

AN INTRASPECIFIC COMPARATIVE ANALYSIS OF CHARACTER DIVERGENCE BETWEEN SYMPATRIC SPECIES

PETER B. MARKO

Department of Marine Sciences, University of North Carolina, Chapel Hill, North Carolina 27599-3300

E-mail: pmarko@unc.edu

Abstract.—Although sympatric character divergence between closely related species has been described in a wide variety of taxa, the evolutionary processes responsible for generating these patterns are difficult to identify. One hypothesis that can explain sympatric differences is ecological character displacement: the sympatric origin of morphologically divergent phenotypes in response to selection caused by interspecific competition. Alternatively, populations may adapt to different conditions in allopatry, with sympatric distributions evolving through selective colonization and proliferation of ecologically compatible phenotypes. In this study, I characterize geographic variation within two sibling species of rocky-shore gastropods that have partially overlapping distributions in central California. In sympatry, both *Nucella emarginata* and *N. ostrina* show significant differences in shell shape and shell ornamentation that together suggest that where the two species co-exist, divergent phenotypes arose as an evolutionary consequence of competition. To examine the evolutionary origins of divergent characters in sympatry, I used a comparative method based on spatial autocorrelation to remove the portion of the phenotypic variance among populations that is explained by genetic distance (using mitochondrial DNA sequences and allozyme frequency data). Because the remaining portion of the phenotypic variance represents the independent divergence of individual populations, a significant sympatric difference in the corrected dataset provides evidence of true character displacement: significant sympatric character evolution that is independent of population history. After removal of genetic distance effects in *Nucella*, shell shape differences remain statistically significant in *N. emarginata*, providing evidence of significant sympatric character divergence. However, for external shell ornamentation in both species and shell shape in *N. ostrina*, the significance of sympatric differences is lost in the corrected dataset, indicating that colonization events and gene flow have played important roles in the evolutionary history of character divergence in sympatry. Although the absence of a widely dispersing planktonic larva in the life cycle of *Nucella* will promote local adaptation, the results here indicate that once advantageous traits arise, demographic processes, such as recurrent gene flow between established populations and extinction and recolonization, are important factors contributing to the geographic pattern of sympatric character divergence.

Key words.—Adaptation, character displacement, competition, *Nucella*, predation, shell evolution, speciation.

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When ecologically similar species develop overlapping distributions, natural selection may favor the evolution of morphological differences that reduce the negative effects of competition. This process of ecological character displacement is broadly defined as phenotypic evolution caused by competition for limited habitat and resources (Schluter 1988; Schluter and McPhail 1992). Character displacement has received considerable theoretical attention, but because experimental tests are usually not possible (but see Schluter 1994; Pfennig and Murphy 2002; Pritchard and Schluter 2000), most of the evidence for the phenomenon comes from comparative data (Taper and Case 1992). Phylogenetically based analyses have been particularly useful (e.g., Losos 1990; Richman and Price 1992; Miles and Dunham 1996; Giannasi et al. 2000; Glor et al. 2003) because they can distinguish character displacement, the evolution of novel phenotypes within lineages, from the sorting of species into compatible combinations through processes of differential persistence, extinction, and colonization (e.g., Strong et al. 1984; Armbruster 1986; Schluter 2000). Consideration of evolutionary history has therefore been fundamentally important in reconstructing the historic processes through which communities of species spatially partition limited habitats and resources (Schluter 2002).

Although it is widely accepted that phylogenetic relationships can inform studies of adaptation between species, the influence of population genetic history on patterns of geographic variation within species is often underappreciated.

However, geographic variation within species has always been a central focus for the study of adaptation and character displacement (Futuyma 1998), and some of the most influential work has involved characterization of geographic variation within species that exist in both allopatry and sympatry with potential competitors (e.g., Fenchel 1975; Connor and Simberloff 1979; Grant 1986; Dayan and Simberloff 1994; Robinson and Wilson 1994; Adams and Rohlf 2000; Pfennig and Murphy 2000, 2003). But, as is the case with cross-species studies, interpretation of the geographic and evolutionary origins of intraspecific variation can be confounded by historical factors. For example, at least two distinct processes could contribute to a geographic pattern of sympatric morphological differentiation. The first involves the sympatric origin of novel phenotypes in response to competition: populations that come into contact with an ecologically similar species evolve a morphologically displaced phenotype that reduces overlap in resource use (i.e., character displacement). The second process involves the evolution of compatible assemblages of populations in sympatry through the selective sorting of phenotypes that have adapted to divergent ecological conditions in allopatry. The fundamental distinction between these two processes is that in the former, divergent character states originate in sympatry as the result of directional selection working on phenotypic variants produced within populations by mutation; in the latter, selection favors the colonization and persistence of morphologically

divergent phenotypes that adapted to divergent conditions in allopatry.

Distinguishing between these two alternative scenarios ultimately requires consideration of patterns of geographic variation in a context that allows identification of the portion of the phenotypic variance among populations that can be attributed to their independent evolutionary divergence (Thorpe 1996; Radtkey 1997; Hansen et al. 2000). Although powerful, the widely used comparative method of independent contrasts (Felsenstein 1985; Graffen 1989) is not altogether appropriate for analyses of intraspecific variation because such methods require an explicit set of phylogenetic relationships among the terminal taxa. To address this issue, correlation and regression methods that use genetic distance data have been developed for analyzing patterns of geographic variation within species (Gittleman and Kot 1990; Legendre et al. 1994; Edwards and Kot 1995; Thorpe et al. 1995; Daltry et al. 1996; Thorpe 1996; also see Martins 1996). Despite the growth of phylogeography, and the abundance of data on population structure in both plants and animals (Avice 2004), few studies of morphological geographic variation have incorporated information about population genetic structure or genealogical relationships to address hypotheses concerning adaptive geographic variation (but see Edwards and Kot 1995; Radtkey et al. 1997; Hansen et al. 2000).

