

Genetic Structure in the Sea

From Populations to Communities

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Virtually all species of marine organisms, whether pelagic, planktonic, or benthic, are patchily distributed, consisting of local populations linked to a greater or lesser extent by dispersal. Ecologists are primarily concerned with characterizing this geographic structure in terms of the distributions and movements of individual organisms within and among local populations. Evolutionary biologists, on the other hand, often think in terms of the spatial distribution of genetic variation within and among local populations. Ecological and evolutionary approaches thus differ in their emphasis on the spatial distribution of individuals versus genes; where they converge is in their attempts to understand the processes that cause geographic variation in a species. In other words, ecology shapes the distribution of genetic variation in a species (Endler 1992), whereas genetic structure provides the evolutionary context in which to interpret a species' ecological interactions with its environment.

Genetic structure in marine populations reflects the historical and contemporary interplay among a complex set of ecological, demographic, behavioral, genetic, oceanographic, climatic and tectonic processes (reviewed in Hedgecock 1986; Palumbi 1995; Benzie 1999; Bohonak 1999). The combined effects of these mechanisms, acting across a range of spatial and temporal scales, determine rates and patterns of dispersal of gametes, zygotes, larvae, and adults. It is these movements, along with the survival and successful reproduction of immigrants, that, in turn, control the scale and rate at which random (i.e., genetic drift) and deterministic (i.e., natural selection) processes build or erode structure within and among groups of individuals.

A number of recent papers have explored the population-level ramifications of genetic structure in marine systems, highlighting the relationships among developmental mode,

dispersal, gene flow (i.e., migration of gametes or individuals that leads to the incorporation of their genes into a recipient population), and speciation (e.g., Burton 1983, 1996; Hedgecock 1986; Palumbi 1994, 1995; Benzie 1999; Bohonak 1999). In keeping with the theme of this book, we expand this population-level perspective to the community, and explore four facets of the following basic question: What can information about the spatial distribution of genetic variation within a species, and the processes that generate these patterns, tell ecologists about the nature and outcomes of species' interactions with their biotic and physical environment?

The first aspect of the question relates to the scale at which a species' predators, competitors, parasites, pathogens, and symbionts regulate its population dynamics (Roughgarden and Iwasa 1986; Roughgarden et al. 1988; Possingham and Roughgarden 1990; Gaines and Lafferty 1995). The spatial scales over which marine populations exhibit "open" versus "closed" dynamics are generally not obvious, and they vary according to the magnitude of migration among subpopulations. Genetic structure can be used to place bounds on the spatial scales over which species are likely to be demographically closed.

The second facet concerns the scales over which species exhibit genetic structure, and how these patterns influence responses to spatially varying selection (see papers in Mopper and Strauss 1998 for a terrestrial perspective; for a marine perspective, see Warner 1997). The spatial distribution of neutral genetic variation determines the degree and scale over which subpopulations have been (or are) evolutionarily independent, and consequently free to evolve in response to local variation in selection. With high levels of gene flow among selective regimes, the selective costs of local adaptation increase, perhaps prohibitively. For example, if a polymorphic

predator (or parasite or herbivore) population genetically varies over a finer spatial scale than its prey (or host), it is unlikely that the prey population will evolve local adaptations in response to geographic variation in its predator (e.g., Menge 1976; Vermeij 1978, 1987; Palmer 1984).

Third, a number of recent genetic studies have revealed the existence of sibling species complexes in what were once thought to be a single polymorphic species (Knowlton 1993). Such discoveries suggest that many marine species may have more limited distributions than previously thought and may be far more ecologically specialized as well.

Finally, when set into a phylogenetic context, genetic structure can reveal a great deal about a population's history of subdivision and gene flow, in particular the history of its interactions with other species (Avice et al. 1987; Brooks and McLennan 1993; Avice 1994). Are strong interactions between competitors, predators and prey, or parasites and their hosts the result of a long, shared selective history (Brooks and McLennan 1993), or are these associations the result of recent introductions (e.g., Vermeij 1991)? Do traits that appear to be adaptive in their current selective contexts reflect a genetically based response to selection in a particular place, or were these traits shared by sister taxa prior to the evolutionary and geographic divergence of these taxa? For example, if we can determine that taxa on both sides of the North Atlantic lack geographic subdivision as a result of ongoing gene flow, then we might predict that differences in their morphology, physiology, behavior, or ecology result from environmentally mediated phenotypic, rather than cumulative genetic, responses to different environments. Conversely, if the lack of genetic structure is due to recent colonization with low levels of ongoing gene flow, then cumulative genetic change becomes a more plausible explanation for phenotypic divergence.

The process of characterizing genetic structure, and using this information to estimate gene flow, effective population size, and other ecologically relevant parameters has a long and complex history. Different methods make different assumptions about the equilibrium status of populations, migration patterns, population structure, and the attributes of genetic markers (Gillespie 1998). Not surprisingly, the different approaches can lead to very different conclusions about the distribution of genetic variation, and the historic and contemporary processes that underlie these distributions (Slatkin 1994; Neigel 1997). For this reason, we begin by summarizing the basic methods used to detect genetic structure and estimate gene flow. Because genetically based inferences of population subdivision and gene flow depend on a host of assumptions about migration patterns, mutation rates, selective neutrality, and equilibrium status (Gillespie 1998), we next consider problems associated with developing a mechanistic interpretation of patterns of genetic structure in natural populations. With this foundation in place, we finally return to the basic ecological questions and use a series of case studies to explore how genetic structure can provide crucial insights into the nature and outcomes of species' interactions with their biotic and physical environments.

CHARACTERIZING GENETIC STRUCTURE AND ESTIMATING GENE FLOW

The first quantitative attempts to depict genetic structure originated with Wahlund's (1928) observation that there should be heterozygote deficiencies in structured populations and Wright's (1951) analyses of the expected distribution of neutral genetic variation in spatially subdivided populations. Wright's approach built on the premise that species can be reduced to a set of freely interbreeding (panmictic) units, and that these units will resemble each other depending on the degree of gene flow between them (Slatkin 1994). Wright developed statistics that summarize the distribution of genetic variation within and among sampling units based on the spatial (and sometimes temporal) distribution of gene and genotypic frequencies. However, it was not until the advent of allozyme electrophoresis in the 1960s that population geneticists could build an extensive multilocus database from which to characterize the spatial distribution of gene frequencies in natural populations.

There is no reliable way to infer the genealogical relationships among allozyme variants, because there is no obvious connection between the migration patterns of proteins on an electrophoretic gel and the degree of divergence of the underlying DNA sequences. The development in the 1980s of indirect and direct methods for detecting nucleotide sequence variation made it possible for the first time to reconstruct the ancestral-descendant relationships among genes, populations, and species. With this information, it became possible for the first time to interpret the geographic distribution of alleles, haplotypes, or sequences in terms of their phylogenetic relationships (phylogeography, *sensu* Avice et al. 1987).

Both the gene frequency and genealogical approaches can be used to estimate the degree of geographic subdivision, the amount of gene flow between populations, and effective population size, all critical elements in forging a synthesis between population genetics and community ecology. Gene-frequency approaches have the advantage of using data that are relatively easy to generate, often for multiple loci; but they lack an explicit historical component. In contrast, the main advantage of genealogical methods is their ability to reconstruct the spatial histories of populations. This includes distinguishing between populations whose size has remained constant and populations that have experienced a recent population expansion. In a geographic context, genealogical data can be used to detect introgression between species, and to identify previously unrecognized cryptic species. Finally, when extended to the members of a community, a genealogical approach makes it possible to test hypotheses about the common processes that generate genetic structure, and the geographic histories of interactions among species.

F_{ST}-Based Approaches

CHARACTERIZING GENETIC STRUCTURE USING *F_{ST}*. Wright (1931, 1951, 1965) developed the classic theory for portraying genet-

ic structure by partitioning the population-wide inbreeding coefficient into contributions from population substructure (F_{ST} , the fixation index) and nonrandom mating within subpopulations (F_{IS}). The basic idea is simple: In a subdivided population, individuals are more likely to mate with members of their own subpopulation than with members of other subpopulations. Thus, at the level of the entire population, a subdivided population will have a higher than expected (under completely random mating) frequency of homozygotes.

Wright initially limited his analysis to two levels of structure: subpopulations and the total population, where subpopulations represent panmictic units within the total population. He further assumed that observed genetic structure was a stable feature of a population. However, populations often exhibit structure at a variety of spatial scales (reviewed in Neigel 1997), and genetic structure may only be evident during specific periods of the life cycle (McCauley and Goff 1998). For this reason, more complex hierarchical models of genetic structure have been developed (Nei 1973; Weir and Cockerham 1984).

F_{ST} measures the magnitude of population subdivision in terms of deviations from heterozygosities expected under Hardy-Weinberg equilibrium:

$$F_{ST} = \frac{H_T - \bar{H}_S}{H_T}$$

where H_T is the probability that two alleles drawn at random (with replacement) from the entire population differ in state (i.e., the probability with no population structure), and \bar{H}_S is the probability that two alleles drawn at random from a subpopulation differ in state (which, for a two-allele system, will always be $2p_iq_i$, where p_i is the observed allelic frequency in subpopulation i), averaged over subpopulations. In a completely randomly mating population, $H_T = \bar{H}_S$, and $F_{ST} = 0$. If that population were to become subdivided, with limited migration among subpopulations, then genetic drift would eventually lead to differences in allelic frequencies among subpopulations, and $H_T > \bar{H}_S$. As the magnitude of this difference increases, F_{ST} will approach its maximum value of 1.

It is also possible to define F_{ST} as the standardized variance in allelic frequencies among subpopulations (or any sampling unit). From this perspective, F_{ST} reflects the amount of genetic variance among subpopulations (usually the smallest sampling units) relative to the total variance expected if all subpopulations actually represented a single panmictic unit (Wright 1943, 1951). It is then a small step to think of F -statistics in terms of a nested analysis of variance, in which the distribution of variance of allelic and genotypic frequencies is partitioned within and among sampling units (Weir 1990; Neigel 1997).

With the rapid growth of a database on DNA sequences, techniques have been developed to use this information to characterize genetic structure. For example, the ratio of sequence divergences within and among subpopulations can be used to estimate F_{ST} (reviewed in Hudson et al. 1992).

Other methods explicitly incorporate the nested ANOVA approach by partitioning sequence divergence between alleles into the relative contributions of population subsets from spatially nested samples (AMOVA, Excoffier et al. 1992). It is important to remember that all methods for calculating F_{ST} assume that subpopulations are the same sizes and have equal variances in allelic frequencies (discussed in Whitlock and McCauley 1999). When these assumptions are violated, highly biased inferences about genetic structure and, consequently, gene flow can result (e.g., Palumbi et al. 1997).

INFERRING LEVELS OF GENE FLOW. There are two basic ways that population geneticists estimate gene flow. Direct measurements (sensu Slatkin 1985a) involve the tracking of individual or group movements (e.g., Gerrodette 1981; Burton and Swisher 1984; Olson 1985; Grosberg 1987, 1991; Stoner 1990; Willis and Oliver 1990; Jones et al. 1999; Swearer et al. 1999). In principle, these migration or dispersal patterns could then be translated into estimates of gene flow by determining whether the movements lead to successful breeding within the recipient population. In practice, the difficulties of (1) detecting rare, long-distance movements that can disproportionately contribute to gene flow, (2) tracking small, rare propagules across the expanses of the oceans, and (3) determining whether immigrants successfully reproduce generally doom this direct approach for the vast majority of marine organisms (Hedgecock 1986; Grosberg 1987; Grosberg and Levitan 1992; Johnson and Black 1995; Palumbi 1999).

