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DEPENDENCE OF GENE FLOW ON GEOGRAPHIC DISTANCE IN TWO SOLITARY CORALS WITH DIFFERENT LARVAL DISPERSAL CAPABILITIES

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Abstract.—When the level of gene flow among populations depends upon the geographic distance separating them, genetic differentiation is relatively enhanced. Although the larval dispersal capabilities of marine organisms generally correlate with inferred levels of average gene flow, the effect of different modes of larval development on the association between gene flow and geographic distance remains unknown. In this paper, I examined the relationship between gene flow and distance in two co-occurring solitary corals. *Balanophyllia elegans* broods large, nonfeeding planulae that generally crawl only short distances from their place of birth before settling. In contrast, *Paracyathus stearnsii* free-spawns and produces small planktonic larvae presumably capable of broad dispersal by oceanic currents. I calculated F-statistics using genetic variation at six (*P. stearnsii*) or seven (*B. elegans*) polymorphic allozyme loci revealed by starch gel electrophoresis, and used these *F*-statistics to infer levels of gene flow. Average levels of gene flow among twelve Californian localities agreed with previous studies: the species with planktonic, feeding larvae was less genetically subdivided than the brooding species. In addition, geographic isolation between populations appeared to affect gene flow between populations in very different ways in the two species. In the brooding *B. elegans,* gene flow declined with increasing separation, and distance explained 31% of the variation in gene flow. In the planktonically dispersed *P. stearnsii* distance of separation between populations at the scale studied (10–1000 km) explained only 1% of the variation in gene flow between populations. The mechanisms generating geographic genetic differentiation in species with different modes of larval development should vary fundamentally as a result of these qualitative differences in the dependence of gene flow on distance.

Key words.—*Balanophyllia elegans,* genetic subdivision, isolation by distance, local adaptation, *Paracyathus stearnsii,* philopatry, stepping stone.

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Species with different life-history and reproductive strategies commonly possess associated differences in dispersal capability (e.g. insects: Dingle et al. 1980; Roff 1991; benthic marine invertebrates: Strathmann 1985; Knowlton and Jackson 1993; marine teleosts: Roff 1988; salamanders: Shaffer and Breden 1989). Dispersal differences may in turn produce different patterns of genetic exchange among populations within a species, thereby altering the process by which gene flow, genetic drift, and natural selection interact to produce geographic variation in genetic characters. Broad dispersal should genetically homogenize populations, as immigrants originate in widely different selective environments. In contrast, geographically restricted gene flow enhances differentiation among populations, as the relatively few immigrants arriving from nearby populations tend to resemble residents genetically (Wright 1943; Kimura and Weiss 1964; Endler 1973). Species with limited dispersal capabilities should therefore show higher levels of genetic subdivision than similar species with greater dispersal capabilities for two different (although not completely independent) reasons: (1) fewer migrants move among populations; and (2) the homogenizing effects of gene flow attenuate more rapidly with increasing separation.

In benthic marine organisms, interspecific differences in dispersal are determined primarily by the ontogeny of larvae. This is because adult stages are generally sessile or sedentary and larvae with different ontogenies spend varying amounts of time developing, and presumably dispersing, in the plankton. The variation in larval dispersal capability among species can be enormous: the larvae of some species spend many weeks in the plankton (Strathmann 1987) and can be found thousands of kilometers offshore (Scheltema 1971, 1988); the larvae of other species settle literally in the shadow of their mothers (Ostarello 1976; Gerrodette 1981; Olson 1985; Grosberg 1987). Consequently, interspecific differences in the mode of larval development have been causally linked to differences in geographical range (Scheltema 1971, 1977; Shuto 1974), rates of colonization (Scheltema 1977; Valentine and Jablonski 1983), and levels of gene flow (Scheltema 1977; Hedgecock 1986; Knowlton and Jackson 1993).

A mechanistic understanding of how interspecific differences in reproductive patterns influence the evolution of the species exhibiting these patterns requires knowledge of how levels of gene flow change with increasing geographic separation between populations. Estimates of gene flow (Nm) based on hierarchical measures of subdivision (*F*-statistics) can clearly document the extent of genetic subdivision. To use these estimates to analyze the relationship between gene flow and distance, Slatkin (1993) suggested a regression approach: plot all pairwise estimates of gene flow ($\hat{M}$) between populations against the distances separating those populations. Resulting regression coefficients and correlations can be compared to analytical or simulated expectations for different population structures and dispersal tendencies.

I used this approach to compare the relationship and association between gene flow and geographic distance in two solitary corals that differ in their larval dispersal capabilities. In the limited disperser *Balanophyllia elegans* Verrill, I previously found a strong association between inferred levels of gene flow and geographic distance at a spatial scale of hundreds of meters to tens of kilometers (Hellberg 1995) and a weaker association at a scale of hundreds to thousands of kilometers (Hellberg 1994). Here, I ask whether such changes

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in inferred gene flow with distance also occur in *Paracyathus stearnsii* Verrill, which possesses broadly dispersed, planktonic larvae.