In this paper, I focus on patterns of morphological divergence between two recently diverged sibling species in the rocky-shore gastropod genus *Nucella*. Population genetic analyses of *N. ostrina* and *N. emarginata* indicate that a broad region of sympatry in central California, between San Francisco and Point Conception, was likely achieved by a post-Pleistocene poleward range expansion of *N. emarginata* across the zoogeographic boundary located at Point Conception (Marko 1998; Wares et al. 2001; Marko et al. 2003). In the region of sympatry, the two species are rarely syntopic (Palmer et al. 1990; Marko 1998; Marko et al. 2003); they tend to be found in adjacent habitats that differ with respect to both physical and biological factors: populations of *N. ostrina* are found predominantly on wave-exposed shores along the outer coast, whereas *N. emarginata* is found mainly on wave-protected shores, such as the leeward sides of headlands and other habitats where wave action is diminished or dissipated by shoreline topography (Marko 1998; Marko et al. 2003).

On wave-exposed shores, shell-crushing predators are relatively rare but on wave-protected shores large predators capable of crushing molluscan prey (e.g., crabs) are abundant. In many gastropod species, these abiotic and biotic differences result in characteristic patterns of morphological variation within and between species: snails on wave-exposed shores have thin shells with wide shell apertures and little external shell ornamentation; snails on wave-protected shores typically exhibit relatively thick shells with narrow shell apertures and greater external ornamentation (e.g., Currey and Hughes 1982; Janson 1982, 1983; Janson and Ward 1984; Palmer 1985). Here, using specimens from previous phylogeographic analyses of allozymes and mitochondrial DNA (mtDNA), I have characterized patterns of geographic variation in shell morphology in both allopatry and sympatry to

determine whether significant morphological divergence occurs in the region where *N. ostrina* and *N. emarginata* co-exist.

To examine patterns of geographic variation in the context of population genetic history, I used a comparative method derived from spatial autocorrelation analysis that uses genetic distances in place of spatial distances to both detect and remove the component of the interpopulation phenotypic variance that is explained by patterns of population genetic differentiation (Cheverud et al. 1985; Gittleman and Kot 1990; Gittleman and Luh 1992; Edwards and Kot 1995). The remaining portion of the phenotypic variance that cannot be explained by population history therefore represents the independent divergence of individual populations (Edwards and Kot 1995). The rationale behind this approach is that if morphological differences reflect significant sympatric character evolution (i.e., character displacement), sympatric differences should remain intact after removal of the population genetic component of the variation. Alternatively, if selective colonization and proliferation of phenotypes that originated in allopatry explains the evolution of the geographic pattern of sympatric divergence, sympatric differences should be diminished after removal of the component of the phenotypic variance explained by genetic distance. Geographic sorting of phenotypes that first evolved in allopatry and true character displacement are not necessarily mutually exclusive, such that phenotypes that first evolved in allopatry could diverge further in sympatry (see fig. 2c in Pfennig and Murphy 2003). However, the use of the comparative method provides a means to identify which process has been more important in the generation of the pattern of sympatric character divergence.

MATERIALS AND METHODS

Morphological Analysis

In a previous study, I collected snails from sites with *N. ostrina* and *N. emarginata* from rocky shores along the west coast of North America and characterized patterns of population structure using a combination of allozymes and mtDNA sequences (Marko 1998). The shells from those samples were saved for morphological analyses. Eight linear measurements of the shell (Fig. 1A) commonly used in gastropod morphometrics (e.g., Raup 1966; Vermeij 1971; Dillon 1984; Palmer 1990; Chiba 1993) were recorded with digital calipers from 25 individuals from each of 18 sites of *N. ostrina* and 12 sites of *N. emarginata*. I also measured shell ornamentation on the exterior of the shell (Fig. 1B,C), by scoring shells as possessing: a smooth shell (0), continuous spiral cords (1), spiral cords with some irregularly spaced bumps (2), regularly spaced spiral knobs on all whorls (3), and strong spiral knobs (4).

To place patterns of geographic morphological variation in an ecological context, I also counted the number of sublethal attacks (the number of repaired breaks in shells) on individual snails (Bergman et al. 1983; Geller 1983; Vermeij 1992). Because interpretation of the frequency of repaired damage among populations may be confounded by differences in the average age of individuals within populations (Schoener 1979), I attempted to minimize this effect by scor-

