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RESEARCH ARTICLE

Genetic discontinuity among regional populations of *Lophelia pertusa* in the North Atlantic Ocean

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Abstract Knowledge of the degree to which populations are connected through larval dispersal is imperative to effective management, yet little is known about larval dispersal ability or population connectivity in *Lophelia pertusa*, the dominant framework-forming coral on the continental slope in the North Atlantic Ocean. Using nine microsatellite DNA markers, we assessed the spatial scale and pattern of genetic connectivity across a large portion of the range of *L. pertusa* in the North Atlantic Ocean. A Bayesian modeling approach found four distinct genetic groupings corresponding to ocean regions: Gulf of Mexico, coastal southeastern U.S., New England Seamounts, and eastern North Atlantic Ocean. An isolation-by-distance pattern was supported across the study area. Estimates of pairwise population differentiation were greatest with the deepest populations, the New England Seamounts (average $F_{ST} = 0.156$). Differentiation was intermediate with the eastern North Atlantic populations ($F_{ST} = 0.085$), and smallest between southeastern U.S. and Gulf of Mexico populations ($F_{ST} = 0.019$), with evidence of admixture off the southeastern Florida peninsula. Connectivity across larger geographic distances within regions suggests that some larvae are broadly dispersed. Heterozygote deficiencies were detected within the majority of localities suggesting deviation from random mating. Gene flow between ocean regions appears restricted, thus, the most effective management scheme for *L. pertusa* involves regional reserve networks.

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Introduction

Molecular studies can provide valuable insights into patterns of differentiation and connectivity in marine systems (Levin 2006; Cowan and Sponaugle 2009). Although few molecular studies have been undertaken for deep-sea organisms, strong genetic structuring has been detected at a variety of scales for many species with wide geographic distributions and no obvious isolating barriers (Rogers 2002; Zardus et al. 2006). Closely related (sibling) or morphologically similar (cryptic) species appear to be common in the deep-sea (Rogers 2002).

An ecologically important habitat of deep-sea continental margins, seamounts and fjords is created by the

cold-water coral *Lophelia pertusa* (Rogers 1999). This nearly cosmopolitan species has most commonly been collected in the eastern North Atlantic Ocean (ENAO), but also occurs in all oceans except polar regions (Roberts et al. 2009). Some of the best developed, most extensive reefs in U.S. waters occur on the continental slope off the southeastern coast of the United States (SEUS; Ross and Nizinski 2007), and to a lesser extent in the Gulf of Mexico (GOM; Brooke and Schroeder 2007). Reefs and mounds are formed by successive coral growth, collapse, and sediment entrapment over a time frame of thousands to millions of years (Roberts et al. 2009). Such reefs tend to cluster in 'provinces' where adequate water movement and food supply favor coral growth (Roberts et al. 2006). Cold-water coral reefs created by *L. pertusa* support a rich fauna comprised of many fishes (Ross and Quattrini 2007, 2009) and invertebrates (Rogers 1999; Reed et al. 2006; Roberts et al. 2006).

The valuable food and energy resources available on continental margins (Levin and Dayton 2009) and seamounts (Clark et al. 2010) make these ocean environments increasingly threatened by human activities such as destructive fishing practices, carbon capture and storage, and increased energy exploration and drilling activities (Davies et al. 2007). Additionally, global climate change may alter ocean temperatures and circulation as well as increase acidification; potentially with dramatic consequences to deep coral reefs (Guinotte et al. 2006; Davies et al. 2007; Levin and Dayton 2009).

Marine reserve networks or protected areas can be powerful tools for maximizing resilience of shallow coral reefs to disturbance (Bellwood et al. 2004). The effective design of marine reserves requires a spatially explicit understanding of larval dispersal (Palumbi 2003). Reserve networks are likely to work well as conservation tools if spacing between localities is less than average dispersal distances (Palumbi 2003). Specifically, the direction, distance, and frequency of larval dispersal are of importance to the size and spacing of reserves (Underwood et al. 2009). Likewise, incorporation of information about larval dispersal among deep reefs may allow for effective protection and avoidance measures to be taken.

The patterns and scales of coral larval dispersal are poorly known (VanOppen and Gates 2006), particularly for the deep-sea species. Difficulty in tracking movements of larvae through the vast and complex oceanic environment has hampered our abilities to directly quantify dispersal and connectivity (Cowan and Sponaugle 2009). For many marine organisms, larval duration is positively correlated with dispersal distance (Bohonak 1999; Shanks et al. 2003). Following expectations, several coral species with brooded larvae that settle quickly exhibit higher levels of genetic structuring than spawning species whose larvae spend extended periods of time in the plankton (e.g. Hellberg 1996; Ayre and Hughes 2000; Whitaker 2004; Underwood et al. 2009). However, molecular investigations have shown that numerous marine species are more spatially structured than would be predicted based on life history characteristics or geographic distributions (Barber et al. 2000; Knowlton 2000; Warner and Cowen 2002; Swearer et al. 2002; Taylor and Hellberg 2003; Ayre and Hughes 2004; Baums et al. 2005; Cowen et al. 2006; Fontaine et al. 2007; Rosel et al. 2009). In fact, for broadcast spawning coral species, evidence of limited dispersal between reefs or regions is mounting (Ayre and Hughes 2000, 2004; Whitaker 2004; Underwood et al. 2007, 2009). Such studies highlight that quantification of larval dispersal distance is complicated because both biological and physical factors that influence dispersal vary in space and time, such as oceanographic circulation patterns, timing of reproduction, larval behavior and duration, and the availability of suitable habitat (Cowan and Sponaugle 2009). Therefore, larval dispersal distances may be influenced by many factors, each of which may vary across the range of a species (Sotka et al. 2004; Ayre and Hughes 2004; Selkoe et al. 2008).

The majority of deep-sea coral species surveyed, including *L. pertusa,* produce lecithotrophic (non-feeding) larvae, yet little is known about larval duration or behavior (Waller and Tyler 2005). Thus, predictions of larval dispersal potential for *L. pertusa* are especially challenging. The only previous population genetics study of *L. pertusa* reported substantial genetic structuring between continental margin and fjord populations in the ENAO (LeGoff-Vitry et al. 2004a). Moderate, but significant, genetic differentiation was observed among populations occurring on the eastern Atlantic continental margin, indicating that the majority of recruitment was highly localized. The observed genetic differentiation among populations could not be explained by geographic distances separating populations. Significant inbreeding was detected in several populations suggesting that effective gene flow is spatially restricted and self-recruitment by sexually produced larvae is the predominant form of colonization. Also, the existence of multiple (cryptic) species within *L. pertusa* was suggested by LeGoff-Vitry et al. (2004b) based upon high mitochondrial DNA sequence divergence between the ENAO and Brazil.

The goal of our study was to examine patterns of connectivity among *L. pertusa* communities at various scales across a large portion of the species' range in the NAO from the GOM to Norway (distances of 22–9000 km between sites); and across a wide range of depths (140–1679 m). A novel suite of nine microsatellite markers was utilized to analyze gene flow in *L. pertusa,* concentrating on the GOM and SEUS regions, and including the

New England Seamounts (NES) for the first time. To allow for comparisons with LeGoff-Vitry et al. (2004a), as well as broadening the perspective of connectivity in *L. pertusa*, continental slope and Norwegian fjord communities from the ENAO were analyzed. Although substantial structuring between the ENAO offshore and fjord populations was reported (see above), we hypothesized that gene flow may be higher in the western NAO. Because the overall flows of the Loop and Gulf Stream currents are predictable, generally unidirectional, and overlay the deep-coral habitats, it is likely that these currents facilitate connectivity. Specifically, we aimed to define population structuring across the study area, and to examine patterns of genetic diversity within regions. Results are discussed in terms of effective management of these unique and fragile ecosystems.

Materials and methods

Coral sampling scheme

Small fragments from 401 *L. pertusa* colonies were collected during 12 cruises occurring between June 2003 and February 2008. Samples originated from 16 deep reef localities (Table 1; Fig. 1a): four localities in the GOM

Table 1 Localities, collection sites with location and average depth, sample sizes (number of colonies genotyped), number of genets (unique multi-locus genotypes), and proportion of clones for *L. pertusa* samples analyzed in this study

Ocean region	Locality	Collection site	Latitude °N	Longitude °W	Depth (m)	No. samples	No. genets	No. per locality	Prop. clones
Gulf of Mexico (GOM)	Green Canyon (GC)	Green Canyon 234	27.45	−91.13	501	5	5	7	0
		Green Canyon 354	27.36	−91.50	525	2	2		
	Tanker Gulfpenn (GP)	Mississippi Canyon 497	28.44	−89.32	533	9	6	6	0.333
	Viosca Knoll 862 (VK862)	Viosca Knoll 862	29.06	−88.23	315	23	17	17	0.261
	Viosca Knoll 826 (VK826)	North	29.16	−88.02	455	31	24	74	0.169
		South	29.10	−88.01	462	58	50		
	Total					128	104	104	0.188
Southeastern U.S. (SEUS)	Miami Terrace (MTR)	Pourtales	24.25	−81.79	344	3	3	15	0.211
		North	26.10	−79.84	287	9	5		
		East	25.70	−79.87	350	7	7		
	Cape Canaveral (CCN)	St. Lucie Bump	27.21	−79.60	700	4	4	24	0.143
		South	28.04	−79.61	737	5	3		
		Central	28.29	−79.61	699	4	3		
		Cocoa Beach	28.32	−79.75	430	10	8		
		North	28.80	−79.62	740	5	6		
	Jacksonville (JAX)	South	30.52	−79.66	591	21	19	24	0.077
		North	30.80	−79.64	557	5	5		
	Savannah Banks (SAV)		31.74	−79.20	511	16	16	16	0
	Stetson (STS)	South	31.83	−77.61	680	9	8	38	0.026
		West	32.02	−77.67	626	11	11		
		North	32.26	−77.48	589	19	19		
	Cape Fear (CF)		33.57	−76.46	394	23	20	20	0.130
	Cape Lookout (CLO)	South	34.32	−75.79	386	23	16	58	0.194
		North	34.21	−75.88	398	49	42		
	Total					220		195	0.114
New England Seamounts (NES)	Manning (MAN)		38.22	−60.52	1418	6	6	6	0
	Rehoboth (REH)		37.47	−59.95	1679	7	7	7	0
	Total					13		13	0
Eastern North Atlantic Ocean (ENAO)	Rockall Bank (RB)		55.50	−15.80	562	12	9	9	0.250
	Mingulay Reef (MNG)		56.81	−7.43	153	6	6	6	0
	Trondheimfjord (TRF)		63.28	9.55	140	18	14	14	0.222
	Total					36		29	0.194
Total						401		341	0.150