Materials and Methods

Natural History of Corals

The solitary scleractinian corals *P. stearnsii* and *B. elegans* both live subtidally along the Pacific Coast of North America. They share a common geographic range extending from northern Baja California to at least northern British Columbia (Durham and Barnard 1952). These two species occupy similar microhabitats, often co-occurring on vertical rock faces at depths of 7–15 m (Chadwick 1991). Densities of *P. stearnsii* in these habitats may reach 25 per m^2 (Fadlallah and Pearse 1982a). Densities of *B. elegans* at similar depths can be an order of magnitude greater (Gerrodette 1981; Fadlallah 1983a). Both species are dioecious, with nearly even sex ratios, and exhibit reproductive peaks in the late winter and early spring (Fadlallah and Pearse 1982a,b).

Female *B. elegans* brood up to 50 large (2–3 mm), nonfeeding planulae annually. These larvae disperse very locally, often attaching within 40 cm of their mother after crawling over hard substrata for only a few days (Gerrodette 1981; Fadlallah 1983a).

Mature female *P. stearnsii* may harbor over 10^5 oocytes. In contrast to *B. elegans,* ova are fertilized and develop outside of the mother. The larvae of *P. stearnsii* are among the smallest known for any scleractinian (160 × 95 μm). Although feeding by these larvae has not been observed directly, their small size, abundant ciliation, and the presence of an anterior invagination all suggest that these larvae are planktotrophic (Fadlallah and Pearse 1982a). Laboratory-reared larvae swam for over four weeks, but never settled. Dispersal distances in nature remain unknown.

Collection of Samples

I collected individuals of both *P. stearnsii* and *B. elegans* from each of the same 12 localities spanning most of the coast of California (Figure 1). Adjacent localities were between 8 km and 302 km apart. At each locality, I gathered individuals from within an area of 100–1000 m^2. I gathered *B. elegans* from three to eight circular patches (radius < 33 cm). Adjacent patches were 4–6 m apart. *Paracyathus stearnsii* were collected (usually on the same dive) as encountered while sampling *B. elegans.* I collected only adult corals (those greater than approximately 6 mm in diameter). All samples were taken from between 5 m and 20 m below mean lower low water. I sampled all localities between April 1990 and July 1993. I removed encrusting algae and epifauna from coral samples before freezing them in liquid nitrogen in the field. Samples were subsequently stored at −80°C.

Electrophoresis

For *P. stearnsii,* I characterized six-locus genotypes for all individuals. I ran all samples using 12% (w/v) starch gels. Enzyme stains and electrophoretic conditions were modified from Selander et al. (1971). I assayed three loci—hexokinase (*Hk,* EC 2.7.1.1), phosphoglucose isomerase (*Pgi,* EC 5.3.1.9), and triosephosphate isomerase (*Tpi,* EC 5.3.1.1)—using the pH 8.0 Tris-citrate buffer system of Selander et al. (1971). I added 4 μl of 2-mercaptoethanol to 300 ml starch gels just before pouring to improve the resolution of *Pgi* bands. Three other loci—peptidase (*Pep,* EC 3.4.11/13., leucyl alanine substrate), and two forms of aspartate aminotransferase (*Aat,* EC 2.6.1.1)—were assayed using the more dilute pH 8.0 Tris-citrate buffer system of Ward and Beardmore (1977). *Aat-1* migrated farther than *Aat-2.* Two additional loci, phosphoglucomutase (*Pgm,* EC 2.7.5.1), and mannose-phosphate isomerase (*Mpi,* EC 5.3.1.8), were initially screened, but ultimately their extremely high levels of variation and limited separation of electromorphs precluded consistent scoring. Alleles were numbered to indicate their percent mobility relative to the most common allele at that locus. I included two internal standards in two lanes within each gel.