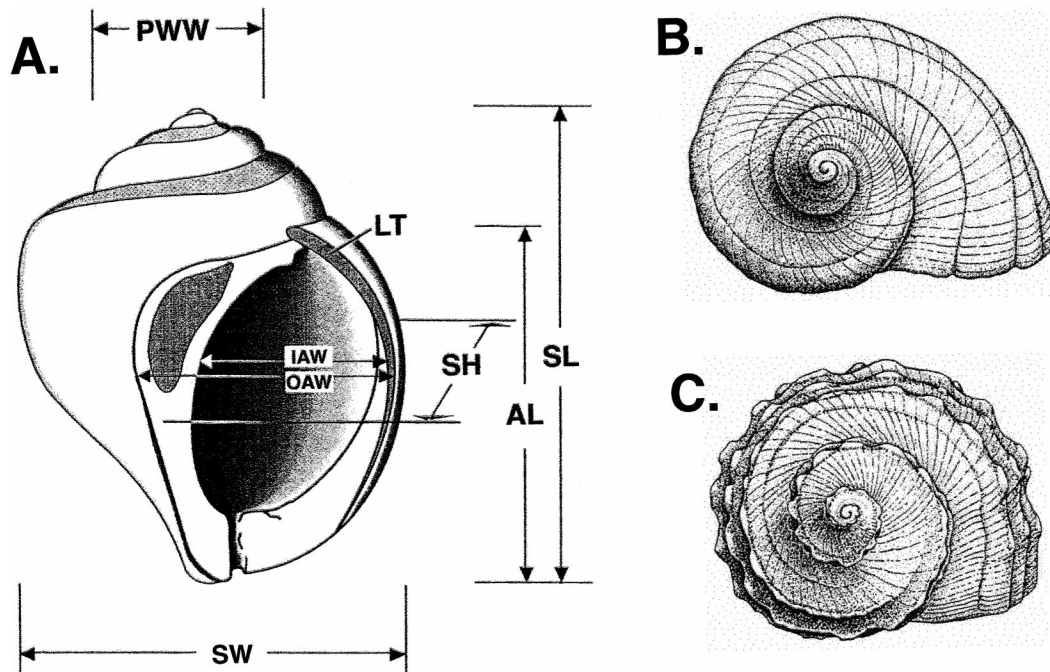


FIG. 1. (A) Linear measurements taken from the shells of *Nucella ostrina* and *N. emarginata*. Abbreviations defined in Table 1. (B) Apical view of continuous spiral cords. (C) Apical view of spiral knobs.

ing only substantial breaks in the final shell whorl (i.e., the most recently produced whorl). I then calculated the average number of repaired breaks per shell at each collection locality.

To characterize patterns of shell shape, I conducted a principal component analysis (PCA) with SYSTAT (ver. 5.0; Wilkinson 1989) on log-transformed linear shell measurements. Parametric *t*-tests were used to compare patterns of variation between sympatric and allopatric populations; patterns of variation in shell traits were compared to geographic variation in repaired shell damage using standard correlation procedures. I also used a discriminant function analysis (DFA, SYSTAT ver. 5.0) to characterize variation between species. For the DFA, shells of *N. ostrina* and *N. emarginata* were classified a priori according to their genotype at *IDH-2*, a diagnostic allozyme locus (Marko 1998).

Detection and Removal of Genetic Distance Effects

To identify and remove the portion of phenotypic variance that can be explained by population history, I used the PA software package (Luh et al. 1994). PA implements a comparative method based on spatial autocorrelation that has been described in detail elsewhere (Cheverud et al. 1985; Gittleman and Kot 1990; Gittleman and Luh 1992; Edwards and Kot 1995) and thus is only outlined briefly here. Spatial autocorrelation is defined as the relationship among values of a single variable that comes from the spatial arrangement in which those values occur (Cliff and Ord 1973, 1981) and can be used to test whether the observed value of a variable at one locality is dependent on values of the variable at neighboring localities (i.e., autocorrelation). Spatial autocorrelation can therefore be easily modified for use in evolutionary comparative studies (Cheverud et al. 1985) by using a matrix

of patristic genetic distances as a weighting matrix (rather than a matrix of geographic distances).

The first step of this approach involves the use of Moran's (1950) *I* autocorrelation coefficient as a diagnostic test for the presence of morphological correlations among samples of populations that are related to genetic differentiation. Moran's *I* is a conventional measure of autocorrelation, similar in interpretation to the Pearson's product moment correlation statistic in that both statistics range between -1.0 and 1.0 (Sokal and Oden 1978). In the context of the comparative method, positive values of Moran's *I* represent positive autocorrelation (genetically similar populations are also alike morphologically), while the converse is true for negative values of the statistic (genetically similar populations differ morphologically); a value of zero represents no autocorrelation. Calculating this statistic for samples separated by a variety of genetic distances allows construction of an autocorrelogram, which is a plot of genetic distance versus Moran's *I*. For the present study, mtDNA and allozyme distances among populations of *N. ostrina* and *N. emarginata* were taken from Marko (1998). Because only relative distances rather than absolute distances are necessary for comparative analyses, I added mtDNA sequence divergence to allozyme distance for each pairwise comparison among populations. Cliff and Ord (1981) showed that the distribution of *I* is normal and that *I* may be transformed and tested for its significance as a standard normal deviate, *z*, in which *z*-scores greater than 1.96 are used to reject the null hypothesis of no autocorrelation (also see Gittleman and Kot 1990; Edwards and Kot 1995).

I calculated Moran's *I* for shell morphological measurements taken from populations of *N. ostrina* and *N. emarginata*, generating correlograms for two traits that showed statistically significant morphological differences between spe-

TABLE 1. Loadings of the nine linear morphological measurements of shells of *Nucella ostrina* and *N. emarginata* on the first two principal component axes. Linear measurements are defined in the text and correspond those in Figure 2.

Linear measurement	PC1	PC2
Shell length (SL)	0.980	0.410
Aperture length (AL)	0.965	-0.077
Inner aperture width (IAW)	0.835	-0.516
Shell height (SH)	0.884	0.048
Penultimate whorl width (PWW)	0.839	0.381
Shell width (SW)	0.985	-0.054
Lip thickness (LT)	0.779	0.505
Outer aperture width (OAW)	0.898	-0.366
Eigenvalue	6.70	1.213
% of total variation	72.4	12.3

cies in sympatry. If correlograms for morphological traits among populations revealed significant autocorrelation with respect to genetic distance, variation in traits was then subdivided with Cheverud et al.'s (1985) phylogenetic autoregressive method using $y = \rho W y + \varepsilon$ to partition variation in each trait (y) into phylogenetic ($\rho W y$) and specific (ε) effects, where W is a matrix of patristic genetic distances and ρ is a constant (the autocorrelation coefficient) that is estimated as part of the procedure. Because the present study focuses on intraspecific variation, I will refer to the phylogenetic and specific components of phenotypic variation hereafter as the *genetic* and *population* components, respectively. The genetic component corresponds to the portion of the variation explained by genetic distance, whereas the population component is the remaining variance unaccounted for

by genetic distance; this latter portion of the phenotypic variance represents the independent evolutionary divergence of populations (Edwards and Kot 1995). Although Rohlf (2001) proposed an alternative procedure for estimating ρ , I have used only the procedure associated with the original description of the method. Martins et al. (2002) have subsequently shown that Cheverud et al.'s (1985) method performs well in simulations under a variety of evolutionary conditions.

