INTRODUCTION

Seamounts, undersea mountains that rise from the sea floor, constitute a distinct deep-sea environment characterized by accelerated currents, exposed hard-substrates, and relatively high biomass and biodiversity (reviewed by Rogers 1994). It has been hypothesized that the topographic and hydrographic conditions associated with seamounts contribute to faunal isolation and the accumulation of highly endemic taxa (reviewed by Rogers 1994). While this hypothesis has been tested for multiple taxonomic groups in the Pacific, it has rarely been addressed in the Atlantic. We tested the null hypothesis that the geographic ranges of corals from NW Atlantic seamounts are restricted to individual seamounts. We examined 188 octocoral and 50 antipatharian colonies (representing 6 and 2 genera, respectively) from 14 seamounts, spanning 1700 km, and the adjacent continental margin and estimated their genetic variation using mitochondrial loci (msh1 for all octocorals, as well as an intergenic region for isidids, and 3 multi-gene spanning segments for antipatharians). Well-sampled haplotypes were not geographically isolated on individual seamounts, thus refuting the hypothesis of local endemism of coral fauna on the New England and Corner Seamounts. The narrow geographic distribution of rare haplotypes is most likely due to undersampling rather than endemism. Our results do not preclude that cryptic variation and endemism not revealed by mitochondrial DNA may become evident should more variable markers be developed.

KEY WORDS: Endemism · Biogeography · Marine connectivity · Dispersal · Chrysogorgiidae · Paramuricea · Black coral · Anthozoa

Deep-sea octocorals and antipatharians show no evidence of seamount-scale endemism in the NW Atlantic

Jana N. Thoma*, Eric Pante*, Mercer R. Brugler, Scott C. France**

University of Louisiana at Lafayette, Department of Biology, PO Box 42451, Lafayette, Louisiana 70504, USA

ABSTRACT: Seamounts are undersea mountains commonly characterized by accelerated currents, exposed hard-substrates, and relatively high biomass and biodiversity. Hydrographic features associated with seamounts have led authors to hypothesize that benthic invertebrate populations from geographically separated seamounts (and the continental slope) may experience varying degrees of genetic isolation, resulting in high levels of endemism. While this hypothesis has been tested for multiple taxonomic groups in the Pacific, it has rarely been addressed in the Atlantic. We tested the null hypothesis that the geographic ranges of corals from NW Atlantic seamounts are restricted to individual seamounts. We examined 188 octocoral and 50 antipatharian colonies (representing 6 and 2 genera, respectively) from 14 seamounts, spanning 1700 km, and the adjacent continental margin and estimated their genetic variation using mitochondrial loci (msh1 for all octocorals, as well as an intergenic region for isidids, and 3 multi-gene spanning segments for antipatharians). Well-sampled haplotypes were not geographically isolated on individual seamounts, thus refuting the hypothesis of local endemism of coral fauna on the New England and Corner Seamounts. The narrow geographic distribution of rare haplotypes is most likely due to undersampling rather than endemism. Our results do not preclude that cryptic variation and endemism not revealed by mitochondrial DNA may become evident should more variable markers be developed.

KEY WORDS: Endemism · Biogeography · Marine connectivity · Dispersal · Chrysogorgiidae · Paramuricea · Black coral · Anthozoa

*Jana N. Thoma and Eric Pante have contributed equally to this project
**Corresponding author. Email: france@louisiana.edu

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Contribution to the Theme Section ‘Conservation and management of deep-sea corals and coral reefs’
Therefore, gathering data allowing us to identify species pools, at local, regional and global scales, to determine the geographic distribution of seamount taxa and to establish faunal affinities between biogeographic regions is still central to seamount research.

McClain (2007) and Stocks & Hart (2007) suggested that a more synthetic understanding of the uniqueness of seamount fauna will come from (1) reducing sampling bias by visiting seamounts from a wider geographical range, (2) estimating endemism at different, well-defined spatial scales, and (3) incorporating molecular methods in the evaluation of faunal isolation. To date, research efforts have been highly skewed toward the Indo-Pacific region, and most of the data on Atlantic seamounts were gathered on northeastern chains (see Wilson & Kaufmann 1987, Mironov & Gebruk 2006, Stocks & Hart 2007 for a review of worldwide seamount endemism to mid-2005). The New Atlanticic, on the other hand, has been given very little attention. Also, most studies compare faunal assemblages from seamounts and slopes, or from seamounts belonging to different seamount chains. On the other hand, few studies focus on finer spatial scales, such as the geographical distribution of individual taxa within and among seamounts (Wilson & Kaufmann 1987, McClain 2007, Stocks & Hart 2007). Finally, most estimates of endemism on seamounts rely on the identification of specimens from morphological characters, which can be biased by phenotypic plasticity as well as convergent evolution and cryptic variation (e.g. Avise 2004).