For *B. elegans,* I scored seven loci (*Hk, Pgi, Tpi, Pep-LA,*

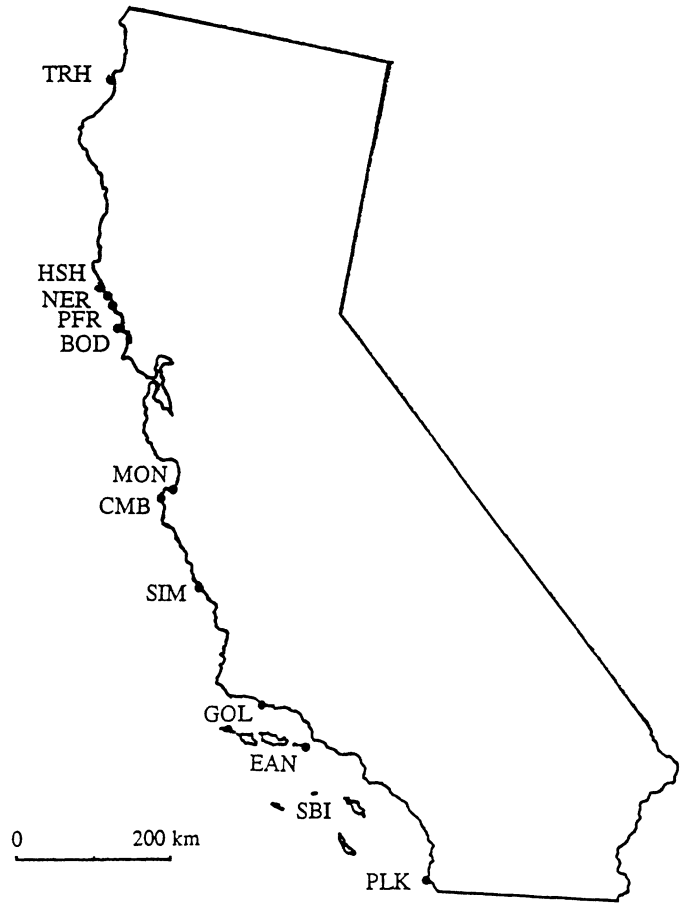

FIG. 1. The 12 Californian localities from which *Paracyathus stearnsii* and *Balanophyllia elegans* were sampled. Abbreviations: TRN (Trinidad Harbor, 41°03′N, 124°08′W), HSH (Horseshoe Point, 38°36′N, 123°22′W), NER (Nereocystis Ridge, 38°34′N, 123°19′W), PFR (Northwest Cape, Fort Ross, 38°31′N, 123°15′W), BOD (off Bodega Head, 38°20′N, 123°00′W), MON (Monterey, 36°34′N, 121°52′W), CMB (Carmel, Monastery Beach, 36°31′N, 121°55′W), SIM (San Simeon, 35°37′N, 121°08′W), GOL (Goleta, 34°26′N, 119°57′W), EAN (East Anacapa Island, 34°01′N, 119°22′W), SBI (Santa Barbara Island, 33°28′N, 119°02′W), and PLK (Point Loma Kelpbeds, 32°43′N, 117°16′W).

Aat, Pgm, and *Lap,* EC 3.4.11.1/2) as described previously (Hellberg 1994). Alleles were numbered to indicate their percent mobility relative to the most common allele at that locus from Santa Cruz.

Analysis

I used Wright's *F*-statistics (Wright 1978) to characterize overall genetic subdivision. These statistics partition total heterozygote deficiency (as compared to populations under panmixia) (F_{IT}) into components due to deficiencies within populations (F_{IS}) and subdivision among populations (F_{ST}). Gene flow (Nm), the average effective number of migrants exchanged between populations each generation, can be estimated from this measure of genetic subdivision using the relationship $Nm = (1 - F_{ST})/4F_{ST}$, assuming that genes move with equal likelihood among all populations. This relationship also assumes that gene flow and genetic drift have equilibrated, that the rate of migration greatly exceeds that of mutation, and that the genetic markers employed are selectively neutral.

Wright's parameters were calculated using the estimators of Weir and Cockerham (1984), which should accurately estimate average Nm if 10 or more populations are sampled and the migration rate (m) is less than 0.1 (Slatkin and Barton 1989; Cockerham and Weir 1993). I computed allele frequencies and hierarchical *F*-statistics from genotype frequencies using the program of Weir (1990). The program estimated standard errors by jackknifing over loci.

To infer the pattern of gene flow between proximate populations from spatial patterns of genetic differentiation, I used $\hat{M}$, the estimate of Nm calculated separately for pairs of populations. In a linear array of populations in which gene flow is restricted to immediately adjacent populations, the expected slope of a regression of $\log_{10}$ ($\hat{M}$) versus $\log_{10}$ (distance of separation) is -1.0. In a two-dimensional array, the expected slope of the log-log regression is -0.5 (Slatkin and Maddison 1990; Slatkin 1993). $\hat{M}$ should be viewed not as the actual number of migrants between a pair of populations each generation, but rather as equivalent to the number of migrants necessary to account for observed genetic differences if migrants could move directly between populations (rather than passing through intermediaries, as may be the case).

I computed $\hat{M}$ based on θ (Weir and Cockerham 1984) and G_{ST} (Nei 1973) for all pairwise combinations of populations using a program provided by M. Slatkin. Estimates of $\hat{M}$ based on G_{ST} ($\hat{M}_{GST}$) should be about twice those based on θ ($\hat{M}_{\theta}$) for pairwise comparisons (Slatkin 1993; Cockerham and Weir 1993). Because G_{ST} is bounded positive and has a lower variance than θ, estimates of $\hat{M}_{GST}$ correlate slightly more strongly with separation than do estimates of $\hat{M}_{\theta}$, especially when $\hat{M}$ levels of gene flow are high (Hellberg 1995). In contrast, θ is unbiased but may go negative when gene flow is high. In these instances, its inverse function $\hat{M}$ will be undefined. I estimated the shortest nautical distance between localities from 24,000:1 and 1,000,000:1 scale maps.

I used ordinary least-squares (OLS) regression, with degrees of freedom adjusted to the number of populations sampled (not the number of pairwise comparisons), to determine whether the slope of the regression was different from zero. The significance of the relationship between log ($\hat{M}$) and log (distance of separation) could not be evaluated using standard regression techniques, as the regression is based on nonindependent, pairwise comparisons. The confidence intervals of these adjusted OLS regressions are identical (to two decimal places) to confidence intervals from Mantel's test (Hellberg 1994). These confidence intervals were also used to determine whether the relationship between gene flow and distance differed between the two species.

