DISPERSAL, GENE FLOW, AND POPULATION STRUCTURE

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ABSTRACT

The accuracy of gene flow estimates is unknown in most natural populations because direct estimates of dispersal are often not possible. These estimates can be highly imprecise or even biased because population genetic structure reflects more than a simple balance between genetic drift and gene flow. Most of the models used to estimate gene flow also assume very simple patterns of movement. As a result, multiple interpretations of population structure involving contemporary gene flow, departures from equilibrium, and other factors are almost always possible. One way to isolate the relative contribution of gene flow to population genetic differentiation is to utilize comparative methods. Population genetic statistics such as F_{ST}, heterozygosity and Nei's D can be compared between species with differing dispersal abilities if these species are otherwise phylogenetically, geographically and demographically comparable. Accordingly, the available literature was searched for all groups that meet these criteria to determine whether broad conclusions regarding the relationships between dispersal, population genetic structure, and gene flow estimates are possible. Allozyme and mtDNA data were summarized for 27 animal groups in which dispersal differences can be characterized. In total, genetic data were obtained for 333 species of vertebrates and invertebrates from terrestrial, freshwater and marine habitats. Across these groups, dispersal ability was consistently related to population structure, with a mean rank correlation of -0.72 between ranked dispersal ability and F_{ST}. Gene flow estimates derived from private alleles were also correlated with dispersal ability, but were less widely available. Direct-count heterozygosity and average values of Nei's D showed moderate degrees of correlation with dispersal ability. Thus, despite regional, taxonomic and methodological differences among the groups of species surveyed, available data demonstrate that dispersal makes a measurable contribution to population genetic differentiation in the majority of animal species in nature, and that gene flow estimates are rarely so overwhelmed by population history, departures from equilibrium, or other microevolutionary forces as to be uninformative.

A CENTRAL challenge for organismal biologists is to establish links between the ecology and the evolution of species. One such link is provided by quantifying the relationship between dispersal ability and the magnitude and spatial scale over which populations differ genetically (hereafter referred to as the level of population genetic differentiation). This is because an in-depth understanding of microevolution requires a quantification of how the movement of genes among populations (i.e., gene flow) interacts with genetic

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The Quarterly Review of Biology, March 1999, Vol. 74, No. 1

0033-5770/99/7401-0002$2.00

drift, natural selection and mutation. Studies of population genetic differentiation are particularly helpful in this regard, as they permit inferences about how microevolutionary forces have interacted throughout the history of a species. For example, population genetic differentiation can reflect natural selection on the markers of interest, the vicariant history of the populations, and the amount of gene flow that has historically occurred between them. (Vicariant distributions are those that are now discontinuous, although the organisms once occuppied a continuous range). Because genetic differences provide the raw material for natural selection, population genetic differentiation can also indicate the potential for local adaptation or speciation in the future.

Despite genetic studies of population structure in numerous taxa over the past three decades, few generalities have become apparent. In particular, investigators have disagreed over whether gene flow estimates are accurate, biased, or entirely misleading (e.g., Boileau et al. 1988; Bohonak et al. 1998; Bossart and Prowell 1998). If populations do not exist long enough to approach an equilibrium between gene flow and drift, then population structure should be interpreted in terms of history (e.g., founder effects, vicariance events, range expansions) rather than gene flow. For any particular population genetic study, there are often insufficient behavioral, ecological and biogeographic data to allow discrimination among hypotheses that consider these factors in various combinations. Thus, multiple interpretations of population structure are often possible, and the relative importance of factors such as gene flow, departures from equilibrium, and natural selection remain unresolved.

For this reason, testable hypotheses regarding the effects of different microevolutionary forces on population differentiation are generally preferable to post hoc speculation. Comparisons among taxa provide one way of generating these types of hypotheses. For example, one might hypothesize that the distribution of genes among populations is primarily the result of vicariance events, rather than a balance between drift and gene flow. This hypothesis can be tested indirectly by searching for common phylogeographic breaks in additional sympatric taxa in the region (see Avise et al. 1987; Avise 1992). Similarly, the hypothesis that dispersal (and presumably gene flow) has a measurable influence on population differentiation can be tested by searching for a correlation between dispersal propensity and differentiation, with species as independent data points (see caveats below). Although comparisons of this type have been conducted for particular taxa (e.g., Waples 1987; Ward 1990; Hellberg 1996; Hairston and Bohonak 1998), there is currently no quantitative review of population genetic studies in species that differ in dispersal ability.

Many issues in evolutionary biology cannot be adequately addressed without an understanding of how evolutionary patterns are linked to ecological processes such as dispersal. These include the potential for local adaptation, the nature of speciation, and the accuracy of gene flow estimates (e.g., Hedgecock 1986; Roderick 1996; Garcia-Ramos and Kirkpatrick 1997; Bossart and Prowell 1998). If there is no correlation between the genetic structure of populations and dispersal (i.e., the movement of individuals between populations) in most taxa, this limitation should be recognized and quantitative interpretations of simple estimates of population differentiation should be abandoned. However, if demonstrable relationships are found consistently in a variety of species and habitats, then population genetic data could be informative concerning the movement of individuals, despite their limitations.

DISPERSAL AND GENE FLOW

HISTORICAL PERSPECTIVE

Genetic analyses of population structure have become commonplace since the advent of protein electrophoresis in the late 1960s. Over the past two decades, many reviews have attempted to relate genetic variation in natural systems to a variety of individual, population and species-level traits (Selander 1976; Nevo 1978; Chow and Fujio 1987; Sole Cava and Thorpe 1991; Palumbi 1994; Ward et al. 1994; Peterson and Denno 1998). However, the relationships among population structure, indirect estimates of gene flow, and dispersal remain ambiguous and resistant to generalization (e.g., Burton 1983; Larson et al.

1984; Liebherr 1988; Boileau et al. 1992; Pogson et al. 1995). Whether population structure consistently bears any relationship to dispersal ability often seems to depend on the specific taxon, population or gene being studied.

Early attempts to characterize these associations centered primarily on marine groups, where a wide variety of taxa include species that vary in larval behavior, development time and mode of development (Gooch et al. 1972; Snyder and Gooch 1973; Gaines et al. 1974). For example, pelagic eggs and larvae permit passive movement by oceanic currents for weeks or months at a time, which should translate into large dispersal distances and genetically homogeneous populations. In this context, Gooch (1975), expecting a direct relationship between pelagic dispersal and genetic differentiation in marine taxa, cited some early examples with one to four loci. By the early 1980s, however, Burton (1983) had concluded that, although populations of sedentary species without pelagic larvae were often differentiated at a local scale, time in the plankton was not always inversely proportional to the amount of population genetic differentiation. Hedgecock (1986) was more optimistic about the strength of the relationship, but also cited a number of widely recognized reasons why dispersal potential might not be interpreted in terms of gene flow. For example, in marine groups, the apparent continuity of dispersal can be limited by physical, chemical, or biological barriers. In addition, natural selection can result in adaptation to local conditions which, in turn, can lead to low juvenile survival, even after dispersal barriers have been overcome. Palumbi (1994; 1995) reaffirmed that, while a general match between larval dispersal and gene flow exists, exceptions are easy to find, and interpretations of population structure are often complicated by both biotic and abiotic factors.

In further support of these conclusions, comparative studies that focused on marine species that vary in dispersal potential have consistently found a relationship between time in the plankton and genetic structure of populations. In fish (Waples 1987; Lacson 1992; Doherty et al. 1995), gastropods (Hoagland 1986; Ward 1990), decapods (Duffy 1993), sea urchins (McMillan et al. 1992) and corals (Hellberg 1996), estimates of population differentiation are higher when dispersal is inferred to be lower. Apart from marine groups, clear dispersal differences among taxonomically and phylogenetically comparable animal species are less common.

Whereas some investigators have noted a negative correlation between dispersal ability and population structure in nonmarine taxa (e.g., crickets: Zera 1981; cave-dwelling arthropods: Caccone and Sbordoni 1987), others have not found clear associations. In mark-and-recapture studies, Taylor et al. (1984) could not explain genetic structuring in the well-studied *Drosophila obscura* group through dispersal differences. Larson et al. (1984) concluded for a group of salamander species that gene flow estimates "may contain information more relevant to historical patterns of gene exchange than to the current population dynamics." This conclusion was also stressed by Liebherr (1988) for five species of carabid beetles. For mtDNA data, Avise (1992) observed that the largest proportion of intraspecific variation across a wide variety of North American animals seemed to be related to vicariant histories dating to the Pleistocene. However, he also noted that population divergence on a local level appeared "plausibly related to probable gene flow regimes of several of the species."