RESULTS

Principal Components Analysis

Two principal components (PC1 and PC2) that explain over 84% of the variation among individuals were extracted from the correlation matrix. All of the variables load heavily and positively on PC1 (Table 1), indicating that PC1 can be interpreted as explaining size variation. Because some characters load positively and others load negatively on the second principal component, PC2 describes variation in shape. Shell length, penultimate whorl width, and lip thickness all load positively on PC2, whereas inner aperture width and outer aperture width both load negatively on PC2. Therefore, low PC2 scores describe shells that are short spired, relatively narrow near the apex, and have thin shells with wide shell apertures (Fig. 2). In contrast, high PC2 scores describe shells that are relatively tall, wide near the apex, but also possess thick apertural lips and narrow shell apertures (Fig. 2).

Sympatric Morphological Divergence: Uncorrected Data

The uncorrected data show sympatric morphological differences between *N. ostrina* and *N. emarginata* in both shell

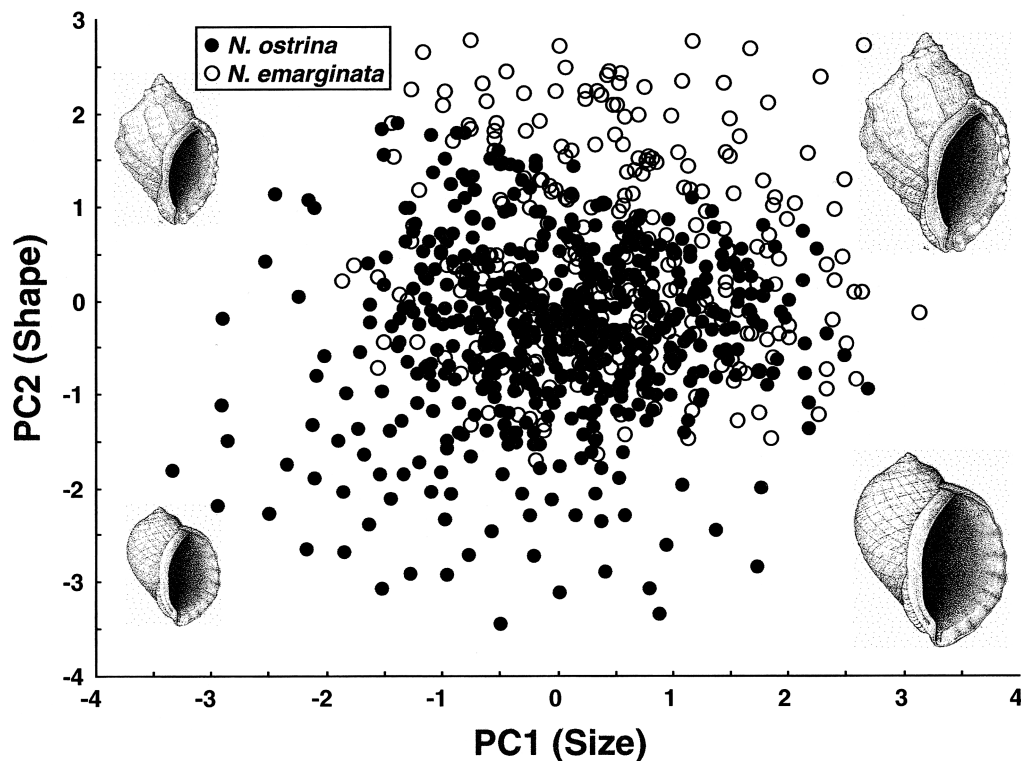


FIG. 2. Principal component (PC) scores for *Nucella ostrina* and *N. emarginata* and corresponding variation in shell morphology associated with each axis. Changes in size and shape reflect the character loadings on PC axes.

shape (PC2) and shell ornamentation (Figs. 3A,B). Standardized scores for shell shape (Fig. 4A) are highly significantly different between species in sympatry ($t = -7.75$, $df = 12$, $P = 0.0001$), with *N. ostrina* exhibiting relatively low PC2 scores and *N. emarginata* possessing relatively high PC2 scores. In contrast, allopatric PC2 scores of the two species (Fig. 4A) do not differ ($t = -0.177$, $df = 14$, $P = 0.8623$). Within species, PC2 scores are significantly different between allopatric and sympatric populations for both *N. ostrina* and *N. emarginata* ($t = 2.24$, $df = 16$, $P = 0.0399$ and $t = 4.71$, $df = 10$, $P = 0.0008$, respectively). Discriminant analysis and subsequent classification of shells based on their shape also reflects sympatric interspecific divergence in shell shape. In sympatry, 406 of 467 individuals (87%) were correctly classified according to their a priori grouping based on their *IDH-2* genotype. In contrast, only 151 of 363 (42%) allopatric individuals were classified correctly as either *N. ostrina* or *N. emarginata* by the DFA.