Asymmetric 95% confidence intervals about the slope of reduced major axis (RMA) regressions were calculated following McArdle (1988), using degrees of freedom appropriate for the number of populations sampled. RMA regression better estimates the relationship between gene flow and proximity than does OLS regression when geographic distance approximates the number of dispersal steps between populations (Hellberg 1994). OLS regression underestimates the slope of the regression in such cases because OLS regression assumes the independent variable (the number of dispersal steps separating populations in this case) is measured without error. However, RMA regression coefficients by their definition cannot equal zero, so the OLS regression is more appropriate for significance testing.

I calculated expected heterozygosities (Nei 1978) at each locality using allele frequency data for each locus, and then averaged over the six loci surveyed, using BIOSYS (Swofford and Sëlander 1989).

Results

The six loci surveyed in *P. stearnsii* were highly polymorphic in all localities sampled (Appendix). The average heterozygosity within localities was 0.43 (SD = 0.030). Bootstrapped 95% confidence intervals were significantly greater than zero for F_{ST}, but not F_{IT} or F_{IS} (Table 1), indicating a small, but significant heterozygote deficit between localities, but no deviation from panmixia within localities. F_{ST} appeared concordant across marker loci, although *Hk* was (nonsignificantly) negative. The mean F_{ST} of 0.0039 is equivalent to over 60 immigrants arriving at each locality per generation.

The Appendix also lists allele frequencies for the two localities from which *B. elegans* had not previously been sampled. Allele frequencies for the remaining ten populations, and for the 26 additional populations refered to below, are published elsewhere (Hellberg 1994, 1995). In contrast to the weak genetic subdivision evident in *P. stearnsii, B. elegans* exhibited strong subdivision both within and among populations (Table 2). The mean F_{ST} for *B. elegans* (= 0.20) is equivalent to genetic homogenization resulting from one immigrant per generation.

Simulations show $\hat{M}$ and geographic separation should be inversely correlated (slope = -1.0) in linearly distributed populations obeying the assumptions of the stepping stone model (Slatkin and Maddison 1990; Slatkin 1993; Hellberg 1994). For *B. elegans* sampled from the same twelve localities as *P. stearnsii,* the OLS regression between log ($\hat{M}$) and log (distance of separation) was significant ($P < 0.001$) and distance explained 31% of the variation in levels of gene flow (Fig. 2). However, the relationship was generally weaker than

TABLE 1. Weir and Cockerham (1984) estimates of Wright's *F*-statistics calculated separately for each locus for *Paracyathus stearnsii* collected from 12 localities. Means and standard errors were obtained by jackknifing over loci. Confidence intervals were obtained by bootstrapping over loci.

Locus	$F = F_{IT}$ (within total)	$\Theta = F_{ST}$ (among localities)	$f = F_{IS}$ (within localities)
Hk	−0.0362	−0.0006	−0.0036
Pgi	−0.0117	0.0027	−0.1212
Tpi	0.1185	0.0118	0.1080
Pep	0.0445	0.0044	0.0403
Aat-1	0.0948	0.0016	0.0933
Aat-2	0.0067	0.0095	−0.0028
Mean	−0.0161	0.0039	−0.0201
Standard error	0.0374	0.0018	0.0368
95% confidence interval	−0.0734–0.0615	0.0012–0.0079	−0.0756–0.0549

the inverse relationship expected for a linear stepping stone (Table 3). Although the three closest pairwise comparisons in the regression based on *B. elegans* from the twelve common localities largely determined the significance of the relationship between $\hat{M}$ and distance, these three values were typical for populations separated by these distances (Hellberg 1995). Including 26 additional localities from which only *B. elegans* was sampled resulted in a nearly identical RMA regression and even stronger association ($r^2 = 0.60$) between $\hat{M}$ and distance (Table 3).

In the planktonically dispersed *P. stearnsii,* inferred gene flow showed no obvious relationship with distance of separation (Fig. 2, Table 3). The RMA slope of log ($\hat{M}_\theta$) versus log (distance of separation) was −1.19 (−0.37 for $\hat{M}_{GST}$), however these regression coefficients overestimate the actual relationship whenever correlations are very weak, as the RMA regression slope is calculated using a ratio of variances and therefore cannot equal zero. OLS squares regression, more appropriate for significance testing, clearly revealed a nonsignificant relationship between log ($\hat{M}$) and log (distance), with 95% confidence intervals that included zero. Distance explained only a very small proportion of the variance in gene flow between populations of *P. stearnsii.* Because gene flow in *P. stearnsii* was so high, θ went negative for 18 of the 66 pairwise comparisons. As a result, the test for interspecific differences in OLS regression slopes based on θ was very conservative and proved insignificant. Regression slopes based on $\hat{M}_{GST}$ (in which both species have values for all pairwise comparisons) differed interspecifcally (Table 3).