The New England Seamounts (NES) and Corner Seamounts (CS) offer a suitable framework for the evaluation of the seamount endemity hypothesis, even though their fauna have only recently begun to be documented (Moore et al. 2003, 2004 and references therein). These seamount chains were formed by a mantle-plume hotspot at the Mid-Atlantic Ridge and subsequent spreading of the seafloor (Sleep 1990), and extend for approximately 1700 km between the North American continental margin and Mid-Atlantic Ridge (Fig. 1). The oldest seamounts (e.g. Bear Seamount) are found in association with the continental margin (Duncan 1984), which also contains numerous canyons where hard substrates are exposed. Hydrography around the NES is affected by the flow of the Gulf Stream between Kelvin and Rehoboth Seamounts (e.g. Richardson 1981), and predicted current patterns show that the NES and adjacent continental margin may be hydrographically connected to each other but isolated from the eastern CS chain (Qiu 1994), although Bower et al. (2009) showed at least some deep subsurface floats flowed from the CS westward to the NES.

Fig. 1. Study region in the NW Atlantic. The total number of colonies collected and analyzed is given in parentheses for each collection site. Contour lines correspond to 500 m isobaths and extend to 4500 m.
We characterized the geographic distribution of genetic types, or haplotypes, of representative octocorals and antipatharians within and across the NES and CS chains. Octocorals and black corals are common and conspicuous sessile fauna on seamounts (e.g. Rogers et al. 2007), which make them appropriate model systems for the evaluation of endemism on the NES and CS chains. Determining actual levels of endemism is impracticable, since it would require a complete catalog of deep-sea habitats and associated fauna. However, endemism of a particular taxon can be refuted if it is sampled outside of its hypothesized distributional area. Therefore, we evaluated the null hypothesis that haplotypes would be restricted, or endemic, to individual seamount peaks rather than being more widely distributed. We used mitochondrial (mt) DNA markers to avoid the confounding effects of phenotypic variation, cryptic variation and convergent evolution of morphological characters. In addition to geographically mapping the distribution of haplotypes, we constructed a haplotype network for *Paramuricea* (a particularly abundant and diverse octocoral genus in our study area) using specimens from within and outside the NW Atlantic to provide additional insight into biogeographic patterns. Our results provide information on the biodiversity, geographic distribution and inferred dispersal potential of octocorals and black corals, which may prove useful for future management and conservation of the NW Atlantic deep-sea benthic fauna.

**MATERIALS AND METHODS**

**Sampling.** Most specimens were collected during the Mountains in the Sea and Deep Atlantic Stepping Stones expeditions of 2003–2005 (NOAA Ocean Explorer expedition logs, http://oceanexplorer.noaa.gov/explorations/explorations.html). A total of 188 colonies of Octocorallia Haeckel, 1866 (3 families: Chrysogorgiidae Verrill, 1883: *Chryso- gorgia* Duchassaing & Michelotti, 1864, *Iridogorgia* Verrill, 1883, *Metallogorgia* Versluys, 1902 and *Radicipes* Stearns, 1883; Isididae Lamouroux, 1812: *Acan- nella* Gray, 1870; and Plexauridae Gray, 1859: *Paramuricea* Kölliker, 1865) and 50 colonies of Antipatharia Milne Edwards & Haime, 1857 (1 family: Schizopathidae Brook, 1889: *Bathypathes* Brook, 1889 and *Parantipathes* Brook, 1889) were collected from 13 seamount peaks of the NES and CS chains, Muir Seamount and 5 locations on the adjacent continental margin of the eastern USA (200 to 2860 m depth) (Fig. 1, Table 1 in Supplement 1, see www.int-res.com/articles/suppl/m397p025_app.pdf). Additional samples from the North Atlantic, Gulf of Mexico and Pacific were used for wider biogeographic comparisons, including museum specimens collected from seamounts in the vicinity of the Azores that allowed for additional inter-seamount chain comparisons (Table S1).