Indirect methods use the spatial distribution of genetic variation to estimate gene flow, under the assumption that different patterns of dispersal and levels of gene flow will generate distinctive genetic structures at evolutionary equilibrium (Slatkin 1985a). Indirect approaches circumvent some of the logistical problems of direct estimates of gene flow, in part because indirect methods do not require the monitoring of individuals through time. Furthermore, indirect methods only incorporate movements that lead to successful establishment of the genes carried by immigrants, and thus reflect the cumulative effects of gene flow (and perhaps selection), averaged over space and time (Slatkin 1985a). In one sense, this is a virtue of indirect methods; however, indirect methods generally estimate gene flow averaged across subpopulations in an idealized model of migration (Whitlock and McCauley 1999). As such, these estimates almost certainly do not represent actual rates of gene flow everywhere within the total population at a given time and potentially sacrifice crucial details of the processes that produce genetic structure.

Indirect measures of gene flow are expressed in terms of two parameters that are extremely difficult to measure independently: (1) the genetically effective migration rate, m (or the fraction of individuals, on average, that migrate between subpopulations each generation) and (2) the genetically effective population size, N_e (Slatkin 1993; see the section in this chapter entitled Gene Flow, Selection, and Local Adaptation). Roughly speaking, N_e is the size of an idealized population (i.e., stationary dynamics, equal sex ratios, binomial variance

in reproductive success) that loses neutral genetic variation due to drift at the same rate as the “real” population (reviewed in Crow and Kimura 1970; Ewens 1982; Whitlock and Barton 1997). The product of N_e and m yields M , the average number of migrants exchanged between subpopulations per generation. As a general rule of thumb, when M exceeds approximately one individual per generation, gene flow—given sufficient time—will eventually offset the diversifying effects of genetic drift (Slatkin 1994). As we discuss in the section Scale of Population Regulation, the trivial levels of genetically effective migration necessary to homogenize allelic frequencies at neutral loci limit the power of gene flow estimates for reckoning demographically significant migration or dispersal.

The literature devoted to inferring levels of gene flow from allelic frequencies is massive, complex, and often arcane (reviewed by Slatkin 1985a; Slatkin and Barton 1989; Cockerham and Weir 1993; Slatkin 1994; Neigel 1997; Bossart and Prowell 1998; Waples 1998; Hutchison and Templeton 1999; Whitlock and McCauley 1999). By far the most popular methods are based on F_{ST} . With the appropriate spatial model of migration (a term we use interchangeably from here on with gene flow), plus a variety of other assumptions we discuss below, F -statistics can be used to estimate M (reviewed in Neigel 1997). The basic and most widely used formula is based on Wright’s (1931) island model of migration, and assumes equal likelihood of migration throughout a species range. The relationship between F_{ST} and gene flow ($N_e m$ or M) is

$$F_{ST} \approx \frac{1}{1 + 4N_e m} \text{ or } N_e m \approx \frac{1}{4} \left(\frac{1}{F_{ST}} - 1 \right)$$

As values of F_{ST} increase from their theoretical minimum of 0 (which implies that there is no detectable genetic structure and high levels of gene flow) to their maximum of 1 (which implies that subpopulations are fixed for different alleles and there is no gene flow), M declines to 0.

Slatkin (1985b) developed an alternative method for estimating $N_e m$, based on the distribution of alleles uniquely occurring in single subpopulations. The approach builds on the idea that the “lifespan” of such private alleles will depend on the rate at which they arise by mutation (and are lost due to drift) and the rate at which gene flow erases their uniqueness. Thus, at an equilibrium between drift and migration, the distribution of private alleles can be related to migration rate.

ASSUMPTIONS UNDERLYING ESTIMATES OF GENE FLOW. The mathematically simple inverse relationship between F_{ST} and $N_e m$ ($= M$) makes it easy to forget that this equation rests on many unstated and often difficult to verify assumptions (reviewed in Slatkin and Barton 1989; Neigel 1997; Bossart and Prowell 1998; Waples 1998; Whitlock and McCauley 1999). Populations of many marine species likely violate at least some of these assumptions. Therefore, we explore briefly the nature of these assumptions, and some of the effects of their violation on estimates of gene flow.

The first assumption is that sampling, in terms of (1) number of individuals, (2) number of loci, and (3) spatial scale, can accurately reveal underlying genetic structure. Insufficient sampling of individuals, subpopulations, and loci can introduce substantial error into estimates of F_{ST} (and analogous estimators such as G_{ST} and θ), and consequently M (Weir and Cockerham 1984; Weir 1990; Neigel 1997; Waples 1998; Holsinger 1999; Whitlock and McCauley 1999). Moreover, most F_{ST} -based analyses require a priori specification of hierarchical structure (but see Holsinger and Mason-Gramer 1996). When the scale of sampling (or data partitioning) does not match the scale at which a population exhibits genetic structure, structure may be exaggerated or obscured (Husband and Barrett 1996; Rousset and Raymond 1997; Bohonak 1999). This potentially confounds comparisons between taxa or studies that use different sample sizes, sampling regimes, and loci. Additionally, because the relationship between F_{ST} and M is nonlinear, large values of M are nearly impossible to estimate within several orders of magnitude (Templeton 1998). For these reasons alone, estimates of gene flow based on F_{ST} may have large associated errors.

The second assumption is that migration rates (m) must greatly exceed mutation rates (μ). This is because mutation reduces estimates of F_{ST} (Crow and Aoki 1984), and consequently upwardly biases inferred levels of gene flow (Neigel 1997). For most allozyme markers with low mutation rates, this effect will be minimal with respect to other sources of error. However, this assumption will almost certainly be violated for more rapidly evolving markers such as microsatellites. This prompted Slatkin (1995) to develop a statistic, R_{ST} , analogous to F_{ST} , that incorporates a stepwise mutation process potentially applicable to microsatellite loci. Neigel (1997) critically analyzed alternatives that putatively control for the effects of mutation on F_{ST} -based estimates of gene flow inferred from DNA sequence data. He concluded that when significant mutation affects a marker, genealogy-based methods, based on the ancestral-descendant relationships of alleles, may have considerable advantages over gene-frequency approaches (see the section entitled Genealogical Approaches).

Third, the model assumes that there is no selection on the marker alleles (i.e., they are neutral). In theory, weak selection should not greatly bias estimates of gene flow, as long as selection on the marker alleles does not vary spatially (Slatkin and Barton 1989). However, several empirical studies on marine systems suggest that selection on allozymes (and perhaps other markers) may strongly influence the spatial distribution of allelic variation (Koehn et al. 1980; Burton 1986; Karl and Avise 1992; Johannesson et al. 1995; reviewed in Avise 1994; Hilbish 1996; Bohonak 1999). Selection can either increase or decrease estimates of F_{ST} (and consequently inferred levels of gene flow). For example, undetected spatially varying selection on marker loci can enhance differences among subpopulations over that expected for neutral markers. On the other hand, balancing selection on genetic markers may spatially homogenize allelic frequencies, reducing structure at the loci under selection and creating the illusion

of high inferred levels of gene flow (Slatkin and Barton 1989; Karl and Avise 1992).

Fourth, the simple formula that relates F_{ST} to $N_e m$ builds on a classic island model of dispersal in which a species consists of a large number of equally sized subpopulations, all of which have an equal probability of exchanging migrants. As we discuss in the section Genetic Homogeneity, this may be a realistic approximation of dispersal in those species for which the scale of larval dispersal substantially exceeds the scale over which there are suitable patches of habitat. However, migration patterns for those species that live along coastlines or hydrothermal vent systems, especially those whose propagules have limited dispersal potential, may better fit a one-dimensional stepping-stone model of dispersal, in which migrants only move between adjacent linearly arrayed patches of habitat (Slatkin 1993; Vrijenhoek 1997). Similarly, for species with limited dispersal that live in island groups, a two-dimensional stepping-stone model may be a better approximation of actual migration patterns. In both classes of stepping-stone migration model, genetic differentiation should increase with the distance separating subpopulations and inferred gene flow should attenuate (Kimura and Weiss 1964). In theory, the exact migration model should minimally bias estimates of gene flow based on F_{ST} (Slatkin and Barton 1989); however, with more complex patterns of gene flow among subpopulations, the failure to sample on a scale or pattern corresponding to the existing genetic structure can substantially bias F_{ST} -based estimates of gene flow (Husband and Barrett 1996).

Finally, estimates of gene flow based on F_{ST} -like statistics (and even coalescent methods, as described in the next section) assume that populations are at a genetic equilibrium between the homogenizing effects of gene flow and the diversifying effects of genetic drift (Felsenstein 1982). In other words, historical effects no longer leave a signature on genetic structure. As we discuss in some detail in later sections, when populations have not reached an equilibrium between gene flow and drift, inferred gene flow may be highly biased (Whitlock and McCauley 1999), and non- F_{ST} -based methods may be more suitable (Slatkin and Barton 1989; Neigel 1997; Hutchison and Templeton 1999). For example, a large difference in allele frequencies between subpopulations can reflect either restricted gene flow (the equilibrium inference, as assumed by most F_{ST} -based methods), or a recent founding event or bottleneck (McCauley 1993; Hutchison and Templeton 1999). Conversely, subpopulations could be genetically similar either because they are linked by high levels of contemporary gene flow (the equilibrium inference), or because they were relatively recently isolated from each other (Felsenstein 1982).

THE APPROACH TO EQUILIBRIUM AND WHY IT MATTERS. Under an island model of migration, the time, t (in generations), it takes for F_{ST} to approach the equilibrium between the homogenizing effects of gene flow and the diversifying effects of genetic drift is related to N_e and m by the following expression (Crow and Aoki 1984):

$$\frac{1}{2m + \frac{1}{2N_e}}$$

For high migration rates and small effective population sizes, this equilibrium may be approached quite rapidly. However, for the large populations that may typify many species of marine invertebrates, or for the low migration rates characteristic of many clonal forms (Jackson 1986), this time may be on the order of thousands, or even millions, of generations. In addition, a stepping-stone, as opposed to island, pattern of migration can considerably lengthen the time it takes to reach this equilibrium (Slatkin 1993).

This raises the important question of whether many marine invertebrate populations ever reach genetic equilibrium throughout their ranges. Imagine under an island-migration model a population with $N_e = 10^5$, $m = 0.0001$ (i.e., $N_e m = 10$ migrants exchanged between subpopulations), and with a generation time of one year. Following a perturbation to migration patterns, it would take F_{ST} roughly 5000 years to reach its eventual genetic equilibrium (Whitlock and McCauley 1999). As we discuss later, many populations of marine organisms—particularly those more complex patterns of gene flow, larger populations, or lower levels of gene flow—may never have time to attain fully this equilibrium between gene flow and drift before being perturbed again. To the extent this is true, patterns of genetic structure in many species of marine invertebrate may not reflect contemporary levels of gene flow. For example, the last glacial period, approximately 10,000–12,000 years ago, made many intertidal and near-shore temperate and polar habitats unsuitable for numerous species, and drove their distributions equatorially. It also lowered sea level in the tropics, potentially strengthening the isolation between tropical island systems and basins (Paulay 1990; Benzie 1999). Depending upon the period of isolation of these populations, the magnitude of isolation, and their prior histories of isolation, the effect of these glacial periods may be either to inflate or reduce observed F_{ST} 's over that expected at equilibrium between contemporary gene flow and drift.

The fact that allelic frequencies and, consequently, genetic parameters such as F_{ST} may vary even over ecological time scales further cautions against taking estimates of gene flow at face value. For example, a growing number of studies show that allelic frequencies vary from generation-to-generation at a particular site, even in species with extensive dispersal potential (e.g., Johnson and Black 1982, 1984a,b; Watts et al. 1990; Kordos and Burton 1993; Lessios et al. 1994; Edmands et al. 1996; Li and Hedgecock 1998; Ruckelshaus 1998). Thus, historical (e.g., vicariance, founder events/range expansions, rare bouts of dispersal) and demographic (e.g., asexual propagation, low recruitment rates or long generation times, overlapping generations, and temporal variance in reproductive or recruitment rates) processes may be as important as levels of contemporary gene flow in determining the current genetic structure of some marine species (Felsenstein 1982; Hedgecock 1986; Ayre 1990; Cunningham and

Collins 1994, 1998; Palumbi 1995; Hilbish 1996; Benzie 1999; Hutchison and Templeton 1999).