DISCUSSION

Balanophyllia elegans and *Paracyathus stearnsii* possess larvae that differ in dispersal capability. Consequently, dependence of gene flow on geographic distance should differ between these two corals. The data shown in Figure 2 and summarized in Table 3 support this expectation. The inferred levels of gene flow between populations of *B. elegans,* which possesses crawling planulae (Gerrodette 1981; Fadlallah 1983a), declined significantly with increasing distance of separation. However, in *P. stearnsii,* whose larvae disperse planktonically (Fadlallah and Pearse 1982a), distance explained almost none of the variation in inferred gene flow between pairs of populations (Table 3). The relationship between gene flow and geographic distance differed between these two species when $\hat{M}$ was estimated using Nei's G_{ST} (Table 3), despite the high uncertainties associated with pairwise estimates of gene flow (Cockerham and Weir 1993). Interspecific differences in regression slopes were not significant when $\hat{M}$ was estimated using Weir and Cockerham's θ, however the variance in estimates of gene flow based on θ is greater than those based on G_{ST} (Cockerham and Weir 1993), so this comparison was less powerful.

The different relationships between inferred gene flow and geographic separation in these two scleractinians could conceivably result from processes other than larval dispersal. These alternatives include the following: (1) selection acting on the genetic markers used to infer gene flow; (2) conflation of locality-specific and species-specific variation; and (3) species-specific biological differences other than larval dispersal.

TABLE 2. Weir and Cockerham (1984) estimates of Wright's *F*-statistics calculated separately for each locus for *Balanophyllia elegans* collected from 12 localities. Means and standard errors were obtained by jackknifing over loci. Confidence intervals were obtained by bootstrapping over loci.

Locus	$F = F_{IT}$ (within total)	$\Theta = F_{ST}$ (among localities)	$f = F_{IS}$ (within localities)
Hk	0.3013	0.2078	0.1181
Pgm	0.2690	0.2659	0.0042
Pgi	0.1962	0.1382	0.0673
Tpi	0.1637	0.1573	0.0077
Pep	0.2749	0.2957	−0.0296
Aat	0.3098	0.2767	0.0458
Lap	0.1162	0.1058	0.0116
Mean	0.2199	0.1953	0.0306
Standard error	0.0382	0.0363	0.0176
95% confidence interval	0.1650–0.2840	0.1422–0.2624	0.0034–0.0698

