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Habitat continuity and geographic distance predict population genetic differentiation in giant kelp

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Abstract. Isolation by distance (IBD) models are widely used to predict levels of genetic connectivity as a function of Euclidean distance, and although recent studies have used GIS-landscape ecological approaches to improve the predictability of spatial genetic structure, few if any have addressed the effect of habitat continuity on gene flow. Landscape effects on genetic connectivity are even less understood in marine populations, where habitat mapping is particularly challenging. In this study, we model spatial genetic structure of a habitat-structuring species, the giant kelp *Macrocystis pyrifera*, using highly variable microsatellite markers. GIS mapping was used to characterize habitat continuity and distance between sampling sites along the mainland coast of the Santa Barbara Channel, and their roles as predictors of genetic differentiation were evaluated. Mean dispersal distance (σ) and effective population size (N_e) were estimated by comparing our IBD slope with those from simulations incorporating habitat continuity and spore dispersal characteristics of the study area. We found an allelic richness of 7–50 alleles/locus, which to our knowledge is the highest reported for macroalgae. The best regression model relating genetic distance to habitat variables included both geographic distance and habitat continuity, which were respectively, positively and negatively related to genetic distance. Our results provide strong support for a dependence of gene flow on both distance and habitat continuity and elucidate the combination of N_e and σ that explained genetic differentiation.

Key words: connectivity; effective population size; GIS; habitat continuity; isolation by distance; kelp; Macrocystis pyrifera; *marine dispersal; microsatellites; population genetics.*

Introduction

Knowledge of spatial patterns of genetic differentiation of populations is key to understanding processes ranging from evolutionary mechanisms of differentiation to the ecological or conservation consequences of loss of genetic diversity (Manier and Arnold 2006). The roots of such knowledge largely emanate from the work of Wright (1943) on isolation by distance (IBD) and its relationship to dispersal ability and other life history attributes (Bohonak 1999). The two general models that have emerged from this work are the island model (Wright 1943) and the stepping stone model (Kimura and Weiss 1964). These models have been thoroughly compared (Palumbi 2003), but from an ecological and conservation viewpoint the most important difference between the two is that geographic distance and population genetic differentiation are expected to increase together, under some proportional function, in the stepping stone model. This expectation occurs because in natural populations migration is often greater between patches that are near each other (Slatkin 1987). This idea has profound implications for many disciplines in biology, especially conservation biology, where a comprehensive understanding of the effects of habitat corridors, barriers, patch size and spacing on population connectivity and persistence is needed for informed and effective management.

The spatial structure of genetic differentiation is commonly modeled using Euclidean distance as a proxy for population connectivity. Recently, with the advent of landscape genetics (Manel et al. 2003), there has been an effort to formally incorporate landscape variables into analyses of population genetic structure for a variety of terrestrial plants and animals (for a review, see Storfer et al. 2007). Several recent studies have used GIS-landscape ecological approaches to quantify habitat features that relate to population connectivity (Michels et al. 2001, Spear et al. 2005, Epps et al. 2007). These studies have mostly shown that environmental and ecological distances are better predictors of genetic differentiation between populations than simple geographic distances, or revealed cryptic environmental barriers to gene flow. Surprisingly, few if any studies have used a GIS spatial framework to address the effect of population size and

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FIG. 1. *Macrocystis pyrifera* floating canopy (upper panel) allows the remote detection of patch structure and habitat continuity using GIS analysis of SPOT satellite images (lower panel used by permission; CNES 2005, distributed by Terra Image USA, LLC and SPOT IMAGE).

habitat continuity on gene flow, yet these are fundamental parameters needed to examine gene flow using a metapopulation framework.

Studies that have incorporated habitat continuity are almost entirely in non-marine habitats (for exceptions see Riginos and Nachman 2001, Billot et al. 2003, Storfer et al. 2007, Leclerc et al. 2008). The challenges associated with habitat mapping in most marine systems undoubtedly contribute to this bias. One marine habitat that is suitable for such a study is giant kelp (*Macrocystis pyrifera*) forests which form a narrow band that fringes the shoreline along the Pacific coast of temperate North and South America. GIS distribution data for giant kelp and other marine species have been available for years, yet the theoretical expectations linking population size and habitat continuity with genetic differentiation have never been empirically explored.