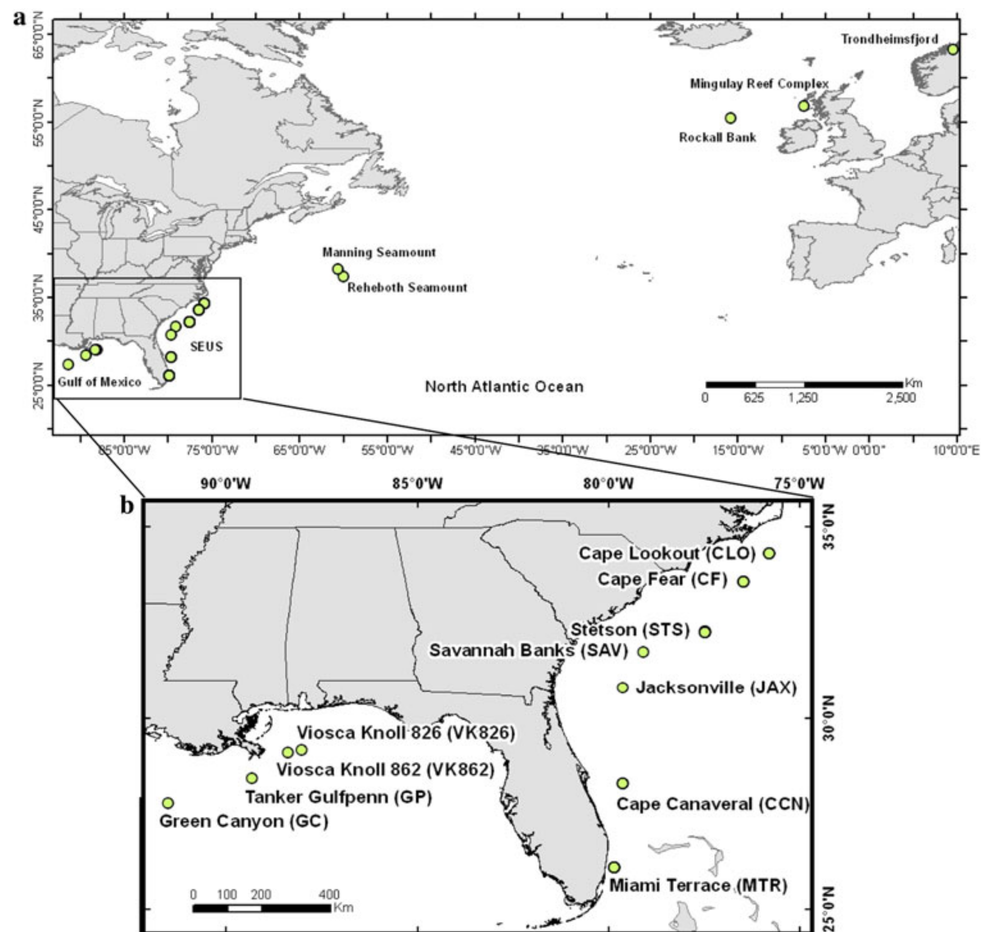

Fig. 1 Map of *L. pertusa* collection localities in **a** the North Atlantic Ocean; and **b** the Gulf of Mexico and western North Atlantic Ocean, off the southeastern U.S. coast

(315–525 m); seven localities in the western NAO off the SEUS (287–740 m); two seamounts off New England (NES, 1418–1679 m); and three localities in the eastern NAO (ENAO, 140–562 m). Small tissue samples were preserved in 95% ETOH, DMSO and/or FTA® Technology Classic card (Whatman®).

The majority of samples from the GOM and SEUS (Fig. 1b) were collected using the *Johnson-Sea-Link* (*JSL*, Harbor Branch Oceanographic Institute) submersible (June 2004–July 2007). Prior to collection with either the *JSL* manipulator claw, the suction sampler, or the Bushmaster Jr. collection device (Urcuyo et al. 2003; Bergquist et al. 2003), collection sites were videotaped and location fixes were established using the Trackpoint II system on the support vessel. Attempts were made to move at least 5 m between *L. pertusa* samples to avoid potentially re-sampling the same genetic individual (clones). Supplemental samples were obtained at a few sites by otter trawl deployed around coral banks to collect benthic megafauna (SEUS, September 2006; GOM, August 2007). Although the trawling objective was to avoid major coral areas, some living *L. pertusa* was collected as the trawl operated close to coral mounds (see Ross and Quattrini 2007 for trawling details).

Lophelia pertusa samples from the Rockall Bank area (June–July 2006) and the Mingulay Reef Complex (July 2006) in the ENAO (Fig. 1a) were obtained using a custom designed boxcore (cylindrical barrel of 50 cm diameter and 55 cm high). Samples from Trondheimsfjord, Norway (Fig. 1a) were collected between 119 and 160 m (February 2008) using the remotely operated vehicle (ROV) *Minerva* (Norwegian University of Science and Technology). At this site, coral colonies grow attached to a vertical wall or beneath overhangs. Samples were collected using a landing net attached to the ROV into which small coral-pieces were scraped off the wall. *L. pertusa* samples from NES were collected (June 2003–August 2005) using the ROV *Hercules* (University of Rhode Island).

Genetic characterization of corals

Total DNA was isolated from preserved coral tissue and/or FTA® card hole-punches using the tissue protocol from the PureGene DNA extraction kit (Gentra Systems Inc., Minneapolis, Minnesota). PCR conditions for amplification of nine microsatellite loci designed for *L. pertusa* are described in Morrison et al. (2008) and were carried out in

20 μl reactions. Amplifications of markers designed for *L. pertusa* from the eastern North Atlantic Ocean (LeGoff and Rogers 2002) were not consistent across all sampled localities; therefore, these data were not included. Fluorescent DNA fragments were analyzed using an ABI PRISM 3100 Genetic Analyzer (Applied Biosystems) with GeneScan-500 ROX size standard. Genescan 2.1 analysis software and Genotyper 3.7 fragment analysis software (Applied Biosystems) were used to score, bin, and output allelic data. The program MICROCHECKER v. 2.2.3 (Van Ooseterhaut et al. 2004) was used to check for scoring errors and large allele dropout. Individuals with identical multilocus genotypes were identified using the program GENECAP (Wilberg and Dreher 2004). The probability of identity (i.e., the probability of two individuals sharing the same genotype) was calculated using GENECAP. A match probability of $P_{SIB} < 0.05$ was set, as suggested by Woods et al. (1999).

Intrapopulation genetic diversity

Loci were tested for fit to statistical assumptions of population genetic analyses. Observed and expected heterozygosities under Hardy–Weinberg equilibrium (HWE), and fixation indices per locus and locality were calculated using GENETIX v. 4.0.5.2 (Belkhir et al. 2001). Exact tests for HWE were performed in Genepop v. 4 (Rousset 2008). To assess levels of inbreeding, Weir and Cockerham's (1984) estimators f and F, analogous to Wright's (1951) F_{IS} and F_{IT}, respectively, were calculated for each locality and tested for statistical significance by 1,000 permutations with GENETIX. As sample sizes at different localities varied, allelic richness, or the number of alleles per locality, was calculated by rarefaction (Kalinowski 2004) to compensate for unequal sample sizes using the program HP-Rare (Kalinowski 2005). Similarly, private allelic richness was calculated by rarefaction for each locality in HP-Rare. Loci were tested for linkage disequilibrium using the exact test of Raymond and Roussett (1995) for all pairs of loci in Genepop. Sequential Bonferroni adjustments for multiple tests (Rice 1989) were used on these and other multiple tests.

Population differentiation

Several techniques were used to describe genetic relationships between populations or individuals as estimated from microsatellite data. First, a Bayesian model-based clustering approach without a priori knowledge of populations (Pritchard et al. 2000) was implemented in STRUCTURE v. 2.3.2 (Hubisz et al. 2009). This method infers the number of genetic clusters (K) from multilocus genotype data by minimizing Hardy–Weinberg and linkage disequilibrium among loci within groups, and then assigns individuals (probabilistically) to each cluster. Because models utilizing collection location information as priors are useful for small data sets and weak structuring (Hubisz et al. 2009), locality designations were included as priors. Settings for all runs also included an admixture model (i.e., individuals may have mixed ancestry), correlated allele frequencies (Falush et al. 2003), and 20,000 MCMC iterations after a burn-in of 10,000 iterations. Ten independent chains were run to test each value of K from $K = 1$–20. The optimum number of clusters was determined by evaluating the values of K as the highest mean ln Pr(X|K) (Pritchard et al. 2000), and ΔK (Evanno et al. 2005). This information was compiled and graphed using STRUCTURE Harvester v.0.56.1 (Earl. 2009, http://taylor0.biology.ucla.edu/struct_harvest). Each cluster identified in the initial STRUCTURE run was analyzed separately using the same settings to identify potential within-cluster structure (Evanno et al. 2005).

Second, pairwise genetic distances between localities were calculated using the chord distance (D_c; Cavalli-Sforza and Edwards 1967) in Populations v. 1.2.30 (Langella, http://bioinformatics.org/~tryphon/populations/). Chord distances were subjected to a neighbor-joining algorithm and strength of support for nodes was tested by bootstrapping over loci for 10,000 replications in Populations.

Third, locality pairwise F_{ST} (Weir and Cockerham 1984) and R_{ST} (Slatkin 1995) estimates were calculated using analyses of molecular variance (AMOVA; Excoffier et al. 1992) and tested for significance (difference from zero) by 9,999 permutations using GenAlEx v. 6.1 (Peakall and Smouse 2006). Both estimates identify the proportion of total genetic diversity between localities; the latter takes into account differences in allele sizes. AMOVAs were also used to partition genetic variation among the clusters suggested by STRUCTURE, and among localities within clusters, using Arlequin v 3.1 (Excoffier et al. 2005).

