Journal of Heredity
doi:10.1093/jhered/est002

Dispersal at a Snail's Pace: Historical Processes Affect Contemporary Genetic Structure in the Exploited Wavy Top Snail (*Megastraea undosa*)

Alison J. Haupt, Fiorenza Micheli, and Stephen R. Palumbi

From the Hopkins Marine Station, Stanford University, 100 Oceanview Blvd, Pacific Grove, CA 93950 (Haupt, Micheli, and Palumbi); and the Northwest Fisheries Science Center, 2725 Montlake Blvd East, Seattle, WA 98112 (Haupt).

Address correspondence to Alison J. Haupt at the address above, or e-mail: ajhaupt@gmail.com.

Abstract

We used population genetics to assess historical and modern demography of the exploited wavy top snail, *Megastraea undosa*, which has a 5–10 day pelagic larval duration. Foot tissue was sampled from an average of 51 individuals at 17 sites across the range of *M. undosa*. Genetic structure at the mtDNA locus is strikingly high (Φ_{ST} of 0.19 across 1000 km), and a major cline occurs in northern Baja California (Φ_{CT} of 0.29 between northern and southern populations). Genetic data indicate that the northern region is highly connected through larval dispersal, whereas the southern region exhibits low genetic structure. However, additional analyses based on patterns of haplotype diversity and relationships among haplotypes indicate that *M. undosa* has likely recently expanded into the Southern California Bight or expanded from a small refugial population, and analysis using isolation by distance to calculate dispersal distance indicates surprisingly short estimates of dispersal from 30 m to 3 km. This scenario of a northward expansion and limited larval dispersal is supported by coalescent-based simulations of genetic data. The different patterns of genetic variation between northern and southern populations are likely artifacts of evolutionary history rather than differences in larval dispersal and this may have applications to management of this species. Specifically, these data can help to inform the scale at which this species should be managed, and given the potentially very small dispersal distances, this species should be managed at local scales. Consideration of the evolutionary history of target species allows for a more accurate interpretation of genetic data for management.

Key words: *fisheries, larval dispersal, management, phylogeography, population genetics, range expansion*

Knowledge of population connectivity—the movement of individuals between subpopulations—is critical to understanding population dynamics and the effective design of management strategies (Kinlan and Gaines 2003; Palumbi 2003; Cowen and Sponaugle, 2009). A majority of marine fishes and invertebrates are characterized by a bipartite life cycle that includes a pelagic larval stage that may last several months, possibly allowing larvae to travel hundreds or thousands of kilometers (Thorson 1950; Strathman 1987). Assuming successful recruitment to adult populations, the spatial scale of larval dispersal defines the scale of contemporary population connectivity (Kinlan and Gaines 2003; Palumbi 2004).

Many of the problems encountered in managing natural resources arise because of a mismatch between the scale of management and the scale(s) of the ecological processes being managed (Prince et al. 1998; Shanks et al. 2003; Hilborn et al. 2005; Cumming et al. 2006; Prince 2010; White and Costello 2011). For example, abalone in Australia exhibit regional variation in growth, reproduction, and the size at which sexual maturity is attained (Prince 2005). If minimum size limits for the fishery are the same across the entire region, then quickly growing abalone may enter the fishery before first reproduction (Prince 2005, 2010). Effective management strategies, including stock delineation and marine reserve placement, require knowledge of the spatial scale at which target species disperse (Sale et al. 2005; Costello et al. 2010). By modeling the effects of networks of marine protected areas, Costello et al. (2010) demonstrated that spatial information, specifically knowledge of dispersal scale, greatly improves management efficiency and increases the economic value of a fishery. However, because of the difficulty of tracking small larvae, larval dispersal scales are often unknown and are rarely integrated into management.

Without the ability to physically track larvae, many researchers have turned to population genetic techniques for estimation of dispersal (Hellberg et al. 2002; Selkoe and Toonen 2006; Hedgecock et al. 2007).

Ecological, physical, historical, and anthropogenic factors act in concert to drive contemporary patterns of dispersal for marine species (Grantham et al. 2003; Cowen and Sponaugle 2009). When dispersal distances are nearly equal to the geographic range of the species, this can lead to panmixia, an openly mixing population. In contrast, when dispersal occurs on smaller geographic scales, the potential for population subdivision exists. The combination of a long pelagic larval phase and ocean currents may aid in long distance dispersal and more open populations, reflected by a lack of genetic structure throughout the range (Largier 2003; Siegel et al. 2003; Gawarkiewicz et al. 2007; Addison et al. 2008). Conversely, larval behavior and oceanographic features may act to limit dispersal (Cowen 2000; Kingsford et al. 2002; Largier 2003). These contemporary processes drive dispersal and successful delivery of larvae from one population to another as well as influence genetic structure of a species. Population genetic studies can give us insight into whether marine populations are connected by larval transport or if there are barriers to dispersal and therefore successful recruitment is more local (Hedgecock et al. 2007; Hellberg 2007; Weersing and Toonen 2009; Dawson et al. 2010; Pinsky et al. 2010). Particularly, studies that use patterns of genetic isolation by distance (IBD) to estimate dispersal kernels may provide further insight into connectivity of separated populations (Kinlan and Gaines 2003; Palumbi 2003; Pinsky et al. 2010).

Although genetic data can be used to infer potential dispersal distances of larvae, they also reflect evolutionary processes, which can make estimates difficult and possibly lead to incorrect inferences of contemporary dispersal (Avise et al. 1987; Hewitt 1996; Benzie 1999; Hewitt 2000; Jacobs et al. 2004, Marko and Hart 2011). Population expansions, contractions, and bottlenecks may leave indelible clues within genetic patterns (Slatkin and Hudson 1991; Harpending et al. 1998). Environmental and anthropogenic drivers (e.g., climate change, human fishing pressure, and habitat destruction) can also change species distributions and population sizes and consequently, alter genetic structure (Selkoe et al. 2010; Puritz and Toonen 2011). Genetic data are often employed to examine these evolutionary patterns in species demographics (Benzie 1999; Hewitt 2000; Jacobs et al. 2004; Hart and Marko 2010; Marko and Hart 2011), which can cause a population to be out of equilibrium and affect estimates of gene flow (Rousset 1997). Range expansions can lead to disparate patterns of genetic structure in the historical range and in a newly expanded range (Hellberg et al. 2001). In the historical portion of the range, the population may be closer to equilibrium and have had time to diversify, whereas in the more recently colonized area, the genetic diversity may be low due to founder effects and a population further from equilibrium (Ibrahim et al. 1996).

Using population genetics to estimate gene flow and infer rates of dispersal assumes that the population is at equilibrium, and if populations are not yet at equilibrium, contemporary genetic patterns may be more reflective of evolutionary processes such as a range expansion rather than contemporary dispersal patterns (Wright 1978). Work by Slatkin (1993) on patterns of IBD indicates that the amount of time for a population to reach equilibrium may be a strong function of effective population size, which in many marine populations may be much lower than local census size (Roman and Palumbi 2003). In marine populations where effective management is contingent on assessment of larval dispersal, it is critical to elucidate whether observed genetic patterns reflect contemporary connectivity or historical population changes (Bird et al. 2007).

In this study, we seek to discover if and how past demographic processes influence contemporary genetic estimates of larval dispersal and connectivity. We combine analyses of empirical genetic data and coalescent-based simulated data sets to explore the contribution of past demographic processes and contemporary dispersal in influencing the genetic structure of a harvested marine benthic invertebrate, the wavy turban snail *Megastraea undosa*, which ranges from southern California, United States to southern Baja California, Mexico. We use these data to investigate regional structure and assess population connectivity across the range of *M. undosa*. Our empirical results reveal two regimes of genetic structure, which could be driven by either differences in dispersal or historical processes. Coalescent-based simulations support the hypothesis that these patterns arise from a historical range expansion and that dispersal may be limited throughout the range despite differences in genetic structure.

Methods

Study Species and Management

Megastraea undosa is a large (5–10 cm), herbivorous gastropod ranging from Point Conception, California, United States (34.5 °N) to Abreojos, Baja California Sur, Mexico (26.7 °N; *M. undosa* is present south of this area to Bahia Magdalena, 25.5 °N, at much lower densities) in rocky intertidal and subtidal habitats (Taniguchi and Rogers-Bennett 2001). This snail is a broadcast spawner that releases gametes into the water column prior to fertilization. *Megastraea undosa* lives to be 12 years and reproduction begins at age 4 and high levels of fecundity are reached beginning at 8 years (Martone and Micheli 2012). Reproduction can occur throughout the year but peaks in October (Belmar-Pérez 1991). Larvae are competent to settle after 5–10 days (Guzmán del Próo et al. 2003).