EFFECTIVE POPULATION SIZE. N_e , or effective population size, is a crucial element of any analysis of the relationship between genetic structure and ecology. N_e is one of the two parameters (the other being m , the per generation migration rate) that together determine gene flow. Moreover, the value of N_e determines the relative importance of selection, drift, and mutation, and especially a population's potential for long-term adaptive genetic response to changing selective regimes (Hill 1985; also discussed here in the next section). Selection and mutation generally play a relatively less important role than drift and gene flow in determining gene frequencies in populations with a small effective population size. In addition, populations with a small N_e typically reach an equilibrium between gene flow and genetic drift relatively quickly. Such populations may be far more prone to extinction due to demographic stochasticity, reduction in gene diversity, or accumulation of deleterious mutations (Lynch and Gabriel 1990; Lande 1993, 1994; Hastings and Harrison 1994; Lynch et al. 1995).

In species that exhibit some combination of high individual variance in reproductive success, large changes in population size, or local extinctions and recolonizations, N_e can be much smaller than the censused number of individuals in a population (Nei and Tajima 1981; Waples 1989; Gilpin 1991; Nunney 1996, 1999; reviewed in Luikart and England 1999; also see the later section Range Expansion and Population Growth). It is notoriously difficult to obtain the demographic data necessary to estimate effective population size. However, temporal and spatial variation in allelic frequencies (Nei and Tajima 1981; Pollack 1983; Waples 1989; Li and Hedgecock 1998), as well as linkage disequilibrium (Hill 1981) and heterozygote excess (Pudovkin et al. 1996) can also be used to estimate N_e (given many of the assumptions cited above).

The few genetically based estimates of N_e for marine populations have so far yielded some unexpected results. Analysis of temporal variation in allelic frequencies in oysters indicates that the effective numbers of breeders in a population may be only a few percent, or less, of the censused population (Hedgecock et al. 1992; Li and Hedgecock 1998). Other high fecundity free-spawners, such as sea urchins, may also have surprisingly small effective population sizes (e.g., Edmands et al. 1996). Nunney (1996) contended that there is no theoretical reason to expect that high fecundity predisposes a population to low N_e relative to its census population size, and that reported differences may be largely methodological. However, Li and Hedgecock (1998) countered that the discrepancy between N_e and census population size in free-spawning marine invertebrates is not necessarily an artifact of the way N_e is inferred, but instead results from enormous among-individual variation in their genetic contributions to the next generation. It remains to be seen how general this pattern is. If small N_e is widespread in numerically large marine populations, then it has profound implications for how they will respond to selection.

GENE FLOW, SELECTION, AND LOCAL ADAPTATION. Gene flow hastens the spread of alleles across a species' range. In so doing, gene flow can either augment or counteract the effects of selection, depending on the spatial scale over which selection varies (Slatkin 1985a; 1994). What follows is a tremendous oversimplification of how gene flow and selection interact; the aim is to give a basic picture. For neutral alleles, in an island model of population structure, if $N_e m$ substantially exceeds one migrant per generation, then gene flow will ultimately prevent local genetic differentiation at neutral loci. Adding the effects of selection to those of gene flow gets complicated fast, especially when populations exhibit complex genetic structure and extinction-recolonization dynamics (Nunney 1999). In the simplest form, if different alleles are favored in different subpopulations, then the equilibrium frequency (p) of an allele favored in a subpopulation will be $1 - \frac{s}{m}$, where s is the selection coefficient in favor of that allele and m is the immigration rate of the alternative, unfavored allele, when $s > m$ (Haldane 1930; Nagylaki 1975). (When $s < m$, $p = 0$.) The time it takes to reach this equilibrium is approximately.

So, the details aside, gene flow can offset some or all of the differentiating effects of drift and spatially variable selection. When gene flow among subpopulations inhabiting distinct selective regimes is high, local adaptation is less likely to occur (Endler 1977; Hedgecock 1986; Johnson and Black 1995). Selection should favor either a reduction in dispersal potential or the evolution of phenotypic plasticity. Conversely, when gene flow among subpopulations is low, small and persistent differences in selective regimes among subpopulations can eventually lead to their adaptive genetic divergence (but see Holt and Gomulkiewicz 1997).

Genealogical Approaches

F_{ST} , GENE GENEALOGIES, AND COALESCENCE. Many evolutionary biologists are familiar with using DNA sequence information to reconstruct species-level phylogenetic relationships. Our concern in this chapter is with depicting patterns of genetic structure (and gene flow) *within* species. F -statistics and their analogues use the spatial distribution of allelic frequencies, usually at multiple loci, to portray genetic structure and to estimate rates of migration. F_{ST} -based approaches explicitly assume that the primary determinant of genetic structure is a balance between gene flow and drift, and do not consider that every pair of alleles in a species has descended from a common ancestor sometime in the past. Ignoring the relationships between alleles is a necessary evil for some kinds of data, such as studies based on allozyme variation. However, for the last two decades, restriction enzyme analysis and direct sequencing have made it possible to use DNA sequences to characterize genetic structure. Sequence information has two major advantages over allozymes. First, allozyme studies reveal differences only at the amino acid level, whereas DNA studies can detect substitutions that do not affect the amino acid sequence. Second, allozyme studies do not identify which amino

acid has changed in a protein, making it impossible to infer relationships between alleles. Sequence information, on the other hand, can be used to deduce genealogical relationships between alleles by any of a number of standard phylogenetic approaches (Hudson 1990; Avise 1994).

The development of coalescence theory has provided a powerful framework for interpreting these gene genealogies in a population genetic framework. This framework has generated novel insights into patterns of genetic structure and the historical mechanisms that can generate genetic structure (e.g., Hudson 1990; Barton and Wilson 1995; Templeton 1998). Coalescent theory analyzes the structure of the tree moving backward in time (i.e., from the top of the tree to its base), with time usually measured in number of generations. Each of the nodes represents the point in time at which two allelic lineages “coalesce” or merge in their most recent common ancestor.

In this section, we first introduce a coalescent approach for estimating gene flow from gene genealogies. We then consider how genealogical approaches are useful for diagnosing especially deep divergences (reciprocal monophyly) between geographically separated populations, and the importance of reciprocal monophyly for reconstructing the history of genetic subdivision. We conclude this section by analyzing some of the crucial differences between intraspecific versus interspecific phylogenies, and between gene genealogies and population phylogenies.

CHARACTERIZING GEOGRAPHIC STRUCTURE AND GENE FLOW USING GENE GENEALOGIES. In DNA-based studies, alleles are defined as sets of homologous sequences that differ by at least one substitution. If the sequences are from mitochondrial genes, alleles are referred to as haplotypes. The first step in a phylogenetically based analysis of intraspecific genetic structure is to reconstruct the genealogical relationships among alleles using parsimony or some alternative method (reviewed in Swofford et al. 1996). These gene genealogies can also be referred to as gene trees. The geographic distribution of the sampled alleles can then be mapped onto a genealogy, and the pattern and degree of association between genealogical and geographic structure assessed (see the section Genetic Homogeneity later in this chapter). For example, if groups of closely related alleles are consistently found in the same geographically restricted areas, then limited gene flow over long periods of time is the simplest explanation.

Slatkin and Maddison (1989, 1990) were the first to develop a coalescent approach to estimating migration rates from gene genealogies. Their method considers the collection locality of an allele as a character state. If closely related alleles are collected in different locations, then parsimony will infer a migration event between the locations. Slatkin and Maddison’s method uses parsimony to calculate the minimum number of migration events across the entire gene genealogy. This method is easiest to employ if phylogenetic methods find a single gene genealogy; however, it is possible to calculate the mean number of migration events across alternative

trees using MacClade 3.0 (Maddison and Maddison 1992). Slatkin and Maddison (1989, 1990) used a simulation approach that assumes both evolutionary equilibrium and constant population size to relate the minimum number of inferred migration events on a gene genealogy to M (defined above). The method is easy to apply, and recombination has surprisingly little effect on estimates of M (Hudson et al. 1992).

Slatkin and Maddison’s parsimony approach has one conspicuous limitation: it does not consider variation in branch lengths when reconstructing migration events. In other words, the method implicitly assumes that the probability of a migration event is independent of branch length. This is unrealistic because longer branch lengths indicate that more time has passed between nodes. Recently developed maximum likelihood methods are more realistic because they assume that migration events are more likely on long branches than on short ones (Nath and Griffiths 1996; Beerli and Felsenstein 1999). However, it remains to be seen how well these methods perform when applied to real data.

As with F_{ST} -based measures, coalescent approaches can use randomization methods to test whether a reduced level of gene flow between populations represents significant geographical subdivision. For example, if the minimum number of migration events between two populations is significantly lower than expected from a distribution of random trees, then the degree of population subdivision is considered significant (Maddison and Slatkin 1991).

THE HISTORY OF POPULATION SUBDIVISION AND THE IMPORTANCE OF RECIPROCAL MONOPHYLY. Significant geographic subdivision can occur between populations that still occasionally exchange individuals, but are at an equilibrium between gene flow and drift. However, significant genetic structure can also result when an historical event has permanently interrupted gene flow between the populations being considered. These historical interruptions of gene flow violate the assumption of equilibrium that are at the heart of traditional population genetic theory. Although allele-frequency approaches can be used to detect nonequilibrium situations (e.g., Slatkin 1993), these approaches offer few insights into the historical processes that produce genetic structure.

Genealogical methods, are particularly well-suited to detecting ancient interruption of gene flow. Whenever gene flow between populations ceases, a combination of mutation and random extinction of lineages (lineage sorting) will eventually generate reciprocal monophyly, where alleles from each location form a monophyletic group relative to the alleles collected from the other location (Figure 3.1; Neigel and Avise 1986; Avise 1994; see the section Range Expansion and Population Growth, later in this chapter). In terms of coalescence theory, reciprocal monophyly occurs when the alleles from each locality each have a unique common ancestor, meaning that they coalesce with each other before they coalesce with alleles in the other subpopulation. This process takes on the order of $4N_e$ generations (Neigel and Avise 1986).

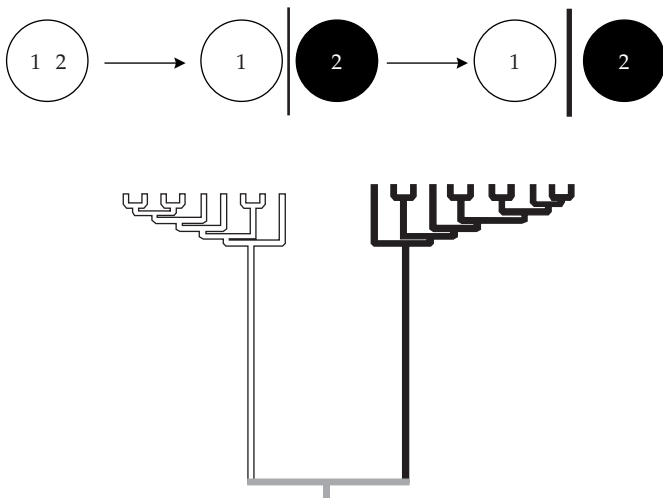


Figure 3.1 The establishment of reciprocal monophyly in subdivided populations. Reciprocal monophyly takes on the order of $4N_e$ generations, and results when a combination of mutation and lineage sorting in a pair of isolated subpopulations eventually causes all of the alleles in each subpopulation to be more closely related to each other than they are to any alleles in the other subpopulation.

The establishment of reciprocal monophyly has several important implications for population and community ecologists. First, reciprocal monophyly between spatially disjunct subpopulations demonstrates a lack of genetically effective migration between the subpopulations. Second, because reciprocal monophyly takes a considerable time to evolve, its existence indicates that both subpopulations have resisted local extinction for at least that much time (Cunningham and Collins 1998; discussed further in the section entitled Community Assembly and the History of Species Interactions).