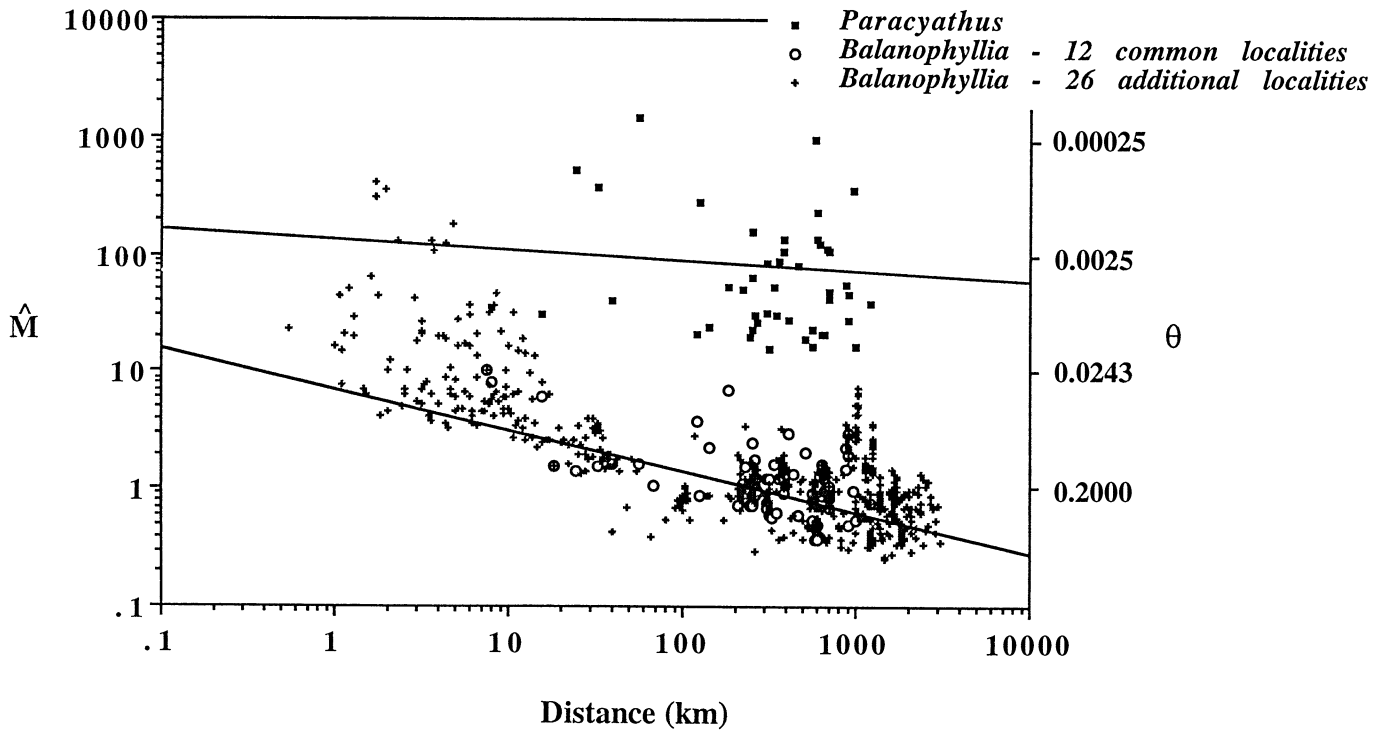

FIG. 2. Ordinary least-squares (OLS) regressions of inferred gene flow ($\hat{M}$, individuals/generation) versus geographical distance of separation (km) for all pairwise combinations of 12 localities of *Paracyathus stearnsii* (closed squares) and *Balanophyllia elegans* (open circles). Pairwise comparisons for *B. elegans,* which include an additional 26 localities (crosses), are also shown (no line shown). Axes are logarithmically scaled. See Table 3 for regression equations. $\hat{M}$ was based on an average of six or seven electrophoretically polymorphic enzyme loci, respectively, as estimated by θ (Weir and Cockerham, 1984). One point for *P. stearnsii* ($\hat{M}_\theta$ = 12,883 at 564 km) does not appear, but was included in regression calculations. Eighteen pairwise comparisons for *P. stearnsii* resulted in negative θs (and thus undefined $\hat{M}_\theta$) and were excluded from the regression.

Natural selection on allozyme markers does not appear to have created the contrasting patterns of genetic structure in the two corals. Variation among loci within each species does not implicate strong selection because patterns of subdivision revealed by hierarchical *F*-statistics (Table 2) are largely concordant across loci in *B. elegans. Paracyathus stearnsii* likewise shows general concordance across loci, with all loci except *Hk* exhibiting slight heterozygote deficits among localities (Table 1). Excluding *Hk* (or any other single allozyme marker) from the regression analysis did not significantly alter the relationship between $\hat{M}$ and distance in *P. stearnsii*: slopes remained insignificant and r^2 was never greater than 2.4% (results not shown). Balancing selection might conceivably homogenize the allele frequencies I found at different localities (Karl and Avise 1992), however, such balancing selection would have to be far stronger within *P. stearnsii* than within *B. elegans* to account for the differences I reported.

Interspecific differences in the relationship between gene flow and distance could be confounded with differences spe-

TABLE 3. Ordinary least squares (OLS) and reduced major axis (RMA) regression equations of log ($\hat{M}$) as a function of log (distance) for *Paracyathus stearnsii* and *Balanophyllia elegans.* $\hat{M}$ was calculated using both Θ (Weir and Cockerham 1984) and G_{ST} (Nei 1973). Regressions for *B. elegans* were calculated separately for 12 populations from which *P. stearnsii* was also sampled, and for 38 populations, which included 26 additional localities.

		OLS				RMA	
	N	Intercept	Slope	Slope 95% CI*	r^2	Slope	Slope 95% CI
$\hat{M}_\Theta$							
P. stearnsii	12	2.089	−0.106	$-0.498 \le b \le 0.286$	0.008	−1.191**	$-0.62 \le v \le -2.29$
B. elegans	12	0.881	−0.325	$-0.191 \le b \le -0.459$	0.311	−0.582	$-0.33 \le v \le -1.01$
	38	1.197	−0.431	$-0.405 \le b \le -0.457$	0.603	−0.554	$-0.45 \le v \le -0.68$
$\hat{M}_{GST}$							
P. stearnsii	12	1.527	−0.042	$-0.145 \le b \le 0.061$	0.013	−0.372**	$-0.19 \le v \le -0.56$
B. elegans	12	1.107	−0.302	$-0.175 \le b \le -0.429$	0.308	−0.541	$-0.31 \le v \le -0.94$
	38	1.353	−0.387	$-0.365 \le b \le -0.409$	0.631	−0.487	$-0.40 \le v \le -0.60$

* CI based on $N - 2$ df, not on the total number of pairwise comparisons.
** RMA estimates of slope become unreliable where OLS slopes are not significantly different from zero.

cific to particular sampled localities if the two species were not collected from the same places. For example, if only one of the species had been collected from a locality unusual in its selective environment, then inferred levels of gene flow between this unusual locality and others could be either inflated or deflated by selection on the allozyme markers themselves (directly altering the frequencies of the markers used to infer gene flow), or on the success of incoming migrants (altering the actual pattern of genetic exchange). This selective effect would influence the relationship between gene flow and distance for one species, but not the other. Inferred gene flow also might differ among equidistant localities due to unequal levels of either past or present-day gene flow due to corridors (e.g. currents) or barriers (e.g. headlands, unsuitable habitat) to dispersal. I collected samples of both species from the same twelve localities, usually on the same dive, and often within centimeters of each other. The possibility remains that differences between alternative sets of localities differentially affect the two species, so that the relationships between gene flow and distance reported here could vary for other sets of localities. However, including 26 additional sites for *Balanophyllia elegans* showed that the relationship between gene flow and distance revealed by the twelve localities considered here were typical for this species (Fig. 2).