Megastraea undosa is harvested in California, United States, and Baja California, Mexico, by divers. In California, catch is largely unregulated: the only requirement is the need for a valid fishing license and—other than no-take marine protected areas (MPAs) that afford protection to all species—there is no spatial management for this species (Taniguchi and Rogers-Bennett 2001). The only sampled site that falls within a no-take MPA is Anacapa Island Landings Cove (Site 1). The major concentration of the fishery is in Baja

California Sur, Mexico, from Punta Eugenia 27.8 °N to La Bocana 26.8 °N, and fishermen in this region are organized into 9 fishing cooperatives, where management of invertebrate species occurs cooperatively with government agencies that regulate Mexican fisheries (McCay et al. forthcoming). Unlike California—where *M. undosa* is managed as 1 region—Baja California Sur, Mexico is managed at the local scale of the fishing cooperative. These cooperatives are granted concessions, or exclusive access, for certain invertebrate fisheries, including *M. undosa*, and have the authority to make decisions about fishing season, quotas, and size limits as long as these are within the limits set by the federal government (McCay et al. forthcoming).

Sample Collection and Sequencing

Foot tissue samples (~1 cm^3) of 27–62 (average = 51; standard deviation [SD] = 9.6) individuals were collected nonlethally via SCUBA from 17 sites across the range of *M. undosa* from the years 2005–2008 (Figure 1; Table 1). Tissue samples were preserved in 95% ethanol. This study was specifically designed to sample across the range of *M. undosa* rather than to examine 1 particular area of interest.

Total genomic DNA was extracted with NucleoSpin DNA extraction kit (BD Biosciences, San Jose, CA) per the manufacturer's protocol. A 605-base-pair segment of the mitochondrial cytochrome oxidase subunit-I (COI) gene was amplified and sequenced using primers HCO-2198 and LCO-1490 (Folmer et al. 1994) following standard PCR and sequencing protocol from Folmer et al. (1994) using EconoTaq. PCR products were sequenced on an ABI 3100 sequencer (Applied Biosystems, Inc., Foster City, CA). Individuals were sequenced in forward and reverse directions and visually scored for accuracy and polymorphisms using Sequencher version 4.8 (Gene Codes Corporation).

Population Structure

Aligned sequences were exported from Sequencher into Arlequin 3.5 (Excoffier et al. 2005) to calculate Φ statistics: a measure of the amount of variance among samples that can be attributed to differences among populations. Using Arlequin, we ran an analysis of molecular variance (AMOVA) to calculate Φ_{ST}, Φ_{SC}, and Φ_{CT} values as well as pairwise Φ_{ST} values between all sites. All AMOVAs were performed using pairwise distance with 10 000 permutations in

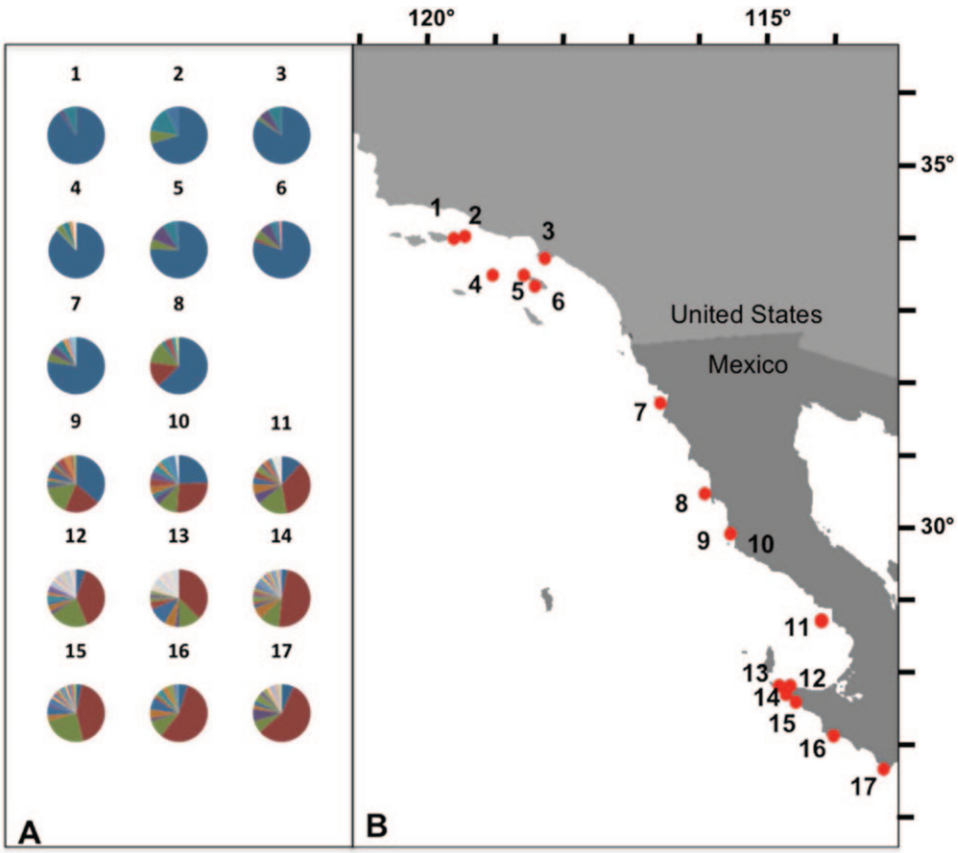

Figure 1. Distribution of COI mtDNA haplotypes along the range of *Megastraea undosa*. (**a**) Each pie chart represents distribution of haplotypes at each site. Each color represents a unique haplotype and numbers above pie charts correspond to site numbers in Table 1. (**b**) Red dots represent sampling locations.

Table 1 Sampling localities of *Megastraea undosa* and corresponding site numbers

Site no	Site name	Region	Latitude	Longitude	N	H	H_u	h	H_e	π
1	Anacapa Landings Cove	North	34.014	−119.418	27	4	0	0.4900	2	0.00173
2	Santa Cruz Island Yellowbanks	North	33.991	−119.565	42	4	0	0.2230	1	0.00090
3	Catalina Island Salta Verde	North	33.32	−118.453	60	7	1	0.3571	2	0.00121
4	Catalina Island Eagle Rock	North	33.473	−118.604	54	6	1	0.4416	2	0.00171
5	Palos Verdes	North	33.711	−118.318	52	5	0	0.3122	1	0.00105
6	Santa Barbara Island Graveyard	North	33.474	−119.029	50	5	1	0.2261	1	0.00089
7	Ensenada	North	31.723	−116.718	40	7	2	0.4000	2	0.00146
8	Isla San Martin	South	30.485	−116.097	48	8	1	0.5824	2	0.00209
9	Punta Baja	South	29.929	−115.753	55	14	2	0.8074	5	0.00300
10	Isla San Geronimo	South	29.784	−115.79	48	16	2	0.8777	8	0.00321
11	Esmerelda	South	28.517	−114.072	57	18	3	0.8546	7	0.00303
12	Punta Eugenia Sur	South	27.846	−115.084	55	19	10	0.8387	6	0.00287
13	Punta Eugenia Norte	South	27.839	−114.931	48	22	10	0.8108	5	0.00304
14	Bahia Tortugas Punta Quebrada	South	27.722	−114.99	62	22	10	0.7546	4	0.00237
15	Bahia Tortugas Punta Clam Bay	South	27.618	−114.842	61	17	11	0.7617	4	0.00273
16	Bahia Asuncion	South	27.148	−114.329	66	13	2	0.6770	3	0.00213
17	Punta Abreojos	South	26.7	−113.644	44	13	4	0.6723	3	0.00195

Region refers to if the site was assigned to the northern or southern region; N is the number of samples per site; H is the number of haplotypes found; H_u is the number of unique haplotypes; h is haplotype diversity; $H_e = 1/(1 - h)$ is the number of effective haplotypes; and π is nucleotide diversity for the COI mtDNA locus.

Arlequin. As post hoc test, we manually performed hierarchical groupings of sites to determine the geographic areas that contained the largest Φ_{CT} differences. The largest Φ_{CT} was found by dividing the populations into 2 groups rather than 3 or 4 groups. There is no clear genetic break in the data, rather a cline in central Baja Mexico. Because there is no clear genetic break between northern and southern populations, it is difficult to draw a clear line between north and south for further analyses. However, the common southern haplotype disappears between Ensenada (Site 7) and Isla San Martin (Site 8) and Ensenada and from here on, these groups of sites will be referred to as north and south (Table 1). We also looked within these groupings to see how genetic structure differed throughout the range of *M. undosa* by performing AMOVAs separately to obtain global Φ_{ST} values within the northern region and within the southern region separately to get an estimate of Φ_{SC} for the 2 regions. These Φ_{ST} values allowed for assessment of potential relative levels of genetic connectivity within the northern and southern regions. We were specifically interested to see if genetic structure was evenly distributed along the range: if levels of Φ_{ST} for the north were similar to levels of Φ_{ST} in the south. We were interested to see if the different management schemes in the 2 different regions matched the patterns of larval dispersal inferred through Φ_{ST}.

Historical Demography

To explore the historical demography of this species, we employed 3 techniques: first, we looked at diversity measures; second, at mismatch distributions of haplotypes; and finally, we examined the relationships among haplotypes for signals of past demographic processes in contemporary genetic patterns.