Finally, when populations isolated for a long period of time come into secondary contact, F_{ST} -based approaches should generally reveal significant subdivision if the secondary contact is recent, or along a sharply defined hybrid zone. One of the best-known marine examples is the zone of contact between Gulf and Atlantic populations of numerous distantly related marine species at Cape Canaveral in Eastern Florida (reviewed in Avise 1992). In this case, F_{ST} -based approaches reveal significant geographic subdivision, but cannot distinguish whether the genetic subdivision is due to an extended historical interruption of gene flow, or an ongoing but significant reduction of gene flow. Gene genealogies, however, reveal that the contacting populations are reciprocally monophyletic, and clarify the status of the populations as evolutionarily independent units (Cunningham and Collins 1994).

GENE GENEALOGIES VERSUS SPECIES-LEVEL PHYLOGENIES. Like species-level phylogenies, *intraspecific* gene genealogies can be inferred from DNA sequences or restriction fragment profiles using conventional search methods implemented in such widely used software packages as PAUP* 4.0 (Swofford 1999) or PHYLIP (Felsenstein 1999). There are, however, two

important differences between species-level phylogenies and *intraspecific* gene genealogies that are crucial to constructing and interpreting gene genealogies (reviewed by Crandall and Templeton 1996).

First and most importantly, the nodes in *inter*-specific phylogenetic trees represent ancestral populations that have gone extinct. In contrast, truly ancestral alleles are almost always found in *intraspecific* gene genealogies. Although counterintuitive, this situation is expected because not every actual bifurcation in an *intraspecific* gene genealogy is reflected by a mutation. Consider a mother who passes on her mitochondria to two daughters. Only the first daughter's mtDNA experiences a mutation, whereas the other daughter's does not. The first daughter's offspring will inherit a derived allele, while the second daughter's offspring will inherit the ancestral allele. In this way, alleles that are identical to the true ancestor remain in the population. These ancestral alleles are easily identified in parsimony analyses because they (1) have no unique substitutions (i.e., autapomorphies), (2) are deeply nested, and (3) are often quite common in the population (Figure 3.2). When one searches for gene genealogies using parsimony or other method, zero-length branches should be collapsed to reflect the existence of actual ancestors in the population (Figure 3.2B).

Second, the traditional outgroup method for rooting *inter*-specific phylogenies is not reliable for *intraspecific* gene genealogies. This is because the distance to the outgroup for an *intraspecific* gene genealogy is vastly greater than the distance between individuals in the population (Castelloe and

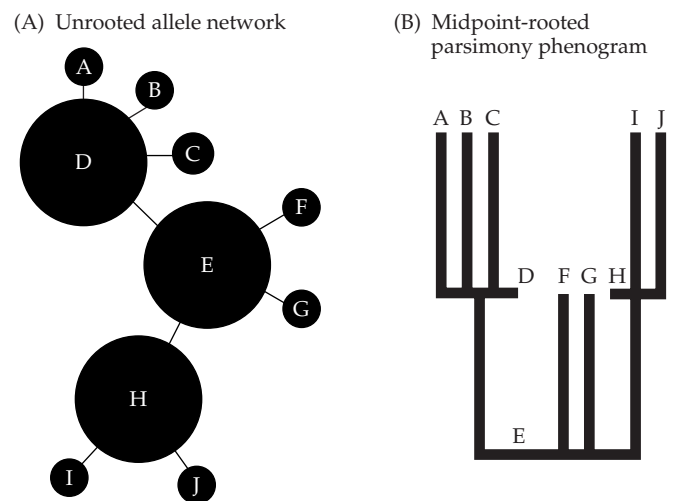


Figure 3.2 (A) An unrooted allele (or haplotype) genealogy. The letters denote a unique haplotype, the size of the circles corresponds to the relative frequency of that haplotype, and the lines connecting the circles represent a single base pair substitution. (B) Midpoint-rooted parsimony phenogram of the same genealogy shown in (A) from PAUP* (Swofford 1999), with zero-length branches collapsed. As expected from the retention of ancestral haplotypes in population-level genealogies, haplotypes D, E, and H have no branch length of their own.

Templeton 1994; Crandall and Templeton 1996). This means that any site along the outgroup branch may have experienced multiple substitutions, thereby erasing the historical signal [similar to “long branch attraction” in interspecific phylogenies (Felsenstein 1978)]. One option is to present a gene genealogy as an unrooted allele network (Avice 1994; Crandall 1994; Smouse 1998). Alternatively, there are several methods that use coalescent theory to root the network (Castelloe and Templeton 1994; Griffiths and Tavaré 1994). These methods build on the premise that the oldest alleles should be the most deeply nested in the network, because they will have had more time to generate descendants.

GENE GENEALOGIES VERSUS POPULATION PHYLOGENIES AND F_{ST} -BASED APPROACHES. The preceding discussion focused on gene genealogies based on alleles sampled from *individuals*. There are, however, many cases in which populations, not individuals, represent the taxonomic units in a phylogeny. For allozyme data, the genealogical relationships between individual alleles are unknown. Instead, allele frequencies are used to generate distances between populations (e.g., Cavalli-Sforza and Edwards 1967; Nei 1972), and population phylogenies are inferred from these distances. Population phylogenies can be built from almost any kind of frequency data, such as DNA allele frequencies, microsatellite allelic frequencies, or—of course—allozymes.

Unlike gene genealogies, population phylogenies have the benefit of being estimated from multiple loci, and usually from relatively large samples. In contrast, most gene genealogies are inferred from relatively small samples of individuals at a single locus. It is important, however, to keep in mind that a population phylogeny does not necessarily predict the relationship of any two individuals from distinct populations. If there has been recent migration between long-isolated subpopulations, the populations will exhibit sharp differences in allele frequencies, even though some individuals in the two populations share closely related alleles due to the recent migration (e.g., Van Syoc 1994). Moreover, because population phylogenies are based on distances inferred from allele frequencies, they are subject to many of the same pitfalls as pairwise F_{ST} 's calculated from gene frequencies (see F_{ST} -Based Approaches).

On the other hand, gene genealogies represent the history of only a single locus, and are not necessarily equivalent to organismal or population-level phylogenies. For several reasons, the genealogy inferred from one gene may be contradicted by other loci collected from the same individual. For example, interspecific hybridization can lead to mitochondrial introgression from one species into another, leading nuclear and mitochondrial genes from the same individual to have very different histories (e.g., Lamb and Avice 1986; Quesada et al. 1995). Similarly, in recombining loci, different parts of the same gene may have distinct histories (Slatkin 1994). This difficulty can be overcome by generating gene genealogies from multiple loci. When multiple loci yield congruent patterns, then confidence in the inferred history is greatly increased.

Conclusions

With the appropriate significance tests (reviewed in Weir 1996; Neigel 1997), F_{ST} and analogues [e.g., G_{ST} (Nei 1973), θ_{ST} (Weir and Cockerham 1984), N_{ST} (Lynch and Crease 1990), and R_{ST} (Slatkin 1993)] provide simple indices of the magnitude and scale over which populations exhibit significant genetic structure, based on readily obtainable data. F_{ST} -based approaches are best-suited to large samples, with data from multiple, independent loci (Slatkin and Barton 1989; Neigel 1997). F_{ST} -based approaches have the virtue (and evil) of reducing potentially very complex genetic structures into simple metrics, facilitating comparisons on the one hand, and obscuring differences on the other (Gillespie 1998). The fact that F -statistics and inferences of gene flow may be time-, locus-, and scale-dependent is also both a blessing and a curse. This sort of variation can provide critical insights into the ways that mating patterns, dispersal, and selection influence genetic structure. However, this variation cautions against taking estimates of gene flow at face value, especially when they involve different spatial and temporal scales, different loci, and different species.

Perhaps the most important limitation of approaches based on the spatial distribution of allelic and haplotypic frequencies is that estimates of gene flow assume that a population is in evolutionary equilibrium with respect to gene flow and genetic drift, and that historical effects no longer persist. Some genealogical methods for estimating migration rates and the magnitude of genetic subdivision make similar equilibrium assumptions, and the number of loci and individuals that are usually sampled limits their power. However, to the extent that populations of marine organisms deviate from migration-drift equilibria, genealogical approaches at the level of the individual and populations may be essential for deciphering the imprint of history on genetic structure and the nature and outcomes of species interactions.

INTERPRETING PATTERNS OF GENETIC STRUCTURE IN MARINE POPULATIONS

The main problem with interpreting genetic patterns in natural populations arises because a particular pattern may be generated by both historical and contemporary processes, acting singly or combined, at different spatial and temporal scales. Many of the methods for detecting patterns of genetic structure and inferring gene flow assume that the genetic signature of past historical events has been erased by a combination of migration and drift. The assumption of an equilibrium between migration and genetic drift also underlies the most important generalization in the evolutionary genetics of benthic marine organisms. Larval dispersal ability should be the primary determinant of genetic structure (Palumbi 1995; Bohonak 1999), and ultimately rates and patterns of speciation and extinction (Jablonski and Lutz 1983; Palumbi 1994; cf. Hedgecock 1986).

Of course, the pattern of genetic structure at equilibrium depends on many factors, including developmental mode,

larval behavior, circulation patterns, distribution of suitable habitats, and geographical scale of sampling (reviewed in Lessios et al. 1998; Benzie 1999; Bohonak 1999). At one extreme, a species with exceptionally broadly dispersing larvae should be panmictic over all but perhaps the largest spatial scales. Species with somewhat more limited dispersal potential may show panmixia over fine and moderate spatial scales, and isolation by distance (sensu Wright 1943; Malécot 1968) at much larger scales. At the other extreme, species with effectively nondispersing larvae should show a pattern of isolation by distance at all but the very finest spatial scales.

In the most recent review of the subject, Bohonak (1999) found a statistically significant relationship between larval dispersal ability and degree of geographic subdivision (measured by F_{ST}). However, like his predecessors (e.g., Burton 1983; Hedgecock 1986; Ayre 1990; Palumbi 1994, 1995; Hilbish 1996; Cunningham and Collins 1998; Ruckelshaus 1998), Bohonak (1999) identified numerous cases in which dispersal potential only weakly predicted genetic structure (also see Cunningham and Collins 1994, 1998; Hellberg 1994; Marko 1998; Benzie 1999). These exceptions emphasize that our understanding of how contemporary processes generate genetic structure in the sea is, not surprisingly, incomplete. Moreover, several lines of evidence suggest that the imprint of historical processes on contemporary genetic structure may be both pervasive and persistent. For example, genetic breaks may not correspond to known barriers to dispersal (reviewed in Cunningham and Collins 1994, 1998; Shulman and Bermingham 1995; Palumbi 1997; Benzie 1999), genetic continuity may occur where there are no obvious contemporary dispersal pathways (e.g., Palumbi et al. 1997), and phylogeographic analysis may reveal that sister taxa are nonadjacent (e.g., Marko 1998).

One of the best-studied marine examples of this kind concerns the distribution of genetic variation among benthic invertebrates along the coast of the southeastern United States (also see examples from the Indo-Pacific in Benzie 1999). Here, many species, regardless of their dispersal potential, are subdivided into two reciprocally monophyletic populations in the Atlantic and the Gulf of Mexico, with a narrow hybrid zone at Cape Canaveral (reviewed in Avise 1992, 1994). It is not certain whether local adaptation or oceanographic barriers maintain the genetic distinctions between these populations (see Hare and Avise 1996). What is certain is that a massive vicariant event interrupted gene flow for many co-occurring taxa, regardless of their dispersal ability, and that larval dispersal has yet to restore genetic homogeneity between the Gulf and Atlantic populations, even in those species with broadly dispersing larvae.

In this section, we analyze some of the problems of distinguishing the contributions that historical and contemporary processes make to genetic structure. We first evaluate from equilibrium and nonequilibrium perspectives the two simplest and most extreme patterns expected at genetic equilibrium: genetic homogeneity and isolation by distance. We note that true uniformity may be difficult to detect, and that apparent examples of both homogeneity and isolation by dis-

tance may reflect the operation of a mixture of historical, as well as contemporary, processes. We then review some statistical methods that can be used to identify historical contributions to genetic structure, especially the effects of range expansions (and contractions) and population growth.