Macrocystis, the world's largest alga, grows on rocky reefs in shallow waters (5–30 m water depth) worldwide (Wormersley 1954). Unlike most species of marine algae, its fronds extend through the water column and form a dense canopy at the seawater surface that is detectable from the air (Fig. 1), making it one of the few marine species whose adult populations are routinely geo-referenced (Reed et al. 2006). Although subtidal rocky habitats often have three-dimensional components, the presence of adult *Macrocystis* populations fundamentally alters the habitat by providing complexity throughout the entire water column, enhancing local diversity, productivity, and ecosystem structure and function (Dayton 1985, Graham 2004, Graham et al. 2007).

In this study, we took advantage of explicit GIS habitat mapping of *Macrocystis pyrifera* along the mainland coast of the Santa Barbara Channel, California and the recent development of highly polymorphic loci (Alberto et al. 2009) to evaluate the roles of habitat continuity and spatial distance as predictors of population genetic differentiation, a proxy for gene flow connectivity. Our analyses revealed a high dependence on both factors. We also estimated dispersal and effective population size using a genetic based simulation model. These results were compared to dispersal estimates derived from empirical and theoretical dispersal models (Reed et al. 2004, 2006, Gaylord et al. 2006), revealing high consistency in dispersal estimates across genetical, empirical, and theoretical approaches.

METHODS

Macrocystis life history and constraints on gene flow

The kelp life history has unique implications for population connectivity, namely an alternation of generations between macroscopic diploid sporophytes, producing haploid spores, and microscopic haploid gametophytes, producing gametes. Spore dispersal, the primary dispersive stage, lasts hours to days and occurs over transport distances ranging from meters to kilometers (Reed et al. 1992, Gaylord et al. 2002). Following dispersal spores settle on the bottom and germinate into microscopic male and female gametophytes. Thus, in contrast to most marine organisms, fertilization in kelps occurs after dispersal. A pheromone released by female gametophytes triggers the liberation of sperm from male gametophytes and guides the sperm to the non-motile egg, a process believed to be effective at distances <1 mm (Boland et al. 1983). Consequently, sporophyte recruitment is largely confined to areas of relatively dense spore settlement (approximately >1 spore/mm^2), with high probability of sperm–egg encounters to ensure fertilization (Reed et al. 1991). Thus, spore dilution is a major constraint limiting kelp dispersal distances over, non-colonized habitat, a constraint that decreases with increasing size of the source population (Anderson and North 1966, Reed et al. 1997). In addition to spore dispersal, gene flow in *Macrocystis* may occur over larger distances via the transport of large fertile sporophytes that become dislodged and set adrift (Hobday 2000).

Sample collection and study area

Samples were collected in July 2006 at nine sites along the mainland coast of the Santa Barbara Channel in southern California (Fig. 2), these sites have been regularly monitored since 2001 by the Santa Barbara Coastal Long Term Ecological Research project. Approximately 50 sample units, each constituted by a single *Macrocystis* blade, were collected haphazardly from

different individuals separated by at least 2 m. A 2-cm^2 section was excised from the blade, carefully cleaned and preserved in silica drying crystals.

Microsatellite amplification and scoring

Genomic DNA was extracted with the NucleoSpin 96 Plant Kit (Macherey-Nagel, Düren, Germany). All individuals were genotyped for 12 microsatellite loci, for which PCR reactions using forward 5′ fluorochrome labeled primers on a GeneAmp 9700 thermocycler (Applied Biosystems, Foster City, California, USA) are described in Alberto et al. (2009). Fragment length was analyzed on an ABI PRISM 3130 DNA analyzer (Applied Biosystems) using the GeneScan-500 LIZ standard. Raw allele sizes were scored with STRand (program *available online*)[6] and binned into allele classes using the R package msatAllele (Alberto 2009).

Genetic analyses

Factorial correspondence analysis (AFC, implemented using GENETIX [Belkhir et al. 2001]) was used to visualize the levels of genetic differentiation among the giant kelp forests sampled along the Santa Barbara coast. A synthetic map illustrating the geographic variation of the first axis of the AFC was generated with the image function of R (R Development Core Team 2008).