We looked for patterns of genetic diversity by comparing nucleotide diversity (π) (Nei and Jin 1989), number of haplotypes, and effective number of haplotypes (Jost 2007; Timmers et al. 2012) calculated in Arlequin, throughout the range. We used mismatch distributions to look for a possible pattern of expansion in the northern and southern populations. Population expansion and contraction influence patterns of genetic sequence divergence and frequency and so mismatch distributions can be used to infer patterns of past demography (Slatkin and Hudson 1991; Rogers and Harpending 1992). Populations that have undergone recent expansion will have a higher frequency of 0 mismatches. This is because the population is likely to be dominated by a few common haplotypes present in the founding individuals (Harpending 1994). The statistic Harpending's Raggedness Index (HRI), which evaluates the raggedness of the mismatch distribution, was calculated using Arlequin. The resulting mismatch distributions for the northern and southern regions were compared with a chi-square test to see if the distributions were significantly different from each other.

Unique haplotypes were identified using DNAsp and then imported into TCS version 1.21 (Clement et al. 2000) to create haplotype networks. TCS calculates the number of differences among haplotypes to create a parsimonious connection and then joins haplotypes into networks (Clement et al. 2000). The proportion of individuals from the northern or southern group was determined for each haplotype.

Estimating Dispersal: IBD

We looked for a pattern of IBD by plotting pairwise genetic distance (pairwise $F_{ST}/(1 - F_{ST})$ and pairwise Euclidian geographic distance. For the IBD curve, we used only comparisons from the southern portion of the range. Conventional F_{ST} as calculated by Arlequin 3.5 is based solely on frequencies of haplotypes unlike Φ_{ST}, which considers relatedness (number of mutations) between haplotypes as well

as differences in frequency (Excoffier et al. 2005). When pairwise conventional F statistics were calculated, we saw a strange pattern for pairwise comparisons of northern sites with other northern sites where these values were much higher than expected (Supplementary Figures 1 and 2). For example, the F_{ST} between Sites 1 and 4 (both dominated by the same haplotype) is 0.670, whereas the F_{ST} between Sites 1 and 15 (which have entirely different suites of haplotypes) is 0.353. By contrast, the pairwise Φ_{ST} values are consistent with the observed pattern of differences in haplotype frequencies among populations. Pairwise F_{ST} and Φ_{ST} values are generally highly correlated, but this relationship breaks down in these data for pairwise comparisons of northern sites with other northern sites (Supplementary Figure 2). It is possible that the low diversity in the northern portion of the range combined with these sites being dominated by 1 main haplotype creates F_{ST} values that are higher than expected for comparisons of northern populations. These F_{ST} values are correct estimates of differentiation based solely on frequency but may be potentially misleading. Because of this, northern sites were excluded from the IBD plot. Pairwise geographic distance was calculated by importing latitude and longitude coordinates into a geographic distance matrix generator. This pattern should represent a balance between drift and migration and allow us to estimate dispersal distance using the following equation (Rousset 1997):

$$\sigma = \sqrt{\frac{1}{4 D_e m}},$$

where σ is the spread, or width, of the dispersal kernel, m is the slope of IBD plot, and D_e is effective density. The significance of the relationship was determined by performing a Mantel test in Arlequin. Rousset (1997) uses a one-dimensional formula, where the length of the habitat is greater than the width; the coastline along the eastern Pacific basin generally fits this assumption. However, the habitat is not continuous and this patchy nature could influence estimates of dispersal (Pinsky et al. 2012).

To obtain estimates of effective density (D_e), we integrated census density estimates with data on reproductive maturity of *M. undosa*. We used data from a previous study that surveyed densities of *M. undosa* in 2006 at 15 sites from Bahia Tortugas to Punta Abreojos, Baja California Sur, Mexico (Martone et al. unpublished data). Surveyed *M. undosa* were broken into 10-mm size bins and these data were integrated with known percentage of reproductively mature females at each size bin (Martone and Micheli 2012). Densities and sizes were similar among sites in Baja; so for ease of calculation, we chose to use size frequency data from one site (Punta Clam Bay, Bahia Tortugas 27.6 °N) to estimate density of reproductive individuals. With this method, we were able to translate census density of *M. undosa* to an estimate of density of reproductive individuals. This was used as an estimate of D_e over the entire range but could have been an over estimation of D_e because we cannot estimate the number of individuals who are actually contributing to the next generation and this number is likely smaller than the density of reproductive individuals. To evaluate how sensitive our measure of dispersal distance is to D_e, we recalculated σ given values of D_e up to 4 orders of magnitude lower.

Coalescent Simulations

We used the coalescent-based program SIMCOAL 2.0 (Laval and Excoffier 2004) to determine expected patterns of genetic diversity with different dispersal and evolutionary histories. SIMCOAL 2.0 uses Kingman's backward-based coalescent approach to construct gene genealogies based on demographic patterns such as migration and population growth and simulates DNA sequences forward from the most recent common ancestor (Kingman 1982a, 1982b). The purpose of these simulations was to explore what patterns of genetic diversity might be produced under different scenarios of dispersal and evolutionary history of expansion. We examined combinations of 2 demographic history scenarios—northward range expansion or no range expansion—and 2 dispersal scenarios—low (10 km) and high (100 km) dispersal distances. These simulated data were then analyzed using Arlequin to assess genetic diversity in each simulation output and compared results with our empirical data.

We simulated 30 populations along a linear coastline each separated by 30 km with effective population sizes of 10 000 individuals. Our empirical sampling design included 17 sites separated by an average of 65 km (range: 8–240 km), and our estimate of effective population size using our empirical estimate of D_e is of the same order of magnitude of the 10 000 individuals used for the simulation. To mimic our sampling design as closely as possible, the first 12 sites were part of the northern population and the remaining 18 were part of the southern population. We ran 1000 replicate runs of each scenario. Fifty individuals were sampled at each of these sites. Migration matrices were calculated using a Gaussian dispersal kernel in R (R Development Core Team 2008) centered around 10 and 100 km for the low and high dispersal simulations, respectively. We simulated 605 base pairs of DNA sequence at a single locus and mutation rate for all simulations scenarios was set at 10^{-7} per base pair (Hugall et al. 2002; Kelly et al. 2010). Simulations with a northward range expansion were simulated with a historical range contraction 1000 generations ago when the first 12 populations (simulated northern range) were reduced to 0 and the founder population for the expansion was 100 individuals. *Megastraea undosa* reaches reproductive maturity at 4 years, reaches high levels of fecundity at 8 years, and lives for approximately 12 years (Martone and Micheli 2012). The generation time of *M. undosa* is likely about 8 years and so an expansion 1000 generations about would correspond to roughly 8000 years ago and fall sometime after the last glacial maximum when conditions in the Southern California Bight were similar to contemporary conditions—rather than colder conditions during Pleistocene glacial cycles—and may have allowed for the species to expand northward (Kennett and Ingram 1995; Kennett and Venz 1995; Graham et al. 2003). Output files were run in Arlequin as batch files to assess differences in

genetic diversity between northern and southern sites and were then compared with the diversity measurements of the actual data.

Results

Population Structure

We detected highly significant genetic structure throughout the range (Φ_{ST} = 0.187, $P < 0.0001$; Table 2). Populations in the north were dominated by 1 haplotype that declined but was still present in the southern portion of the range at a lower frequency (Figure 1). In contrast, the southern populations are dominated by a different haplotype that is nearly exclusive to this region: only 1 individual at Catalina Island (Site 6) possessed this haplotype (Figure 1).

Hierarchical AMOVAs among groups of sites revealed that the largest difference was between Isla San Martin (Site 8) and Punta Baja (Site 9), (Φ_{CT} = 0.28620, $P < 0.0001$). Table 2 shows the results of different hierarchical analyses with different north–south groupings of samples. There is no clear genetic break but rather a gradient present in north central Baja. Because the dominant southern haplotype disappears between Ensenada (Site 7) and Isla San Martin (Site 8; Figure 1), for all other analyses, sites from Ensenada to the northern range limit are considered northern and sites from Isla San Martin to the southern limit are southern (Table 1).

We found different patterns of genetic connectivity among populations in the northern and southern regions (Table 2). Among the northern sites, no genetic structure was detected (Φ_{ST} = −0.004, P = 0.683), whereas in the southern sites there was significant structure (Φ_{ST} = 0.044, $P < 0.001$). Among the northern populations, there are no significant pairwise Φ_{ST} population comparisons, but among the southern populations, there are multiple significant comparisons (Table 3). The southern region encompasses a slightly larger area (northern = 359 km of coastline; southern = 483 km of coastline), and so it is possible that the differences we see in structure are due to the smaller northern area. However, we can reject this hypothesis because if we isolate a smaller area in the center of the southern region, significant genetic structure is present (Ensenada–Esmerelda, 294 km; Φ_{ST} = 0.058, $P < 0.001$), and if we consider the island coastlines of the Channel Islands, the northern area may be larger.