Genetic Homogeneity

The lack of obvious physical barriers to dispersal in many of the world's oceans led early marine population geneticists to predict that species with broadly dispersing larvae should exhibit little genetic structure across their ranges (reviewed in Burton 1983; Hedgecock 1986; Benzie 1999). The presence of larvae from near-shore species in the middle of the Atlantic and Pacific Oceans reinforced this expectation (Scheltema 1986), and several recent genetic studies on fish (reviewed in Graves 1998; Waples 1998) and invertebrates suggest that broadly dispersing larvae (and adults) can maintain genetic cohesiveness over large distances. For example, in an allozyme study of a solitary coral (*Paracyathus stearnsii*) with planktonic larvae, Hellberg (1996) found no significant geographic subdivision over thousands of kilometers along the West Coast of the United States. Similarly, both solitary and clonal forms of the freely spawning sea anemone *Anthopleura elegantissima* lack significant genetic structure over the same geographic range (McFadden et al. 1997). Perhaps the most spectacular and best-documented example of genetic homogeneity concerns the sea urchin *Echinothrix diadema* (Lessios et al. 1998). *E. diadema* is one of the few species whose distribution spans the Eastern Pacific Barrier (EPB), 5400 km of abyssal water without any shallow habitats that could serve as stepping stones for dispersal. Neither nuclear (allozymes) nor mitochondrial markers reveal any geographic structure reflecting restricted gene flow across the Eastern Pacific Barrier, leading Lessios et al. (1998) to propose that El Niño events propel larvae across the EPB sufficiently often to homogenize genetic structure at this vast scale.

Equilibrium explanations invoking panmixia over broad geographic expanses should, however, be interpreted cautiously for several reasons. First, in several cases, extension of a sampling regime to include the entire range of a species changed the initial inference of panmixia and extensive gene flow. For instance, allozyme studies of genetic structure in the free-spawning giant clam *Tridacna gigas* (Benzie and Williams 1992) and the starfish *Linckia laevigata* (Williams and Benzie 1996) revealed little genetic differentiation over thousands of kilometers in Australia. In both cases, expanded sampling revealed significant geographic subdivision (Benzie and Williams 1995; Williams and Benzie 1998). Similarly, Palumbi and Wilson (1990) reported that mitochondrial DNA diversity was homogeneous over a range of 1,500 km in the sea urchin *Strongylocentrotus purpuratus*. Wider sampling, however, revealed subtle but significant genetic differentiation between two California locations south of Point Conception (Edmunds et al. 1996).

Second, some early reports of broad genetic uniformity based on allozymes have been contradicted by subsequent

analysis using DNA markers (reviewed in Hilbish 1996). Buroker's (1983) allozyme study of the American oyster *Crassostrea virginica* is a classic example. Buroker (1983) reported panmixia from Georgia to Texas; however, subsequent analysis using mitochondrial (Reeb and Avise 1990) and nuclear DNA markers (Karl and Avise 1992) showed reciprocal monophyly between the Atlantic and the Gulf of Mexico. Whether there is geographic structure in the allozyme dataset is debatable (Cunningham and Collins 1994); however, there is no doubt that in the absence of migration allozyme frequencies can fail to reach genetic equilibrium even after millions of years of isolation. For example, geminate pairs of the sea urchin genus *Diadema* (Bermingham and Lessios 1993) and the snapping shrimp *Alpheus* (Knowlton et al. 1993) show no significant allozyme divergence on either side of the Isthmus of Panama. In both cases, mitochondrial DNA showed deep divergences whereas allozymes did not (reviewed in Cunningham and Collins 1994). Similarly, allozymes failed to reveal any genetic structure across the Indo-Pacific in the sea star *Linckia laevigata* (Williams and Benzie 1996), whereas a subsequent analysis using mtDNA revealed significant differentiation among some populations (Williams and Benzie 1997).

Finally, there are several surprising examples of genetic uniformity that challenge equilibrium explanations, because they occur in species with demersal larvae and limited dispersal potential. These include an allozyme study of North Sea and Irish Sea populations of the sea anemone *Urticina equus* (Solé-Cava et al. 1994), and mitochondrial DNA analyses of genetic structure in three benthic invertebrates found on both sides of the North Atlantic: the gastropods *Nucella lapillus* and *Littorina obtusata*, and the isopod *Idotea baltica* (Wares et al., in press). These populations may currently be panmictic over these regional scales; however, their dispersal potential suggests that they should exhibit isolation by distance (see the next section). Consequently, nonequilibrium alternatives should be seriously considered (Slatkin 1993). For example, if a vicariant event recently subdivided the formerly panmictic North and Irish Sea populations of *U. equus*, divergence in allozymes due to drift may not have had time to accumulate to detectable levels (Solé-Cava et al. 1994).

Isolation by Distance

If the geographic range of a species is large relative to the dispersal potential of its propagules, then genetic drift will lead to divergence between subpopulations, even at equilibrium (isolation by distance, sensu Wright 1943; Malécot 1968). Under this isolation-by-distance scenario, the relationship between genetic differentiation and spatial separation of subpopulations can be described in terms the \log_{10} of \hat{M} (the amount of inferred gene flow between pairs of populations as defined above) versus the \log_{10} of geographic distance. At equilibrium, this relationship should have a characteristic slope, the value of which depends upon (1) whether gene flow follows a one- or two-dimensional stepping-stone model (Kimura and Weiss 1964) and (2) the spatial distribution and

separation of suitable habitats (Slatkin 1993; Hellberg 1996; Hutchison and Templeton 1999). Values of \hat{M} can be estimated by any of the methods described earlier (in the sections Inferring Levels of Gene Flow and The History of Population Subdivision and the Importance of Reciprocal Monophyly; Slatkin 1993). Isolation by distance can also be detected using spatial autocorrelation (e.g., McFadden 1996), which circumvents some of the scale-dependent biases of F -statistics, or by nested clade analysis (Templeton 1994, 1998). A full discussion of these methods is beyond the scope of this paper.

The pattern of isolation by distance should be most apparent in species that live in continuously distributed habitats and whose propagules have limited dispersal potential (e.g., Ayre and Dufty 1994; reviewed in Knowlton and Jackson 1993). For instance, the cup coral *Balanophyllia elegans* internally broods large, sexually produced, demersal larvae, and lives in the shallow subtidal and low intertidal along the West Coast of North America (Gerrodette 1981; Fadlallah 1983). Hellberg (1994, 1995, 1996) found a highly significant negative relationship between genetic (\hat{M} , inferred from allozymes) and geographic distance in *B. elegans*. Over scales less than 50 km, the 95% confidence intervals of this slope include the predicted value of 1.0 for a one-dimensional stepping-stone model at equilibrium between limited larval dispersal and genetic drift (Hellberg 1995). However, beyond approximately 50 km the magnitude of genetic differentiation no longer increased (Hellberg 1994, 1995). Similar observations in marine systems of the genetic signal of isolation by distance fading at larger regional scales occur in the intertidal gastropod *Nucella emarginata* (Marko 1998), the splash-zone harpacticoid copepod *Tigriopus californicus* (reviewed in Burton 1998), and the mangrove littorine *Littoraria cingulata* (Johnson and Black 1998).

The failure to find a pattern consistent with isolation by distance at larger scales may be due to an historical disruption of genetic structure, caused by events such as the Pleistocene glaciations in the Northern Hemisphere. Following such a disruption, neighboring populations should achieve equilibrium before more distant ones. The resulting pattern of genetic structure could be quite complex, especially when the historical events produce multiple barriers to dispersal, across which reequilibration occurs at different rates. In fact, Hellberg (1995) estimated that the time to reach an equilibrium between migration and gene flow in *B. elegans* is on the order of 40,000 years. Because this exceeds the amount of time between major climatically induced fluctuations in sea level, temperate species such as *B. elegans* and *N. emarginata*, whose larvae have a very limited capacity for dispersal, may only rarely reach an equilibrium between migration and gene flow throughout their ranges.

Taken together, these examples imply that even when there is a significant relationship between the magnitude of genetic subdivision and geographic distance at some spatial scales, historical processes may contribute to the pattern at other spatial scales. Furthermore, apparent isolation by distance can be generated by distinctly nonequilibrium processes.

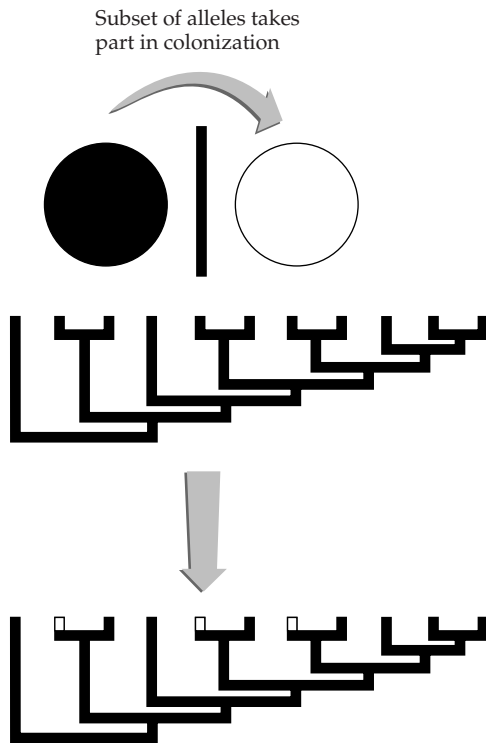


Figure 3.3 The effects of range expansions or long-distance dispersal on gene genealogies. When a source population (in black) colonizes a new area (in white), the newly founded population will likely contain a subset of the haplotypic diversity in the source population. Thus, the newly founded population will be less diverse than the source population, and the haplotypes in the newly founded population will be phylogenetically nested within haplotypes of the source population (bottom panel).

es (Slatkin 1993; Barton and Wilson 1995). For example, in a widely ranging species that consists of several reciprocally monophyletic populations inhabiting geographically restricted areas, genetic distances between areas will tend to be large, whereas distances within areas will tend to be small. This can produce a regional pattern that resembles isolation by distance at equilibrium, despite the absence of any ongoing migration among areas.

Range Expansion and Population Growth

We have argued that, at least in temperate regions, the ranges of many nearshore species of marine organisms are unlikely to be static over the periods necessary to establish a range-wide equilibrium between gene flow and drift. It is possible to use information about genetic structure to reconstruct the history of range expansions (and contractions). This is because, after a species expands its range—whether by way of gradual expansion or long-distance colonization—the newly colonized area will generally carry only a subset of the alleles in the source population (Figure 3.3; Hewitt 1996; Templeton 1994, 1998). This leads to three straightforward predictions about genetic structure following recent range expansions. First, newly colonized areas should have significantly lower

genetic diversity than the parent population (Hewitt 1996; Grant and Bowen 1998; Marko 1998). For DNA sequence data, the significance of a difference in genetic diversity can be assessed by simple permutation. Second, alleles in the colonized area should be phylogenetically nested within the diversity of alleles from the source area (Templeton 1994, 1998). Third, rapid population growth is more likely in newly colonized areas compared to source areas, and this should leave a characteristic signature on a gene genealogy (see below).

Figure 3.4 illustrates the rationale for the first two predictions. The figure shows an invasion of North America from Europe in terms of geographical maps of allele genealogies. Because we are considering mitochondrial data, alleles that differ by at least one substitution will be referred to as haplotypes. The invading species initially exists only in Europe, with at least six unique haplotypes (Figure 3.4A). The species subsequently colonizes North America (Figure 3.4B). At this point, all haplotypes sampled from North America will be identical to one another and to one of the European haplotypes from which they descended. If there is no further migration from the European source, new haplotypes (from mutation)—descended from the invading haplotype—will appear in North America (Figure 3.4C).