As with shell shape, standardized scores for shell ornamentation (Fig. 4B) are also significantly different between species in sympatry ($t = -10.156$, $df = 14$, $P = 0.0001$), with *N. ostrina* and *N. emarginata* showing mean ornamentation scores of 2.3 and 3.9, respectively (Fig. 3B). Within species, sympatric populations differ from conspecific allopatric populations (Fig. 4B): *N. ostrina* exhibits lower shell ornamentation scores ($t = 2.612$, $df = 16$, $P = 0.0193$) and *N. emarginata* shows greater shell ornamentation ($t = 2.974$, $df = 10$, $P = 0.014$) in the region of sympatry (as compared to conspecific allopatric samples). However, unlike for shell shape, shell ornamentation also differs significantly between allopatric populations ($t = -3.533$, $df = 14$, $P = 0.003$).

Geographic Variation in Repaired Shell Damage

Sympatric differences in shell morphology appear to be related to geographic patterns of shell damage (Fig. 3C). Between species, differences in repaired shell damage are not significant in allopatry ($t = -1.526$, $df = 14$, $P = 0.1493$) but are highly significant in sympatry ($t = -7.075$, $df = 12$, $P = 0.0001$), with *N. emarginata* exhibiting greater frequencies of repaired shell breaks in the region of sympatry. For both species, the frequency of repaired shell damage is also correlated significantly with both shell shape ($r = 0.603$, $P < 0.05$) and shell ornamentation score ($r = 0.409$, $P < 0.05$).

Presence and Removal of Autocorrelation

Correlograms for shell shape and shell ornamentation reveal high autocorrelation (positive values of Moran's I) among populations with respect to genetic distance (Fig. 5). The correlogram is typical of those observed in other taxa, with positive autocorrelation among closely related samples and negative autocorrelation among those separated by larger genetic distances (e.g., Edwards and Kot 1995; Luh and Croft 1998). Significantly positive autocorrelation in both shell shape ($R^2 = 0.307$) and shell ornamentation ($R^2 = 0.552$) was found for combined allozyme/mtDNA genetic distances less than 0.15–0.20 (corresponding to mtDNA sequence divergences of less than 2%). Negative autocorrelation was observed in shell shape among populations separated by ge-

netic distances of more than 0.25 and in shell ornamentation for populations differing by more than 0.45.

Removal of genetic distance effects and subsequent analyses of the population components of shell morphology changed the outcomes of comparisons of allopatric and sympatric populations. Although the trend of greater differentiation in sympatry than in allopatry remains, the population components for shell ornamentation (Fig. 4D) exhibit no statistically significant difference between species in sympatry ($t = 1.82$, $df = 12$, $P = 0.093$). In contrast, the population components for shell shape (Fig. 4C) did remain significantly different between species in sympatry ($t = -3.75$, $df = 12$, $P = 0.0028$). However, the significance of sympatric differences in the population component of shell shape is asymmetrical with respect to the two species: allopatric and sympatric populations of *N. emarginata* differ with respect to shell shape ($t = 2.32$, $df = 10$, $P = 0.043$), but allopatric and sympatric populations of *N. ostrina* show no significant difference ($t = 0.98$, $df = 16$, $P = 0.342$).

DISCUSSION

Nucella ostrina and *N. emarginata* exhibit highly significant differences in shell morphology and habitat use where their geographic ranges overlap. Populations of *N. ostrina*, which are found predominantly on wave-exposed shores in central California, have significantly lower shell shape (PC2) and shell ornamentation scores than either conspecific allopatric populations or sympatric populations of *N. emarginata*. In contrast, *N. emarginata*, which tends to be limited to central California sites that are sheltered from the action of breaking waves, possesses significantly higher shell shape and shell ornamentation scores than both sympatric *N. ostrina* and allopatric *N. emarginata*. Variation in these shell traits is known to have important functional significance for rocky-shore gastropods living in spatially heterogeneous environments. Specifically, most of the shell measurements that load heavily on PC2 are known to affect the resistance of snails to shell-breaking predators. For example, thick shells with broad whorls, narrow apertures, and strong external ornamentation show increased resistance to predators in experimental assays (Kitching et al. 1966; Rossi and Parisi 1973; Kitching and Lockwood 1974; Vermeij 1976, 1978, 1982, 1987; Zipser and Vermeij 1978; Hughes and Elner 1979; Palmer 1979, 1985; Vermeij and Currey 1980; Seeley 1986). In contrast, wide shell apertures, relatively thin shells, and shorter-spined shells with a reduced projected area are all features characteristic of populations living in wave-exposed environments where shell-breaking predators are relatively scarce (Kitching and Lockwood 1974; Berry and Crothers 1974; Currey and Hughes 1982; Crothers 1983, 1985; Brown and Quinn 1988; Etter 1988). Given the apparently adaptive relationships that exist between spatial variation in these shell traits and the frequency of repaired shell damage (Fig. 3), the geographic pattern is consistent with a sympatric origin of divergent character states. In sympatry *N. ostrina* shows a lower incidence of repaired shell damage and possesses a less predator-resistant shell morphology. In contrast, sympatric populations of *N. emarginata* exhibit greater incidences