Ideally, comparisons of the genetic consequences of different modes of larval dispersal would not only sample the same localities and use the same genetic markers, but would contrast sister taxa that differed solely in their mode of larval development. Although *P. stearnsii* and *B. elegans* belong to different families, the Caryophylliidae and Dendrophylliidae respectively, larval dispersal characteristics vary little within the dendrophylliid clade. As far as is known, all members of the genus *Balanophyllia* (Gerrodette 1981; Kinchington 1981; Fadlallah 1983a), and some members of its probable sister group, *Tubastrea* (Babcock et al. 1986), release only crawling larvae. Indeed, most dendrophylliids brood nonfeeding planulae (Fadlallah 1983b). Thus, it was necessary to look outside the species most closely related to *B. elegans* for a comparison to planktonically dispersing larvae. *Paracyathus stearnsii* and *B. elegans* differ in many aspects of their life histories (Gerrodette 1981; Fadlallah and Pearse 1982a,b; Fadlallah 1983a), as well as in their aggressiveness (Chadwick 1991). But beyond the difference in mode of larval dispersal, these differences would not obviously modify their genetic structure.

Two types of evidence support the hypothesized correlation between levels of gene flow and mode of larval development. First, species with philopatric larvae exhibit greater capacity for adaptive change to geographically variable selective regimes (Vermeij 1982; Janson 1983; Behrens Yamada 1989) than do species with larvae that spend long periods in the plankton (Strathmann et al. 1981). Second, geographic surveys of allozyme markers consistently indicate lower levels of average gene flow in species with limited larval dispersal than in closely related, co-occurring taxa possessing broadly dispersed larvae (Berger 1973; Janson 1987; Waples 1987; Duffy 1993; Hunt 1993).

Although the magnitude of gene flow (the number of immigrants) differs among species possessing different larval dispersal potential, several lines of evidence suggest that the association between gene flow and geographic distance may not vary as dramatically among such taxa. First, species with limited larval dispersal may sometimes disperse to distant (nonadjacent) populations by rafting of adults (Highsmith 1985; Jokiel 1991). Second, many clades do not conform to the generalized correlation between larval dispersal and geographic range (Jackson 1986; O'Foighil 1989; Vermeij et al. 1990). Likewise, species with feeding larvae do not necessarily make better colonizers (Johannesson 1988). Furthermore, several mechanisms may geographically restrict gene flow affected by the dispersal of planktonic larvae, including larval behavior (Burton and Feldman 1982), postsettlement mortality (Koehn et al. 1976; Johnson and Black 1984; Hedgecock 1986), and passive transport mediated by coastal geography and currents (Berglund and Lagercrantz 1983; Ebert and Russell 1988; Bertness and Gaines 1993), so that levels of gene flow, although large relative to species with nonfeeding larvae, might nonetheless decline with increasing separation between populations.

Patterns of DNA sequence variation further support the notion that planktotrophic species may not disperse as broadly as once thought. Geographic variation in mtDNA (Reeb and Avise 1990) and scnDNA (Karl and Avise 1992) among Atlantic populations of the American oyster (*Crassostrea virginica*) suggest gene flow may be geographically restricted despite the apparent wide dispersal capabilities of this species' pelagic larvae. However, this strong genetic differentiation may stem in part from the recent hybridization of populations formerly isolated during Pleistocene climatic fluctuations, which apparently divided many marine species currently inhabiting the southeastern coast of the United States (Bert 1986; Reeb and Avise 1990; Cunningham et al. 1992). Along the Pacific Coast of North America, the few studies of molecular variation to date agree with the conclusions reached here. The brooding tidepool copepod *Tigriopus californicus,* a limited disperser, exhibits geographically concordant patterns of mitochondrial and nuclear sequence variation that, in addition to revealing a phylogenetic break not apparent from allozyme data, evince a close association between genetic similarity and geographic proximity (Burton and Lee 1994). In contrast, geographic surveys of the planktonically dispersed urchin *Strongylocentrotus purpuratus* have revealed no evidence of a dependence of gene flow on distance (Palumbi and Wilson 1990). The planktonically dispersed sea cucumber *Cucumaria miniata* exhibits high mtDNA haplotype diversity and no evidence for population structure over a broad geographic range, while a single common haplotype tends to dominate in populations of its congeneric brooder *C. pseudocurata* (A. Arndt, pers. comm. 1995).

If, as seems likely then, the different patterns of genetic change with distance in *P. stearnsii* and *B. elegans* truly reflect differences in the dispersal capabilities of their respective larvae, then mechanisms generating geographic diversity within similar species should vary depending on their mode of development. Assuming that proximate populations inhabit more similar selective regimes than do distant populations and that these selective conditions remain constant over time (Bell 1992), the progeny of species with geographically limited dispersal should experience a pattern of selection similar to those of their parents. Additionally, most im-

migrants will genetically resemble residents, further facilitating the accumulation of locally differentiated genotypes over generations (Janson 1983, Behrens Yamada 1989). These differences may become so great that further genetic exchange is curtailed, and increasing differentiation may result (Burton 1987).

In contrast, the offspring of species with broad, geographically unbiased dispersal will commonly find themselves in selective environments quite different from those of previous generations. In obligately sexual species with planktonic larval dispersal, then, adaptive differentiation among populations will require either strong postsettlement selection each generation (Koehn et al. 1976; Johnson and Black 1984; Hilbish 1985; Hedgecock 1986; Watts et al. 1990), or physical barriers (such as inlets) that partially isolate populations (Berglund and Lagercrantz 1983; Bertness and Gaines 1993).