Because the expected shape of the gene genealogy at equilibrium is well known, coalescent theory can be used to distinguish between populations that have undergone recent growth from those that have remained at a constant size. This makes it possible to explore the third prediction of rapid population growth in the newly founded populations. The genetic signatures of rapid population growth were originally explored using the simple distributions of pairwise distances (Slatkin and Hudson 1991; Rogers and Harpending 1992). Two recent advances now make it possible to use patterns of genealogical relationships to characterize population dynamics. The first approach predicts the number of lineages through time under models assuming either constant population size or exponential growth (e.g., Nee et al. 1995; Rambaut et al. 1997), and then tests the fit of linear transformed empirical data to the models (software End-Epi, <http://evolve.zps.ox.ac.uk>; Rambaut et al., 1997). These transformations can be interpreted graphically so as to distinguish between exponential and linear growth, and whether a population has been growing exponentially at a changing rate.

Kuhner et al. (1998) recently developed a maximum likelihood method that simultaneously estimates θ (effective population size \times mutation rate), as well as a growth parameter. A sampling procedure is used to estimate these parameters across many alternative trees (software Fluctuate, <http://www.evolution.genetics.washington.edu/lamarc/fluctuate.html>). Given an independent estimate of mutation rate, a trajectory of effective population size through time can be estimated from this approach. An old population that has had no recent bottleneck should have a shallow growth trajectory, whereas a recently founded population should have experienced explosive growth from a few founding individuals. Although this approach makes unrealistic assumptions, such as assum-

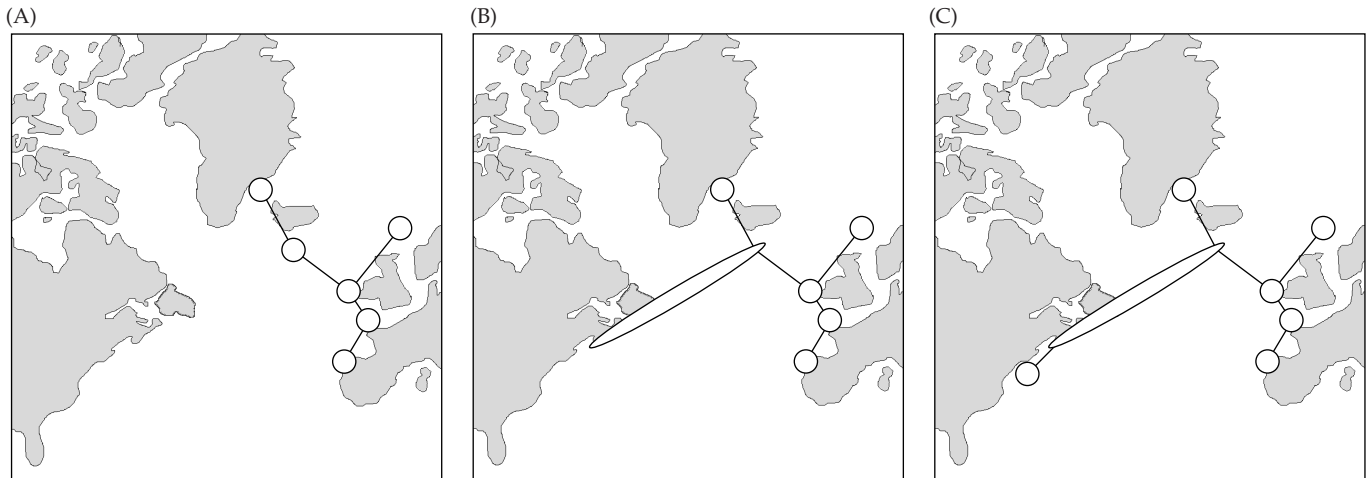


Figure 3.4 An unrooted gene genealogy illustrating the process of colonization of North America from Europe by a single mitochondrial haplotype. Each circle (or oval) represents a single haplotype, and approximates the geographical range of that haplotype. (A) Prior to the colonization event, the species is endemic to Europe. (B) A propagule (or propagules) carrying a single

European haplotype colonizes North America. (C) Mutation and drift will eventually cause the North American haplotypes to diverge from their European progenitors. In the absence of subsequent colonization from European sources, all new haplotypes in North America will be descended from the founding haplotype.

ing that the shape of the curve will always be exponential (Kuhner et al., 1998), it may be useful to distinguish between very different classes of histories.

Range expansions often occur naturally, especially following climatic or tectonic changes. However, human-mediated introductions are becoming distressingly common in the sea (Carlton and Geller 1993). With adequate genetic sampling, it should be possible to rule out human-mediated transport if there are at least a few unique alleles in the newly colonized area (Ó Foighil and Jozefowicz 1999). The evidence against human-mediated colonization is especially strong if most or all of these unique alleles are descended from one of the common, or “founding” alleles (as in Figure 3.4B). If, however, all alleles in the colonized area are shared with the hypothetical source population, other information, including historical records, must be incorporated into the reconstruction of colonization.

Summary and Conclusions

As others have argued (e.g., Palumbi 1994; Hilbish 1996; Benzie 1999), the evidence summarized in this section suggests that there are relatively few marine species that fully satisfy the expectations of equilibrium between genetic drift and migration across their entire ranges. At one extreme, the absence of significant genetic structure cannot always be equated with true equilibrational panmixia. It may take millions of years following subdivision for allozyme markers to reveal genetic structure. Although mtDNA-based markers may be more sensitive to vicariance, migration models that assume equilibrium will yield low but detectable levels of migration between populations that have long since stopped exchanging migrants. Similarly, recently founded populations and their putative sources may not show significant genetic dif-

ferences; however, their levels of genetic diversity should significantly differ. In all of these cases, the absence of detectable genetic structure cannot necessarily be equated with significant present-day gene flow.

At the other extreme, a simple correspondence between geographical distance and genetic distance (or inferred migration rate) does not necessarily mean that populations are at equilibrium. The details of scale, once again, count: If the correspondence occurs only across small spatial scales, then it suggests that subpopulations have yet to equilibrate at regional scales (Hutchison and Templeton 1999). When a population consists of an aggregate of more-or-less contiguous local populations that are internally panmictic, but that do not exchange migrants with the other subpopulations, an analysis of genetic structure that includes both within- and among-subpopulation comparisons can yield a significant relationship between genetic and geographic distances, despite the absence of gene flow among subpopulations.

We conclude that the present-day genetic structure of many species of marine invertebrates often reflects the operation of *both* contemporary gene flow and historical factors, and that populations are often not in equilibrium throughout their ranges. More specifically, in species with extensive dispersal potential, and at local scales, the effects of gene flow and drift may predominate; in species with less extensive dispersal potential, or at relatively larger spatial scales, nonequilibrium processes may prevail. With allele frequency approaches to the analysis of genetic structure, the relative contributions of historical and contemporary are often impossible to distinguish. Phylogeographic approaches, on the other hand, now make it possible to begin to assess the relative contributions that historical factors and contemporary gene flow make to current genetic structure. The few studies of marine organisms that

employ such methodologies suggest that many species of marine invertebrates consist of genetically differentiated subpopulations whose evolutionary histories geographically vary. To the extent that this is generally true, it raises a critical series of questions for the community ecologist concerning the spatial and temporal scales over which populations of marine organisms interact with their competitors, predators, and pathogens.

FROM POPULATIONS TO COMMUNITIES

In this section, we return at last to the question posed at the beginning of this chapter: What can information about patterns of genetic variation within a species, and the historical and recent processes that generate these patterns, tell us about the ecological and evolutionary outcomes of species interactions? We first consider the strengths and weaknesses of using genetic structure to address questions concerning open and closed ecological systems, and the scales over which interacting species can influence each other's population dynamics. We then extend this analysis into predicting the nature of genetic and phenotypic responses to spatially varying selection. Third, we consider how genetic information can be used to distinguish sibling species, and the importance of these distinctions for understanding the evolution of ecological specialization. Finally, we explore how genetic structure can be used to reconstruct the history of species interactions, specifically to distinguish long-term, locally adapted residents from recent arrivals with less potential for local adaptation.

Scale of Population Regulation

The spatial scale and magnitude of demographic connection among subpopulations of the species that compose a local community depend on species-specific modes of development, larval behavior, and local and regional patterns of water movement (Gaines and Roughgarden 1985; Possingham and Roughgarden 1990; Gaines and Bertness 1993; Todd 1998; reviewed in Booth and Brosnan 1995; Caley et al. 1996; Cowen et al. 2000). The debate over whether populations of marine organisms exhibit open or closed dynamics was ignited in the early 1980s when marine ecologists rediscovered the importance of recruitment limitation to the demography of benthic invertebrates and reef fish populations (Doherty 1981; Underwood and Denley 1984; Gaines and Roughgarden 1985; Roughgarden et al. 1985; Young 1987; Hughes 1990; Grosberg and Levitan 1992; Booth and Brosnan 1995; Caley et al. 1996; Waples 1998). Recruitment levels can affect population dynamics and species interactions by regulating the intensity of competition (both intra- and interspecific) and predation (Menge and Sutherland 1987; Connolly and Roughgarden 1999). To the extent that the adults of many marine organisms are relatively sedentary and their propagules are relatively motile, the supply of recruits to a local population of adults could be governed by processes occurring outside the local population, instead of by local reproductive output (Menge and Olson 1990). This is what is conventionally meant by "open" population dynamics.

In most benthic marine communities, occupants of different trophic levels, and competitors at the same trophic level, often have different developmental modes. For example, two of the keystone predator genera of the Northern Hemisphere rocky intertidal have dramatically different dispersal potential. The major gastropod predator *Nucella* has direct development, whereas the predatory seastars *Asterias* and *Pisaster* have planktotrophic larvae. Since the major prey of all of these predators are mussels and barnacles, both of which have planktotrophic larvae with extensive dispersal potential, the scales over which prey abundance regulates predator population dynamics (or vice versa) should differ for interactions with *Nucella* compared to those involving *Asterias* and *Pisaster*. Gaines and Lafferty (1995) developed a series of models exploring the dynamics of predators and prey, competitors, and hosts and pathogens, when interacting species exhibited different combinations of locally closed versus open populations. These models nearly uniformly yield dramatically different dynamics than conventional models in which interacting species are closed or open at matching spatial scales.

From the perspective of community ecology, the critical problem is therefore to determine not only the magnitude and scale of demographic exchange among subpopulations (i.e., how open or closed are they?) of each interacting species, but also the degree to which the population dynamics of interacting species spatially correspond (McLaughlin and Roughgarden 1993; Holt 1993; Underwood and Petraitis 1993; Booth and Brosnan 1995; Gaines and Lafferty 1995; Connolly and Roughgarden 1999). This problem has remained an unanswered challenge in most marine systems because of the difficulties of directly tracking migration of motile propagules. One approach, widely used in agricultural systems, is to breed "genetically engineered" stocks that carry rare markers, introduce them into natural or experimental arrays, and sample offspring for the marker gene. Such genetic tags have also been used in marine invertebrates (e.g., Grosberg and Quinn 1986; Grosberg 1991) and fish (Wilson et al. 1997; Wilson and Donaldson 1998; Perez-Enrique and Tanigushi 1999). It is now also possible to track fish larvae using natural or artificial chemical tags (Campana et al. 1995; Jones et al. 1999; Swearer et al. 1999).

The value of naturally occurring genetic markers for characterizing demographic units (and identify larval sources) relies on the presence of detectable genetic differences among subpopulations (Utter and Ryman 1993; Hedgecock 1994; Burton 1994, 1996; Palumbi 1995; Waples 1998). In turn, the existence of such differences depends upon the relationship between the genetically effective migration rate, m , and the mutation rate, μ . In general, if m is greater than μ for a marker, then at equilibrium, the marker will not reveal differences among subpopulations. If, however, m is less than μ , new alleles will arise within subpopulations more frequently than they are exchanged with adjacent subpopulations, and unique alleles characteristic of that specific subpopulation should be detectable in at least some individuals.

If selectively neutral markers reveal genetic structure at a particular spatial scale, and this structure is temporally stable, then the genetically distinct subpopulations cannot be experiencing much present-day gene flow (e.g., Bulnheim and Scholl 1981; Burton et al. 1979; Todd et al. 1988; Burton and Lee 1994; Lessios et al. 1994; Lewis and Thorpe 1994; Burton 1997; Edmands et al. 1996; see Waples (1998) for caveats when F_{ST} is small (< 0.05), but nonetheless, significant). Such subpopulations ought to be independently regulated by their parasites, pathogens, predators, and competitors, with substantially different population dynamics than would be the case in demes connected by extensive migration (Antonovics 1994; Gaines and Lafferty 1995).