Historical Demography

We found that nucleotide diversity in the north (π = 0.00125, SD = 0.001019) was less than half of that in the south

Table 2 AMOVA results for *Megastraea undosa* at the COI mtDNA locus

	Variance	% Total	Φ Statistics	*P*
Global				
Among populations	0.14755	18.69	Φ_{ST} = 0.18687	<0.0001
Within populations	0.64203	81.31		
North only				
Among populations	−0.00158	−0.42	Φ_{ST} = −0.00419[a]	0.6835
Within populations	0.37703	100.42		
South only				
Among populations	0.03651	4.36	Φ_{ST} = 0.04363[a]	<0.0001
Within populations	0.80038	95.64		
California vs. Mexico				
Among groups	0.21420	23.72	Φ_{SC} = 0.06787	<0.0001
Among populations within groups	0.04674	5.18	Φ_{ST} = 0.28898	<0.0001
Within populations	0.64203	71.1	Φ_{CT} = 0.23721	0.00020
North (7: Ensenada) vs. South (8: Isla San Martin)				
Among groups	0.25036	27.37	Φ_{SC} = 0.03350	<0.0001
Among populations within groups	0.02247	2.46	Φ_{ST} = 0.29521	<0.0001
Within populations	0.64203	70.18	Φ_{CT} = 0.27078	0.0001
North (8: Isla San Martin) vs. South (9: Punta Baja)				
Among groups	0.26177	28.62	Φ_{SC} = 0.01570	<0.0001
Among populations within groups	0.01082	1.18	Φ_{ST} = 0.29674	0.0003
Within populations	0.64203	70.2	Φ_{CT} = 0.28553	0.0003
North (9: Punta Baja) vs. South (10: Isla San Geronimo)				
Among groups	0.23750	26.37	Φ_{SC} = 0.03217	<0.0001
Among populations within groups	0.02115	2.35	Φ_{ST} = 0.28790	<0.0001
Within populations	0.64203	71.28	Φ_{CT} = 0.26423	<0.0001
North (10: Isla San Geronimo vs. South (11: Esmerelda)				
Among groups	0.21470	24.09	Φ_{SC} = 0.05094	<0.0001
Among populations within groups	0.03446	3.87	Φ_{ST} = 0.27958	<0.0001
Within populations	0.64203	72.04	Φ_{CT} = 0.24091	0.0002

Global Φ_{ST} refers to the entire range of the species. Northern Φ_{ST} refers to north of and including Ensenada, Baja California, Mexico, to the northern edge of the range. Southern Φ_{ST} refers to sites south of and including Isla San Martin, Baja California, Mexico, to the southern edge of the range. Hierarchical AMOVA results are also reported.

[a] This is an approximation of Φ_{SC}.

Table 3 Above the diagonal pairwise Φ_{ST} comparisons are listed for *Megastraea undosa* at the COI mtDNA locus

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1		0.00773	0.00377	−0.01076	0.00402	0.01515	−0.01152	0.02257	**0.11481**	**0.15942**	**0.23751**	**0.30006**	**0.2529**	**0.2919**	**0.30057**	**0.31098**	**0.30933**
2	0.2973		−0.00802	0.00917	−0.01611	−0.01669	−0.01378	**0.08558**	**0.20625**	**0.26462**	**0.34062**	**0.41242**	**0.36097**	**0.39906**	**0.40926**	**0.4213**	**0.43348**
3	0.30631	0.63964		−0.0067	−0.01086	−0.00102	−0.01537	**0.05479**	**0.17657**	**0.23318**	**0.3111**	**0.38345**	**0.33172**	**0.36579**	**0.37966**	**0.38255**	**0.38666**
4	0.55856	0.1982	0.57658		−0.00002	0.02097	−0.01174	0.02085	**0.11826**	**0.16494**	**0.24021**	**0.30757**	**0.25933**	**0.29181**	**0.30694**	**0.30442**	**0.29896**
5	0.27928	0.93694	0.78378	0.36937		−0.00508	−0.01611	**0.07656**	**0.19588**	**0.25373**	**0.32796**	**0.39937**	**0.35006**	**0.38284**	**0.39806**	**0.40202**	**0.40817**
6	0.12613	0.97297	0.41441	0.06306	0.55856		−0.00771	**0.0916**	**0.22005**	**0.28119**	**0.35973**	**0.4324**	**0.37865**	**0.4175**	**0.42537**	**0.43964**	**0.45412**
7	0.63964	0.76577	0.91892	0.7027	0.82883	0.61261		**0.04227**	**0.1517**	**0.20303**	**0.27936**	**0.34676**	**0.2983**	**0.33471**	**0.34652**	**0.35252**	**0.3531**
8	0.17117	<0.00001	0.02703	0.09009	<0.00001	<0.00001	0.04505		**0.03396**	**0.07**	**0.14491**	**0.20734**	**0.15438**	**0.19025**	**0.19797**	**0.2015**	**0.20206**
9	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	0.03604		−0.00503	**0.02993**	**0.06646**	**0.03283**	**0.05802**	**0.05656**	**0.05986**	**0.06357**
10	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	0.61261		0.00551	**0.0418**	0.00237	**0.03529**	**0.0272**	**0.03498**	**0.04782**
11	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	<.00001	<0.00001	<0.00001	<0.00001	0.24324		−0.00058	−0.00847	−0.00217	0.00151	−0.00267	0.00691
12	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	0.00901	<0.00001	0.42342		0.00647	−0.00385	0.00315	−0.00574	0.00382
13	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	0.31532	0.86486	0.17117		0.00595	−0.00543	0.00655	**0.02246**
14	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	0.57658	0.6036	0.20721		0.0121	−0.01071	−0.00589
15	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	0.0991	0.2973	0.21622	0.62162	0.12613		0.01111	**0.03408**
16	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	0.45045	0.71171	0.18919	0.99099	0.14414		−0.00549
17	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	0.00901	0.18018	0.28829	0.00901	0.76577	0.03604	0.71171	

Significant comparisons ($\alpha = 0.05$) are boldfaced and these comparisons that are significant after Bonferroni corrections (corrected $\alpha = 0.0003$ for 153 comparisons) are underlined. *P* values are listed below the diagonal.

($\pi = 0.002755$, SD = 0.001793; *t*-test: $P < 0.0001$), with 13 and 82 haplotypes, respectively. Mismatch distributions of both northern and southern regions indicate a pattern of expansion measured by HRI (north: HRI = 0.3996, $P = 0.41$ and south: 0.0376, $P = 0.41$; Harpending, 1994; Figure 2). However, the large proportion of 0 mismatches in the northern region indicates that the northern expansion may be more recent and pronounced. These two distributions were significantly different ($\chi^2 = 41851.638$, degrees of freedom [df] = 6, $P < 0.0001$).

The haplotype network shows that the dominant southern haplotype is the root of the diversity for this species (Figure 3). All of the diversity in this system may radiate off of this 1 southern haplotype, whereas the most common northern haplotype is just one of many radiating off of the dominant southern haplotype. This star phylogeny—with one very common haplotype surrounded by many less common variants—also indicates an expansion (Slatkin and Hudson 1991; Avise 2000).

Estimating Dispersal

We found a significant relationship between geographic and genetic distance (Mantel test: correlation coefficient = 0.5708, $P = 0.005$; Figure 4) using only pairwise comparisons from the southern portion of the range. Our estimate of effective density, which incorporated data on reproductive maturity of *M. undosa* (Martone and Micheli 2012), was 0.76 individuals/m^2. Using this D_e estimate and the slope of the IBD relationship (0.0005), the estimated dispersal kernel is 25 m. With a D_e of 1, 2, 3, and 4 orders of magnitude lower the estimated dispersal kernel is 79, 250, 793, and 2508 m, respectively.

Coalescent Simulations

Genetic diversity estimates of northern versus southern populations were consistent with our empirical results only for the scenario that included a northward range expansion with limited dispersal (10 km; Table 4). Scenarios that included long distance dispersal and/or lack of a range expansion resulted in no difference in genetic diversity (measured by π) between northern and southern regions.

Discussion

We found high levels of global genetic structure throughout the contemporary biogeographic range of *M. undosa*. However, when the range is parsed into northern and southern regions, there are conflicting patterns of genetic structure: no detectable structure in mtDNA Φ_{ST} was found in the north and significant structure in the south. These differences translate into different levels of inferred genetic connectivity via larval dispersal: high connectivity in the north and low in the south. This result might indicate that contemporary management regulations set at a fine spatial scale in the south but not in the north appropriately reflect different patterns of population connectivity within these 2 regions. However, an examination of evolutionary processes, such

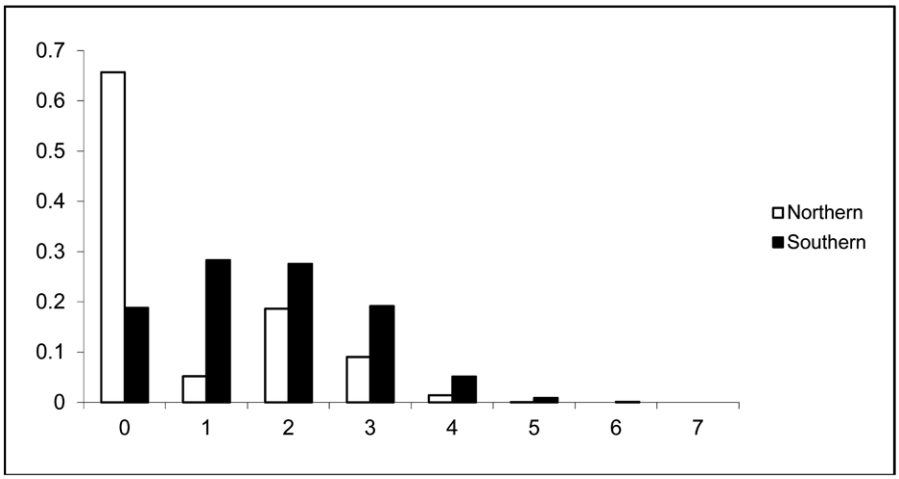

Figure 2. Number of COI mtDNA sequence mismatches for *Megastraea undosa* is shown on the *x* axis and frequency on the *y* axis. The northern population is represented in white and the southern in black.