Departure from Hardy-Weinberg equilibrium was assessed with the inbreeding coefficient F_{IS}, estimated with f (Weir and Cockerham 1984), followed by a probability test of the null hypothesis of random union of gametes (H_0: $F_{IS} = 0$; Rousset and Raymond 1997). Levels of differentiation were described by the F_{ST} estimator θ (Weir and Cockerham 1984), and significant departures from H_0 of no differentiation were tested for with an appropriate Fisher exact test using GENEPOP 4 (Rousset 2008). The hypothesis of isolation-by-distance (IBD; Wright 1943, Rousset 2001), the increase of genetic differentiation with distance, was analyzed by the regression between pairwise estimates of differentiation, as $F_{ST}/(1 - F_{ST})$, and linear distance between sites. A Mantel test provided by the ISOLDE routine in GENEPOP 4.0, was used to test the null hypothesis of no correlation between genetic and geographical distances between populations. The analysis was repeated with F_{ST} estimates corrected for the presence of null alleles because when null allele frequency is high, genetic differentiation (F_{ST}) is expected to be overestimated. The ENA method, implemented by the software FreeNA (Chapuis and Estoup 2007), was thus used to estimate the F_{ST} matrix corrected for null alleles.

Spatial sampling

We used the California Department of Fish and Game kelp cover GIS layer to estimate habitat continuity and geographic distance among pairs of sites (GIS layer data *available online*).[7] This data layer is a composite of annual data from 1988 to 2003 and represents the maximum extent of kelp habitat in the study region during a time period that is relevant to our study. The stretch of coastline sampled is a nearly linear east-west feature with kelp habitat occurring as a series of discrete patches along the coast (see Fig. 2). Using this GIS database, we generated a matrix of geographic distances between all pairs of sites and a matrix of estimates of the area of kelp in hectares per kilometer of linear coastline between all pairs of sites, which we considered to be an estimate of habitat continuity.

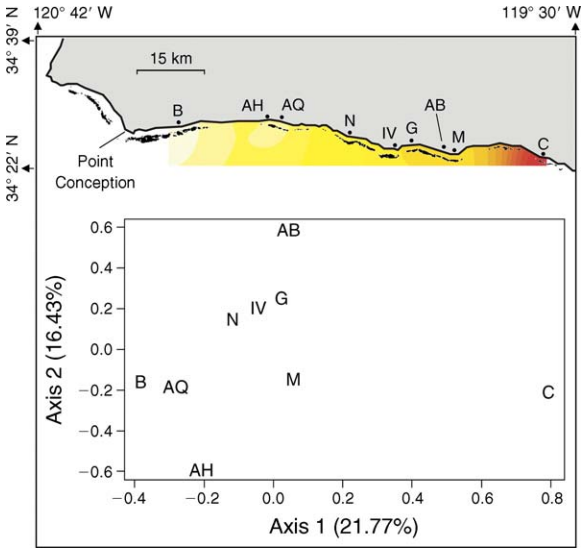

FIG. 2. Synthetic map illustrating genetic differentiation of *Macrocystis pyrifera* along the mainland coast of the Santa Barbara Channel. Colors represent the position of each spatial location along the first axis of a factorial correspondence analysis (AFC) of microsatellite alleles (shown below the map). Points indicate collection sites; sample codes are detailed in Appendix A. The surface canopy of giant kelp, as detected by aerial infrared photography in 2003, is shown to illustrate the level of habitat continuity of giant kelp forests in our study area.

Relating genetic distance to habitat continuity

We used a multiple regression approach to assess models linking geographical distance and habitat continuity to genetic distance. Unlike approaches that aim at relating two main matrices of interest while controlling for the effects of other variables, as in partial Mantel tests, our regression approach is well suited for assessing the additive contribution of independent factors (here geographic distance and habitat continuity) on genetic distance as the dependent variable (Manier and Arnold 2006). The key assumptions of multiple regression analysis were met: (1) bivariate normality

[6] ⟨http://www.vgl.ucdavis.edu/informatics/strand.php⟩

[7] ⟨http://www.dfg.ca.gov/biogeodata/gis/mr_nat_res.asp⟩

(tested using residual analysis), (2) linear relationships between both independent factors and genetic distance (tested using single factor regressions) and (3) non-colinearity between the independent factors (tested using tolerance values and condition indices). Four model outcomes were possible: lack of fit for any model, only geographic distance was explanatory, only habitat continuity was explanatory, both geographic distance and habitat continuity were explanatory. Model selection followed the relative Akaike Information Criterion, R-AIC (Burnham and Anderson 1998).