Dispersal estimates obtained in the field (e.g., from mark-and-recapture studies) are limited in space and time (Table 1). In contrast, the genetic structure of a species is averaged over thousands of generations or more, and integrated geographically over many populations. This suggests that some apparent discrepancies between gene flow estimates and dispersal estimates, as well as departures from equilibrium, might occur because evolutionarily significant dispersal events are frequently undetected in ecological studies (as stressed by Slatkin 1985a; 1994; see Kiester et al. 1982 for an example). Further, although dispersal patterns in nature are often complicated (Nürnberger and Harrison 1995), population structure is most commonly quantified using the simple island model of Wright (1931). As a result, some species might appear to possess population structures that depart markedly from simplistic expectations (e.g., the tide-

TABLE 1
Categories of dispersal and gene flow estimates by temporal scale of resolution

	Dispersal	Gene Flow
Direct, short-term estimates	Mark-and-recapture studies	Tracking marker alleles over a short number of generations
Indirect, long-term estimates	Conservative life history traits	Statistics derived from allele frequencies

pool copepod *Tigriopus californicus*: Burton and Feldman 1981; Burton 1994; Burton and Lee 1994; Dybdahl 1994). Well-studied organisms such as *T. californicus* are important reminders that interpreting population structure requires an in-depth knowledge of basic biology and historical biogeography. However, the complicated patterns of population structure found in these taxa do not necessarily indicate that empirical generalities are impossible.

ALLOZYME-BASED STUDIES

Protein electrophoresis has had many advantages over other types of genetic analysis; historically it has been the fastest, cheapest, and easiest way to screen genetic variation in large numbers of individuals. Accordingly, many genetic studies of populations have used allozyme frequencies derived from electrophoresis. Unlike mitochondrial DNA (mtDNA), allozyme data can be obtained for a number of independent loci, permitting error estimation for population differentiation statistics by applying data resampling methods such as the jackknife or the bootstrap across loci (Weir 1990; Sokal and Rohlf 1995). Unusual patterns at any individual locus can be determined through departures from Hardy-Weinberg equilibria, unusual geographic clines (e.g., Johannesson et al. 1995), or other sensitivity analyses.

Allozyme-based studies of population structure and gene flow may be biased in a number of ways, however. The inability to separate all alleles electrophoretically can lead to inaccurate estimates of heterozygosity (H) and population differentiation. In addition, the nonneutrality of specific metabolic protein alleles, long suspected, has been demonstrated conclusively in some organisms (e.g., Watt et al. 1983; Hilbish and Koehn 1985; McDonald and Kreitman 1991; Watt et al. 1996). More importantly, the possibility that the maintenance of most or all protein polymorphisms might be owing to some type of balancing selection suggests that even qualitative inferences regarding gene flow should be examined carefully (Karl and Avise 1992; Pogson et al. 1995; Raybould et al. 1996; but see Houle 1989; McDonald et al. 1996).

Studies of population structure in the oyster *Crassostrea virginica* highlight the difficulties of inferring natural selection on allozyme loci, even in well-studied groups. Low levels of population genetic differentiation have been found for allozymes in *C. virginica* (Buroker 1983). These results are consistent with high rates of gene flow expected in a marine species possessing planktonic eggs and larvae. In contrast, mtDNA and four anonymous nDNA loci show a pronounced phylogeographic break that separates Gulf of Mexico and Atlantic populations of this species (Karl and Avise 1992). Hare et al. (1996) found qualitatively similar results for two of these loci after correcting for methodological problems. From these results, Karl and Avise (1992) concluded that balancing selection was probably acting on most or all of the polymorphic allozyme loci. However, later studies found no reproductive barriers between Gulf and Atlantic populations of *C. virginica* (Hare and Avise 1996), no phylogeographic structure in genealogies of three nuclear loci (Hare and Avise 1998), and very little population subdivision in six additional anonymous nuclear loci (McDonald et al. 1996). It is difficult to interpret all of these studies within the simple hypothesis that natural selection is acting on all allozyme loci, yet differentiation in the other markers represents selectively neutral patterns of evolution (Karl and Avise 1992). Hare and Avise (1998) discuss a number of scenarios that might reconcile the data currently available.

FROM POST HOC EXPLANATIONS TO TESTABLE HYPOTHESES

How might the contribution of ongoing gene flow to differentiation among populations be determined statistically? At least four approaches are possible. First, concordance among a variety of genetic markers can allow for detailed conclusions about the interplay of migration, drift and mutation, or highlight genes that appear to depart from selective neutrality. The preceding discussion of population genetic studies in *C. virginica* illustrates this point (see also Nelson et al. 1987; Burton 1994; Burton and Lee 1994).

Second, gene flow estimates can be compared with direct dispersal estimates from ecological studies (e.g., Bohonak 1999). However, dispersal may not translate into gene flow for a variety of reasons: failure of immigrants to breed, unequal migration rates between demes, small sample size and sampling at the wrong scale, and nonequilibrium conditions (Larson et al. 1984; Caccone 1985; Caccone and Sbordoni 1987; Scheepmaker 1990; Grant and Little 1992).

Because gene frequencies inherently provide long-term averages that require hundreds or thousands of generations to equilibrate (Boileau et al. 1992; Cockerham and Weir 1993; Slatkin 1993, 1994), a third approach for ascertaining the relationship between dispersal and gene flow is to abandon gene frequency data in favor of direct, short-term measures of gene flow. Gene flow can be estimated between generations by repeatedly assaying multilocus genotypes in asexual species (Goodwin et al. 1995) or releasing marker alleles into a population (Burton and Swisher 1984; Berry et al. 1991; Grosberg 1991; see also Slatkin 1985a and citations within). But even though gene flow estimates from these techniques are comparable to mark-and-recapture estimates of dispersal, they are not feasible for most animals in nature. Direct estimates of gene flow are also subject to the same spatial and temporal limitations as direct estimates of dispersal, which limits their use for interpreting genetic structure of populations.

A more objective way to evaluate long-term estimates of gene flow is with long-term estimates of dispersal (Table 1). Such an estimate should effectively integrate over many generations and over all interacting populations. Life history, morphological, behavioral and habitat-associated traits all contribute to dispersal ability, and can provide the basis for long-term dispersal estimates. If variation in these traits exists among species, if that variation can be unambiguously translated into dispersal ability, and if the traits are conservative (little changed) over the lifetime of a species, the resulting evaluation will be more objective than one based on ecological estimates of dispersal.

In practice, categorizations of life history, morphology and behavior are based on short-term observations, but if these traits are well understood biologically, they can provide reliable, qualitative rankings of dispersal. If the traits fall into discrete categories, then these relative rankings will also be unambiguous. Thus, although benthic (bottom-dwelling) marine invertebrates with planktonic larvae might occasionally disperse less than species lacking planktonic larvae, ranking these species as possessing, on average, "high" and "low" dispersal ability generates conservative, testable hypotheses. In studies of single species, contrasts of this type are not possible. Accordingly, post hoc interpretations of population structure are necessarily based on conjecture rather than falsifiable hypotheses. Because drift, population history, natural selection, and gene flow can interact in complicated ways, it is always possible to invoke different combinations of these factors that are equally plausible.

Confounding factors will undoubtedly limit the strength of any comparative approach. For example, a ranking of dispersal ability in an insect taxon based only on wing morphology may miss the potential importance of other behavioral or morphological traits. If the species of interest are not sympatrically distributed, differences in their vicariant histories may also obscure or confound the underlying patterns. These limitations are unavoidable when direct experimentation is not possible, and hypotheses can only be tested by correlative data. When a phylogeny is available for the taxon, methods that attempt to control for the phylogenetic nonindependence of species can be helpful (Felsenstein 1985; Miles and Dunham 1993). Thus, across multiple species,

gene flow estimates should correlate best with dispersal when the species are closely related and have few other ecological differences: the ideal contrast would be between sister species occurring sympatrically and differing *only* in their ability to disperse.

Comparative studies of this type have been relatively rare outside of marine groups (reviewed by Burton 1983; Hedgecock 1986). Only a handful of studies have analysed population structure in a consistent manner for sympatric species with dispersal differences (e.g., Waples 1987; Liebherr 1988; Boileau et al. 1992; Doherty et al. 1995). In the majority of these investigations, the species considered are only distantly related. Studies that have focused on a single genus are often limited to two species (e.g., Janson 1987; McMillan et al. 1992), presumably because it is difficult to find many sympatric, closely related taxa with unambiguous dispersal differences.