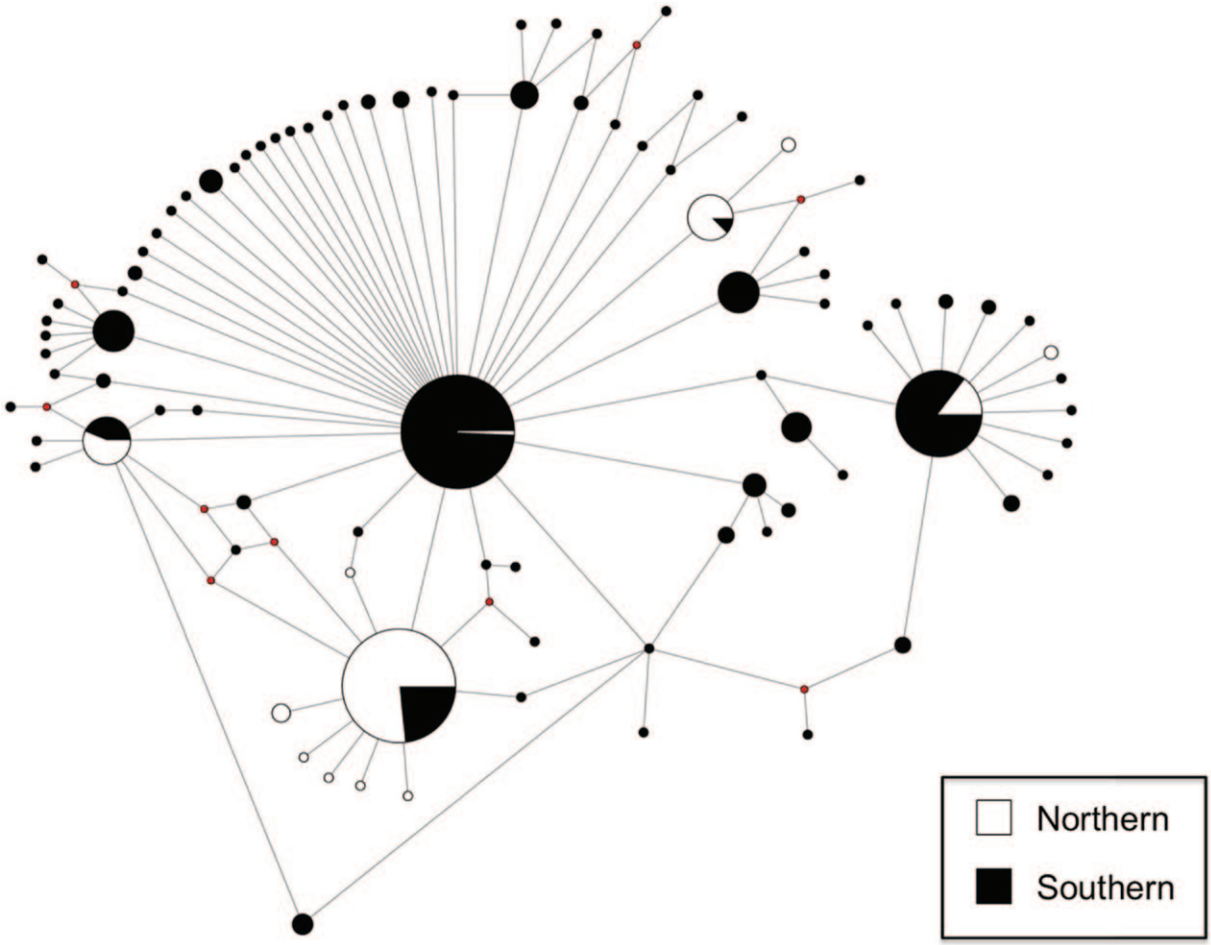

Figure 3. COI mtDNA haplotype network for *Megastraea undosa*. Each circle represents a unique haplotype. Size of circle is proportional to number of individuals that possess the haplotype. White represents the proportion of individuals from the north and black from the south. Red circles represent necessary missing—or unsampled—haplotypes to connect existing haplotypes.

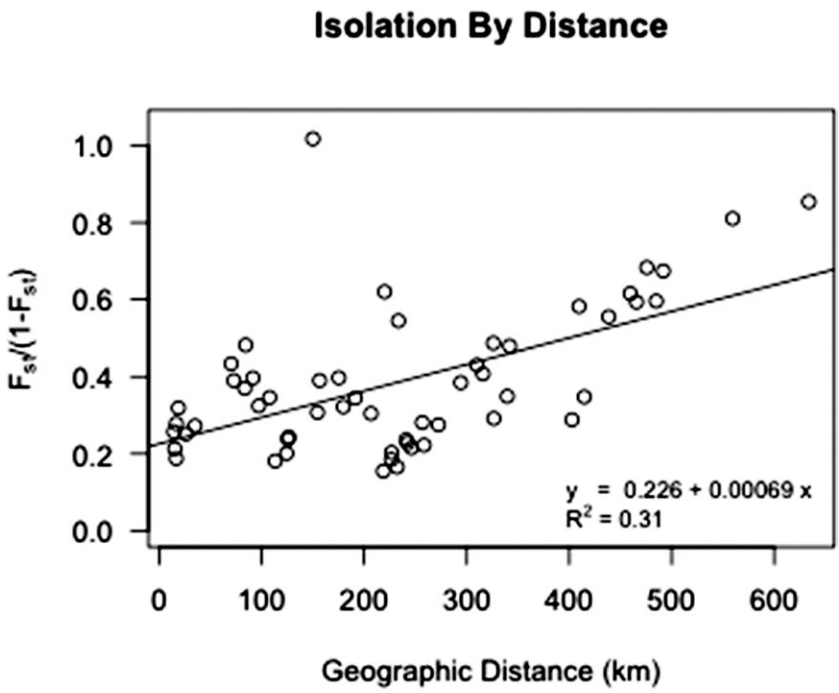

Figure 4. IBD plot for *Megastraea undosa* at the COI mtDNA locus. Pairwise Euclidian geographic distance graphed against pairwise genetic difference ($F_{ST}/(1 - F_{ST})$; Mantel test: correlation coefficient = 0.5708, $P = 0.005$).

Table 4 Ratio of northern or southern diversity for simulated scenarios and the empirical data for *Megastraea undosa* COI mtDNA

History	Dispersal	Northern/southern diversity
Expansion	100	0.9253
Expansion	10	**0.4438**
No Expansion	100	0.9247
No Expansion	10	1.0068
Actual data		**0.4250**

The only scenario that matches the empirical ratio is with a northward range expansion and limited dispersal.

as range expansions and bottlenecks, and potential demographic history indicates that this snail may have undergone a northward range expansion and/or a northern population expansion after the end of the last glacial maximum into the Southern California Bight—the northern region—and this process yielded lower genetic diversity in the north. A selective sweep could have also caused lower genetic diversity; although, we are unable to rule out this possibility, it is unlikely that only the north would have been affected by a selective sweep as there is no obvious selective pressure that is unique to the Southern California Bight.

Larval transport of *M. undosa* is likely to be influenced by oceanography on a number of spatial scales throughout the range. At a regional scale, the range is dominated by the offshore-equatorward flowing California Current, but at local scales, each portion of the range is subject to a different set of oceanographic conditions including coastal eddies, upwelling centers, oceanographic fronts, and poleward flowing water (Simpson and Lynn 1990; Hickey 1998; Zaytsev et al. 2003; Woodson et al. 2012). Oceanographic patterns in the Southern California Bight have been well studied, and recent research using circulation simulations to estimate potential and realized dispersal for fishes and an invertebrate species found that larval connectivity was heterogeneous in the Southern California Bight (Watson et al. 2010). In the fall months when *M. undosa* spawns, higher flow was seen from southern sites to northern sites, which likely impacts connectivity between the Southern California Bight and the southern portion of the range. Oceanographic patterns associated with the southern portion of the range in Baja California are not as well understood or studied, but it is likely that the major headland of Punta Eugenia influences these patterns (Bernardi and Talley 2000; Zaytsev et al. 2003; Haupt et al. in review).

Although differences in oceanography likely influence local dispersal patterns of *M. undosa*, they are unlikely to fully explain the observed differences in genetic differentiation and diversity throughout the range. Coalescent-based computer simulations indicate that this pattern could have been created by a range expansion and maintained by limited dispersal. Taken together, these results show that evolutionary processes influence patterns of contemporary genetic structure and need to be taken into account when making recommendations for management and conservation.