Dispersal and effective population size

To better understand the relationship between effective dispersal, effective population size, and IBD, we conducted simulations aimed at estimating the combinations of parameter values that yielded an estimate similar to our empirically observed IBD slope. This relationship was estimated using population simulations based on empirically observed values for habitat continuity and allelic diversity (our data), and maximum dispersal and dispersal distribution shape parameters fitted to represent the current velocities that are found in these kelp beds (from Reed et al. 2006) and varying effective population sizes. The approach of comparing empirically derived IBD slopes with those predicted by simulations has been used before (Kinlan and Gaines 2003, Palumbi 2003); here we extend it by simulating much more realistic scenarios where we include multiple alleles, fragmented habitat, different dispersal distribution parameters and different population sizes with the use of a recently developed software IBDsim (Leblois et al. 2009).

IBDsim uses a coalescent algorithm to derive various IBD models with continuous or discrete subpopulations. The simulated metapopulation was represented in a one-dimension lattice population model, each node representing one km of coast. Habitat continuity in the study area was simulated by including empty nodes in the lattice in areas where GIS analyses showed no historical presence of kelp. Spore dispersal distribution was modeled using a truncated variant of the discrete Pareto, with the probability of moving k steps in one direction depending on M, the dispersal probability, and on n, the kurtosis (Leblois et al. 2009). M and n were fitted to represent the dispersal distributions of spores under four scenarios of ocean current velocity observed by Reed et al. (2006) in the study region. Scenarios with higher and more variable current velocities were simulated with higher dispersal probability (M) and lower kurtosis (n). The number of alleles allowed in the model was 20 (the average number of alleles observed) and a generalized stepwise mutation (GSM) model with a 1×10^{-3} mutation rate was chosen. For each current velocity scenario, we conducted three replicates of 110 simulations with variable population size (22 values from 50 to 2500) and variable maximum dispersal distance (five values from 12 to 20 km) consistent with Gaylord et al. (2002). Population size here represents the effective population size, given IBDsim assumes Hardy–Weinberg equilibrium within each node. Each combination of dispersal distribution (set by M and n) and maximum dispersal defines a mean per generation parent-offspring distance (sporophyte to sporophyte), hereafter called mean dispersal distance, σ. In the case of *Macrocystis*, σ represents the mean distance travelled by spores that contribute genes to the next sporophyte generation.

Results

Genetic diversity

The microsatellite loci used to genotype *Macrocystis pyrifera* samples from the Santa Barbara Channel revealed high levels of genetic diversity. The total number of alleles observed per locus ranged from 7 to 50, and on a single population from 2 to 27 at locus Mp-BC-8 and Mpy-17, respectively. Allelic richness, standardized for equal sample size for inter-site comparisons at each locus, was very similar across sites and ranged from 10.55 to 11.32, at Bulito and Mohawk respectively (see Appendix A). Null alleles were present, as indicated by MICROCHECKER analyses (Van Oosterhout et al. 2004) and suspected from the observation of loci that failed to amplify on some samples even when many independent reactions were attempted. The loci suspected to have null alleles and having F_{IS} values higher than expected under Hardy-Weinberg equilibrium, were not consistent, across populations with the exception of three loci more severely affected than others (see Appendix B). Mean F_{IS} across populations was high (0.166), but decreased considerably (to 0.092) when these three loci thought to be more influenced by null alleles were removed.