Genetic variation is analysed below for animals that differ categorically in dispersal potential. This approach forgoes a detailed examination of dispersal and historical influences for a small number of case studies in favor of a broad quantitative summary across many independent groups. The results for a number of well-characterized taxa (e.g., Smith and Fujio 1982; Gyllenstein 1985; Ward 1990; Avise 1992) are combined with novel data sets in an analysis of 27 animal groups for which the relationship between population genetic statistics (e.g., F_{ST}, heterozygosity) and qualitative rankings of dispersal ability can be evaluated. The unambiguous conclusion from this analysis is that such statistics denote demonstrable relationships with dispersal ability in most animal taxa.

Analysis of Comparative Studies

A literature review was undertaken to find all groups of animal species in which dispersal differences could be reliably ranked, and for which information on population genetic structure was available. Although ideal groups would be composed of closely related and sympatric species, studies of this type are rare. Accordingly, I have summarized correlations between dispersal and population structure across a large number of groups to look for consistent patterns despite geographic, taxonomic and phylogenetic complications (Table 2). An attempt was made to find all groups in which dispersal ability could be directly related to life history, behavior or morphology. Because many researchers view the continuity of habitats as dictating the ability of species to disperse (e.g., open marine systems versus freshwater lakes), studies contrasting taxa from different habitats were included.

Twenty-seven groups of animal species conformed to these criteria (Table 2). Many of these groups consist of marine invertebrates; however, vertebrate and invertebrate taxa from terrestrial and freshwater habitats are also represented. In some cases, data were extracted from the original studies for reanalysis; in others, the original data were augmented with newer studies. Eight of the data sets were assembled specifically for this review. In five groups, raw data from the original investigation were not available, and averages for entire categories of species had to be used. In the 22 groups for which data were available at the species level or lower, the number of taxa varied from 2 to 82, with a median of 7.

Within each group, I ranked species for relative dispersal ability ($\mathbf{D_r}$), with $D_r = 1$ for all species in the lowest dispersing category, $D_r = 2$ for the next category, and so forth (Table 2). In nearly all cases, the criteria by which dispersal ability was ranked were determined by researchers in the corresponding studies (see references in Table 2; complete list of rankings in Bohonak 1998 and available on request from the author). For marine taxa, this ranking was based on the presence or absence of planktonic eggs and larvae (groups 2, 6, 8, 11–13, 24), larval time in the plankton (groups 4–5), or a combination of these factors (groups 1, 3, 9). For example, group 3 (Lacson 1992) contains one species of fish with benthic eggs and no pelagic larvae ($D_r = 1$), 4 species with benthic eggs and pelagic larvae ($D_r = 2$) and one species with pelagic eggs and larvae ($D_r = 3$). In groups 14–19 and 21–22, dispersal ability in terrestrial, freshwater (landlocked), anadromous, and marine taxa was assumed to increase in that order ($D_r = 1$, 2 and 3). In group 23, $D_r = 1$ for freshwater taxa and $D_r = 2$ for marine taxa and one bird species (Avise 1992). Dispersal ability of four amphipods was based on their behavior and the distribution

of their preferred microhabitats (group 20: $D_r = 1$ for two species restricted to sponges and $D_r = 2$ for two free-living species; Yampolsky et al. 1994).

For waterstriders (group 7), D_r was assumed be highest in long-winged species, followed by seasonally winged species and, finally, wingless species. Wing morphology and behavior was used for group 26 (two sets of ranking criteria; Liebherr 1988). For water mites (group 10), D_r was based on the dispersal ability of insect taxa that each species parasitizes. Nonparasitic species were given a rank of $D_r = 1$ (Smith 1998), and parasitic species that disperse on midges, mosquitos and odonates (dragonflies and damselflies) were given ranks of 2, 3 and 4 respectively (Bohonak 1998). Dispersal ability of stream-dwelling arthropods (group 27) was based on mobility of adults and immature stages. The relatively immobile beetle *Psephenus herricki* was ranked lowest, followed by amphipods ($D_r = 2$), cambarid decapods ($D_r = 3$), the caridean decapod *Paratya australiensis* (which possesses a planktonic immature stage: $D_r = 4$), blackflies (winged adult stage: $D_r = 5$) and stoneflies and caddisflies (winged adults and relatively active larvae: $D_r = 6$). Within each of the 27 groups, the number of dispersal categories varied between 2 and 7 with a median of 3.

Although mtDNA data were available for two of the groups, the remainder of the data were based on allozymes. For each species or taxon, the following measures were obtained:

F_{ST} or G_{ST}: as calculated by the original researchers. These estimates of population differentiation should decrease from a maximum of 1 (complete fixation of different alleles in each population) to 0 (no population subdivision) with increasing dispersal ability. G_{ST} (Nei 1973) is one of several estimators of F_{ST}, introduced by Wright (1961, 1965; see also Weir 1990). Within any particular group, only one estimator (e.g., Weir's θ or Nei's G_{ST}) was typically used. However, in groups 3 and 5, two estimators were used by the original researcher, and each was analysed separately here.

Nm: The estimated number of migrants exchanged between local populations per generation, derived from the frequency of "private" alleles, those found in only one local population (Slatkin 1985b). When Nm estimates only reflecting a simple transformation of F_{ST} were available, this category was omitted. As a measure of gene flow, Nm should increase with dispersal.

Nei's D: this measure of genetic distance is based on the genetic similarity of two populations (Nei 1972). Here, the average value of D for all pairs of populations was used. Nei's D is expected to decrease with increasing dispersal.

H, H_S: Individual heterozygosity averaged by individual (H) or by subpopulation (H_S). These differ when sample sizes are not the same in all populations. Because gene flow among populations increases effective population size and slows the rate of fixation, heterozygosity should increase with increasing dispersal. With one exception, observed instead of expected heterozygosities were used. Only studies with data from six or more loci (both monomorphic and polymorphic) were included.

P: Percentage of loci that are polymorphic, for studies with six or more loci. Polymorphic loci are defined here as those for which the overall frequency of the most common allele is ≤ 0.95. Although gene flow should promote the maintenance of alleles within any single population, no relationship is expected between gene flow and the maintenance of variation at the level of the species. Accordingly, P should be unrelated to dispersal ability.

The relationship between dispersal ranking and each genetic statistic was determined using Spearman rank correlation coefficients (R). This statistic is a nonparametric analog of the usual Pearson product-moment correlation coefficient, and appropriate for assessing correlations when one or both variables contain ranked data (Sokal and Rohlf 1995, p 598). Where multiple entries for a genetic statistic were available for the same species, mean values were used to calculate R. Complete data matrices are available on request from the author, and provided in Bohonak (1998).

Across systems, the "consistency" of each population genetic statistic was determined by comparing how often the sign of R (positive or negative) matched its expected sign. A statistic that is always positively correlated with dispersal ability (i.e., R always >0) can be considered a good indirect measure of dispersal.