Lastly, isolation by distance (IBD; Wright 1943) was examined by testing the correlation between genetic and marine geographical distances between locality pairs at several geographic scales. The regression of genetic distance ($F_{ST}/(1 - F_{ST})$ versus the logarithm of geographic distance was tested using Mantel randomization tests (Mantel 1967), as shown to be satisfactory for populations in two-dimensional habitats (Rousset 1997). Separate Mantel tests were run for the entire data set, as well as for the GOM and SEUS populations which had sufficient sampling. Straight-line marine geographic distances between populations were estimated using ARCGIS v. 9.2 (Environmental Systems Research Institute). Mantel tests were performed using the MXCOMP routine in NTSYS-PC v. 2.10 (Rohlf 2000) using 9,999 permutations.

Results

Intrapopulation genetic diversity

Genotypes at 9 microsatellite loci were determined for 401 *L. pertusa* colonies representing 28 collections at 16 localities from the GOM, SEUS, NES and ENAO (Fig. 1). Using the program MICROCHECKER, we did not find evidence of scoring errors due to stuttering or large allele drop-out, and likewise, using the program GENECAP, we did not find any multi-locus genotypes that differed by only one or two alleles, often indicative of scoring errors.

Of the 401 *L. pertusa* genotyped, 60 individuals (15%) had non-unique multi-locus genotypes (MLGs, Table 1). The proportion of clones was generally low (average 0.13) and varied by locality, ranging from 0 to 0.33 (Table 1). The majority of identical MLGs were represented twice, but a few were represented three times, and all identical genotypes were from the same collection site (GOM = VK826 and VK862; SEUS = all sites except SAV; ENAO = RB, TRF). Given the low probability that two unrelated individuals sampled from the same population share identical MLGs ($P_{SIB} = 4.32 \times 10^{-5}$), these individuals were considered clonemates produced by asexual fragmentation. Only one of each unique multilocus genotype was included in further analyses.

The employed microsatellite markers were highly polymorphic with 348 alleles detected, ranging from 12 alleles at *Lpe*A5 to 69 alleles at *Lpe*D3 and averaged 38.7 alleles per locus (Table 2). The mean number of alleles per locus found at one locality varied from 4.65 in the Manning Seamount locality to 24.33 in the Cape Lookout locality (Table 2). Observed heterozygosities were high in the majority of locus-by-population comparisons, ranging between 0.11 and 1.0 (Table 2). Private alleles were detected at a majority of localities, with the exception of Green Canyon and the *Gulfpenn* shipwreck in the western and central GOM, respectively (Table 2). After rarefaction to compensate for unequal sample sizes, the Stetson Banks and Cape Fear localities in the SEUS had the highest allelic richness and private allelic richness, while the Manning Seamount locality had the lowest (Fig. 2).

When organized by collection localities, randomization tests showed that the 341 unique multilocus genotypes were consistent with HWE for the majority of locus-by-collection comparisons (Table 2). However, significant heterozygote deficits (positive F_{IS} values) were detected in 28 out of 144 locus-by-locality comparisons (19%, Table 2). Significant heterozygote deficits were detected at seven of the nine loci, and in 12 of 16 localities. Since heterozygote deficits were not detected across all populations for any locus, these results were not consistent with presence of null alleles. Instead, the observed positive values of f indicated that inbreeding was apparent in all localities and was significant in 14 of 16 localities when estimated across loci (Table 2). No linkage disequilibrium was detected among loci, as none of the 576 tests for linkage disequilibrium were significant after adjustment for multiple tests ($\alpha = 0.05$, $P < 0.0009$).

Population differentiation

Posterior probability values from the STRUCTURE analysis suggested the data were best explained by three genetic groupings (clusters) of *L. pertusa* localities ($K = 3$, Fig. 3). Ten independent runs at $K = 3$ produced the same clustering solution illustrated in Fig. 3, corresponding to geographic groupings of localities into oceanic regions as follows: GOM [A], SEUS [B], and NAO [C], which included both NES and ENAO localities. Additional hierarchical STRUCTURE runs were performed on each of the initial $K = 3$ clusters: sub-structuring was detected only for the North Atlantic cluster [C], which was further subdivided into NES [C1] and ENAO [C2] sub-clusters (Fig. 3, bottom). Results from the subsequent run of STRUCTURE indicated that average proportion of membership to cluster-of-origin was stronger for cluster C2 (ENAO) than for the C1 (NES) cluster (Table 3).

For the majority of localities, a high proportion of individuals were assigned to the STRUCTURE-defined cluster from which they were collected (cluster-of-origin ≥90%, Table 3). Exceptions, where individual membership assignments to cluster-of-origin averaged less than 90%, included Miami Terrace and Cape Canaveral localities off the coast of southern Florida [B], as well as Mingulay and Trondheimfjord localities [C] (Table 3).

To investigate evolutionary relationships in allele frequencies, pairwise genetic distances (D_C) were calculated among localities, with several localities from close geographic proximity grouped together in order to increase power of the analysis due to increased sample sizes (GP and GC = western GOM; MAN and REH = NES; RB and MNG = eastern Atlantic). The chord distance matrix is illustrated as an unrooted neighbor-joining tree (Fig. 4). In concordance with results produced by the STRUCTURE analysis, *L. pertusa* localities formed three groupings corresponding to ocean regions, and NES formed an independent grouping within the NAO cluster (Fig. 4; 100% bootstrap).

Fixation index (F_{ST}) estimates between populations (Table 4, below diagonal), ranged from 0 to 0.178, and were more variable than chord distances. Although it should be noted that sample sizes were small for the NES, pairwise estimates of F_{ST} were highest and significant for comparisons between NES and other localities (0.133–0.178, average = 0.156). Trans-Atlantic pairwise

Table 2 Genetic diversity and differentiation in 16 *L. pertusa* sampling localities characterized using 9 microsatellite markers

Locality	Locus	*Lpe*A5	*Lpe*C120	*Lpe*C142	*Lpe*C151	*Lpe*C44	*Lpe*C52	*Lpe*C61	*Lpe*D3	*Lpe*D5	Mean (P)	f
GC	A (P)	5	5	9	4	8	7	12	9	5	7.11 (0)	
	H_O	0.714	0.833	0.857	0.143	0.714	0.571	1.000	1.000	0.571	0.712	
	H_E	0.673	0.667	0.847	0.663	0.847	0.786	0.908	0.857	0.735	0.776	
	F	0.016	−0.163	0.065	0.813	0.231	0.343	−0.024	−0.091	0.294		**0.160**
GP	A (P)	5	5	8	3	8	6	11	10	4	6.67 (0)	
	H_O	0.667	0.667	0.833	0.600	0.800	0.500	1.000	1.000	0.667	0.748	
	H_E	0.736	0.611	0.819	0.540	0.860	0.750	0.903	0.875	0.681	0.753	
	F	0.184	0.000	0.074	0.000	0.180	0.412	−0.017	−0.053	0.111		0.101
VK862	A (P)	7	11	14 (1)	6 (1)	17 (1)	9	16	13 (1)	6	11.0 (4)	
	H_O	0.625	0.824	0.765	0.313	0.667	0.706	0.941	0.706	0.529	0.675	
	H_E	0.730	0.804	0.881	0.689	0.922	0.766	0.907	0.749	0.661	0.790	
	F	0.176	0.007	0.161	**0.569**	**0.309**	0.109	−0.008	0.088	0.228		**0.176**
VK826	A (P)	9	14	23	8	33	15	34 (1)	33 (2)	12 (1)	20.11 (4)	
	H_O	0.857	0.507	0.851	0.521	0.814	0.712	0.931	0.851	0.353	0.711	
	H_E	0.756	0.660	0.912	0.715	0.939	0.787	0.947	0.874	0.733	0.814	
	F	−0.127	0.238	**0.073**	**0.277**	0.140	0.101	0.025	0.033	**0.524**		**0.133**
MTR	A (P)	6	10	11	5	20 (1)	8	20	14	10 (2)	11.56 (3)	
	H_O	0.667	0.600	0.867	0.357	0.857	0.667	1.000	0.600	0.385	0.667	
	H_E	0.769	0.767	0.844	0.541	0.926	0.727	0.929	0.873	0.793	0.797	
	F	0.167	0.250	0.008	0.372	0.111	0.117	−0.042	**0.344**	**0.544**		**0.198**
CCN	A (P)	7	14	15	6	22 (1)	13 (1)	24	24	10	15.0 (2)	
	H_O	0.870	0.708	0.864	0.350	0.636	0.583	0.792	0.833	0.542	0.686	
	H_E	0.775	0.821	0.878	0.638	0.941	0.571	0.949	0.922	0.646	0.793	
	F	−0.100	0.158	0.040	0.471	**0.345**	0.000	**0.186**	0.117	0.182		**0.157**
JAX	A (P)	8	18	17	7	19	13	25	24 (3)	15 (2)	16.2 (5)	
	H_O	0.870	0.792	0.833	0.409	0.609	0.542	0.958	0.792	0.583	0.710	
	H_E	0.803	0.885	0.893	0.698	0.890	0.608	0.943	0.933	0.681	0.815	
	F	−0.060	0.127	0.088	**0.433**	**0.336**	0.130	0.005	**0.172**	0.164		**0.151**
SAV	A (P)	7	12 (1)	14 (1)	7 (1)	15	10	19	19 (1)	15 (2)	11.0 (6)	
	H_O	0.750	0.733	0.929	0.571	0.533	0.563	0.938	0.688	0.688	0.710	
	H_E	0.807	0.860	0.895	0.684	0.911	0.736	0.934	0.928	0.756	0.835	
	F	0.102	0.181	0.000	0.200	0.443	0.266	0.028	**0.289**	0.122		**0.182**
STS	A (P)	9	24 (5)	24	11 (3)	31 (3)	17 (4)	33	37	14	22.22 (15)	
	H_O	0.868	0.842	1.000	0.424	0.657	0.649	0.921	0.763	0.343	0.719	
	H_E	0.776	0.937	0.936	0.713	0.956	0.760	0.952	0.961	0.688	0.853	
	F	−0.106	**0.114**	−0.055	**0.418**	**0.325**	0.160	0.046	**0.219**	**0.512**		**0.171**
CFR	A (P)	7	12 (1)	17	5	23 (1)	12 (2)	24	27 (5)	18 (1)	16.11 (10)	
	H_O	0.850	0.842	0.947	0.684	0.600	0.800	0.900	0.700	0.650	0.775	
	H_E	0.806	0.875	0.928	0.735	0.945	0.801	0.945	0.954	0.804	0.866	
	F	−0.029	0.065	0.006	0.097	**0.387**	0.027	0.073	**0.191**	**0.216**		**0.131**
CLO	A (P)	10	23	27 (1)	9 (1)	33 (2)	19 (3)	28	45 (1)	25 (2)	24.33 (10)	
	H_O	0.828	0.776	0.897	0.346	0.623	0.690	0.875	0.860	0.473	0.707	
	H_E	0.812	0.895	0.928	0.707	0.949	0.735	0.946	0.957	0.693	0.850	
	F	−0.011	**0.142**	0.043	**0.518**	**0.353**	0.071	0.084	**0.110**	**0.327**		**0.174**
MAN	A (P)	2	8	6	1	3 (1)	2	4	10	5	4.56 (1)	
	H_O	0.167	0.833	0.667	0	0.500	0.000	0.000	0.833	0.400	0.378	
	H_E	0.375	0.819	0.750	0	0.625	0.278	0.720	0.889	0.780	0.582	
	F	0.615	0.074	0.200		0.500	1.000	1.000	0.153	0.568		**0.461**