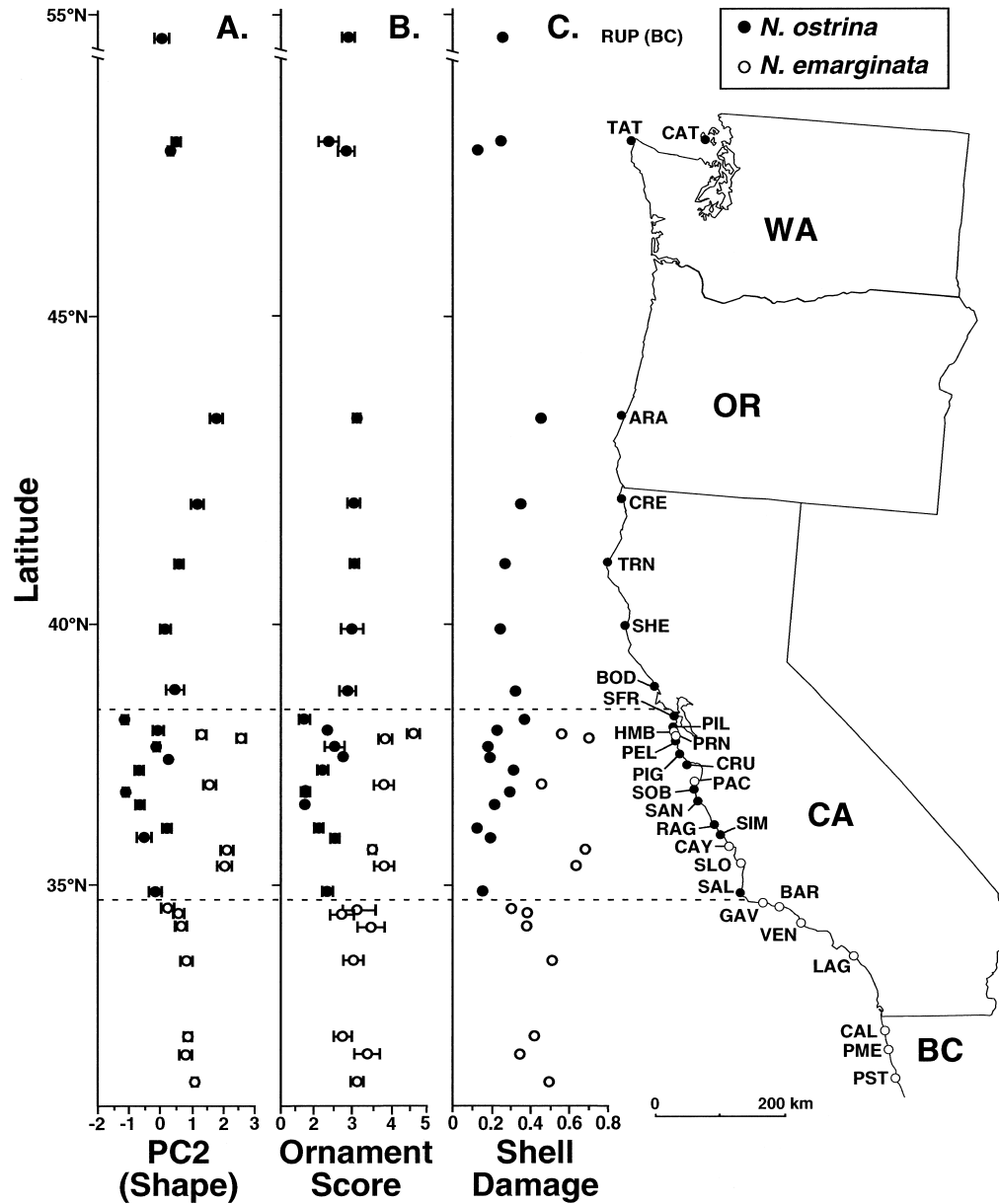


FIG. 3. Geographic variation in (A) shell shape (PC2), (B) ornamentation score, and (C) repaired shell damage among populations of *Nucella ostrina* and *N. emarginata*.

of repaired shell damage and exhibit more predator-resistant shell morphologies.

In the absence of a historical phylogeographic perspective, geographic variation in *Nucella* would appear to provide a clear ecogeographic pattern that is fully consistent with the idea that character divergence first arose in sympatry. However, use of the comparative method has an impact on the interpretation of the geographic origins of these differences. Even though the pattern of sympatric differentiation is present in both the uncorrected and corrected datasets, the significance of this result is substantially diminished for some traits when population genetic data are taken into account. For example, although uncorrected shell ornamentation scores show a highly significant pattern of sympatric divergence (Fig. 4B), significance disappears when the portion of

the variation explained by genetic distance is removed from the shell morphology data (Fig. 4D). Similarly, although a significant difference in shell shape exists between sympatric and allopatric populations of *N. emarginata*, the sympatric shift in shell shape in *N. ostrina* (Fig. 4A) loses statistical significance after analysis of only the population components for this trait (Fig. 4C). Therefore, the assumption that each population represents an evolutionarily independent data-point would wrongly imply that each population provides an independent replicate of the evolutionary response to sympatric overlap, artificially inflating the number of degrees of freedom in statistical analyses of the geographic pattern.

The absence of significant sympatric differences for some traits in the corrected dataset indicates that more of the phenotypic variation between allopatric and sympatric regions