Unfortunately, the absence of genetic structure may say relatively little about *demographic* interconnectedness, because a demographically insignificant amount of gene flow among subpopulations—on the order of one migrant per generation—will eventually homogenize allelic frequencies at neutral loci. As we discussed earlier (in the section entitled *The Approach to Equilibrium and Why It Matters*), the time it takes to reach this equilibrium depends on the migration rate, effective population size, and mutation rate (Takahata 1983). With low mutation rates, and demographically plausible migration rates, this equilibrium will be reached quickly, even in relatively large populations, leaving no detectable genetic signature. However, as the mutation rate, μ , of a marker increases with respect to the migration rate, m , the rate of approach to equilibrium will be slowed.

In this respect, the development of hypervariable markers such as microsatellites has dramatically improved the power to distinguish previously undetectable levels of genetically effective migration among subpopulations. Coupled with a variety of recent statistical innovations, hypervariable markers potentially allow more detailed inferences about the pattern, scale, and history of gene flow than has been possible with less variable markers (e.g., Bertorelle and Excoffier 1999; Waser and Strobeck 1998; reviewed in Luikart and England 1999). For example, hypervariable markers such as some microsatellite loci can be used [with some caveats about mutational models, estimating allelic frequencies, and so forth; see papers in Goldstein and Schlötterer (1999)] to estimate gene flow using the procedures described earlier for F_{ST} -like statistics (e.g., R_{ST}). Such indirect estimates of gene flow can then be compared to direct estimates based on genetic identification of the sources of individual immigrants. One way to do this is to “engineer” genetically or chemically migrants so that they can be distinguished from residents upon resampling. Alternatively, if populations are even slightly genetically differentiated, hypervariable markers dramatically improve the prospects for using likelihood methods to assign individual genotypes in a sample to their correct source population (reviewed in Waser and Strobeck 1998; also see <http://www.biology.ualberta.ca/jbrzusto/Doh.html>). Similarly, maximum-likelihood methods can be sometimes be used to distinguish between sets of subpopulations with the same F_{ST} 's that are linked by gene flow (i.e., in equilibrium)

from those that are partially or fully independent (Beaumont and Bruford 1999).

To some, these advances promise to bridge the gap between the shortcomings of direct and indirect measures of gene flow. A more precise understanding of the short- and long-term outcomes of the interaction between spatially varying selection and gene flow should follow (see the next section). Nonetheless, for all but the lowest rates of exchange among subpopulations, it is unlikely that naturally occurring genetic markers alone will ever be able to reveal fully the geographic sources of immigrants to a population and the magnitude of demographic connections.

Responses to Spatially Varying Selection

When populations are at equilibrium, the scale and magnitude of genetic subdivision strongly reflects the extent to which (1) individuals experience different selective regimes over their lifetimes and (2) subpopulations can independently evolve in response to spatially varying selection. Thus, the correspondence between the scale and magnitude of genetic structure and the scale over which diversifying selection operates determines the likelihood of cumulative genetic change and local adaptation (Endler 1992). In general, species with limited gene flow should be more likely than species with extensive gene flow to exhibit local adaptation to spatially varying selection (Holt and Gaines 1992). They should also do so on finer spatial scales than species with more widespread gene flow. Genetically differentiated subpopulations may ultimately diverge to such an extent that they become reproductively isolated.

At the other extreme, when the spatial scale of gene flow exceeds the scale over which selection varies, cumulative adaptive genetic changes are unlikely to occur. In other words, spatially varying selection favoring a specific genotype in a particular location can overcome the homogenizing effects of gene flow within generations; however, a continuing flow of recruits from neighboring populations limits the opportunity for the accumulation of genetically based local specialization to spatially varying selection (Ament 1979; Strathmann and Branscomb 1979; Strathmann et al. 1981; Warner 1997). Selection should instead favor the evolution of generalist phenotypes or reduced dispersal (Slatkin 1973; Gooch 1975; Endler 1979; Hedgecock 1986; Warner 1997). When the appropriate environmental cues exist, phenotypic plasticity or habitat selection may also evolve (Adler and Harvell 1990). Thus, there should be a tradeoff between the expected degree of local genetic adaptation and the magnitude of dispersal.

Does empirical reality in marine species match these predictions? Many of the classic marine studies of the scale of genetic differentiation concern spatially varying selection imposed by the physical environment (reviewed in Janson and Ward 1984; Hedgecock 1986; Behrens Yamada 1989; Ayre 1995; Warner 1997). Behrens Yamada (1989) contrasted geographic variation in life-history traits in two species of *Littorina*, an intertidal, herbivorous snail common in temperate waters of the eastern Pacific. *L. sitkana* embryos directly develop

into crawl-away juveniles, whereas *L. scutulata* larvae develop in the plankton. Both species exhibit significant geographic variation in the expression of growth rates and reproductive timing, attributed to selection imposed by variation in desiccation stress (Behrens Yamada 1989). These life-history differences persisted in common garden experiments as well as reciprocal transplants, suggesting that at least some of the demographic variation is heritable. Consistent with the predicted tradeoff between scale of local adaptation and dispersal potential, the scale of geographic differentiation for these traits is on the order of tens of kilometers in the directly developing *L. sitkana* versus hundreds of kilometers in *L. scutulata*. Unfortunately, the study lacked a genetic assessment using neutral markers of geographic structure, making it impossible to reject the scenario that the regional pool of recruits is genetically homogeneous, with post-recruitment selection within generations producing the observed local pattern.

Other studies of the response to spatial variation in the physical environment that explicitly consider genetic structure also support some of the basic predictions of the tradeoff model. *Tigriopus californicus* is an intertidal and supralittoral harpacticoid copepod common in tidepools along the West Coast of North America. The life history of *T. californicus* implies that it should have very limited dispersal potential, a prediction verified by high levels of temporally stable genetic differentiation at very fine spatial scales (reviewed in Burton 1998). Patterns of micro-geographic and regional variation at several allozyme loci associated with osmoregulation strongly correspond to spatial variation in salinity and temperature along both intertidal and latitudinal gradients. Physiological studies and transplant experiments confirm that these loci are under selection by the thermal and salinity regime. Whether selection favored the evolution of reduced dispersal in *T. californicus* remains to be seen; nevertheless, it appears that limited gene flow in this species permits selection to cause cumulative adaptive change at very fine spatial scales.

In species with extensive dispersal potential, such as barnacles (Hedgecock 1986; Schmidt and Rand 1999) and mussels (e.g., Hilbish and Koehn 1985), genetic data, either in the form of allozymes or mtDNA data, show that cohorts of new recruits appear to be genetically well-mixed over local and sometimes regional scales. However, at some loci (associated with thermal, salinity, or desiccation tolerance), the genetic composition of cohorts recurrently diverges following recruitment, presumably due to diversifying selection imposed by local variation in temperature or salinity. In these examples, the perhaps unexpected product of the interaction between high gene flow and fine-scale post-recruitment selection appears to be the short-term maintenance of a balanced genetic polymorphism within populations for variation in the physiological traits under selection, rather than phenotypic plasticity or reduced dispersal.

The effects of spatial variation in predation intensity on phenotypic variation in prey populations are far better studied than the effects of other species interactions such as competition or parasitism. What are the effects of genetic struc-

ture on the evolution of this phenotypic variation, and to what extent does this variation represent local adaptation versus predator-induced phenotypic plasticity? Conspecific populations of many marine gastropods, including members of the genera *Nucella* and *Littorina*, often exhibit site-specific variation in shell thickness that corresponds to the intensity of predation by crabs (Janson 1982, 1987; Palmer 1985, 1990; Trussell 1996). Thin-shelled morphs are more resistant to dislodgement by waves, and predominate on exposed shores where crab predators are relatively rare; in adjacent protected waters, where crab predation intensifies, thick-shelled morphs predominate (reviewed in Trussell 1996).

The whelk genus *Nucella* consists entirely of directly developing species with demersal, crawl-away juveniles. Studies of genetic structure based on both allozymes (e.g., Day 1990; Day et al. 1993) and mtDNA sequences (Marko 1998) show that populations exhibit extensive genetic structure at spatial scales corresponding to phenotypic variation in shell thickness and the abundance of predators. Unlike the previously cited barnacle and mussel examples, where it appears that recruits are well mixed (at least at local scales), the existence of substantial genetic structure at a scale roughly corresponding to that over which selection varies suggests that phenotypic variation in shell thickness signifies true local adaptation. However, several experimental studies indicate that much of the phenotypic variation in shell thickness can be induced by crab predators (Appleton and Palmer 1988; Palmer 1990), and thus may not entirely represent local genetic adaptation.

In the North Atlantic, two species of *Littorina* have been especially well characterized in terms of genetic structure and geographic variation in shell structure. Like the North Pacific species pair studied by Behrens Yamada (1989), *L. saxatalis* is a direct developer, with crawl-away juveniles; *L. littorea* is sympatric with *L. saxatalis*, but its larvae remain in the plankton for 4–6 weeks (Janson 1987). Allozyme studies show the expected genetic patterns, with *L. saxatalis* exhibiting fine-scale genetic structure on the order of meters (Janson 1987) and *L. littorea* lacking detectable genetic structure over hundreds of kilometers (Berger 1973; Janson 1987). In both species, the degree of variation in shell morphology corresponds to the pattern of genetic structure. *L. saxatalis* displays variation in shell-thickness according to local variation in wave exposure, and *L. littorea* lacks such phenotypic variation (Curry and Hughes 1982; but see Dudley 1980).

Once again, the question is, does the variation in the shell morphology of the direct-developing *L. saxatalis* represent genetic differentiation or phenotypic plasticity? As with *Nucella*, the answer remains equivocal. Newkirk and Doyle (1975) showed that variation in shell morphology is partially under genetic control in *L. saxatalis*, a result consistent with the expectation of local adaptation. However, a recent study on *L. obtusata* (also a direct developer) demonstrated that crab-predation can directly induce a substantial increase in shell thickness (Trussell 1996), suggesting a role for phenotypic plasticity.

To what extent can information about the genetic structure of marine populations be used to predict a species response to spatially varying selection? The answer at this point remains equivocal. Species with minimal structure and extensive gene flow that we might expect to exhibit phenotypic plasticity often do not. Species with substantial structure and minimal gene flow often exhibit phenotypic plasticity. Studies conducted at different scales and on different populations can produce conflicting results.

Part of the failure to match expectations is almost certainly due to our extremely limited knowledge of the nature of spatial and temporal variation in selection. In addition, our understanding of the genetics of adaptation remains in its infancy (Orr 1998). But just as importantly, we still know remarkably little about genetic structure and the history of gene flow in natural populations of marine organisms. In terms of the response to selection, the details of genetic structure and the equilibrium status of populations are critical: Populations with identical inferred levels of gene flow may differ in their actual degree of isolation from one another. For instance, populations may lack significant genetic structure for neutral markers either because they are currently exchanging migrants, or because they have been recently subdivided and not yet reached evolutionary equilibrium (e.g., Benzie 1999). Conversely, populations that appear to be equally differentiated may actually represent a mosaic of formerly isolated subpopulations, some of which are now interconnected (but have yet to reach equilibrium), and others of which remain unconnected. In both situations, subpopulations with the same apparent genetic structure may differ in their responses to spatially varying selection because some subpopulations may be partially or fully evolutionarily independent, whereas others may only appear to be.