Table 2 continued

Locality	Locus	*Lpe*A5	*Lpe*C120	*Lpe*C142	*Lpe*C151	*Lpe*C44	*Lpe*C52	*Lpe*C61	*Lpe*D3	*Lpe*D5	Mean (*P*)	*f*
REH	*A* (*P*)	3 (1)	12	7	1	5 (1)	3	5	10 (2)	5 (1)	5.67 (5)	
	H_O	0.286	0.714	0.571	0	0.400	0.571	0.429	0.857	0.667	0.496	
	H_E	0.255	0.908	0.816	0	0.720	0.561	0.765	0.878	0.792	0.633	
	F	−0.044	0.286	0.368		0.529	0.059	**0.500**	0.100	0.245		**0.290**
RB	*A* (*P*)	5	6	11	5	12	2	10	11	5 (1)	8.78 (1)	
	H_O	1.000	0.778	0.889	0.833	0.778	0.111	1.000	0.889	0.111	0.710	
	H_E	0.728	0.691	0.864	0.764	0.895	0.105	0.889	0.864	0.525	0.703	
	F	−0.321	−0.067	0.030	0.000	0.188		−0.067	0.030	**0.810**		0.053
MNG	*A* (*P*)	6	4	10	5 (1)	9	1	11	11	5	11.89 (1)	
	H_O	0.667	0.833	0.833	0.500	0.833	0	1.000	0.833	0.400	0.656	
	H_E	0.750	0.708	0.889	0.736	0.875	0	0.903	0.903	0.680	0.716	
	F	0.200	−0.087	0.153	0.400	0.138		−0.017	0.167	0.500		**0.177**
TRF	*A* (*P*)	8	9	15	7	14	1	17	16	6 (1)	10.11 (1)	
	H_O	0.714	0.786	0.786	0.500	0.857	0	0.929	0.786	0.167	0.614	
	H_E	0.837	0.760	0.918	0.555	0.872	0	0.923	0.911	0.740	0.724	
	F	0.182	0.004	0.181	0.151	0.055		0.032	0.173	**0.792**		**0.191**
Sample (341)	*A* (*P*)	12 (1)	57 (7)	31 (3)	43 (7)	37 (11)	35 (10)	17 (1)	69 (15)	47 (13)	348 (68)	0.163

Given are numbers of observed (*A*) and private (*P*) alleles; H_O and H_E: proportions of observed and expected heterozygotes per locus and site; *F* and *f*: Weir and Cockerham's (1984) estimators of inbreeding calculated and tested for significance (bold) in GENETIX (Belkhir et al. 2001). For each locality and locus, numbers in bold represent significant deviations from Hardy–Weinberg equilibrium after sequential Bonferroni corrections (α = 0.05, $P < 0.0004$). Locality abbreviations given in Table 1

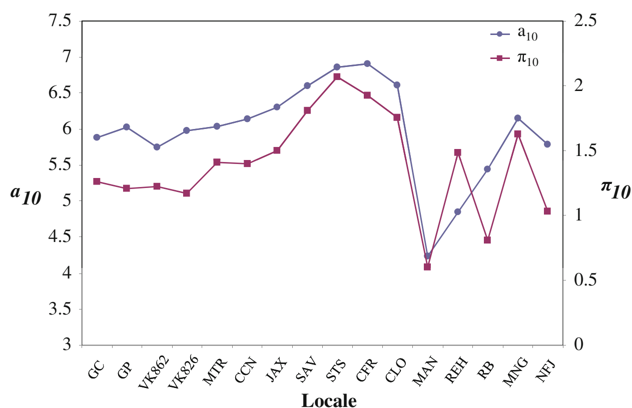

Fig. 2 Allelic richness (a_{10}) and private allelic richness (π_{10}) estimated for each sampled *L. pertusa* locality using rarefaction based on 10 genes per locality. Collection localities (below graphic) are sorted from West to East

estimates of F_{ST} were also significant and ranged from 0.065 to 0.166 (average = 0.089). Although magnitudes of F_{ST} estimates between GOM and SEUS localities were similar across localities, (ranging from 0.005 to 0.026, and averaging = 0.019), more of the comparisons between SEUS and Viosca Knoll localities were significant relative to comparisons with western GOM localities (Green Canyon and *Gulfpenn*). Due to the small sample size for the western GOM, power to detect structure was likely low.

Among SEUS *L. pertusa* localities, estimates of F_{ST} ranged from 0 to 0.018 (average = 0.005), with highest estimates calculated for comparisons between Miami Terrace and other SEUS localities, yet none these comparisons were statistically significant (Table 4). Among GOM localities, estimates of F_{ST} were low for all comparisons (0–0.013), average pairwise F_{ST} was 0.007, and no pairwise F_{ST} estimates were statistically significant. In concordance with results from ENAO *L. pertusa* populations (LeGoff-Vitry et al. 2004a), continental slope localities (Eastern Atlantic) were significantly differentiated from the fjord locality (Trondheimfjord, $F_{ST} = 0.035$). Patterns of differentiation between populations were similar whether estimated by R_{ST} or $F_{ST,}$ yet estimates were considerably higher using R_{ST} (Table 4, above diagonal), indicating that sufficient numbers of mutations have occurred to increase differentiation over that expected through random genetic drift alone.

Quantitative estimates of hierarchical gene diversity (AMOVA) indicated significant genetic population structure at all levels tested, with the greatest variance observed within localities (Table 5). Variation was maximally distributed when localities were defined by four clusters suggested by the subsequent STRUCTURE analysis, with 4.4% (F_{ST}) and 14.9% (R_{ST}) of variance among clusters ($P < 0.001$; Table 5). Estimates of R_{ST} were at least three times that of F_{ST}. Significant structuring was also detected

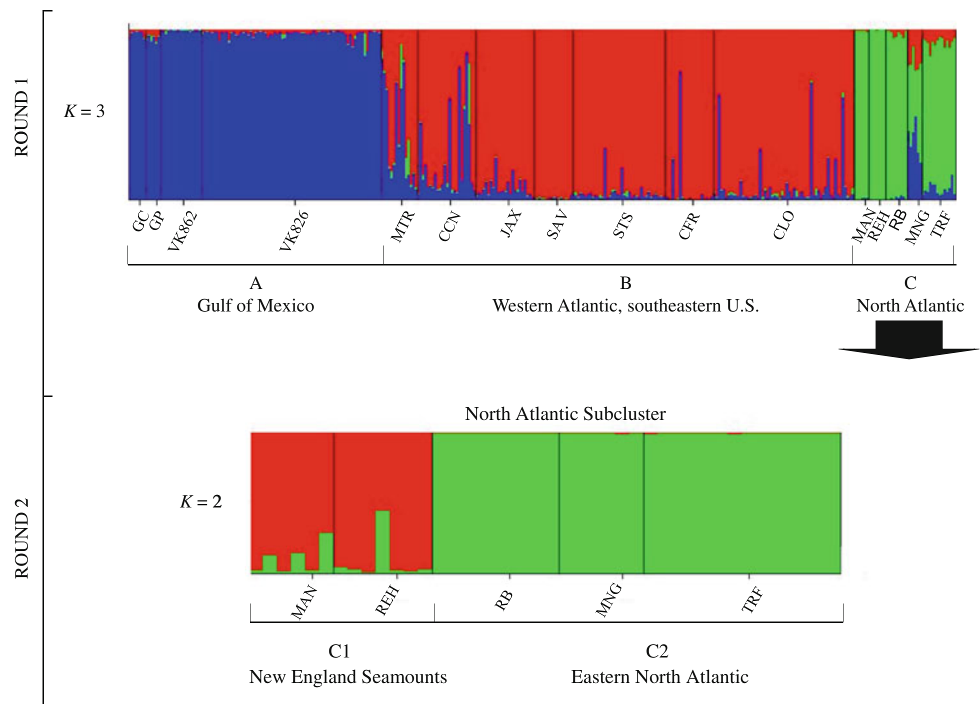

Fig. 3 Proportional membership of *L. pertusa* individuals from sequential cluster analyses using the program STRUCTURE. The three initial clusters (*top*, $K = 3$, A–C) are shown with *vertical bars* representing each individual broken into colored segments based on the proportion of the genome estimated to have originated from each of the three clusters. Collection localities (below graphic) are sorted from West to East. The North Atlantic cluster contained additional structuring identified by subsequent STRUCTURE runs (*bottom*, $K = 2$, C1–C2)

Table 3 Average proportion of membership by locality for the clusters identified by STRUCTURE

Region	Locality	STRUCTURE cluster ($K = 3$)			STRUCTURE subcluster ($K = 2$)	
		Cluster A	Cluster B	Cluster C	Cluster C1	Cluster C2
Gulf of Mexico (A)	GC	0.973	0.023	0.003		
	GP	0.955	0.034	0.011		
	VK862	0.954	0.039	0.007		
	VK826	0.979	0.015	0.006		
Southeastern U.S. (B)	MTR	0.395	0.551	0.054		
	CCN	0.225	0.753	0.022		
	JAX	0.096	0.899	0.005		
	SAV	0.035	0.961	0.004		
	STS	0.041	0.953	0.006		
	CFR	0.084	0.909	0.007		
	CLO	0.082	0.907	0.011		
New England seamounts (C1)	MAN	0.008	0.005	0.987	0.812	0.188
	REH	0.006	0.007	0.987	0.884	0.116
Eastern North Atlantic (C2)	RB	0.019	0.042	0.939	0.004	0.996
	MNG	0.317	0.234	0.449	0.004	0.996
	TRF	0.071	0.074	0.855	0.005	0.996

between the GOM and SEUS clusters, with 1.7% (F_{ST}) and 1.8% (R_{ST}) of variance among clusters ($P < 0.001$; Table 5). Relatively weak structure was also detected among localities in the SEUS (0.6 and 1.6% of variance among localities based on F_{ST} and R_{ST}, respectively, $P < 0.05$; Table 5).