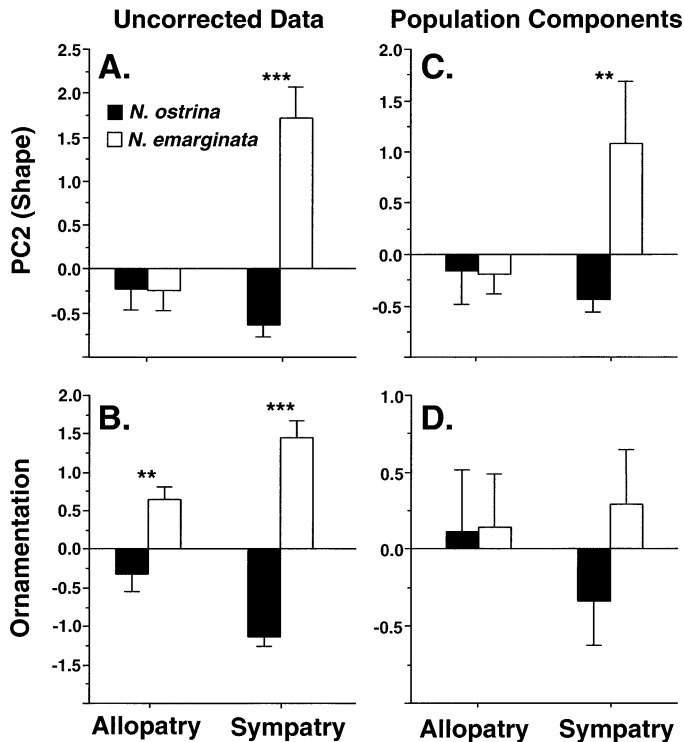


FIG. 4. Normalized allopatric and sympatric scores for shell shape (A and C) and shell ornamentation score (B and D) for *Nucella ostrina* and *N. emarginata*. Mean values and standard errors are shown for uncorrected data and after removal of correlations explained by population genetic distances. ** $P < 0.01$; *** $P < 0.001$.

is explained by population genetic history than by the independent divergence of populations in sympatry. At face value, the loss of statistical significance for the relationship between morphology and ecology in the corrected dataset, such as was observed in both species for shell ornamentation, could mean that some of the morphological differences in central California did not evolve in response to sympatric overlap. Alternatively, the discrepancy between the uncorrected and corrected datasets could mean that the population genetic component of the phenotypic variance is itself adaptive, that is, that sympatric character divergence occurred once in each species but divergent phenotypes then spread throughout the region of sympatry. Given that sympatric overlap was established by a northward post-Pleistocene range expansion by *N. emarginata* into central California (Marko 1998), shell ornamentation differences in *N. emarginata* observed today in sympatry with *N. ostrina* could have arisen from the evolution of novel phenotypes upon first contact between species at the periphery of their geographic ranges. The broad range of sympatry may have subsequently evolved through selective colonization and proliferation of ecologically compatible phenotypes of *N. emarginata*; ecologically compatible populations of *N. ostrina* likely persisted while incompatible populations were lost to extinction.

However, an allopatric origin for divergent shell ornamentation in *N. emarginata* seems more likely for several reasons. First, both species show no significant differences between allopatric and sympatric populations in corrected

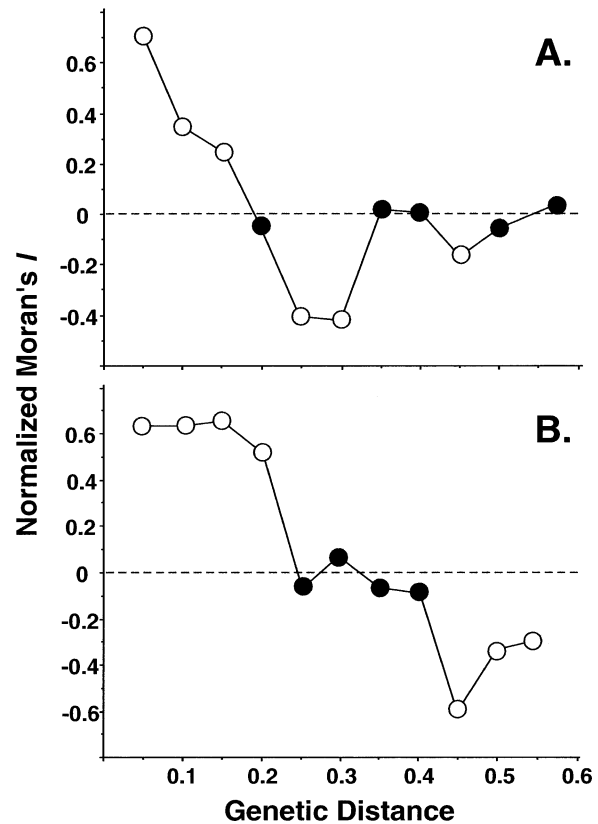


FIG. 5. Phylogenetic correlograms: plots of normalized values of Moran's I (I/I_{max}) against total genetic distance for uncorrected shell shape data (A) and shell ornamentation score (B) in *Nucella*. Trait values whose z-scores fall outside 95% confidence intervals around $z = 0$ (no autocorrelation) are indicated with open circles.

shell ornamentation scores (Fig. 4D). Second, some individual *N. emarginata* in southern California possess ornamentation scores that are nearly as large as the mean sculpture score observed in central California (Fig. 3B) with allopatric differences existing in the uncorrected dataset (Fig. 4B). This combination of results indicates that allopatric evolution of shell ornamentation in *N. emarginata* likely played a role in permitting range overlap and coexistence in central California. Although a single sympatric origin cannot be conclusively distinguished from an allopatric origin, under either scenario the comparative analysis of shell ornamentation scores indicates that gene flow and colonization events have played a significant role in generating the pattern of sympatric character divergence in *N. emarginata* as it expanded its geographic range into central California.