The data presented here strongly suggest that different modes of larval development result in qualitatively different relationships between the magnitude of gene flow and geographic distance (see Shaffer 1984, for a terrestrial analog). These differences imply that geographic differentiation in genetic characters is established by different mechanisms in species with different larval dispersal capabilities. Studies that simultaneously estimate gene flow between localities (and around barriers) and measure local adaptive differences between these same localities (e.g., Stearns and Sage 1980) are needed to define more soundly the evolutionary consequences of different life-history patterns in benthic marine invertebrates.

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APPENDIX. Allele frequencies for 12 localities of *Paracyathus stearnsii* and two localities of *Balanophyllia elegans*. Localities are listed left to right in descending southward order. For *P. stearnsii*, alleles are numbered to indicate percent mobility relative to the most common allele at that locus. For *B. elegans*, alleles are numbered to indicate mobility relative to the most common allele from Santa Cruz. Alleles with the same number from different species do not have the same mobility. *N* = number of individuals per locality.

		P. stearnsii													*B. elegans*	
Locus	Allele	Locality *N*	TRH 28	HSH 53	NER 52	PFR 46	BOD 47	MON 38	CMB 11	SIM 24	GOL 57	EAN 33	SBI 29	PLK 24	Locus	Allele	CMB 32	SBI 32
Hk	104						0.011	0.079			0.018		0.034	0.021	*Hk*	113	0.016	
	100		0.643	0.651	0.577	0.478	0.553	0.618	0.618	0.604	0.553	0.652	0.552	0.521		106		0.047
	93		0.107	0.113	0.106	0.087	0.106	0.066	0.091	0.104	0.167	0.061	0.103	0.063		100	0.890	0.609
	88		0.196	0.170	0.221	0.293	0.234	0.184	0.227	0.208	0.184	0.212	0.207	0.333		93	0.094	0.344
	79		0.054	0.066	0.077	0.130	0.074	0.053	0.136	0.063	0.079	0.076	0.103	0.063	*Pgm*	100	0.047	0.328
	70				0.019	0.011	0.021									91	0.906	0.672
	67									0.021						78	0.047	
Pgi	264				0.010										*Pgi*	100	0.453	0.641
	230					0.022			0.045	0.042				0.042		85	0.547	0.359
	185		0.161	0.255	0.183	0.174	0.128	0.145	0.045	0.125	0.158	0.197	0.155	0.188				
	141		0.196	0.255	0.279	0.283	0.266	0.237	0.182	0.333	0.228	0.197	0.328	0.167				
	100		0.643	0.462	0.490	0.478	0.574	0.461	0.591	0.438	0.553	0.545	0.466	0.563				
	68			0.028	0.038	0.043	0.032	0.158	0.091	0.063	0.061	0.061	0.052	0.042				
	18								0.045									
Tpi	126		0.089	0.038	0.019	0.022	0.064	0.158		0.021	0.009		0.052	0.042	*Tpi*	100	1.000	1.000
	100		0.893	0.887	0.933	0.870	0.862	0.776	0.909	0.958	0.904	0.909	0.931	0.875				
	71					0.011												
	68		0.018	0.057	0.038	0.087	0.074	0.053	0.091	0.021	0.070	0.076	0.017	0.083				
	32			0.019	0.010	0.011		0.013			0.018	0.015						
Pep-la	125		0.018							0.021				0.021	*Pep*	102		0.094
	117		0.107	0.113	0.096	0.065	0.085	0.053	0.045	0.083	0.079	0.106	0.017	0.042		100	0.828	0.859
	113		0.161	0.170	0.202	0.185	0.106	0.158	0.091	0.250	0.228	0.227	0.241	0.146		97		0.016
	100		0.518	0.585	0.606	0.663	0.670	0.724	0.818	0.521	0.640	0.545	0.655	0.646		92	0.172	0.031
	97		0.143	0.085	0.058	0.043	0.053	0.013	0.045	0.021	0.026	0.030		0.146				
	90		0.054	0.028		0.033	0.074	0.053		0.083	0.026	0.045	0.017		*Lap*	111	0.640	0.594
	79			0.019	0.038	0.011	0.011			0.021		0.030	0.052			106	0.172	0.234
	71											0.015	0.017			100	0.188	0.125
																96		0.047
Aat-1	114		0.054	0.009	0.019	0.022	0.032	0.039	0.045	0.042	0.026	0.030	0.034	0.021	*Aat*	100		0.547
	100		0.875	0.915	0.933	0.978	0.957	0.868	0.909	0.917	0.921	0.894	0.897	0.979		92	0.063	
	81		0.071	0.075	0.048		0.011	0.092	0.045	0.042	0.053	0.076	0.069			82	0.937	0.453
Aat-2	154				0.019	0.022	0.021					0.015						
	131				0.058	0.022	0.096	0.039	0.045	0.104	0.044	0.106	0.052	0.063				
	122		0.214	0.142	0.048	0.228	0.117	0.132	0.045	0.167	0.175	0.061	0.052	0.063				
	100		0.768	0.736	0.798	0.663	0.723	0.750	0.818	0.688	0.675	0.758	0.810	0.833				
	84			0.123	0.058	0.065	0.043	0.066	0.091	0.042	0.105	0.061	0.086	0.042				
	22		0.018		0.019			0.013										