Genetic differentiation between pairs of localities increased significantly with marine geographic distance (Fig. 5, $R^2 = 0.26$, $P < 0.003$). Therefore, an IBD pattern of population structuring was supported at the broadest scale of this study. Comparisons involving NES localities fell well above the regression line, indicating greater genetic distances between these and other localities separated by similar geographic distances. Therefore, the NES appear more isolated from other NAO *L. pertusa* populations. When NES are removed from the analysis, the

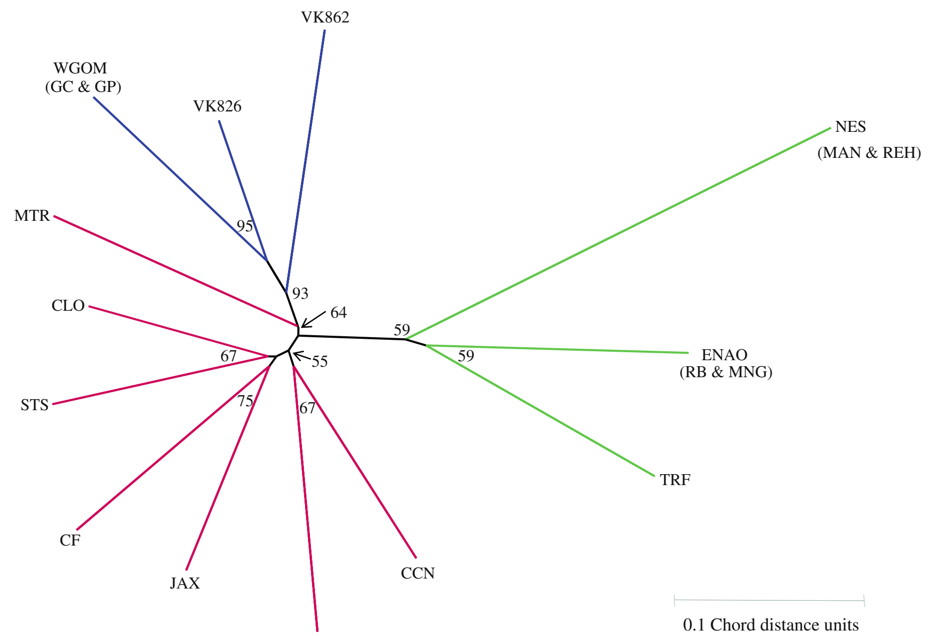

Fig. 4 Unrooted neighbor-joining tree generated from pairwise genetic distances (chord distance, Cavalli-Sforza and Edwards 1967) between *L. pertusa* localities or locality groups (see Table 1 for abbreviations). Branches are color-coded according to clusters identified in STRUCTURE analysis (Fig. 3): *blue* Gulf of Mexico; *red* southeastern U.S.; *green* North Atlantic Ocean. Bootstrap support values >50% given at nodes

Table 4 Pairwise F_{ST} (below diagonal) and R_{ST} (above diagonal) estimates between localities for *L. pertusa* based on a survey of nine microsatellite loci

	WGOM	VK-862	VK-826	MTR	CCN	JAX	SAV	STS	CF	CLO	NES	ENA	TRF
Western GOM		0.1039	0.0241	0.0310	0.0794	*0.1406*	0.1486	*0.1362*	0.0401	*0.0934*	*0.3129*	*0.1719*	*0.2218*
VK-862	0.0125		0.0413	0.0152	0.0061	0.0331	0.0690	0.0368	0.0000	0.0000	*0.3920*	*0.3863*	*0.4172*
VK-826	0.0000	0.0091		0.0000	0.0046	0.0388	0.0557	*0.0553*	0.0179	*0.0308*	*0.3677*	*0.1815*	*0.2097*
Miami	0.0049	0.0143	0.0142		0.0000	0.0430	0.0913	0.0618	0.0131	0.0236	*0.3885*	*0.2609*	*0.2915*
Cape Canaveral	0.0164	0.0191	*0.0158*	0.0091		0.0000	0.0252	0.0292	0.0079	0.0000	*0.4230*	*0.2686*	*0.3042*
Jacksonville	0.0199	*0.0251*	*0.0261*	0.0149	0.0000		0.0000	0.0107	0.0235	0.0010	*0.4930*	*0.3310*	*0.3789*
Savannah	0.0137	*0.0258*	*0.0206*	0.0123	0.0000	0.0057		0.0063	0.0222	0.0136	*0.5345*	*0.3722*	*0.4441*
Stetson	*0.0226*	*0.0188*	*0.0243*	0.0131	0.0050	0.0031	0.0000		0.0048	0.0067	*0.4794*	*0.3536*	*0.4047*
Cape Fear	0.0204	0.0193	*0.0243*	0.0179	0.0111	0.0029	0.0000	0.0000		0.0000	*0.3748*	*0.2978*	*0.3436*
Cape Lookout	0.0152	*0.0182*	*0.0200*	0.0095	0.0036	0.0000	0.0000	0.0000	0.0000		*0.4093*	*0.2992*	*0.3356*
NE Seamounts	*0.1733*	*0.1717*	*0.1620*	*0.1784*	*0.1671*	*0.1575*	*0.1585*	*0.1461*	*0.1333*	*0.1460*		*0.5246*	*0.5094*
Eastern Atlantic	*0.0962*	*0.1022*	*0.0902*	*0.0795*	*0.0779*	*0.0827*	*0.0772*	*0.0840*	*0.0730*	*0.0807*	*0.1655*		0.0476
Trondheimfjord	*0.1026*	*0.1011*	*0.0945*	*0.0934*	*0.0800*	*0.0736*	*0.0798*	*0.0739*	*0.0654*	*0.0709*	*0.1128*	*0.0345*	

Estimates in italics indicate significance based on 9,999 permutations after sequential Bonferroni correction ($\alpha = 0.05$, $P < 0.0006$)

correlation between genetic and geographic distances improved (Fig. 5, $R^2 = 0.67$, $P < 0.0001$). Correlations between geographic and genetic distances among SEUS localities were also weakly statistically significant ($R^2 = 0.35$, $P < 0.012$, not shown).

Discussion

This study of the nearly cosmopolitan deep-sea coral species *L. pertusa* included populations inhabiting vast geographic (9000 km) and depth (140–1679 m) ranges throughout the NAO. Strong genetic discontinuities between ocean regions (GOM, SEUS, NES, and ENAO, with genetic affiliation suggested between the latter two groupings) were detected through concordant population genetic analyses and may indicate vicariant events or regional adaptation. At this broad scale, a pattern of IBD was detected indicating that gene flow is restricted among geographically distant populations. Our data suggests that multiple processes that influence gene flow and connectivity at different spatial and temporal scales contribute to patterns of differentiation in *L. pertusa* in the NAO.

Table 5 Results from analysis of molecular variance (AMOVA) among clusters suggested by STRUCTURE for *L. pertusa*

Variation	F_{ST}				R_{ST}		
	df	% Variation	*P*	F_{ST}	% Variation	*P* value	R_{ST}
STRUCTURE grouping, 4 clusters							
Among clusters	3	4.36	<0.001	0.050	14.88	<0.001	0.166
Among localities within clusters	13	0.64	<0.010		1.75	<0.010	
Among individuals within localities	665	95.00	<0.001		83.36	<0.001	
Total	681						
GOM vs. SEUS [clusters A vs. B]							
Among clusters	1	1.66	<0.001	0.022	1.81	<0.001	0.039
Among localities within clusters	9	0.52	NS		2.13	<0.010	
Among individuals within localities	587	97.82	<0.010		96.06	<0.050	
Total	597						
SEUS [cluster B]							
Among localities	6	0.56	<0.050	0.006	1.62	<0.050	0.016
Among individuals within localities	383	99.44			98.38		
Total	389						

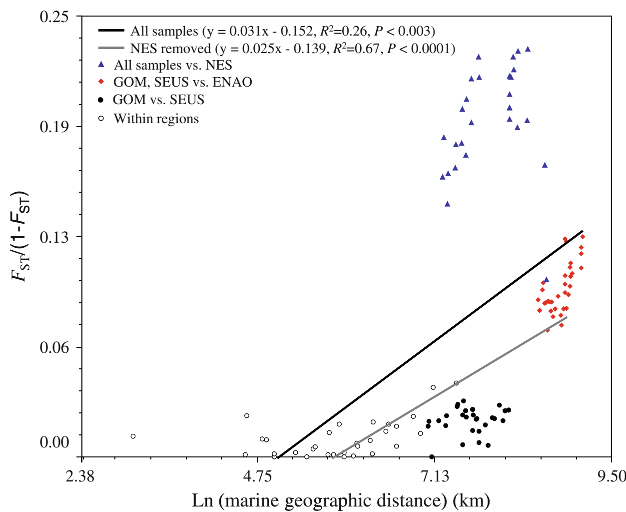

Fig. 5 Mantel tests for correlation between geographic and genetic distances between *L. pertusa* localities. Scatterplots and regressions shown for all sampled localities

Broad-scale genetic structuring

A positive correlation between genetic and geographic distance (IBD) may provide a means of estimating dispersal in marine systems (Hellberg et al. 2002; Palumbi 2004; Bradbury and Bentzen 2007). An IBD spatial genetic pattern is expected if realized dispersal is much less than the scale of the study, assuming spatially homogeneous gene flow and a balance between loss of alleles due to genetic drift (mutation) and replacement of alleles by dispersal (gene flow) (Slatkin 1993; Bradbury and Bentzen 2007). For *L. pertusa*, an IBD pattern appears scale-dependent across the North Atlantic Ocean. At smaller spatial scales, such as within the ENAO (LeGoff-Vitry et al. 2004a), no IBD pattern was detected. However, at larger spatial scales, such as within the SEUS region (maximum distance = 1032 km), or across the study area (9000 km), IBD was detected. For *L. pertusa*, restricted gene flow at these larger spatial scales was suggested from cluster analyses. Therefore, the significant IBD pattern is unlikely to represent homogeneous gene flow throughout the surveyed area, as is often assumed in models of gene flow (Slatkin 1993; Garnier et al. 2004), and estimates of contemporary dispersal processes based upon an IBD pattern should be made cautiously.