Even though *N. ostrina* shows no population genetic evidence of a similar range expansion into the region of sympatry (Marko 1998), analysis of the population components of both shell ornamentation and shell shape also indicates that population history explains much of the morphological variation among populations. Therefore, even in the absence of a regionwide colonization event, gene flow, in the form of either recurrent exchange between established populations or extinction and recolonization, has also likely played a significant role in the sympatric spread of adaptive morphological traits in *N. ostrina*. The concept that gene flow may

promote evolutionary change is not new (see Wright 1931; Futuyma 1987; Slatkin 1987), but for marine species like *Nucella* that lack a planktonic larval stage in their life cycles, gene flow is regarded primarily as a constraining evolutionary force; local adaptation is thought to be pervasive due to restricted gene flow between adjacent populations (Scheltema 1971; Gooch 1975; Crisp 1978; Crothers 1983; Janson 1982; Burton 1983; Hedgecock 1986; Behrens Yamada 1989; Boulding 1990). Although restricted gene flow in species with nonplanktonic larvae should provide widespread opportunities for genetic drift and local adaptive evolution, the comparative analyses in *Nucella* imply that if adaptive phenotypes arise in one location, they often become geographically widespread through dispersal among ecologically similar sites.

Genetic distances could also be correlated with geographic morphological variation for other reasons. For example, if genetic distance were related to geographic distance and geographic distance is in turn related to ecological factors shaping patterns of shell morphological variation, removal of genetic distance effects would simultaneously remove the ecogeographic component of the variation in shell traits. To address this possibility, for each species I multiply regressed all pairwise geographic and genetic distances among populations on Euclidean distances derived from shell damage frequencies. Because matrix variable data do not obey the assumption of independence, the statistical significance of the regression parameters was tested by permutation of the dependent matrix in the Permute software package (Legendre et al. 1994). The regression analysis indicates that although shell damage and geographic distance exhibit a significant linear relationship in both *N. ostrina* ($P = 0.027$) and *N. emarginata* ($P = 0.038$), genetic distance is not strongly related to geographic distance in either species ($P = 0.232$ and $P = 0.340$, respectively). Therefore, the comparative method should not have inadvertently removed the ecogeographic or adaptive component of the variation.

For shell shape in *N. emarginata*, the hypothesis of a sympatric origin of divergent phenotypes is supported given the presence of significant sympatric differences in this trait after removal of genetic distance effects. Although geographic sorting of pre-existing variation and true character displacement are not mutually exclusive processes, the persistence of a significant ecogeographic pattern after removal of genetic distance effects suggests that a significant amount of character divergence has occurred in sympatry independently of allopatric populations. Whether competition was necessarily important in the evolution of shell shape in *N. emarginata* or still maintains morphological differences between sympatric populations of *N. ostrina* and *N. emarginata* is not well understood. Habitat segregation is widely regarded as the main mechanism allowing coexistence among many intertidal species within biogeographic provinces (Borkowski and Borkowski 1969; Branch 1975; Hughes 1971; Taylor 1976; Vermeij 1971; Spight 1981) and *N. emarginata* and *N. ostrina* do show some trophic differentiation in sympatry, with *N. emarginata* consuming a wider range of intertidal prey (West 1986; Palmer et al. 1990). However, patterns of geographic variation that are consistent with character displacement can often be explained by other hypotheses (Schluter and McPhail

1992; Taper and Case 1992). For example, because sympatric morphological divergence between *N. ostrina* and *N. emarginata* involves antipredator traits, divergence in sympatry could also be caused by apparent competition (Holt 1977; Abrams 2000; Abrams and Chen 2002). Predation and other causes of mortality may also facilitate character displacement (Rundle et al. 2003). Future field experiments are therefore necessary to determine the competitive effects of one species on the other.

The statistically significant sympatric shift in shell shape in *N. emarginata* could also reflect phenotypic plasticity, which has been described in rocky-shore gastropods, including some species of *Nucella* (Appleton and Palmer 1988; Palmer 1985; Trussell 1996). Ecophenotypic variation is not expected to be related to population history and should remain intact in the corrected data, such as is the case for shell shape in *N. emarginata*, and could therefore represent an example of facultative character displacement (Pfennig and Murphy 2002). However, even if some ecophenotypic variation in shell shape exists, common garden experiments involving *Nucella* typically also show significant genetic variation for plasticity (Appleton and Palmer 1988; Palmer 1985). For example, when raised under identical conditions in the laboratory, juvenile *N. ostrina* hatched from egg cases from wave-protected habitats (i.e., exposed to greater relative predation risk) produce thicker shells with smaller shell apertures than do animals from wave-exposed populations, where shells are typically less predator-resistant (Marko 1991).

Conclusions

For marine organisms, secondary contact following allopatric speciation may be a common phenomenon because oceanographic barriers that are responsible for initiating speciation are often transitory in nature (Valentine and Jablonski 1983; Palumbi 1994; Marko 1998). As a consequence, many recently diverged sibling species have completely or partially overlapping geographic distributions in the marine environment (Murphy 1978; Knowlton 1993; Duffy 1996; Hellberg 1998; Marko 1998), creating the potential for direct contact between morphologically and ecologically similar species. If the morphological differences between *N. ostrina* and *N. emarginata* arose as a consequence of a post-Pleistocene range expansion by *N. emarginata*, the analysis of geographic variation here indicates that in addition to local adaptation *de novo*, population history is an important factor explaining the geographic distribution of adaptive morphological traits.

The inability of discriminant analyses to distinguish allopatric populations of *N. ostrina* from *N. emarginata* suggests that no differentiation in shell shape between species can be attributed to the allopatric phase of speciation. Thus the sudden appearance in the marine fossil record of new shell shapes alongside their putative ancestral species (e.g., Eldredge and Gould 1972; Williamson 1981) could reflect secondary contact and subsequent morphological divergence rather than speciation by peripheral isolation followed by invasion of a morphologically divergent daughter species. Very limited morphological differentiation has been documented between other marine sibling species that are per-

manently geographically isolated but that have not developed sympatric distributions (e.g., Lessios and Weinberg 1994; Marko and Jackson 2001). For such taxa, secondary contact and subsequent ecological interactions may be fundamentally important in generating morphological diversity among species.

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