TABLE 2
Summary of groups analysed

Group	Lowest taxonomic resolution	T_r	N_t	No. of dispersal categories	Ref.
GROUPS IN WHICH DISPERSAL IS INFERRED FROM LIFE HISTORY AND MORPHOLOGICAL DATA:					
1 Sea stars	Class Asteroidea (Echinodermata)	3(3, 6)	11(6, 9)	6	1–6
2 Marine prosobranch gastropods	Subclass Prosobranchia (Mollusca)	4(4, 8)	16(2–13)	3	7–18
3 Caribbean fish	Superorder Teleostei (Vertebrata)	5	6	3	19
4 Great Barrier Reef fish	Superorder Teleostei (Vertebrata)	5	7(5–7)	7	20
5 Pacific fish	Superorder Teleostei (Vertebrata)	5	10	6	21
6 Corals	Order Scleractinia (Cnidaria)	6	2	2	22
7 Water striders	Family Gerridae (Arthropoda)	8	4(2–3)	3	23–26
8 Shipworms	Family Teredinidae (Mollusca)	8(8, 10)	7(2, 7)	3	27
9 Oysters	Family Ostreidae (Mollusca)	8	8	7	28, 29
10 Water mites	Genus *Arrenurus* (Acari)	10	11(7–11)	4	30
11 Sea urchins	Genus *Heliocidaris* (Echinodermata)	10	2	2	31
12 Periwinkles	Genus *Littorina* (Mollusca)	10	12(4–12)	3	18, 32–50
13 Sponge-dwelling decapods	Genus *Synalpheus* (Arthropoda)	10	2	2	51
GROUPS IN WHICH DISPERSAL IS INFERRED FROM THE HABITAT IN WHICH EACH SPECIES LIVES:					
14 Outcrossing gastropods*	Class Gastropoda (Mollusca)	3	3*	3	52
15 Facultatively selfing gastropods*	Class Gastropoda (Mollusca)	3	3*	3	52
16 Fish*	Superorder Teleostei (Vertebrata)	5	4*(2,4)	3	53
17 Fish*	Superorder Teleostei (Vertebrata)	5	3*	3	54
18 Decapods	Order Decapoda (Arthropoda)	6	82(23–70)	3	55–84
19 Calanoid copepods	Order Calanoida (Arthropoda)	6	17(2–12)	2	85–96
20 Lake Baikal amphipods	Suborder Gammaridae (Arthropoda)	7	4(3–4)	2	97
21 Atlantic salmon	Species *Salmo salar* (Vertebrata)	11	2	2	98
22 Brown trout	Species *Salmo trutta* (Vertebrata)	11	2	2	99

TABLE 2 *continuation*
Summary of groups analysed

Group	Lowest taxonomic resolution	T_r	N_t	No. of dispersal categories	Ref.
GROUPS IN WHICH DISPERSAL IS INFERRED FROM LIFE HISTORY AND HABITAT:					
23 Atlantic marine and coastal taxa	Multiple phyla: Arthropoda, Mollusca, Vertebrata	1	12	2	100
24 Marine fish*	Superorder Teleostei (Vertebrata)	5	9*	7	101
GROUPS IN WHICH DISPERSAL IS INFERRED FROM BEHAVIOR AND HABITAT:					
25 Cave-dwelling arthropods	Phylum Arthropoda	2	32(6–26)	3	102–112
GROUPS IN WHICH DISPERSAL IS INFERRED FROM BEHAVIOR AND HABITAT:					
26 Carabid beetles	Tribe Platynini (Arthropoda)	9	5	5	113
27 Stream-dwelling arthropods	Phylum Arthropoda	2	59(21–46)	6	56,70,71, 114–127

N_t is the number of taxa in each group, and T_r is a ranking of the lowest taxonomic resolution, from $T_r = 1$ (multiple phyla) to $T_r = 11$ (within species comparisons). The number of dispersal categories within each group is provided. Numbered references are indexed below. When values for N_t and T_r vary across genetic statistics owing to incomplete data sets, ranges are also indicated. * indicates data that have been summarized elsewhere, and for which information was unavailable at the species level. These groups were analysed by dispersal category rather than by species.

References:

1 (Benzie and Stoddart 1992); 2 (Hunt 1993); 3 (Johnson and Threlfall 1987); 4 (Kwast et al. 1990); 5 (Stickle et al.1992); 6 (Williams and Benzie 1993); 7 (Campbell 1978); 8 (Day and Bayne 1988); 9 (Gooch et al. 1972); 10 (Grant and Utter 1988); 11 (Hoagland 1984); 12 (Holborn et al. 1994); 13 (Johnson and Black 1984); 14 (Johnson and Black 1991); 15 (Johnson et al. 1993); 16 (Liu et al. 1991); 17 (Mitton et al.1989); 18 (Snyder and Gooch 1973); 19 (Lacson 1992); 20 (Doherty et al.1995); 21 (Waples 1987); 22 (Hellberg 1996); 23 (Preziosi and Fairbairn 1992); 24 (Varvio-Aho 1979); 25 (Varvio-Aho and Pamilo 1979); 26 (Zera 1981); 27 (Hoagland 1986); 28 (Buroker 1983); 29 (Buroker 1985); 30 (Bohonak 1998); 31 (McMillan et al. 1992); 32 (Beardmore and Morris 1978); 33 (Berger 1973); 34 (Berger 1977); 35 (Boulding et al. 1993); 36 (Fevolden and Garner 1987); 37 (Janson 1985a); 38 (Janson 1985b); 39 (Janson 1987); 40 (Janson and Ward 1984); 41 (Janson and Ward 1985); 42 (Johannesson 1992); 43 (Knight et al. 1987); 44 (Mastro et al. 1982); 45 (Noy et al. 1987); 46 (Ward 1990); 47 (Ward and Janson 1985); 48 (Ward and Warwick 1980); 49 (Wilkins and O'Regan 1980); 50 (Wilkins et al. 1978); 51 (Duffy 1993); 52 (Brown and Richardson 1988); 53 (Gyllenstein 1985); 54 (Ward et al. 1994); 55 (Armada et al. 1993); 56 (Attard and Pasteur 1984); 57 (Berglund and Lagercrantz 1983); 58 (Boulton and Knott 1984); 59 (Brown 1981); 60 (Busack 1988); 61 (Chow et al. 1987); 62 (Chow and Fujio 1985); 63 (Chow and Fujio 1987); 64 (Chow et al. 1988); 65 (Costa and Bisol 1978); 66 (Hedgecock et al. 1977); 67 (Hedgecock et al. 1979); 68 (Hedgecock et al. 1982); 69 (Huber 1985); 70 (Hughes et al. 1995); 71 (Ingold et al. 1988); 72 (Kartavtsev 1994); 73 (Lester 1979); 74 (Lester 1983); 75 (Mashiko and Numachi 1993); 76 (Mulley and Latter 1980); 77 (Nelson and Hedgecock 1980); 78 (Nemeth and Tracey 1979); 79 (Redfield et al. 1980); 80 (Smith and McKoy 1980); 81 (Stevens 1990); 82 (Tracey et al. 1975); 83 (Turner and Lyerla 1980); 84 (Valentine 1976); 85 (Afanas'ev et al. 1989); 86 (Boileau 1991); 87 (Boileau and Hebert 1988); 88 (Boileau and Hebert 1991); 89 (Boileau and Taylor 1994); 90 (Bucklin 1989); 91 (Bucklin 1991); 92 (Bucklin and Marcus 1985); 93 (Cervelli et al. 1995); 94 (Hairston and Bohonak 1998); 95 (Carol Eunmi Lee, pers. comm. 1996); 96 (Trujillo-Ortiz et al. 1995); 97 (Yampolsky et al. 1994); 98 (Hindar et al. 1991); 99 (Verspoor 1994); 100 (Avise 1992); 101 (Smith and Fujio 1982); 102 (Caccone 1985); 103 (Caccone et al. 1986); 104 (Caccone and Sbordoni 1987); 105 (Cesaroni et al. 1992); 106 (Crouau-Roy 1989a); 107 (Crouau-Roy 1989b); 108 (Dickson et al. 1979); 109 (Gooch and Hetrick 1979); 110 (Koppelman and Figg 1995); 111 (Laing et al. 1976); 112 (Sbordoni et al. 1981); 113 (Liebherr 1988); 114 (Funk and Sweeney 1990); 115 (Funk et al. 1988); 116 (Guinand 1994); 117 (Jackson and Resh 1992); 118 (Lop and Oliver 1989); 119 (Robinson et al. 1992); 120 (Scheepmaker 1990); 121 (Schmidt et al. 1995); 122 (Siegismund and Müller 1991); 123 (Snyder and Linton 1984); 124 (Sweeney and Funk 1991); 125 (Sweeney et al. 1986); 126 (Sweeney et al. 1987); 127 (White 1989).

Two statistical tests of consistency were conducted for each measure using sign tests. One test for matching signs was made using all R values, and a second was conducted using only those rank correlations in which R was significant at a level of $\alpha \leq 0.05$.

SOURCES OF ERROR AND BIAS

The pooling of genetic data collected in multiple studies might be misleading if geographic scale or the number of populations in each original study were confounded with rankings of dispersal ability. For example, if widely dispersing species are sampled on larger geographic areas than species with restricted dispersal, island-model F_{ST} estimates for these species may not be comparable. Unequal numbers of species or different levels of taxonomic resolution within each of the groups could also introduce biases. Accordingly, an attempt was made to determine if geographic scale, sample size or taxonomic resolution influenced the correlations in any way.