Although the New England seamounts occur in a geographic location that may be a potential corridor, or stepping-stone, for gene flow between eastern and western Atlantic Ocean *L. pertusa* populations, these seamount populations do not appear to act as such. Given the large and significant genetic distances observed between other sampled *L. pertusa* localities and the NES, lower levels of genetic diversity, and the decreased correlation of genetic and geographic distances when the NES localities are compared, the seamount localities appear more isolated than other populations surveyed. However, the combination of small sample size and highly polymorphic markers may compromise estimates of genetic distance (Nei 1973, 1978). Therefore, additional sampling will be required before isolation of the seamount populations can be adequately assessed. If in fact the seamounts are more isolated than continental slope *L. pertusa* populations, several factors may contribute to their genetic isolation. First, these seamounts occur deeper (>1000 m) than other *L. pertusa* localities sampled and therefore may be influenced by currents differently. At depths greater than 1000 m, current

flow is dominated by the Deep Western Boundary Current (containing portions of North Atlantic Deep Water) that flows in the opposite direction of the Gulf Stream (Pickart and Watts 1990). The different current regimes could create a boundary to gene flow between the upper slope *L. pertusa* reefs and those at the NES. Alternatively, the change in depth between upper slope and NES populations may create a strong physiological gradient. As such, NES populations may be locally adapted to this unique physiological environment, enhancing genetic differentiation. Although depth is an obvious difference between the NES and other sampled *L. pertusa* localities, the NES are also geographically isolated from other sampled localities, and from other well developed *L. pertusa* reefs. Vast expanses of open ocean act as a barrier to gene flow for coral species along the western coast of Australia (Ayre and Hughes 2004). In our sampling scheme, the Cape Lookout locality lies within closest proximity to the NES (1400 km away), approximately twice the distance separating genetically isolated coral populations in western Australia (Ayre and Hughes 2004). Sampling shallower *L. pertusa* closer to the NES, if such a locality exists, would be informative to test hypotheses involving isolation by depth or distance. Lastly, larval retention may be enhanced due to the complex hydrography that often surrounds seamounts (Clark et al. 2010).

Based on major current patterns, higher population connectivity was expected among *L. pertusa* reefs in U.S. waters than was observed in this study. The GOM Loop Current feeds directly into the Florida Current, which impacts most of the water column at continental slope depths off the SEUS (Bane et al. 2001), and then continues northeastward across the Atlantic as the Gulf Stream. However, GOM and SEUS *L. pertusa* populations fell into separate clusters in the STRUCTURE analysis, suggesting restricted gene flow, with admixture between the SEUS and GOM clusters for the southern Florida (Miami and Cape Canaveral) populations. Additionally, the significant structuring detected using AMOVA suggested restricted dispersal. However, the localities sampled in the north-central GOM are generally outside the Loop Current. The northward penetration of the current varies and often produces anticyclonic eddies that drift westward, producing an active mesoscale eddy field (Morey et al. 2003). Thus, *L. pertusa* larvae from these sites may have reduced opportunity to enter the Loop Current and disperse into the Atlantic Ocean. Future analyses of *L. pertusa* sampled from the West Florida slope (within the Loop Current influence) may resolve this issue as we hypothesize that these may be more closely related to Atlantic populations.

The coastal waters off central Florida are a transitional area between temperate (Carolinian) and subtropical (Caribbean) zoogeographic provinces (Briggs 1974). Due to climatically driven changes in sea levels and temperature during the last glacial maximum, the GOM and Atlantic marine faunas have a complex history structured by repeated episodes of vicariance and dispersal (Avise 1994). These historical vicariant events, along with present-day currents and latitudinal selection gradients, have lead to varying degrees of genetic discontinuities (such as sharp changes in allele frequencies) for many marine organisms in the Cape Canaveral region (reviewed by Avise 1994; Cunningham and Collins 1998; Avise 2000; Eytan et al. 2009). Although *L. pertusa* occurs much deeper than marine taxa with known phylogeographic breaks in the Cape Canaveral region, our data suggest the presence of a transition from GOM to Atlantic genotypes in this same area. Additional sampling of *L. pertusa* from off Florida may help to determine the geographic extent of the genetic discontinuity for *L. pertusa* in this area. Moreover, long-term ocean current observations (e.g. White et al. 2010) from this transitional area may improve our ability to interpret this complex genetic structuring.

Whether or not regionally isolated populations of *L. pertusa* represent cryptic species requires further morphological examination and additional biological evidence. For instance, there may be biological differences in the timing of reproduction among trans-Atlantic populations of *L. pertusa*. The reproductive cycle of *L. pertusa* has been partially described for populations in the ENAO (Waller and Tyler 2005) and the GOM (Brooke et al. 2007). There appears to be a trans-Atlantic offset in timing of spawning, which occurs in January and February for ENAO populations (Waller and Tyler 2005), March in Trondheimfjord, Norway (Brooke and Järnegren, unpubl. data) and September to October in GOM and SEUS (Brooke et al. 2007; S. Brooke, unpubl. data). Although spawning cues are unknown, early spring seasonal blooms of surface primary production were suggested as a potential cue for initiation of gametogenesis in ENAO *L. pertusa* populations (Waller and Tyler 2005). In the eastern GOM, a tongue of high concentration of chlorophyll *a* exists in July–August, coincident with freshwater discharge by large rivers in the northern GOM (Morey et al. 2003). Since the seasonality of primary production varies between oceanic regions, this could potentially act as a selective force driving differentiation in timing of reproduction, and ultimately, could lead to reproductive incompatibility and speciation.

Species diversity within communities has been hypothesized to co-vary with genetic diversity within populations because locality processes influence these two levels of diversity in parallel (Vellend and Geber 2005). In the present study, parallels exist between the patterns of genetic differentiation observed among regional *L. pertusa* populations and regional patterns of species diversity in

both deep-sea corals and fishes. For example, Cairns and Chapman (2001) examined regional relationships of deep-water scleractinian species and identified three main superclusters corresponding to eastern and western Atlantic and boreal North Atlantic regional groupings. Similarities exist between those zoogeographic patterns and the regional subdivisions we observed in *L. pertusa*. In our analyses, eastern and western Atlantic Ocean *L. pertusa* populations were clearly distinctive. Additionally, the GOM and SEUS clusters were unique yet closely related.

Based on community structure analyses of abundance and distribution patterns, the SEUS deep reef fish communities also appeared to differ from fish groupings on GOM coral banks, fish communities north of Cape Hatteras, as well as those occurring shallower (<200 m) and deeper (>1000 m) than SEUS deep coral banks (Ross and Quattrini 2009). Within the 300–1000 m depth band such fragmentation was unexpected for fishes whose larvae and adults are highly mobile. Ross and Quattrini (2009) suggested that these patterns could be caused by physical differences (primarily temperature and depth) among sample sites or differences in habitat structure and relationships. Small scale oceanographic features (e.g., Grasmueck et al. 2006; Davies et al. 2010) may serve to isolate fauna to varying extents, and these should be investigated further. Shared patterns of species diversity and genetic structuring across unrelated taxa using similar habitats suggests overarching organizing or isolating mechanisms (Vellend and Geber 2005; Johnson and Stinchcombe 2007).

Regional patterns of differentiation

Within regions, our genetic analyses suggest that connectivity between *L. pertusa* populations is complex but is generally weak to moderate with long-distance dispersal occurring with enough frequency to produce regional cohesion. Significant genetic structuring was detected in the SEUS region through both AMOVA (Table 5) and a significant IBD pattern. Localities within this region had high heterozygosities, allelic richness and contained the majority of private alleles (Table 2; Fig. 2). It should be noted that sampling was geographically extensive and sample sizes adequate in this region.

The strong genetic structuring between fjord and continental margin ENAO populations reported by LeGoff-Vitry et al. (2004a) was not fully supported by our analyses, we note that the power of our analyses are likely lower than that of the previous study given fewer samples of *L. pertusa* from the ENAO. The STRUCTURE analysis included both fjord and continental margin populations in one cluster (Fig. 3, cluster C2; Table 3). However, evidence of differentiation between fjord and offshore populations was observed in high pairwise F_{ST} and R_{ST} estimates (Table 4).

Intrapopulation diversity and reproduction

Similar to the findings of LeGoff-Vitry et al. (2004a), heterozygote deficits were detected in the majority of populations examined, thus confirming the generality of such local genetic patterns for *L. pertusa* in the NAO. In the ENAO, LeGoff-Vitry et al. (2004a) explained significant inbreeding by spatially restricted gene flow and high rates of self-recruitment of sexually produced larvae. In a given *L. pertusa* population, abundance of genets may be less than otherwise expected based upon observed live coral coverage. A high proportion of clones at a site strengthen the chance of few genets producing the majority of larvae. Over time, as genet abundance decreases, the probability of matings among close kin increases.

Heterozygote deficits, along with large and positive F_{IS} values, have frequently been observed in marine invertebrates (Bohonak 1999), including the majority of corals surveyed (Ayre and Hughes 2000; VanOppen and Gates 2006). A broad association between heterozygote deficiencies and one life history trait, spermcasting, was supported in a review of available literature for marine invertebrates, though casual links remain unclear (Addison and Hart 2005). For corals, highly localized recruitment and unrecognized within population structuring (Wahlund effect) have been inferred (e.g. Whitaker 2004; Underwood et al. 2007). Small-scale spatial genetic structuring makes defining population boundaries for long-lived sessile species especially challenging (Ayre and Hughes 2000; Underwood et al. 2007; Ledoux et al. 2010). Exhaustive sampling of several localities would allow for characterization of levels of self-recruitment and help to define the mating system of *L. pertusa*.

