeton, A. R., E. Routman, and C. A. Phillips. 1995. Separating population structure from population history: A cladistic analysis of the geographical distribution of mitochondrial DNA haplotypes in the tiger salamander, *Ambystoma tigrinum*. *Genetics* 140:767-782.
- Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biological Review* 25:1-45.
- Turner, T. F., and J. C. Trexler. 1998. Ecological and historical associations of gene flow in darters (Teleostei: Percidae). *Evolution* 53:1781-1801.
- Turner, T. F., J. C. Trexler, J. L. Harris, and J. L. Haynes. 2000. Nested cladistic analysis indicates population fragmentation shapes genetic diversity in a freshwater mussel. *Genetics* 154:777-785.
- Turner, T. F., J. P. Wares, and J. R. Gold. 2002. Genetic effective size is three orders of magnitude smaller than adult census size in an abundant, estuarine-dependent marine fish (*Sciaenops ocellatus*). *Genetics* 162:1329-1339.
- Vaughn, C. C., and C. M. Taylor. 2000. Macroecology of a host-parasite relationship. *Ecography* 23:11-20.
- Vernmeij, G. J. 1987. *Evolution and Escalation*, Princeton University Press.
- Vernmeij, G. J. 1991. Anatomy of an invasion: The trans-Arctic interchange. *Paleobiology* 17:281-307.
- Vernmeij, G. J. 1992. Time of origin and biogeographical history of specialized relationships between northern marine plants and herbivorous molluscs. *Evolution* 46:657-664.
- Viard, F., F. Justy, and P. Jarne. 1997. The influence of self-fertilization and population dynamics on the genetic structure of subdivided populations: A case study using microsatellite markers in the freshwater snail *Bulinus truncatus*. *Evolution* 51:1518-1528.
- Wade, M. J., and D. E. McCauley. 1988. Extinction and recolonization: Their effects on the genetic differentiation of local populations. *Evolution* 42:995-1005.
- Wares, J. P. 2000. Abiotic influences on the population dynamics of marine invertebrates. Ph.D. thesis, Duke University.
- Wares, J. P. 2002. Community genetics in the Northwestern Atlantic intertidal. *Molecular Ecology* 11:1131-1144.
- Wares, J. P., and C. W. Cunningham. 2001. Comparative phylogeography and historical ecology of the North Atlantic intertidal. *Evolution* 55:2455-2469.
- Wares, J. P., S. D. Gaines, and C. W. Cunningham. 2001. A comparative study of asymmetric migration events across a marine biogeographic boundary. *Evolution* 55:295-306.
- Wares, J. P., D. S. Goldwater, B. Y. Kong, and C. W. Cunningham. 2002. Refuting a controversial case of a human-mediated marine species introduction. *Ecology Letters* 5:577-584.
- Watson, D. C., and T. A. Norton. 1987. The habitat and feeding preferences of *Littorina obtusata* (L.) and *L. mariae* Sacchi et Rastelli. *Journal of Experimental Marine Biology and Ecology* 112:61-72.
- Wesselingh, F. P., G. C. Cadee, and W. Renema. 1999. Flying high: On the airborne dispersal of aquatic organisms as illustrated by the distribution histories of the gastropod genera *Tryonia* and *Planorbarius*. *Geologie en Mijnbouw* 78:165-174.
- Wilke, T., and G. M. Davis. 2000. Intraspecific mitochondrial sequence diversity in *Hydrobia ulvae* and *Hydrobia ventrosa* (Hydrobiidae: Rissooidea: Gastropoda): Do their different life histories affect biogeographic patterns and gene flow? *Biological Journal of the Linnean Society* 70:89-105.
- Wilding, C. S., J. Grahame, and P. J. Mill. 2000. Mitochondrial DNA COI haplotype variation in sibling species of rough periwinkles. *Heredity* 85:62-74.
- Williams, J. D., M. L. Warren, K. S. Cummings, J. L. Harris, and R. J. Neves. 1993. Conservation status of freshwater mussels of the United States and Canada. *Fisheries* 18:6-22.
- Wilson, A. B., K. A. Naish, and E. G. Boulding. 1999. Multiple dispersal strategies of the invasive quagga mussel (*Dreissena bugensis*) as revealed by microsatellite analysis. *Canadian Journal of Fisheries and Aquatic Science* 56:2248-2261.
- Wollenberg, K., and J. C. Avise. 1998. Sampling properties of genealogical pathways underlying population pedigrees. *Evolution* 52:957-966.
- Wootton, M. C., K. T. Scribner, and M. H. Smith. 1988. Genetic variability and systematics of *Gambusia* in the southeastern United States. *Copeia* 1988:283-289.
- Wright, S. 1977. *Evolution and the Genetics of Populations: A Treatise*. Vol. 4. Variability Within and Among Natural Populations. University of Chicago Press, Chicago.
- Zourou, E. 2000. The exceptional mitochondrial DNA system of the mussel family Mytilidae. *Genes and Genetic Systems* 75:313-318.