Determining the influence of varying geographic scales is not simple, because comparable scales are typically not sampled by different researchers, and sampling details are often omitted. Nonetheless, a geographic scale was determined for every study that possessed site descriptions. In most cases distances between populations were not reported and had to be estimated from maps. Sampling in three of the groups (4, 13, 16) was sufficiently disjunct that the data had been analysed by the original investigators on two separate scales. As a result, I separated these data into "large" and "local" scales as well. In other groups (3, 5, 6, 8, 11, 20, 21, 22, 23) species were sampled on comparable scales. Five groups contained insufficient data to examine the influence of geographic scale (9, 14, 15, 17, 24).

For each of the ten remaining groups, I examined scatterplots of the statistics quantifying genetic differentiation among populations (F_{ST}, Nei's D, private allele estimates of Nm) as a function of "geographic scale," defined as the maximum distance between any pair of populations in the study of that species. Each point in these plots was a separate species. The graphs were examined visually for evidence of bias, made easier by using a different symbol/color combination for each dispersal rank (similar to plots in Williams and Guries 1994; Bohonak 1999). This procedure was supplemented by the corresponding analysis of covariance (ANCOVA) for each plot. (D_r was treated as a categorical independent variable, and scale as the covariate. Logarithmic transformations of scale and/or the population statistic were used as necessary to meet linearity assumptions.) For statistics measuring population differentiation, a more appropriate way to examine the influence of scale would be to recalculate the statistics for every pair of populations and then plot these as a function of geographic distance (sensu Slatkin 1993; 1994) for all species in the group (see Figure 4 in Janson 1987 for a two-species example). However, the data necessary for such an analysis were rarely available in the original studies.

In most cases, the null hypothesis that F_{ST}, Nm, H, Nei's D or P was unrelated to geographic scale could not be rejected. Examination of the scatterplots also revealed no evidence of bias in these groups, and usually D_r categories were represented at a range of geographic scales. However, geographic scale was highly disjunct and complicated the interpretation of group 7 (water striders). As a result, the data for this group were divided into "local" and "large" scales ($\leq$10 km and $\geq$900 km) for separate analyses.

Similar graphical and statistical analyses were conducted to determine whether the number of populations per species in each original study influenced the rank correlations between dispersal and the five genetic statistics. No such dependence was detected.

As phylogenetic distance between species increases, differences other than dispersal ability will increasingly add errors to the rank correlations. The importance of this bias can be ascertained by examining the strength of R across groups at different taxonomic levels of resolution. A rank value for taxonomic resolution ($\mathbf{T_r}$) was assigned to each of the 27 groups based on the Linnean hierarchy: $T_r = 1$ for group 23 (which included many phyla), $T_r = 2$ for groups 25 and 27 (one phylum), and so on. The highest level of T_r (11) was assigned to groups 21 and 22, which contrasted anadromous and nonanadromous populations of the same fish species.

A new rank correlation was calculated between R and T_r, and termed $\mathbf{R_{R,T}}$. R might be expected to approach 1 as the phylogenetic distance among species decreases, because the number of extraneous differences other than dispersal decreases. Similarly, one might expect R values near zero for taxa in different orders or phyla. I used this approach despite the likelihood that it is a weak test of bias. It is doubtful that Linnaean categories above the level of species provide comparable information in different taxa (e.g., phylogenetic distance and ecological differences among species in an order of insects may not be comparable to those for an order of corals).

The R values were also examined for correlations with the number of taxa in each group ($\mathbf{N_t}$), and the rank correlation between R and N_t was termed $\mathbf{R_{R,N}}$. It is possible that very small sample sizes might provide misleading results concerning the relationship between population genetic structure and dispersal (e.g., for $N_t = 2$, the only possible values for R are 1, −1 and 0).

In summary, estimates of F_{ST}, D, Nm from private alleles, H and P were obtained for as many species as possible in each of 27 groups. Dispersal rankings for each species in each group (D_r) were assigned using life history, behavioral, morphological and/or habitat-specific criteria. Within each group, rank correlations (R) were calculated between each of the five genetic statistics and D_r, and these R values were assessed for consistency across groups. This assessment consisted of seeing how often the sign of R matched its predicted sign. For each of the five genetic statistics, correlations with taxonomic resolution in each group ($R_{R,T}$) and the number of species in each group ($R_{R,N}$) were examined. Statistical significance for these correlations may indicate potential biases.

Statistical analyses were conducted using DataDesk 6.0 for Macintosh (Velleman 1997).

RESULTS OF ANALYSIS

Estimates of population differentiation (F_{ST} or G_{ST}) were available for 20 of the 27 groups (Table 3). These included marine, freshwater and terrestrial invertebrates, and fishes. In 19 of 20 cases, the rank correlation R was negative: increased dispersal was associated with decreased differentiation among populations (see Figure 1). Apart from water mites (R = 0.24), R values ranged between −0.17 and −1.00 with a mean of −0.78 and a median of −0.80 (mean R = −0.73 for all 20 groups, see Table 4). In 10 of the 13 groups for which sample size was large enough to assess significance (i.e., four or more species), the rank correlation was statistically significant. Consistency tests showed that R values for population differentiation were negative more often than could be expected by chance alone, and this result did not depend on the exclusion of 10 groups in which R was not statistically different from zero (sign tests; $p \leq 0.001$ and $p \leq 0.005$; see Table 4).

Gene flow estimates from private alleles increased with increasing dispersal ability in four out of five groups for which they were available, with a mean R of 0.44. In contrast, average values of Nei's D between populations in each species were not related to dispersal as consistently, with only six out of eleven possessing a negative R value (mean R = −0.25). However, the correlation between Nei's D and dispersal was negative in all five cases where it was large enough to be significant ($p \leq 0.05$ for sign test).

The mean R between heterozygosity and dispersal was 0.51, and the median was 0.70. The heterozygosity correlations were positive in 15 out of 21 groups, resulting in marginal significance for consistency (sign test: $p \leq 0.05$). R was positive in four out of five cases in which it was statistically different from zero (Table 4). P, the percentage of loci that were polymorphic, showed no clear relationship with dispersal across 19 groups despite significant rank correlations within mites, oysters, prosobranch gastropods and fish from the Great Barrier Reef (Table 3).

The correlations in Table 3 did not appear to be biased by variation in T_r (taxonomic resolution) across groups ($p > 0.05$ for all values of $R_{R,T}$; see Table 5). However, the number of taxa (N_t) in each group was strongly correlated with R values for two of the five genetic statistics. Larger sample sizes were associated with weaker (i.e., less negative) correlations between dispersal and F_{ST} ($R_{R,N}$ = 0.74, $p < 0.001$; see Figure 2). The relationship between heterozygosity and dispersal also may have

TABLE 3

Spearman rank correlations (R) between dispersal ranking and population genetic statistics

Group	F_{ST} or G_{ST}	Nm‡	Nei's D	H, H_S	P
GROUPS IN WHICH DISPERSAL IS INFERRED FROM LIFE HISTORY AND MORPHOLOGICAL CRITERIA:					
1 Sea stars	−0.69* (9)			−0.75, 0.82*[PP] (6)	−0.21 (6)
2 Marine prosobranch gastropods	−0.80* (6)		0.16 (7)	1.00 (2)	−0.51* (13)
3 Caribbean fish	−0.17,−0.51 (6)	−0.17 (7)	0.00 (7)		−0.46 (7)
4 Great Barrier Reef fish: Large scale	−0.79* (7)		−0.96*** (7)	−0.14 (7)	−0.71* (7)
Great Barrier Reef fish: Local scale	−0.30 (5)				
5 Pacific fish	−0.82***, −0.88**** (10)	0.56* (10)	−0.72* (10)	−0.01 (10)	0.18 (10)
6 Corals	−1.00 (2)				
7 Water striders: Large scale	−1.00 (3)			1.00 (2)	0.50 (3)
Water striders: Local scale	−1.00 (2)				−1.00 (2)
8 Shipworms			1.00 (2)	0.87** (7)	−0.14 (7)
9 Oysters				0.90*** (8)	0.92***(8)
10 Water mites	0.24 (7)			0.45, 0.38 (11)	0.65* (9)
11 Sea urchins (mtDNA)	−1.00 (2)				−1.00 (2)
12 Periwinkles	−0.60* (11)		0.00 (4)	0.17, −0.04 (12)	0.01 (12)
13 Sponge-dwelling decapods: Large scale	−1.00 (2)				0.00 (2)
Sponge-dwelling decapods: Local scale	−1.00 (2)				1.00 (2)
GROUPS IN WHICH DISPERSAL IS INFERRED FROM THE HABITAT IN WHICH EACH SPECIES LIVES:					
14 Outcrossing gastropods				1.00 (3 groups)	
15 Facultatively selfing gastropods				1.00 (3 groups)	
16 Fish: Large scale	−0.63 (4 groups)				
Fish: Local scale	−0.95* (4 groups)			0.11, 1.00[PP] (4, 2 groups)	
17 Fish	−1.00 (3 groups)				
18 Decapods	−0.59*** (23)		0.02 (25)	0.16, −0.07 (40, 37)	−0.06 (70)
19 Calanoid copepods	−0.29 (10)		−0.64* (10)	−1.00 (2)	−0.21 (12)
20 Lake Baikal amphipods	−0.87 (3)			0.71 (4)	0.00 (4)
21 *Salmo salar*	−1.00 (2)			1.00 (2)	1.00 (2)
22 *Salmo trutta*				1.00, 1.00 (2)	
GROUPS IN WHICH DISPERSAL IS INFERRED FROM LIFE HISTORY AND HABITAT:					
23 Atlantic marine and coastal taxa (mtDNA)		0.59*, 0.49 (12)			
24 Marine fish				0.92**** (9 groups)	