Conservation implications and future research

All *L. pertusa* populations harbor substantial genetic diversity, thus providing the potential for adaptive evolution should environmental conditions change. Gene flow between ocean regions appears restricted, thus the most effective management scheme for *L. pertusa* involves regional reserve networks in the GOM, SEUS, NES and NEAO regions. As a step towards protecting fragile deep-sea coral habitats, the South Atlantic Fisheries Management Council, and the U.S. Department of Commerce have recently approved (June 2010) four large Coral Habitat Areas of Particular Concern off the SEUS coast.

Population genetic theory suggests that the New England seamount *L. pertusa* populations may be especially vulnerable to disturbance given low heterozygosities

and allelic richness. Since these localities appear highly isolated, serious long-term consequences could result from disturbance since it is unlikely that new recruits would re-colonize the seamounts.

The SEUS *L. pertusa* populations harbor high genetic diversity, and thus are also important to protect. Within the SEUS region, the Stetson Banks and Cape Fear populations stand out, with the highest allelic richness.

While the state of cold-water coral ecosystems in the Gulf of Mexico remains unclear after the Deepwater Horizon oil spill, experiences from past oil spills and laboratory experiments suggest that corals and invertebrates will be negatively impacted by direct exposure to crude oil and dispersants (e.g. Haapkyla et al. 2007; Fuller et al. 2004). Additionally, deprivation of surface-derived food sources could have devastating indirect effects to the deep reef community. The Viosca Knoll localities may represent the most well developed *L. pertusa* reefs known in the GOM (Brooke and Schroeder 2007), harboring substantial genetic diversity, and lying within 50 km of the oil spill site. Although sampling of additional, comparative GOM localities was limited in the current analyses, gene flow within the GOM appears adequate to potentially replenish the Viosca Knoll localities should they be severely impacted. Circulation patterns in the GOM also appear adequate to provide a means of benthic transport of organic material (Jochens and DiMarco 2008). However, given the net westward deep current flow in the north-central GOM (Morey et al. 2003), availability of recruits may require a sporadic long-distance dispersal event.

While the data included in this study were geographically extensive and often included large sample sizes, we caution that a more complete view of Atlantic Ocean *L. pertusa* populations is needed. Due to the difficulties and costs involved in sampling deep coral communities, sample sizes in this study were uneven, and in some cases, small. For example, the NES and western GOM populations relied on sample sizes of less than ten individuals. The combination of small sample sizes and highly polymorphic markers may lead to spurious results (Nei 1973, 1978). Sampling each population more extensively should increase confidence in the biological meaning of results. Additionally, increasing the geographic scope of sampling in the Atlantic Ocean is necessary. Specifically, the inclusion of *L. pertusa* samples from the Caribbean, Bahamas, the mid-Atlantic Ridge, and sites in the South Atlantic Ocean, such as Brazil and the Gulf of Guinea, would contribute towards our understanding of basin-wide gene flow. Although little gene flow is expected, genetic comparisons between *L. pertusa* in Atlantic and Pacific Ocean basins would be informative to this analysis. Furthermore, while the indirect genetic methods applied in this study lend valuable insights into connectivity patterns that would have been difficult to obtain by other means, these patterns are representative of long-term gene flow, integrated over generations, and focusing on successful dispersers (Palumbi 2003). Direct genetic assessments, such as kinship analysis (e.g. Wang and Santure 2009), would complement this work, allowing for demographic assessments on local and ecological space and time scales (e.g. Underwood et al. 2009; Christie et al. 2010). Complementing genetic estimates of connectivity with modeling of dispersal, and including data on topography and short- and long-term oceanographic conditions (Selkoe et al. 2008; White et al. 2010), should greatly improve inferences regarding connectivity between *L. pertusa* deep reefs. The examination of functional portions of the *L. pertusa* genome may reveal adaptive differences between populations, adding new insights into the ecology, evolution and protection of deep reefs.

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References

Addison JA, Hart MW (2005) Spawning, copulation and inbreeding coefficients in marine invertebrates. Biol Lett 1:450–453

Avise JC (1994) Molecular markers, natural history and evolution. Chapman & Hall, New York, p 511

Avise JC (2000) Phylogeography. Harvard University Press, Cambridge
Ayre DJ, Hughes TP (2000) Genotypic diversity and gene flow in brooding and spawning corals along the Great Barrier Reef, Australia. Evolution 54:1590–1605
Ayre DJ, Hughes TP (2004) Climate change, genotypic diversity and gene flow in reef-building corals. Ecol Lett 7:273–278
Bane JM Jr, Attkinson LP, Brooks DA (2001) Gulf Stream physical oceanography at the Charleston Bump: deflection, bimodality, meanders, and upwelling. In: Sedberry GR (ed) Island in the stream: oceanography and fisheries of the Charleston Bump, Amer Fish Soc Symp 25, Bethesda, MD, pp 25–36
Barber PH, Palumbi SR, Erdmann MV, Moosa MK (2000) A marine Wallace's line? Nature 406:692–693
Baums IB, Miller MM, Hellberg ME (2005) Regionally isolated populations of an imperiled Caribbean coral, *Acropora palmata*. Mol Ecol 14:1377–1390
Belkhir K, Borsa P, Chikhi L, Raufaste N, Bonhomme F (2001) Genetix: logiciel sous Windows TM pour la génétique des populations. Laboratoire Génome, Populations, Interactions: CNRS UMR. 5000, Université de Montpellier II, Montpellier
Bellwood DR, Hughes TP, Folke C, Nyström M (2004) Confronting the coral reef crisis. Nature 429:827–833
Bergquist DC, Ward T, Cordes EE, McNelis T, Howlett S, Kosoff R, Hourdez S, Carney R, Fisher CR (2003) Community structure of vestimentiferan-generated habitat islands from upper Louisiana slope cold seeps. J Exp Mar Biol Ecol 289:197–222
Bohonak AJ (1999) Dispersal, gene flow, and population structure. Quart Rev Biol 74(1):21–45
Bradbury IR, Bentzen P (2007) Non-linear genetic isolation by distance: implications for dispersal estimation in anadromous and marine fish populations. Mar Ecol Prog Ser 340:245–257
Briggs JC (1974) Marine zoogeography. McGraw-Hill Book Co., New York
Brooke S, Schroeder WW (2007) State of deep coral ecosystems in the Gulf of Mexico region: Texas to the Florida Straits. In: Lumsden SE, Hourigan TF, Bruckner AW, Dorr G (eds) The state of deep coral ecosystems of the United States. NOAA Tech Memo CRCP-3, Silver Spring, MD, pp 233–270
Brooke SD, Young CM, Holmes M (2007) Biological characterization and studies, Part II. In: Characterization of northern Gulf of Mexico deepwater hard bottom communities with emphasis on Lophelia coral. Continental Shelf Associates, Inc., New Orleans, pp 119–147
Cairns SD, Chapman RE (2001) Biogeographic affinities of the North Atlantic deep-water Scleractinia. In: Willison JHM, Jall J, Gass SE (eds) Proceedings of the first international symposium on deep-sea corals. Ecology Action Centre, Halifax, NS, pp 30–57
Cavalli-Sforza LL, Edwards AWF (1967) Phylogenetic analyses: models and estimation procedures. Evolution 21:873–881
Christie MR, Johnson DW, Stallings CD, Hixon MA (2010) Self recruitment and sweepstakes reproduction amid extensive gene flow in a coral–reef fish. Mol Ecol 19:1042–1057
Clark M, Rowden AA, Schlacher T, Williams A, Consalvey M, Stocks KI, Rogers AD, O'Hara TD, White M, Shank T, Hall-Spencer JM (2010) The ecology of seamounts: structure, function, and human impacts. Annu Rev Mar Sci 2:253–278
Cowan RK, Sponaugle S (2009) Larval dispersal and marine population connectivity. Annu Rev Mar Sci 1:443–466
Cowen RK, Paris CB, Srinivasan A (2006) Scaling of connectivity in marine populations. Science 311:522–527
Cunningham CW, Collins TM (1998) Beyond area relationships: extinction and recolonization in molecular marine biogeography. In: De Salle R, Schierwater B (eds) Molecular approaches to ecology, evolution. Birkhauser-Verlag, Basel, pp 297–321
Davies AJ, Roberts JM, Hall-Spenser J (2007) Preserving deep-sea natural heritage: emerging issues in offshore conservation and management. Biol Conserv 138:299–312
Davies AJ, Duineveld GCA, van Weering TCE, Mienis F, Quattrini AM, Seim HE, Bane JM, Ross SW (2010) Short-term environmental variability in cold-water coral habitat at Viosca Knoll, Gulf of Mexico. Deep-Sea Res I 57:199–212
Evanno G, Regnault S, Goudet J (2005) Detecting the number of clusters of individuals using the software structure: a simulation study. Mol Ecol 14:2611–2620
Excoffier L, Smouse PE, Quattro JM (1992) Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. Genetics 131:479–491
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
Eytan RI, Hayes M, Arbour-Reily P, Miller M, Hellberg ME (2009) Nulcear sequences reveal mid-range isolation of imperilled deep-water coral populations. Mol Ecol 18:2375–2389
Falush D, Stephens M, Pritchard J (2003) Inference of population structure using multilocus genotype data: linked loci and correlated allele frequencies. Genetics 164:1567–1587
Fontaine M, Baird S, Piry S et al (2007) Rise of oceanographic barriers in continuous populations of a cetacean: the genetic structure of harbour porpoises in old world waters. BMC Biol 5:30. doi:10.1186/1741-7007-5-30
Fuller C et al (2004) Comparative toxicity of oil, dispersant, and oil plus dispersant to several marine species. Environ Toxicol Chem 23(12):2929–2941
Garnier S, Alibert P, Audiot P, Prieur B, Rasplus J-Y (2004) Isolation by distance and sharp discontinuities in gene frequencies: implications for the phylogeography of an alpine insect species, *Carabus solieri*. Mol Ecol 13:1883–1897
Grasmueck M, Eberli GP, Viggiano DA et al (2006) Autonomous underwater vehicle (AUV) mapping reveals coral mound distribution, morphology, and oceanography in deep water of the Straights of Florida. Geophys Res Lett 33:L23616
Guinotte JM, Orr JC, Cairns SD, Morgan L, George R (2006) Will human-induced changes in seawater chemistry alter the distribution of deep-sea scleractinian corals? Front Ecol Environ 4:141–146
Haapkyla J et al (2007) Oil pollution on coral reefs: a review of the state of knowledge and management needs. Vie et Millieu 57(1–2):95–111
Hellberg ME (1996) Dependence of gene flow on geographic distance in two solitary corals with different larval dispersal capabilities. Evolution 50(3):1167–1175
Hellberg ME, Burton RS, Neigel JE, Palumbi SR (2002) Genetic assessment of connectivity among marine populations. Bull Mar Sci 70(Suppl. 1):273–290
Hubisz MJ, Falush D, Stephens M, Pritchard JK (2009) Inferring weak population structure with the assistance of sample group information. Mol Ecol Resour 9:1322–1332
Jochens AE, DiMarco SF (2008) Physical oceanographic conditions in deepwater Gulf of Mexico in summer 2000–2002. Deep-Sea Res II 55:2541–2554
Johnson MTJ, Stinchcombe JR (2007) An emerging synthesis between community ecology and evolutionary biology. Trends Ecol Evol 22:250–257
Kalinowski ST (2004) Counting alleles with rarefaction: private alleles and hierarchical sampling designs. Conserv Genet 5:539–543
Kalinowski ST (2005) HP-RARE 1.0: a computer program for performing rarefaction on measures of allelic richness. Mol Ecol Notes 5:187–189