Contemporary Patterns of Genetic Connectivity

Using the pattern of IBD, we estimated short dispersal distances ranging from 30 m to ~3 km, depending on estimates

of effective density. Even with a dispersal distance of 1–3 km, obtained using the lowest estimates of effective density, we would still conclude that this snail has limited dispersal. Previous studies that examined larval dispersal of marine gastropods have found both high and low levels of genetic differentiation and inferred connectivity, but gastropods also encompass a large range of pelagic larval durations (PLD; Kelly and Palumbi, 2010). Recent work on blacklip and black abalone, which have a comparable PLD to *M. undosa*, show that these abalone species may have very limited dispersal distance, on the order of 7–10 km for blacklip abalone (Gruenthal and Burton 2008; Miller et al. 2008). By combining oceanographic connectivity matrices with genetic connectivity data, White et al. (2010) determined that the whelk, *Kelletia kelletii*, which has a PLD of 40–60 days (Zacherl D, unpublished data), an order of magnitude longer than *M. undosa*, likely disperses on a scale of 30 km. Oceanographic modeling studies of two commercially fished molluscs—a scallop and a gastropod—in the Gulf of California, Mexico, predict that dispersal potential may be much larger than this (100's of km) and that larvae may be exported out of marine reserves to fished areas, though the authors point out that these models may overestimate potential dispersal because larval behavior could limit distance traveled by larvae (Cudney-Bueno et al. 2009).

By considering the full range of *M. undosa*, rather than focusing solely on northern populations out of context, we see a clear pattern of IBD, which may indicate limited dispersal throughout the range. Separately, however, the north and the south present different patterns: the north has no structure and the south has significant structure. These differing patterns could lead us to infer different levels of connectivity via larval dispersal in these areas. Coalescent-based simulations indicate that to maintain the pattern of reduced genetic diversity in the north for 1000 generations after the northward expansion that dispersal in this snail must be limited. Potentially, the northward expansion and the historical processes drive the patterns in the north, rather than a difference in realized larval dispersal.

Historical Demography

Physiological tolerance to physical factors such as temperature can play an important role in structuring species ranges in response to climatic changes and may be driving range contractions and expansions (Roy et al. 1995). Marine flora and fauna have adapted to climatic changes with range shifts in both historical and contemporary times (Valentine and Jablonski 1993; Barry et al. 1995; Roy et al. 1995; Zacherl et al. 2003; Dawson et al. 2010). During the last glaciation in the late Pleistocene, the water temperatures in the Southern California Bight may have been much cooler, 7–8 °C, whereas current temperatures range from 12 to 20 °C (Kennett and Ingram 1995; Kennett and Venz 1995; Graham et al. 2003). A study by Muhs et al. (2006) examined marine terrace fauna of the eastern Pacific from fossil assemblages dating 120 000 and 80 000 years BP. They discovered that the species assemblages at 120 000 years BP were similar to contemporary assemblages, indicating that paleotemperatures may have been very similar to current temperatures. In contrast, fauna from 80 000 years BP consisted of many species not currently found in this region; these species are currently found in northern, colder areas, indicating that during this era, the Southern California Bight was likely much colder (Muhs et al. 2006). For many southern species, including *M. undosa*, the Southern California Bight may have been too cool during the most recent glaciation to serve as usable habitat until after recession of glaciers in the northern Pacific and subsequent warming of these waters.

Repeated extirpations and recolonizations resulting in founder effects could have kept genetic diversity in the system low. *Megastraea undosa* is found in the Southern California Bight in paleontological studies from 120 000 years ago but not found again until more contemporary studies of Native American middens from 6 000 to 10 000 years ago in the Channel Islands (Forgeng 1992; Erlandson et al. 1998; Roy K, personal communication). During the Holocene, *M. undosa* may have been able to expand into southern California from Mexico; given its potential short dispersal distance combined with the predominant southward currents, this expansion might have occurred very slowly. In modeling kelp forest populations throughout the late quaternary, Graham et al. (2010) indicated large shifts in kelp abundance and productivity of kelp forests throughout time. This would likely translate into major changes in kelp forest communities. Although *M. undosa* is not dependent on the presence of kelp, it is a kelp forest–associated species and is currently found more often in kelp-forested areas than in deforested areas and would likely be affected by large-scale changes in kelp forests (Graham, 2004). Previous work by Selkoe et al. (2010) found that kelp is an important predictor of genetic differentiation in the Southern California Bight and Baja California. Kelp may also play an important role for *M. undosa*, though kelp densities do not seem to correlate to changes in genetic structure and although this species is a kelp forest–associated species and its range extends past southern limit for the range of *Macrocystis pyrifera*.

Effects of climatic changes due to glaciation are commonly found in genetic structure of species in both marine and terrestrial environments (Hewitt 2000). As northern areas cooled during glacial periods, many species contracted into southern warmer areas and recolonized after climate warming (Hewitt 2004). Recent work by Marko et al. (2010) documented that although persistence through the last glaciation of marine species in the northeastern Pacific was common, 5 of 14 species did show evidence of a postglaciation range expansion. Although coastal marine species may have persisted in refugia in the northeastern Pacific (7 of 14 species), some species' ranges were reduced to southern latitudes. Species, even ones closely related, may respond differently to climatic changes. Hickerson and Cunningham (2005) found that with sister species of intertidal fishes, one species persisted despite glaciation and the other experienced a range contraction. These events are often observed in the northeastern Pacific where glaciers were present in coastal systems (Rocha-Olivares and Vetter 1999; Marko 2004; Wilson 2006;

Marko et al. 2010). With *M. undosa*, we see a possible signature of glacial events even though its range does not overlap with glaciated areas.

Applications to Management

The fishery for *M. undosa* is the third most economically important invertebrate fishery in Baja California, Mexico, after lobster and abalone, and management occurs at the local scale of fishing cooperatives (Singh-Cabanillas 1996; Gluyas-Millán et al. 2002; McCay et al. forthcoming). Given the limited dispersal of *M. undosa*, this small scale of management is likely appropriate. Work by Martone and Micheli (2012) suggests that ecological processes such as growth rates and reproduction also vary across a small spatial scale further supporting local rather than regional management. In southern California, management for this species is nearly nonexistent and occurs at the regional scale (Taniguchi and Rogers-Bennett 2001). In this study, the lack of genetic structure in California could support management at a large regional scale. However, when placed in the context of historical demography and evolutionary process, our results indicate that management likely should occur at local scales in California as well. For this reason, managers should be cautious when using data that are not placed in context of an entire range or trying to generalize across species (Bird et al. 2007). Mismatch distributions, genetic diversity patterns, and simulations all support the hypothesis that a recent northward expansion into the Southern California Bight drives the lack of genetic structure in the north. Further, our simulations demonstrate that the most likely dispersal and demographic scenario, of those considered, is a northward range expansion and limited dispersal. Making any assessment about larval dispersal with little to no genetic structure is very difficult (Waples 1998). For *M. undosa*, with the knowledge we gain by looking at the entirety of the range we may be able to recommend that, though we detect no structure in the northern region of the range, management should occur at local scales in both the southern and northern regions.

Newer tools and more quickly evolving markers may aid in avoiding these issues of confusing contemporary and evolutionary patterns to assess connectivity via larval dispersal. Assignment methods, particularly parentage analysis (Jones and Ardren 2003), have shown great promise especially for looking at larval spillover from within marine reserves to outside fished areas (Jones et al. 2005; Planes et al. 2009). The advantage of these methods is that they give actual measurements of contemporary dispersal rather than a long-term average. However, the limitations are that this is a one-time snapshot and without repetition among years a generalization for dispersal patterns cannot be made. Also these types of studies often only capture evidence of limited dispersal because the sample area is small relative to the species range and thus is not collecting potential long distance dispersers, which may be of ecological and conservation significance.

Our results highlight some potential issues and solutions for the use of genetic tools to infer contemporary patterns of larval dispersal. Current genetic structure may reflect evolutionary history but consideration of the entire range of a species as well as exploring historical processes may allow for more accurate inferences of dispersal. In the case study of *M. undosa*, we find that inclusion of the entire range as well as consideration of historical demography indicates potentially limited dispersal in the northern region despite lack of genetic structure.

Supplementary Material

Supplementary material can be found at http://www.jhered.oxfordjournals.org/.

Funding

National Science Foundation Graduate Research Fellowship awarded to A.J.H.; NSF Biocomplexity in the Environment Grant OCE-0410439. Partnership for the Interdisciplinary Study of Coastal Oceans sponsored by the David and Lucile Packard Foundation and the Gordon and Betty Moore Foundation.

Acknowledgments

First and foremost the authors thank the fishing cooperatives of FEDECOOP for their logistical and field support in Baja California. We thank R. Martone, R. Beas, L. Gonzales, S. Guzmán del Próo, E. Serviere, J. Belmar, J. Carillo, F. Lopez, J. Ramirez, C. White, S. Koch, S. Hamilton, J. Wible, E. Hoagland, D. Zacherl, J. Lorda, and C. O'Connell for assistance in the field. We thank A.O. Shelton, M. Pinksy, and S.T. Nixon for computing help. Helpful discussion and feedback were provided by M. Siegle, M. Pespeni, C. Wood, D. Barshis, R. Martone, K. Ruegg, C. Tepolt, G. Somero, M. Pinsky, J. Ladner, R. Kelly, K. Kroeker, and two anonymous reviewers.