TABLE 3 *continuation*
Spearman rank correlations (R) between dispersal ranking and population genetic statistics

Group	F_{ST} or G_{ST}	Nm‡	Nei's D	H, H_S	P
GROUPS IN WHICH DISPERSAL IS INFERRED FROM BEHAVIOR AND HABITAT:					
25 Cave-dwelling arthropods	−0.93** (6)	0.50* (15)	−0.01 (19)	0.49* (13)	0.22 (26)
GROUPS IN WHICH DISPERSAL IS INFERRED FROM BEHAVIOR AND MORPHOLOGY:					
26 Carabid beetles [ranked by					
1) behavior,	−1.00**,	1.00**,	−1.00**,	0.70, 1.00**, 0.60,	−0.70,
2) wing morphology]	−0.50 (5)	0.50 (5)	−0.50 (5)	0.50 (5)	−0.60 (5)
27 Stream arthropods	−0.80**** (21)		−0.81**** (32)	0.12 (32)	0.08 (46)

‡ private alleles
Multiple entries into the same cell occur when several estimates of the statistic were available. Sample sizes are indicated in parentheses. All data are from allozymes, except groups 1 and 8, which are based on mtDNA. Correlations marked with * are significant at $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.005$, and **** = $p \leq 0.001$. Statistical significance is only available for correlations where $n \geq 4$. With correction for 61 tests where $n \geq 4$, **** is equivalent to a Bonferroni-corrected $p \leq 0.061$. [PP] indicates heterozygosity values from common polymorphic loci only.

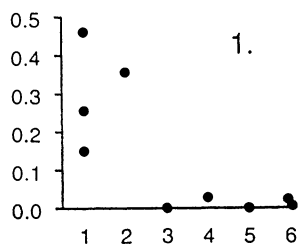
been confounded by number of taxa ($R_{R,N} = -0.55$; $p < 0.005$). No other relationships between R and either T_r or N_t were apparent (Table 5).

Separating the influences of T_r and N_t on the correlations in Table 3 is difficult, because T_r and N_t were significantly correlated for three out of the five genetic statistics. Rank correlations of T_r and N_t ranged between −0.62 and −0.87 for Nei's D, P and private allele estimates of Nm ($p < 0.05$ for all three), reflecting poorer taxonomic resolution in groups with more species. To some extent, this collinearity rested on R values in Table 3 that were calculated from only two taxa, as these groups generally were focused at the generic or species level (see Table 2). However, exclusion of cases where $N_t = 2$ did not substantively change the values of $R_{R,N}$ and $R_{R,T}$ (Table 5) or the qualitative conclusions of the analyses (Table 4).

Thus, population genetic metrics commonly used to quantify differences among populations and to infer gene flow were significantly correlated with dispersal in many groups for which data were available; across groups, they consistently showed associations in the direction predicted. The average correlation between dispersal ability and heterozygosity was also high, although these relationships were less consistent. The relationship between P and dispersal was equivocal. The strength of the associations within any particular group was related to the number of taxa it contained. However, because phylogenetically restricted studies often contain fewer species, it is not possible to entirely separate the biases imposed by sample size and taxonomic resolution.