Knowlton N (2000) Molecular genetic analysis of species boundaries in the sea. Hydrobiologia 420:73–90

Ledoux J-B, Garrabou J, Bianchimani O, Drap P, Feral J-P, Aurelle D (2010) Fine-scale genetic structure and inferences on population biology in the threatened Mediterranean red coral, *Corallium rubrum*. Mol Ecol 19:4204–4216

LeGoff MC, Rogers AD (2002) Characterization of ten microsatellite loci for the deep-sea coral *Lophelia pertusa* (Linnaeus, 1758). Mol Ecol Notes 2:164–166

LeGoff-Vitry MC, Pybus OG, Rogers AD (2004a) Genetic structure of the deep-sea coral *Lophelia pertusa* in the northeast Atlantic revealed by microsatellites and internal transcribed spacer sequences. Mol Ecol 13:537–549

LeGoff-Vitry MC, Rogers AD, Baglow D (2004b) A deep-sea slant on the molecular phylogeny of the Scleractinia. Mol Phylogenet Evol 30:167–177

Levin LA (2006) Recent progress in understanding larval dispersal: new directions and digressions. Integr Comp Biol 46(3):282–297

Levin LA, Dayton PK (2009) Ecological theory and continental margins: where shallow meets deep. Trends Ecol Evol 24(11): 606–617

Mantel N (1967) The detection of disease clustering and a generalized regression approach. Cancer Res 27:209–220

Morey SL, Schroeder WW, O'Brien JJ, Zavala-Hidalgo J (2003) The annual cycle of riverine influence in the eastern Gulf of Mexico basin. Geophys Res Lett 30(16):1867

Morrison CL, Eackles MS, Johnson RL, King TL (2008) Characterization of 13 microsatellite loci for the deep-sea coral, *Lophelia pertusa* (Linnaeus 1758), from the western North Atlantic Ocean and Gulf of Mexico. Mol Ecol Resour 8:1037–1039

Nei M (1973) The theory and estimation of genetic distances. In: Morton NE (ed) Genetic structure of populations. University of Hawaii Press, Honolulu, pp 45–54

Nei M (1978) Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics 89: 583–590

Palumbi SR (2003) Population genetics, demographic connectivity, and the design of marine reserves. Ecol Appl 13(1):S146–S158

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

Peakall R, Smouse PE (2006) GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. Mol Ecol Notes 6:288–295

Pickart RS, Watts DR (1990) Deep western boundary current variability at Cape Hatteras. J Mar Res 48:765–791

Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. Genetics 155:945–959

Raymond M, Roussett F (1995) An exact test for population differentiation. Evolution 49:1280–1283

Reed JK, Weaver DC, Pomponi SA (2006) Habitat and fauna of deep-water *Lophelia pertusa* coral reefs off the southeastern U.S.: Blake Plateau, Straights of Florida, and Gulf of Mexico. Bull Mar Sci 78:343–375

Rice WR (1989) Analyzing tables of statistical tests. Evolution 43:223–225

Roberts JM, Wheeler AJ, Freiwald A (2006) Reefs of the deep: the biology and geology of cold-water coral ecosystems. Science 312:543–547

Roberts JM, Wheeler AJ, Freiwald A, Cairns S (2009) Cold-water corals: the biology and geology of deep sea coral habitats. Cambridge University Press, New York

Rogers AD (1999) The biology of *Lophelia pertusa* (Linnaeus 1758) and other deep-water reef-forming corals and impacts from human activities. Int Rev Hydrobiol 84:315–406

Rogers AD (2002) Molecular ecology and evolution of slope species. In: Wefer G, Billet D, Hebbeln D et al (eds) Ocean margin systems. Springer-Verlag, Berlin, pp 323–337

Rohlf FJ (2000) NTSYS-PC: numerical taxonomy and multivariate analysis systems, Version 2.10. Exeter Software, Setauket

Rosel PE, Hansen L, Hohn AA (2009) Restricted dispersal in a continuously distributed marine species: common bottlenose dolphins *Tursiops truncatus* in coastal waters of the western Atlantic. Mol Ecol 18:5030–5045

Ross SW, Nizinski MS (2007) State of deep coral ecosystems in the U.S. southeast region: Cape Hatteras to Southeastern Florida. In: Lumsden SE, Hourigan TF, Bruckner AW, Dorr G (eds) The state of deep coral ecosystems of the United States. NOAA Tech Memo CRCP-3, Silver Spring, MD, pp 233–270

Ross SW, Quattrini AM (2007) The fish fauna associated with deep coral banks off the southeastern United States. Deep-Sea Res I 54:975–1007

Ross SW, Quattrini AM (2009) Deep-sea fish assemblage patterns on the Blake Plateau (Western North Atlantic Ocean). Mar Ecol 30:74–92

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

Rousset F (2008) GENEPOP '007: a complete re-implementation of the GENEPOP software for Windows and Linux. Mol Ecol Resour 8:103–106

Selkoe K, Henzler C, Gaines S (2008) Seascape genetics and the spatial ecology of marine populations. Fish Fish 9:363–377

Shanks AL, Grantham BA, Carr MH (2003) Propagule dispersal and the size and spacing of marine reserves. Ecol Appl 13:S159–S169

Slatkin M (1993) Isolation by distance in equilibrium and nonequilibrium populations. Evolution 47:264–279

Slatkin M (1995) A measure of population subdivision based on microsatellite allele frequencies. Genetics 139:457–462

Sotka EE, Wares JP, Barth JA, Grosberg RK, Palumbi SR (2004) Strong genetic clines and geographic variation in gene flow in the rocky intertidal barnacle *Balanus glandula*. Mol Ecol 13:2143–2156

Swearer SE, Shima JS, Hellberg ME et al (2002) Evidence of self-recruitment in demersal marine populations. Bull Mar Sci 70:251–271

Taylor MS, Hellberg ME (2003) Genetic evidence for local retention of pelagic larvae in a Caribbean reef fish. Science 299:107

Underwood JN, Smith LD, van Oppen MJH, Gilmour JP (2007) Multiple scales of genetic connectivity in a brooding coral on isolated reefs following catastrophic bleaching. Mol Ecol 16:771–784

Underwood JN, Smith LD, van Oppen MJH, Gilmour JP (2009) Ecologically relevant dispersal of corals on isolated reefs: implications for managing resilience. Ecol Appl 19(1):18–29

Urcuyo IA, Massoth GJ, Julian D, Fisher CR (2003) Habitat, growth and physiological ecology of a basaltic community of *Ridgeia piscesae* from the Juan de Fuca Ridge. Deep-Sea Res I 50: 763–780

VanOppen MJH, Gates RD (2006) Conservation genetics and the resilience of reef-building corals. Mol Ecol 15:3863–3883

Van Oosterhaut C, Hutchinson WF, Wills DPM, Shipley P (2004) MICROCHECKER: software for identifying and correcting genotyping errors in microsatellite data. Mol Ecol Notes 3:535–538

Vellend M, Geber MA (2005) Connections between species diversity and genetic diversity. Ecol Lett 8:767–781

Waller RG, Tyler PA (2005) The reproductive biology of two deep-water, reef-building scleractinians from the NE Atlantic Ocean. Coral Reefs 24:514–522

Wang J, Santure A (2009) Parentage and sibship inference from multilocus genotype data under polygamy. Genetics 181: 1579–1594

Warner RR, Cowen RK (2002) Larval retention of production in marine populations: evidence, mechanisms, and consequences. Bull Mar Sci 70:245–249

Weir BS, Cockerham CC (1984) Estimating F-statistics for the analysis of population structure. Evolution 38:1358–1360

Whitaker K (2004) Non-random mating and population genetic subdivision of two broadcasting corals at Ningaloo Reef, Western Australia. Mar Biol 144:593–603

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

Wilberg MJ, Dreher BP (2004) GENECAP: a program for analysis of multilocus genotype data for non-invasive sampling and capture-recapture population estimation. Mol Ecol Notes 4:783–785

Woods JG, Paetkau D, Lewis D et al (1999) Genetic tagging of free-ranging black and brown bears. Wildl Soc Bull 27:616–627

Wright S (1943) Isolation by distance. Genetics 28:114–138

Wright S (1951) The genetical structure of populations. Ann. Eugenics 15:323–354

Zardus JD, Etter RJ, Chase MR, Rex MA, Boyle EE (2006) Bathymetric and geographic population structure in the pan-Atlantic deep-sea bivalve *Deminucula atacellana* (Schenck, 1939). Mol Ecol 15:639–651