References

Addison JA, Ort BS, Mesa KA, Pogson GH. 2008. Range-wide genetic homogeneity in the California sea mussel (*Mytilus californianus*): a comparison of allozymes, nuclear DNA markers, and mitochondrial DNA sequences. Mol Ecol. 17:4222–4232.

Avise JC. 2000. Phylogeography: the history and formation of species. Cambridge (MA): Harvard University Press.

Avise JC, Arnold J, Ball RM, Bermingham E, Lamb T, Neigel JE, Reeb CA, Saunders NC. 1987. Intraspecific phylogeography: the mitochondrial DNA bridge between population genetics and systematics. Ann Rev Ecol and Syst. 18:489–522.

Barry JP, Baxter CH, Sagarin RD, Gilman SE. 1995. Climate-related, long-term faunal changes in a California rocky intertidal community. Science. 267:672–675.

Belmar-Pérez J. 1991. Madurez gonádica y ciclo reproductor del caracol panocha (*Astraea undosa* Wood, 1828; Gasterópodo: Turbinidae) en Bahía Tortugas, Baja California Sur. Anales del ICMyL UNAM. 18:169–187.

Benzie JH. 1999. Genetic structure of coral reef organisms: ghosts of dispersal past. Int Comp Biol. 39:131–145.

Bernardi G, Talley D. 2000. Genetic evidence for limited dispersal in the coastal California killifish, *Fundulus parvipinnis*. J Exp Mar Biol Ecol. 255:187–199.

Bird CE, Holland BS, Bowen BW, Toonen RJ. 2007. Contrasting phylogeography in three endemic Hawaiian limpets (*Cellana spp.*) with similar life histories. Mol Ecol. 16:3173–3186.

Clement M, Posada D, Crandall KA. 2000. TCS: a computer program to estimate gene genealogies. Mol Ecol. 9:1657–1659.

Costello C, Rassweiler A, Siegel D, De Leo G, Micheli F, Rosenberg A. 2010. The value of spatial information in MPA network design. Proc Natl Acad Sci USA. 107:18294–18299.

Cowen RK. 2000. Connectivity of marine populations: open or closed? Science. 287:857–859.

Cowen RK, Sponaugle S. 2009. Larval dispersal and marine population connectivity. Ann Rev Mar Sci. 1:443–466.

Cudney-Bueno R, Bourillón L, Sáenz-Arroyo A, Torre-Cosío J, Turk-Boyer P, Shaw WW. 2009. Governance and effects of marine reserves in the Gulf of California, Mexico. Ocean Coast Manage. 52:207–218.

Cumming GS, Cumming DHM, Redman CL. 2006. Scale mismatches in social-ecological systems: causes, consequences, and solutions. Ecol Soc. 11:14.

Dawson MN, Grosberg RK, Stuart YE, Sanford E. 2010. Population genetic analysis of a recent range expansion: mechanisms regulating the poleward range limit in the volcano barnacle Tetraclita rubescens. Mol Ecol. 19:1585–1605.

Erlandson JR, Tveskov MA, Byram RS. 1998. The development of maritime adaptations on the southern coast of North America. Arctic Anthropology. 35:6–22.

Excoffier L, Laval G, Schneider S. 2005. Arlequin (version 3.0): an integrated software package for population genetics data analysis. Evol Bioinform Online. 1:47–50.

Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R. 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Mol Marine Biol Biotechnol. 3:294–299.

Forgeng EE. 1992. Archeology, ecology, and site-formation processes at the Daisy Cave midden, San Miguel Island, California [master's thesis]. [Eugene (OR)]: Department of Anthropology, University of Oregon.

Gawarkiewicz GG, Monismith S, Largier J. 2007. Observing larval transport processes affecting population connectivity: progress and challenges. Oceanography. 20:40–53.

Gluyas-Millán M, Quinonez-Velazquez C, Talavera-Maya J. 2002. Effect of El Nino 1997–1998 on the snail *Astraea undosa* (Wood) population along the Baja California western coast. J Shellfish Res. 21:831–834.

Graham M. 2003. Ice ages and ecological transitions on temperate coasts. Trends Ecol Evol. 18:33–40.

Graham MH. 2004. Effects of local deforestation on the diversity and structure of southern California giant kelp forest food webs. Ecosystems. 7:341–357.

Graham MH, Kinlan BP, Grosberg RK. 2010. Post-glacial redistribution and shifts in productivity of giant kelp forests. Proc Biol Sci. 277:399–406.

Grantham BA, Eckert GL, Shanks AL. 2003. Dispersal potential of marine invertebrates in diverse habitats. Ecol Appl. 13:108–116.

Gruenthal KM, Burton RS. 2008. Genetic structure of natural populations of the California black abalone (*Haliotis cracherodii Leach, 1814*), a candidate for endangered species status. J Exp Mar Biol Ecol. 355:47–58.

Guzmán Del Próo S. 2003. Larval and early juvenile development of the wavy turban snail, *Megastraea undosa* (Wood, 1828) (Gastropoda: Turbinidae). Veliger. 46:4.

Harpending HC. 1994. Signature of ancient population growth in a low-resolution mitochondrial DNA mismatch distribution. Hum Biol. 66:591–600.

Harpending HC, Batzer MA, Gurven M, Jorde LB, Rogers AR, Sherry ST. 1998. Genetic traces of ancient demography. Proc Natl Acad Sci USA. 95:1961–1967.

Hart MW, Marko PB. 2010. It's about time: divergence, demography, and the evolution of developmental modes in marine invertebrates. Integr Comp Biol. 50:643–661.

Hedgecock D, Barber P, Edmands S. 2007. Genetic approaches to measuring connectivity. Oceanography. 20:70–79.

Hellberg ME. 2007. Footprints on water: the genetic wake of dispersal among reefs. Coral Reefs. 26:463–473.

Hellberg ME, Balch DP, Roy K. 2001. Climate-driven range expansion and morphological evolution in a marine gastropod. Science. 292:1707–1710.

Hellberg ME, Burton RS, Neigel JE, Palumbi SR. 2002. Genetic assessment of connectivity among marine populations. Bull Mar Sci. 70:18.

Hewitt G. 1996. Some genetic consequences of ice ages, and their role in divergence and speciation. Biol J Linn Soc. 58:247–276.

Hewitt G. 2000. The genetic legacy of the Quaternary ice ages. Nature. 405:907–913.

Hewitt G. 2004. Genetic consquences of of climatic oscillations in the Quaternary. Phil Trans R Soc Lond B. 359:183–195.

Hickerson MJ, Cunningham CW. 2005. Contrasting quaternary histories in an ecologically divergent sister pair of low-dispersing intertidal fish (Xiphister) revealed by multilocus DNA analysis. Evolution. 59:344–360.

Hickey BM. 1998. Coastal oceanography of western North America from the tip of Baja California to Vancouver Island. In: Robinson AR, Brink KH, editors. The sea. New York: John Wiley and Sons. p. 345–393.

Hilborn R, Orensanz JM, Parma AM. 2005. Institutions, incentives and the future of fisheries. Philos Trans R Soc Lond, B, Biol Sci. 360:47–57.

Hugall A, Moritz C, Moussalli A, Stanisic J. 2002. Reconciling paleodistribution models and comparative phylogeography in the Wet Tropics rainforest land snail *Gnarosophia bellendenkerensis* (Brazier 1875). Proc Natl Acad Sci USA. 99:6112–6117.

Ibrahim KM, Nichols RA, Hewitt GM. 1996. Spatial patterns of genetic variation generated by different forms of dispersal during range expansion. J Hered. 77:282–291.

Jacobs DK, Haney TA, Louie KD. 2004. Genes, diversity, and geologic process on the Pacific Coast. Annu Rev of Earth Pl Sci. 32:601–652.

Jones AG, Ardren WR. 2003. Methods of parentage analysis in natural populations. Mol Ecol. 12:2511–2523.

Jones GP, Planes S, Thorrold SR. 2005. Coral reef fish larvae settle close to home. Curr Biol. 15:1314–1318.

Jost L. 2007. Partitioning diversity into independent alpha and beta components. Ecology. 88:2427–2439.

Kelly RP, Oliver TA, Sivasundar A, Palumbi SR. 2010. A method for detecting population genetic structure in diverse, high gene-flow species. J Hered. 101:423–436.

Kelly RP, Palumbi SR. 2010. Genetic structure among 50 species of the northeastern Pacific rocky intertidal community. PLoS ONE. 5:e8594.

Kennett JP, Ingram BL. 1995. A 20,000-year record of ocean circulation and climate change from the Santa Barbara basin. Nature. 377:510–514.

Kingman J. 1982a. On the genealogy of large populations. J Appl Probab. 19:27–43.

Kingman J. 1982b. The coalescent. Stoch Proc Appl. 13:235–248.

Kingsford MJ, Leis JM, Shanks A, Lindeman KC, Morgan SG, Pineda J. 2002. Sensory environments, larval abilities and local self-recruitment. B Mar Sci. 70:309–340.

Kinlan BP, Gaines SD. 2003. Propagule dispersal in marine and terrestrial environments: a community perspective. Ecology. 84:2007–2020.

Largier JL. 2003. Considerations in estimating larval dispersal distances from oceanographic data. Ecol Appl. 13:71–89.