DISCUSSION

There are many reasons why the comparative approach used here should fail to uncover statistically significant associations. As discussed in the introduction, dispersal ability was ranked according to relatively conservative criteria, but other factors that may be important for many taxa were ignored. Even though dispersal ability is not expected to be a perfect indicator of gene flow, I assumed that these discrepancies would be minor in comparison to differences among dispersal categories. Further, many interpretations of population differentiation are based on equilibrium assumptions and simplistic models of gene flow that are unlikely to be met in most natural systems. Certainly some but not all of the 82 decapod species in group 18 are in dispersal-gene flow equilibrium. The 59 species of stream-dwelling arthropods (group 27) are unlikely to have been sampled or genetically assayed in comparable ways. Even the basic assumption that populations are discrete, homogeneous units may be too simplistic for some marine taxa, where detailed studies on small scales have suggested that recruitment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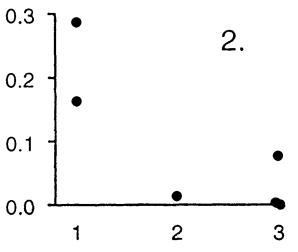
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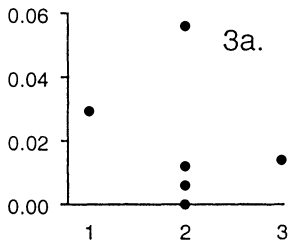
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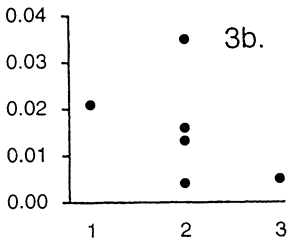
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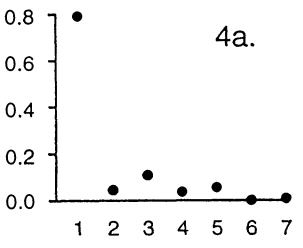
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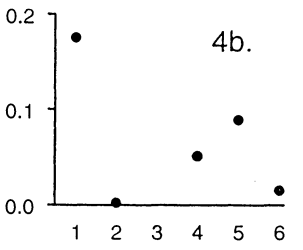
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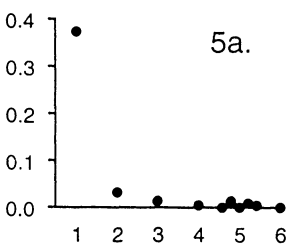
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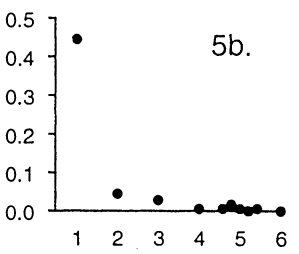
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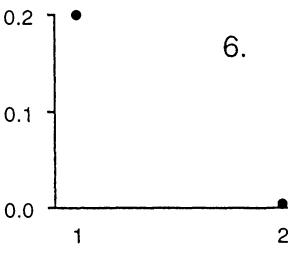
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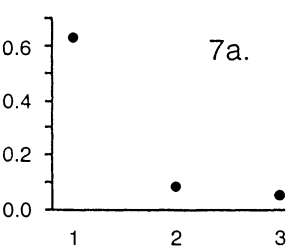
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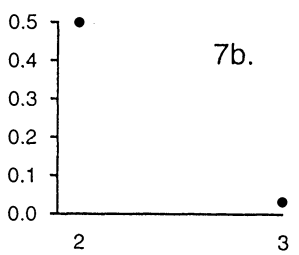
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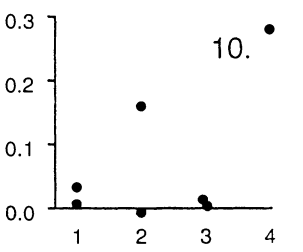
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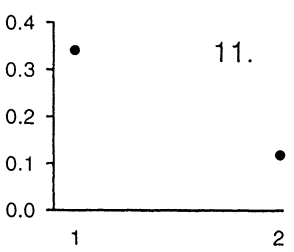
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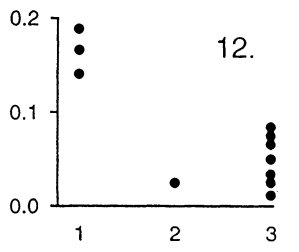
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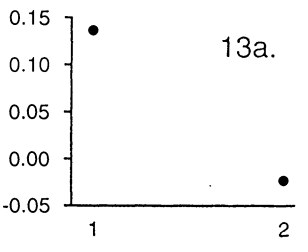
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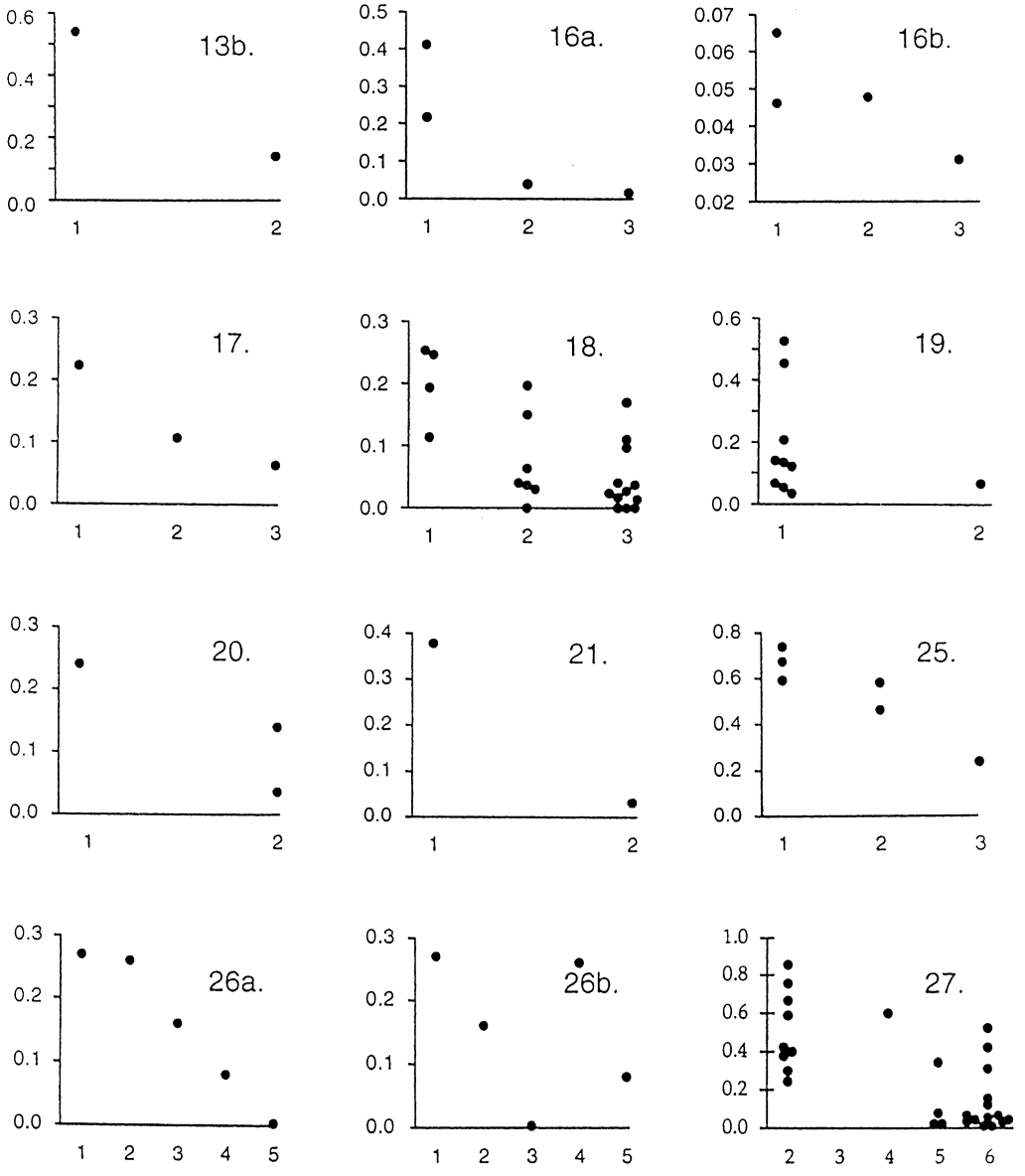

FIGURE 1. RELATIONSHIP BETWEEN POPULATION GENETIC DIFFERENTIATION AND DISPERSAL ABILITY For each group in which estimates of population genetic differentiation were available, the value of F_{ST} or G_{ST} is plotted as a function of the dispersal rank D_r for each species. Group numbers are indicated in each panel. Two plots (**a** and **b**) for groups 4, 7, 13 and 16 reflect division of the data into "local" and "large" scale studies, and F_{ST} was estimated by two methods (**a** and **b**) in groups 3 and 5 (see Table 3). Two sets of ranking criteria (**a** and **b**) were used in group 26. Overlapping points are slightly displaced along the ordinate for clarity.

TABLE 4
Summary of R values

	F_{ST} or G_{ST}	Nm‡	Nei's D	H, H_S	P
Expected sign of *R*	−	+	−	+	?
Mean *R* (by group)	−0.73	0.44	−0.25	0.51	−0.03
Median *R*	−0.80	0.54	−0.01	0.70	−0.06
Consistency of sign of *R* (all groups)	19 of 20****	4 of 5	6 of 11	15 of 21*	9^-, 7^+, $3^{\pm}$
Number of groups in which significance can be assessed ($N_t \geq 4$)	13	5	10	14	15
Consistency (only cases where $p \leq 0.05$ for *R*)	10 of 10***	4 of 4	5 of 5*	4 of 5	2^-, 2^+
Consistency of sign of *R* ($N_t > 2$ only)	15 of 16***	4 of 5	6 of 10	11 of 16	8^-, 6^+, $2^{\pm}$

‡ private alleles

Only one entry per group and population genetic statistic was used. Where two correlations were available for the same group at different scales, or where multiple entries were available for the same cell in Table 2, only one entry was made in Table 4. (If there were differing signs in the same cell , such as heterozygosities for the periwinkle group, that group was conservatively interpreted as not supporting the predicted hypothesis.) *, *** and **** indicate significance at $p \leq 0.05$, $p \leq 0.005$ and $p \leq 0.001$ (one-sided sign test). Statistical significance is available only where $n \geq 4$. With correction for 13 sign tests with $n \geq 4$, *** is equivalent to a Bonferroni-corrected $p \leq 0.065$.

patterns are complex (Johnson et al. 1993; see also Watts et al. 1990; Edmands et al. 1996). Nonetheless, population genetic data tend to correlate with dispersal ability in predictable ways despite myriad complicating factors. It is possible that these 27 groups are not representative of patterns found across all species. However, a more parsimonious conclusion may be that simple population genetic statistics are generally robust for making inferences about the movement of individuals.

For a wide variety of animal taxa, the correlation between dispersal and population genetics is nearly always in the direction predicted. When phylogenetically or ecologically comparable groups of species are evaluated, those with a life history indicative of reduced dispersal almost always show increased F_{ST}, a larger number of private alleles, and, to a lesser extent, reduced heterozygosity (Figure 1, Table 4). These results are in accord with previous qualitative reviews of marine organisms (e.g., Palumbi 1995). Their extension to include freshwater and terrestrial animals indicates that the continuity of marine ecosystems in space and time, when compared with other environments, does not make them unique. This is supported by Peterson and Denno's (1998) recent review of phytophagous insects, which found a good match between gene flow estimates and direct, short-term estimates of dispersal (from mark-and-recapture and invasion studies). Similarly, Govindaraju (1988; 1989) has also found a significant relationship between dispersal ability and gene flow in quantitative reviews of plant species.

There are additional reasons to believe that the influence of dispersal on population genetics is as pervasive as suggested by the summary in Table 4. The consistency of *R* values documented across five genetic statistical measures corresponds with the degree to which dispersal and gene flow should influence them. For example, private allele estimates of gene flow are thought to be less reliable than estimates of Nm from F_{ST} (Waples 1987; Slatkin and Barton 1989), and the consistency of Nm is less than that of F_{ST} (Table 4). Slatkin (1985a) noted that the association between genetic distances such as Nei's D and gene flow remains relatively unexplored statistically, that D takes longer to reach equilibrium than F_{ST} or private alleles, and that some simulations have shown only a weak correspondence between D and gene flow (Slatkin and Maruyama 1975). Consistent with those observations, I found that the sign of *R* for Nei's D matched expectations less often than *R* for either F_{ST} or private allele Nm estimates.