Isolation by distance and habitat continuity

A congruent pattern between geographic origin and genetic relationship was revealed by the factorial correspondence analysis; the gradation of spatial genetic differentiation is well represented by the first axis of this AFC (synthetic interpolated area in Fig. 2). A steep increase in genetic differentiation was observed in the eastern portion of the study area between Mohawk and Carpinteria, corresponding to an area with low kelp abundance between these sites (Fig. 2). Global and pairwise genetic differentiation levels (see Appendix C) were low but significant ($P < 0.001$). Global F_{ST} estimates were approximately the same when using the ENA correction method (0.021) as when using the original data (0.022). This correction did not affect the isolation by distance slope value of 0.0003 (Fig. 3A), nor the fit of the regression model of genetic differentiation with geographical distance $r^2 = 0.325$. Reducing the data set from 12 to 9 loci to remove those most affected by null alleles did not change the IBD slope, but it did decrease the fit of the regression to $r^2 = 0.25$. Accordingly, the best model relating genetic distance to habitat variables included both geographic distance, which was positively

related to genetic distance, and habitat continuity, negatively correlated with genetic distance (see Appendix D; Fig. 3A, B). These results clearly point to the counteracting effects of distance and habitat continuity in determining the genetic structure of giant kelp populations; F_{ST} increased with distance and decreased with area of kelp per km between sites. Using AIC criteria (Appendix D) and an estimate of variance explained, the fit to the two-term model ($r^2 = 0.501$, Fig. 3C) was much better than that of both single-term models (spatial distances $r^2 = 0.325$ and habitat continuity $r^2 = 0.316$; Fig. 3A, B, respectively).

Dispersal and effective population size

The simulated effective population size that resulted in a slope value similar to that found empirically ranged from 50–700 in scenario D to 800–2500 in scenario A (Fig. 4). Conversely the mean dispersal distance, σ, ranged from 1.8 to 2.92 km, and from 0.58 to 0.67 km, at high and low velocity current scenarios, respectively. The solution set for parameter values yielding the observed IBD slope showed a clear trade-off between effective population size and mean dispersal distance. The overall pattern suggests that if effective population sizes are small, higher levels of dispersal are needed to achieve the observed IBD. In contrast, for large effective population sizes, lower levels of dispersal are necessary to achieve the solution.

Discussion

In this study we have shown that implicit consideration of habitat continuity improved the capacity to predict genetic differentiation between patches of the giant kelp *Macrocystis pyrifera* along the southern California coastline, relative to the more common approach of analyzing genetic distance variation with geographic distance. We also provide an approach to quantify the role of habitat continuity on gene flow. Our results indicate that consequences of habitat fragmentation on the metapopulation structure of giant kelp are likely to be severe, which has important implications for conservation management of this key habitat-forming species. An additive model that included both geographic distance and habitat continuity best explained the variance in pair-wise F_{ST} values for patches of *Macrocystis*. That the model was additive indicates that geographic distance and habitat continuity are both important factors that operate independently to influence genetic distance (as noted above distance and habitat continuity did not covary). Increasing geographic distance between patches was associated with increasing genetic distance, while increasing habitat continuity between patches was associated with decreasing genetic distance. This relationship makes particular sense for a species like *Macrocystis* that occurs in discrete patches (Reed et al. 2006), which serve as the stepping stones in the isolation by distance model. Other studies have found that habitat discontinuities increase genetic differentia-