For this reason alone, future studies at the interface between ecology and genetics should incorporate an explicit historical component that utilizes some combination of genealogical methods and high-resolution genetic markers capable of distinguishing low levels of ongoing gene flow from the recent cessation of genetic exchange. In this respect, intraspecific genealogical information can be used in some situations to identify those species in an assemblage with the greatest potential for local adaptation. If a species can be recognized as a recent colonist (see the section entitled Range Expansion and Population Growth), then it may have had little opportunity to respond to local selection. If populations in one area are reciprocally monophyletic with respect to populations in other areas, then it is most parsimonious to infer that the species has survived in both areas with little gene flow between them (see Genealogical Approaches). The length of time populations have persisted in both areas corresponds roughly to the number of substitutions along the internal branch dividing the populations (Figure 3.5). Reciprocally monophyletic populations therefore satisfy two requirements for local adaptation: long-term residence, and little or no genetic exchange with other populations.

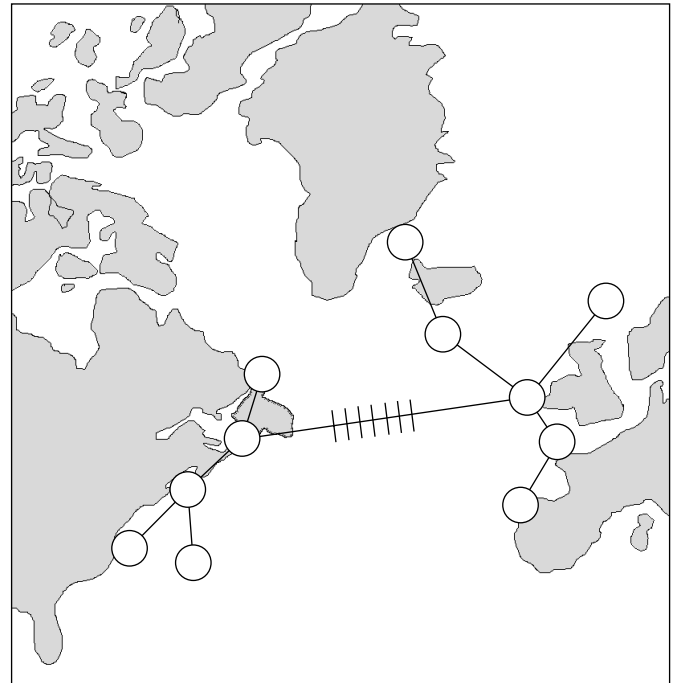


Figure 3.5 Establishment of reciprocal monophyly following the colonization process shown in Figure 3.4. If there is no further migration across the Atlantic, then mutations (represented by hatch marks) will accumulate between European and North American populations, producing a long internal branch in the genealogy (see Templeton 1994). Such a pattern would indicate the independence of resident populations on opposite coasts.

Cryptic Species: Intraspecific Polymorphism versus Interspecific Diversification

In the previous section we concluded that recent and historic patterns of gene flow are key determinants of the evolutionary response of populations to spatially varying selection. Given sufficient time and limited gene flow, diversifying selection and drift can eventually lead to the acquisition of genetically based post- and pre-reproductive isolation between populations (reviewed in Coyne and Orr 1998). In many cases, there are few reliable morphological clues to this transition from a polymorphic species to interspecific diversification, and lab tests of reproductive compatibility are notoriously difficult to implement and interpret. Yet this transition from a state of intraspecific polymorphism to two or more cryptic (“sibling”) species is critical to identify, because in many organisms (plants and corals may be exceptions) it signifies the irreversible evolutionary independence of lineages.

The existence of numerous complexes of sibling marine species is now well established (see review in Knowlton 1993). Although an unambiguous definition of cryptic or sibling species is controversial (for a good discussion see Knowlton and Weigt 1997), cryptic species can often be identified by genetic data, especially when populations show fixed allelic differences or reciprocal monophyly (see the section entitled The History of Population Subdivision and the Importance of

Reciprocal Monophyly). For this reason, Avise and Ball (1990) used gene genealogies as the basis for their concordance species concept. They argued that if multiple unlinked loci show congruent patterns of reciprocal monophyly, the individuals so defined should be considered distinct species.

When they are not diagnosed, cryptic species that have fully or partially sympatric distributions can be confused with stable intraspecific polymorphisms. Such confusion can, in turn, dramatically alter interpretations of outcomes of ecological interactions. For example, the snail *Acanthina angelica* preys on the barnacle *Chthamalus anisopoma*, and induces the production of a hooded morph that is more resistant to predation than the normal conical morph (Lively 1986; reviewed in Lively et al. 2000). The conical morph of *C. anisopoma* occurs throughout the Gulf of California, whereas the hooded morph occurs primarily in the northern Gulf. The predator, *A. angelica*, lives only in the northern Gulf of California, suggesting that geographic variation in the prey's phenotypic polymorphism is the result of environmental induction by the predator. However, Lively et al. (2000) recently showed that barnacles collected from the northern Gulf differed in their inducibility by *Acanthina*, raising the possibility that there is also an underlying genetic polymorphism controlling the amount of phenotypic plasticity in the northern Gulf population.

Why are there noninducible morphs in the northern Gulf? One option is that some sort of balancing selection maintains an equilibrial genetic polymorphism within the northern Gulf (Lively et al. 2000), as appears to be the case in the barnacles and mussels discussed above. An unexplored nonequilibrial alternative is that the inducible and uninducible forms represent genetically differentiated populations, or even cryptic species. Uninducible southern Gulf populations or species may be continually swept into the northern Gulf in such large numbers that they persist in the northern Gulf, maintaining apparent polymorphism for inducibility despite their selective disadvantage in the face of *Acanthina* predation. If this scenario were correct, then our ecological and historical interpretation of the distribution of hooded morphs of *C. anisopoma* would substantially differ from that based on a genetic or environmentally induced intraspecific polymorphism.

One of the most ecologically dramatic examples in marine systems of the importance of distinguishing interspecific differentiation among cryptic species from intraspecific phenotypic polymorphisms concerns the symbiosis between hermatypic corals and their zooxanthellae. Until recently, this symbiosis was thought to represent an association between a diversity of host coral species and a single species of dinoflagellate in the genus *Symbiodinium*. However, Rowan and Powers (1991, 1992), following previous speculation (e.g., Kinzie and Chee 1979; Jokiel and York 1982), challenged the long-standing hypothesis that the *Symbiodinium* that inhabited all hermatypic corals belonged to the same ecologically generalized "cultivar." Using RFLPs of genes encoding small ribosomal RNAs, they showed that there are three very distinct taxa of symbionts, designated *A*, *B*, and *C*. Later work revealed that each of these three cultivars of *Symbiodinium* had different

irradiance optima. At least in the corals *Montastrea annularis* and *M. faveolata*, symbionts *A* and *B* are common in shallow, high irradiance habitats; *C* predominates in deeper, low irradiance habitats (Rowan and Knowlton 1995; Rowan et al. 1997).

The mere discovery that *Symbiodinium* was not a monotypic species, but instead a species complex, consisting of at least three very distinct members with different physiologies, was in and of itself a major revolution in our understanding of the natural history of coral symbioses. It also helped to clarify why there is so much variation within and among coral heads in intensity of bleaching. Rowan et al. (1997) sampled tissue from low and high irradiance parts of individual coral heads, and from corals living at different depths. Samples from a single coral head contained different relative amounts of each symbiont, and the relative abundance of each type of symbiont corresponded to predictions based on irradiance optima (i.e., symbiont *C* was most common in low irradiance positions on individual coral heads, and increased in relative abundance in corals sampled from increasing depth). In other words, there is zonation within and among coral heads, and subsequent experimental manipulations showed that irradiance plays a major role in controlling community composition of the symbionts (Rowan et al. 1997).

These findings do not exclude other important intrinsically driven effects on coral bleaching such as physiological acclimatization of hosts and symbionts, and genetically based physiological differences among host corals. But the data do highlight the existence of previously unknown genetically based differences among the symbionts, and the role that such variation may have in producing the distinct patterns of bleaching so commonly observed throughout the Caribbean. Without this genetic information about the taxonomy of *Symbiodinium*, and the fine-scale distribution of the symbiotic taxa within and among coral heads, the evolutionary and ecological relationships between corals and their algal symbionts, not to mention the ecological interactions and maintenance of diversity among symbionts, would at best be half told stories (Rowan and Knowlton 1995).

Community Assembly and the History of Species Interactions

Do the recurrent similarities and differences that characterize modern species assemblages of marine organisms principally reflect the outcomes of contemporary ecological interactions, repeated in time or space, or do the members of similar assemblages also share a genealogical connection? The great promise of "historical ecology" was that phylogenetic analysis would bring two new perspectives to our understanding of the historical and contemporary contributions to community assembly (Brooks 1985; Brooks and McLennan 1991). First, a phylogeny should allow identification of a species' closest relatives, and thus allow one to reconstruct ancestral and derived character states. With this knowledge, it would be possible to infer which features evolved *in situ*, and which were inherited from its ancestor. For example, ecological character displacement can lead to differences in size be-

tween competing species (e.g., Schluter et al. 1985). If, however, the closest relatives of one or both species were the same size as the competing species, then the size difference between the interacting species more likely represents a retained ancestral difference, rather than the outcome of the ongoing competitive interaction.

Second, phylogeographic analysis should make it possible to identify species that have had a long shared history with one another. If two interacting species collected from the same area have congruent phylogenies, then these species probably shared a long history (reviewed in Cunningham and Collins 1994; Page and Hafner 1996). Conversely, if one of the members of the interaction has been a long-term resident, and the other arrived recently from elsewhere, then the species have had relatively little time to evolve in response to one another.

Shared history can also be inferred if a number of species share congruent patterns of reciprocal monophyly on either side of a genetic break (reviewed in Avise 1994). In the case of the North Atlantic fauna, the set of species that show reciprocal monophyly between Europe and North America must have persisted on both coasts with little appreciable gene flow, despite glacial fluctuations (Cunningham and Collins 1998). If, on the other hand, there is consistent genetic evidence for recent colonization of a particular area by members of an assemblage, then the newly colonizing species may have had a long history in the source—but not the recipient—area (e.g., Europe in Figure 3.5).

SUMMARY

Ecology has two fundamental goals. The first is to identify the processes that regulate species distribution and abundance, and the temporal and spatial scales over which these processes operate. The second is to understand the nature and outcomes of species' interactions with their biotic and physical environments and how these interactions regulate community structure. It remains difficult to identify many of these processes (and their scale of operation) and to predict these outcomes, in part because there has been little concerted effort by systematists and population geneticists to provide marine ecologists with the information necessary to decipher the history of species distributions and the spatial scales over which populations are genetically connected.

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Promising beginnings have been made in the southeastern United States (reviewed in Avise 1994; Cunningham and Collins 1998), the Isthmus of Panama (Knowlton et al. 1993; Collins 1996; Lessios 1998), the Indo-Pacific (reviewed in Benzie 1999), the West Coast of the United States (e.g., Burton 1998), and hydrothermal vent systems (reviewed in Vrijenhoek 1997). These studies, along with the analyses of genetic structure presented in this chapter, suggest that few, if any, marine species are in equilibrium with respect to gene flow, drift, and selection throughout their ranges. To the extent that this proves to be correct, we should expect substantial geographic variation in the nature and outcomes of these interactions, both as a result of ongoing spatial variation in selection, as well as the different histories of selection, colonization, and extinction experienced by different populations.

Understanding the history of species distributions in terms of contemporary and historic patterns of selection, extinction, and colonization also underlies the development of a tradition of “comparative marine ecology.” How do we interpret ecological similarities and differences among communities? To what extent are these similarities the result of shared histories or shared selective regimes? To what extent are differences possible despite shared histories? Do the biogeographic boundaries that define major breaks in community composition correspond to genetic discontinuities in their constituent taxa (Burton 1998; cf. Avise 1994)? Are the species that occupy adjacent biogeographic provinces closely related? For example, the rocky intertidal community of New England differs dramatically from that of the temperate Pacific, yet the New England assemblage consists largely of species that arrived from the Pacific in the past few million years (Vermeij 1991). Answers to these ecological questions fundamentally depend on growing collaboration among ecologists, population geneticists, and systematists. This collaboration remains to be fully implemented, but with it will come a much deeper understanding of the principles that govern community structure and dynamics.

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