For heterozygosity (H), increased levels of gene flow should slow the loss of alleles due to drift, and so H should be positively correlated with dispersal and gene flow. However, heterozygosity is not a measure of population subdivision per se, and H is likely to be influenced by many other factors. This is reflected by a

TABLE 5
Rank correlation of R values in Table 2 with T_r and N_t

	All Groups			Groups where $N_t > 2$		
	$R_{R,T}$	$R_{R,N}$	n	$R_{R,T}$	$R_{R,N}$	n
F_{ST} or G_{ST}	−0.16	0.74****	20	0.30	0.52*	16
Nm	0.46	−0.40	5	0.63	−0.40	5
Nei's D	0.32	−0.34	11	0.11	−0.12	10
H, H_S	0.27	−0.55***	21	−0.03	−0.52*	16
P	0.23	0.14	19	0.11	0.40	16

*, *** and **** indicate significance at $p \leq 0.05$, $p \leq 0.005$ and $p \leq 0.001$. With correction for 20 tests, **** is equivalent to a Bonferroni-corrected $p \leq 0.02$.

less consistent fit of dispersal with H than with the previous three population genetic statistics. Finally, P shows no consistent relationship to dispersal in Table 4, which is in accord with expectations. If polymorphism is measured at the level of the species, then the maintenance of multiple alleles should be only weakly affected by interactions among populations. For example, imagine a single locus with two alleles at equal frequencies. Even in the complete absence of gene flow, when drift is great enough to fix alternate alleles in 50% of the populations, the locus would still remain "polymorphic." The inclusion of P in these analyses provides some assurance that the results are not simply artifacts, because although P does represent some measure of genetic variation, it shows no relationship with dispersal ability. Thus, the relative consistencies for *R* across the five genetic statistical measures provides further evidence that the broad conclusions of this review are valid.

Because more distantly related species tend to differ in larger numbers of ecological and demographic characters, correlations between dispersal and population genetic statistics should become weaker as more inclusive groups are analysed. However, there was no measurable influence of species relatedness on the correlations in this study. This may be due to the conservative nature of the taxonomic ranking criteria. It is also possible that a larger analysis might uncover significance in such an association, as only six groups resolved at the family level or less were used here.

Within a single taxon, contrasts among closely related species possessing dispersal differences should lead to stronger inferences regarding the interplay of evolutionary forces. The single group in which dispersal is positively correlated with F_{ST} provides such an example. Water mites of the genus *Arrenurus* parasitize a variety of winged adult insects that differ in dispersal ability. This association permits a ranking of dispersal in the mites, since it provides the sole means of transport among ponds and lakes. However, across seven species assayed in this genus, five species are essentially panmictic over scales of 150–200 km, and dispersal shows an insignificant but positive relationship to allozyme population differentiation (R = 0.24, Table 3; Bohonak 1998). A more focused set of contrasts is possible in this group because several species have independently lost the ability to parasitize insects. These "direct developers" hatch from eggs into a postlarval stage, and forgo their primary opportunity to disperse. For the two cases in which data are available from a direct-developing species and a parasitic sister species, loss of parasitism has led to an increase in population differentiation (F_{ST}) both times. Thus, although F_{ST} values for allozymes are near zero, and historical influences might be prominent in these species, phylogenetically restricted comparisons are consistent with a limited role for dispersal and gene flow in structuring populations genetically.

The use of species as statistically independent points in correlations and regressions requires a great deal of caution (Felsenstein 1985). Relationships among species possess an historical phylogenetic component that necessarily contributes to (or causes) covariance among traits at the species level. In the animal taxa analysed here, taxonomic scale may ob-

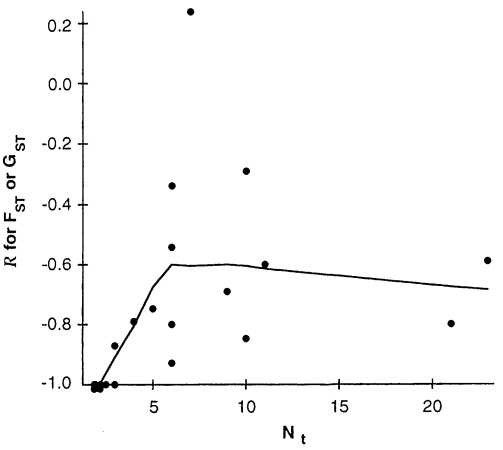

FIGURE 2. RELATIONSHIP BETWEEN *R* FOR POPULATION DIFFERENTIATION AND N_T
R from the "$\mathbf{F_{ST}}$ or $\mathbf{G_{ST}}$" column in Table 3 is plotted as a function of $\mathbf{N_t}$ (number of taxa in each group; see Table 2). A smoothing function is shown to emphasize the trend (locally weighted regression scatterplot smoothing [LOWESS] smoother with a span of 20%; Velleman 1997). The four overlapping points for $N_t = 2$ are slightly displaced for clarity.

scure or bias associations between dispersal and population genetics to an unknown extent. However, the consistency of those correlations despite variation in taxonomic resolution suggests that phylogenetic history generally may play a less important role in structuring populations than dispersal ability. The future analysis of larger groups of closely related individuals with clear dispersal differences will help to resolve these issues. Further, a comparative analysis of these or comparable data sets that explicitly controls for phylogeny (Felsenstein 1985; Harvey and Pagel 1991) would be informative for well-studied groups such as molluscs or decapods.

Finally, inspection of Figure 1 suggests that in some marine taxa, the influence of life history, morphology and development on population differentiation might be important only in extreme cases. Values of F_{ST} are unusually high only for dispersal category 1 in many marine invertebrate groups. For these taxa, $D_r = 1$ typically included species that lack planktonic larvae and have benthic eggs, and species with D_r values of two and higher had larvae that spend increasing amounts of time in the plankton. This suggests that, although the presence of planktonic larvae does slow population differentiation, increasing development time in the plankton may not always have demonstrable population genetic consequences (e.g., Waples 1987; Doherty et al. 1995). These observations are consistent with those made in Burton's (1983) early review of protein variation in marine systems.

SUMMARY

One might wonder whether finding statistically significant correlations between dispersal and population genetic statistics is surprising. If sample sizes are large enough, statistical significance will be found whether dispersal ability accounts for as much as 80%, or as little as 5%, of the variance in F_{ST} across species. What about the other, unexplained variance? Do these types of analyses contribute to a more general understanding of evolutionary pattern and process?

At least two considerations suggest that the answer to the latter question is yes. First, population genetic processes are numerous, complex, and difficult to separate in most single-species studies. Tests of comparative hypotheses provide one way to evaluate broad generalities, and to discover which taxa depart from these generalities. These goals will be met in future work through the continued accumulation of multispecies studies and a greater application of phylogenetic information.

Second, there are numerous opinions about how important gene flow, mutation, natural selection, drift and nonequilibrium factors are in general, as well as in particular species. Population genetic data need to be collected and analysed within a common framework to resolve these issues. The magnitude and role of gene flow has been particularly elusive in this regard. Gene flow has been hypothesized to be extensive in nature (Mayr 1942) or limited (Ehrlich and Raven 1969), to be a creative microevolutionary force (Wright 1932) or a destructive one (by preventing local adaptation, Baur 1986), to prevent speciation (Carson and Templeton 1984) or to cause it through hybridization (Abbott 1992). At one

extreme, the role of gene flow in structuring allozyme variation in natural populations is sometimes characterized as inconsequential or negligible in comparison with natural selection or historical factors (e.g., Gillespie 1991; Bossart and Prowell 1998). The studies reviewed here would suggest that such pessimism regarding the impact of dispersal and gene flow on population genetic structure is unwarranted. Across a wide variety of taxa, allozymes provide a valuable tool for interpreting microevolutionary processes and reflect, at least in part, the movement of individuals among populations.

ACKNOWLEDGMENTS

I thank Carla Cáceres, Corey Freeman-Gallant, Rick Grosberg, Nelson Hairston, Jr., Cami Holtmeier, David Post, Bruce Smith and an anonymous reviewer for commentary and helpful discussion. AJB was supported by grants from the National Science Foundation (DEB-9423603), and a training grant to the Center for Applied Math and Department of Ecology and Systematics at Cornell University.

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