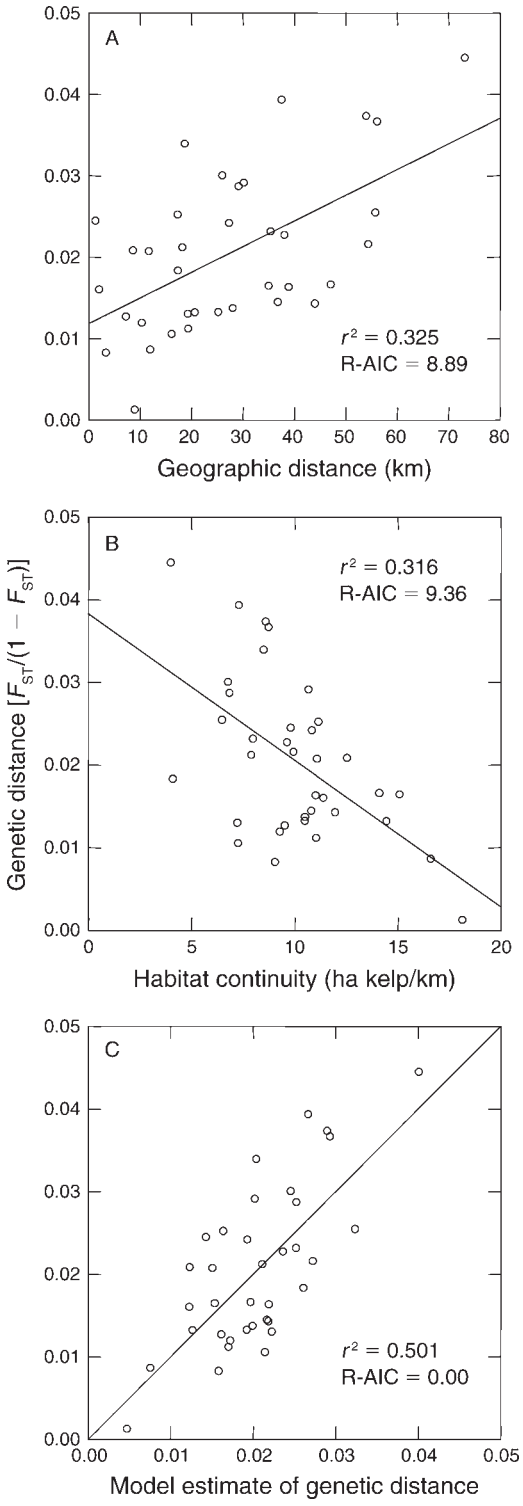

FIG. 3. Relationships between genetic distance and (A) geographic distance, (B) habitat continuity, and (C) two-factor model prediction (geographic distance and habitat continuity). See Appendix D for statistical output.

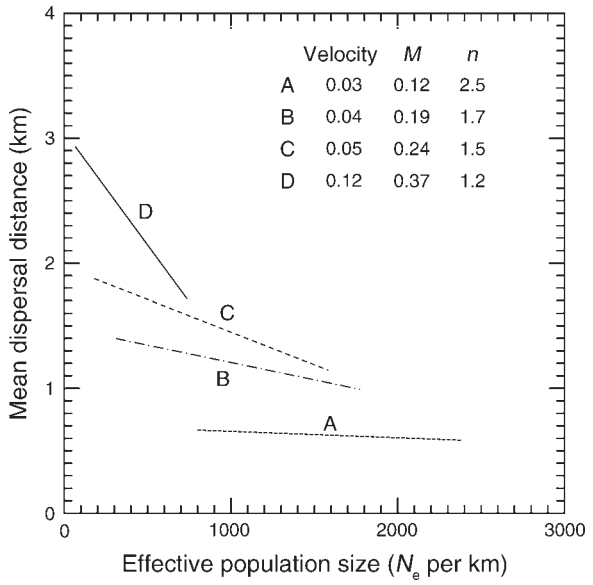

FIG. 4. Lines A–D are the best-fit solutions ($P < 0.00001$ for each line) from the IBDsim simulations of parameter values for effective population size estimated for a spatial scale of 1 km and mean dispersal distance (σ) leading to the observed isolation by distance slope of 0.0003. The four lines represent velocity distributions measured in winter and summer at two study sites (Carpinteria [A, C] and Naples [B, D]) in Reed et al. (2006). These distributions represent the range in current velocities characteristic of our study region. Shown is the measured mean velocity (m/s), for each velocity distribution, the dispersal probability M, and the kurtosis of the Pareto distribution, n, that we used to model in IBDsim the dispersal probabilities in Reed et al. (2006).

tion in marine environments (Riginos and Nachman 2001, Billot et al. 2003). The innovative aspect here is the spatial and regression analyses that quantify and predict the effect of this landscape feature on gene flow.