Laval G, Excoffier L. 2004. SIMCOAL 2.0: a program to simulate genomic diversity over large recombining regions in a subdivided population with a complex history. Bioinformatics. 20:2485–2487.

Marko PB. 2004. "What's larvae got to do with it?" Disparate patterns of post-glacial population structure in two benthic marine gastropods with identical dispersal potential. Mol Ecol. 13:597–611.

Marko PB, Hart MW. 2011. The complex analytical landscape of gene flow inference. Trends Ecol Evol (Amst). 26:448–456.

Marko PB, Hoffman JM, Emme SA, Mcgovern TM, Keever CC, Cox LN. 2010. The "Expansion-Contraction" model of Pleistocene biogeography: rocky shores suffer a sea change? Mol Ecol. 19:146–169.

Martone RG, Micheli F. 2012. Geographic variation in demography of a temperate reef snail: importance of multiple life-history traits. Mar Ecol-Prog Ser. 457:85–99.

McCay BJ, Micheli F, Ponce-Diáz G, Murray G, Shester G, Ramirez-Sanchez S, Weisman W. Forthcoming. Community-based concessions on the Pacific coast of Mexico. Marine Policy.

Miller KJ, Maynard BT, Mundy CN. 2008. Genetic diversity and gene flow in collapsed and healthy abalone fisheries. Mol Ecol. 18:200–211.

Muhs DR, Simmons KR, Kennedy GL, Ludwig KR, Groves LT. 2006. A cool Pacific Ocean at the close of the last interglacial complex. Quat Sci Rev. 25:235–262.

Nei M, Jin L. 1989. Variances of the average numbers of nucleotide substitutions within and between populations. Mol Biol Evol. 6:290–300.

Palumbi SR. 2003. Population genetics, demographic connectivity, and the design of marine reserves. Ecol Appl. 13:146–158.

Palumbi SR. 2004. Marine reserves and ocean neighborhoods: the spatial scale of marine populations and their management. Annu Rev Envir Res. 29:31–68.

Pinsky ML, Montes HR Jr, Palumbi SR. 2010. Using isolation by distance and effective density to estimate dispersal scales in anemonefish. Evolution. 64:2688–2700.

Pinsky ML, Palumbi SR, Andréfouët S, Purkis SJ. 2012. Open and closed seascapes: where does habitat patchiness create populations with high fractions of self-recruitment? Ecol Appl. 22:1257–1267.

Planes S, Jones GP, Thorrold SR. 2009. Larval dispersal connects fish populations in a network of marine protected areas. Proc Natl Acad Sci USA. 106:5693–5697.

Prince J. 2005. Combating the tyranny of scale for haliotids: micro-management for microstocks. B Mar Sci. 76:557–578.

Prince J. 2010. Rescaling fisheries assessment and management: a generic approach access rights, change agents, and toolboxes. B Mar Sci. 86:197–219.

Prince J, Walters C, Ruiz-Avila B, Sluczanowski P. 1998. Territorial user's rights and the Australian abalone (i.) fishery. In: Jamieson GS, Campbell A, editors. Proceedings North Pacific Symposium on Invertebrate Stock Assessment and Management. Ottawa (Canada): National Research Council of Canada. p. 367–375.

Puritz JB, Toonen RJ. 2011. Coastal pollution limits pelagic larval dispersal. Nature Commun. 2:226.

RDC Team (R Development Core Team). 2008. R: A Language and Environment for Statistical Computing. Vienna (Austria): R Foundation for Statistical Computing.

Rocha-Olivares A, Vetter R. 1999. Effects of oceanographic circulation on the gene flow, genetic structure, and phylogeography of the rosethorn rockfish (*Sebastes helvomaculatus*). Can J Fish Aquat Sci. 56:803–813.

Rogers AR, Harpending H. 1992. Population growth makes waves in the distribution of pairwise genetic differences. Mol Biol Evol. 9:552–569.

Roman J, Palumbi SR. 2003. Whales before whaling in the North Atlantic. Science. 301:508–510.

Rousset F. 1997. Genetic differentiation and estimation of gene flow from *F*-statistics under isolation by distance. Genetics. 145:1219–1228.

Roy K, Jablonski D, Valentine JW. 1995. Latitudinal range shifts of Pleistocene marine mollusks thermally anomalous assemblages revisited: patterns in the extraprovincial latitudinal range shifts of Pleistocene marine mollusks. Geology. 23:1071–1074.

Sale PF, Cowen RK, Danilowicz BS, Jones GP, Kritzer JP, Lindeman KC, Planes S, Polunin NV, Russ GR, Sadovy YJ, et al. 2005. Critical science gaps impede use of no-take fishery reserves. Trends Ecol Evol (Amst). 20:74–80.

Selkoe KA, Toonen RJ. 2006. Microsatellites for ecologists: a practical guide to using and evaluating microsatellite markers. Ecol Lett. 9:615–629.

Selkoe KA, Watson JR, White C, Horin TB, Iacchei M, Mitarai S, Siegel DA, Gaines SD, Toonen RJ. 2010. Taking the chaos out of genetic patchiness: seascape genetics reveals ecological and oceanographic drivers of genetic patterns in three temperate reef species. Mol Ecol. 19:3708–3726.

Shanks AL, Grantham BA, Carr MH. 2003. Propagule dispersal distance and the size and spacing of marine reserves. Ecol Appl. 13:159–169.

Siegel D, Kinlan B, Gaylord B, Gaines S. 2003. Lagrangian descriptions of marine larval dispersion. Mar Ecol-Prog Ser. 260:83–96.

Simpson JJ, Lynn RJ. 1990. A mesoscale eddy dipole in the offshore California current. J Geophy Res. 95:13,009–13,022.

Singh-Cabanillas J. 1996. Pesqueria de caracol panocha. In Casas-Valdez M, Ponce-Diaz G, editors. La Paz (Mexico): Estudio del Potencial Pesquero y Acuícola de Baja California. p. 43–58.

Slatkin M. 1993. Isolation by distance in equilibrium and non-equilibrium populations. Evolution. 47:264–279.

Slatkin M, Hudson RR. 1991. Pairwise comparisons of mitochondrial DNA sequences in stable and exponentially growing populations. Genetics. 129:555–562.

Strathman MF. 1987. Reproduction and development of marine invertebrates of the northern Pacific Coast. Seattle (WA): University of Washington Press.

Taniguchi, IK., Rogers-Bennett L. 2001. Wavy turban snail. In California's living marine resources: a status report. In: Leet WS, Dewess CM, Larson Klingbeil RE, editors. CDFG, Univ. of Calif. Agr. Nat. Res. Publ. SG01-11, pp. 140–141.

Thorson G. 1950. Reproductive and larval ecology of marine bottom invertebrates. Biol. Rev. 25:1–45.

Timmers MA, Bird CE, Skillings DJ, Smouse PE, Toonen RJ. 2012. There's no place like home: crown-of-thorns outbreaks in the central pacific are regionally derived and independent events. PLoS ONE. 7:e31159.

Valentine J, Jablonski D. 1993. Species diversity in ecological communities: historical and geographical perspectives. Chicago (IL): University of Chicago Press.

Waples R. 1998. Separating the wheat from the chaff: patterns of genetic differentiation in high gene flow species. J Hered. 89:438.

Watson JR, Mitari S, Siegel DA, Caselle JE, Dong C, McWilliams JC. 2010. Realized and potential larval connectivity in the Southern California Bight. Mar Ecol Prog Ser. 401:31–48.

Weersing K, Toonen R. 2009. Population genetics, larval dispersal, and connectivity in marine systems. Mar Ecol-Prog Ser. 393:1–12.

White C, Costello C. 2011. Matching spatial property rights fisheries with scales of fish dispersal. Ecol Appl. 21:350–362.

White C, Selkoe KA, Watson J, Siegel DA, Zacherl DC, Toonen RJ. 2010. Ocean currents help explain population genetic structure. P Roy Soc Lond B. 277:1685–1694.

Wilson AB. 2006. Genetic signature of recent glaciation on populations of a near-shore marine fish species (*Syngnathus leptorhynchus*). Mol Ecol. 15:1857–1871.

Woodson CB, Tyburczy J, Barth JA, McManus MA, Caselle J, Carr MH, Malone D, Raimondi PT, Washburn L, Menge B, Palumbi SR. 2012. Coastal fronts set recruitment and connectivity patterns across multiple taxa. Limnol Oceanogr. 57:582–596.

Wright S. 1978. Evolution and the genetics of populations. A treatise in four volumes. Volume 4: variability within and among natural populations. Chicago (IL): University of Chicago Press.

Zacherl D, Gaines SD, Lonhart SI. 2003. The limits to biogeographical distributions: insights from the northward range extension of the marine snail, *Kelletia kelletii*. J Biogeogr. 30:913–924.

Zaytsev O, Cervantes-Duarte R, Montante O, Gallegos-Garcia A. 2003. Coastal upwelling activity on the Pacific shelf of the Baja California Peninsula. J Oceanogr. 59:489–502.

Received November 8, 2011; First decision January 24, 2012; Accepted January 21, 2013

Corresponding Editor: Brian W Bowen