Importantly, the results of our genetic analyses are consistent with empirical and theoretical estimates of spore dispersal in *Macrocystis*. Reed et al. (2004) monitored the colonization of unoccupied habitat by giant kelp at varying distances from the nearest source population and found the highest densities of sporophyte recruits within a 1–1.5 km interval. Results from a physical transport model by Gaylord et al. (2006) indicated that scales of connectivity on the order of 1 km should be representative of most kelp forests. These values are within the 0.58–2.92 km range that we estimated for mean dispersal distance σ. An important distinction needs to be made when comparing connectivity estimates derived from metapopulation simulations with those from single source studies such as those of Reed et al. (2004) and Gaylord et al. (2006). Genetic connectivity at the metapopulation scale is not entirely explained by σ; a small proportion of emigrant spores reach distances much larger than the mean dispersal, and indeed maximum dispersal values in our simulation are much higher than σ. These long dispersed emigrants can outcross with local spores that settled at sufficiently high densities to guarantee fertilization, and are expected to maintain low levels of genetic differentiation across the metapopulation (Wright 1931, Slatkin 1987). This is particularly true for giant kelp metapopulation at the Santa Barbara Channel where an important proportion of patches may be connected at the dispersal distances considered here (Reed et al. 2006). Thus the connectivity estimates from Gaylord et al. (2006), that modeled the decaying effect of spore densities from a single source without considering the interaction of dispersal from different sources, should be taken as an underestimate of the metapopulation connectivity.

The effective population sizes that explain our IBD slope (50–2500 per linear km) are much smaller than adult population sizes at comparable spatial scales in our study area, which we estimated to be around 26 000 based on a mean adult density of 0.26 (the average over all nine sites for the period 2001–2008; Santa Barbara Coastal-LTER, *unpublished data*) and the mean kelp area within 1 km stretch of coast (GIS data). Our estimated range in the ratio of effective population size to adult population size (N_e/N) of 0.2% to 9.6% agrees with the expectations for marine organisms that have high rates of fecundity and juvenile mortality, which are expected to have high variance in reproductive success (Hedgecock 1994, but see Frankham 1995). Population size fluctuations are another possible cause of low N_e/N ratios (Frankham 1995) that might play an important role in giant kelp where space occupation (by sporophyte populations) is very dynamic (Reed et al. 2006). Given our σ estimates, even with a N_e/N ratio below 10%, the metapopulation N_e observed at spatial scales "effectively" connected by gene flow should be much higher than the subpopulations N_e (Waples 2002). This may help to explain the high levels of genetic diversity reported here relative to those previously reported for kelps (Coyer et al. 2001, Billot et al. 2003, Engel et al. 2008). Migration may thus play a more predominant role than genetic drift on the dynamics of genetic diversity at this scale. In fact, even the high multilocus F_{IS} values suggestive of inbreeding can alternatively be explained by the incidence of null alleles at some loci, as its population mean estimates drop to half (0.085) when the most affected loci are removed.

It has long been known that population genetic differentiation should be affected by species life history and environmental attributes affecting dispersal of either propagules or adults (Wright 1943, Kimura and Weiss 1964, Bohonak 1999). However, environmental attributes have often been modeled under the general proxy of geographic distance, the main exception to this being the consideration of dispersal barriers (e.g., Keller and Largiader 2003, Sumner et al. 2004). Only recently has there been a surge in studies that formally incorporate other habitat attributes such as landscape migration features (Arnaud 2003) and habitat continuity (Shoemaker and Jaenike 1997), thereby improving spatial

models of population genetic differentiation. In this study we have been able to combine high resolution genetic markers with GIS data sets of population distribution to reveal the role of habitat continuity in mediating gene flow across distant sites. These results serve to increase our understanding of giant kelp forest metapopulation connectivity and have important implications for their effective management. This type of GIS-based approach could be further complemented by incorporating, ecological niche modeling, fine-scale ocean circulation patterns, and asymmetric gene-flow analyses.

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APPENDIX A

Macrocystis pyrifera sites sampled along the mainland coast of the Santa Barbara Channel in California (*Ecological Archives* E091-006-A1).

APPENDIX B

Inbreeding coefficient (F_{IS}) estimates per locus and population of *Macrocystis pyrifera* along the mainland coast of the Santa Barbara Channel in California (*Ecological Archives* E091-006-A2).

APPENDIX C

Pairwise genetic differentiation, measured as θ, F_{ST} estimator, between *Macrocystis pyrifera* sites in the Santa Barbara Channel (*Ecological Archives* E091-006-A3).

APPENDIX D

Comparison of models relating geographic distance and habitat continuity to genetic distance (*Ecological Archives* E091-006-A4).