To better distinguish incomplete sampling from true endemism, we plotted the geographic distribution of haplotypes—unique sequences of haploid mitochondria—as a function of sample size bounded by 2 theoretical expectations (Fig. 2): (1) local endemism (a haplotype is found on a single seamount peak independent of sample size) and (2) pan-distribution (the number of seamount peaks with a particular haplotype equals the number of seamount peaks sampled). We rejected the null hypothesis of seamount-scale endemism if haplotypes were found on more than one peak (see Fig. 2). Below the dotted line in Fig. 2 we cannot reject the null hypothesis that geographic restriction is due to endemism, as we cannot differenti-
ate endemism from undersampling. However, as sampling effort across seamounts increases and haplotypes are still found on one peak (i.e., the lower right part of the plot), the likelihood for endemism increases. It is worth noting that 3 of the seamounts sampled in the present study are characterized by multiple peaks that are separated horizontally by ~50 to 75 km by saddles that range from 1300 to 2300 m deeper than the summits (e.g., Milne-Edwards and Verrill Peaks comprise Caloosahatchee Seamount, Goode and Kükenthal comprise Corner Seamount). Although fauna on the peaks are topographically isolated, it can be argued that this isolation is less significant than for fauna on separate seamounts. However, we observed no case where haplotypes were restricted to only 2 peaks on the same seamount.

**DNA extraction, PCR and sequencing.** Total genomic DNA was extracted from both ethanol (EtOH)-preserved and frozen material using a CTAB (2% hexade- cycttrimethylammonium bromide) protocol (with proteinase K final concentration of 167 µg/mL) and a single chloroform-only extraction (modified from France et al. 1996).

To characterize endemism for a range of coral species on the NES and CS, we chose to sequence mtDNA as it presents few technical challenges and is cost-effective when studying species from a wide taxonomic range. Among mt markers that have been used in octocoral phylogenetics, a mismatch repair gene homolog (msh1) exhibits the highest rate of substitution and appears useful from the intrageneric to interordinal levels (16S, France et al. 1996; msh1, ND3 and ND4L, France & Hoover 2001; cox1, France & Hoover 2002, Calderón et al. 2006; ND2, ND3 and ND6, McFadden et al. 2004). Since msh1 appears to lack intraspecific variation (e.g. Lepard 2003), we associate octocoral haplotypes with individual species. This same reasoning applies to the novel mt markers used for black corals (M. R. Brugler unpubl. data). Microsatellites, which are typically more variable than mtDNA and offer resolution to the population level, were not a viable option for the present study as they generally require species-specific optimization and a larger investment of time and money, as well as greater sample sizes.

Using PCR, we amplified the 5’-region of msh1 for all octocorals plus, for the bamboo coral Acanella, a mt intergenic region and flanking sequence (igr4) (van der Ham et al. in press), and 5 partial genes, 1 tRNA and 3 mt intergenic regions (IGR) for black corals (Table 1). Each PCR reaction contained 1X TaKaRa Ex Taq buffer (Mg2+ free), 0.4 mM dNTPs, 1.5 mM of

<table>
<thead>
<tr>
<th>Amplified gene region</th>
<th>Sequence 5’→3’</th>
<th>Fragment size (primer pairs)</th>
<th>Annealing temp. (time)</th>
<th>Extension temp. (time)</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>msh1(5’) for Octocorallia</td>
<td>TAG TTT TAC TGG CCT CTA C</td>
<td>–990 (1&amp;7)</td>
<td>51°C/20–30 s</td>
<td>72°C/50 s</td>
<td>Brugler &amp; France (2008)</td>
</tr>
<tr>
<td>(1) ND4L2475F</td>
<td>TAC GTG GYA CAA TGG CTG</td>
<td>–845 (2&amp;7)</td>
<td>51°C/30 s</td>
<td>72°C/60 s</td>
<td>Brugler &amp; France (2008)</td>
</tr>
<tr>
<td>(2) ND42625F</td>
<td>GCC ATT ATG GTT AAC TAT TAC</td>
<td>–495 (2&amp;6)</td>
<td>48°C/45 s</td>
<td>72°C/60 s</td>
<td>France &amp; Hoover (2002)</td>
</tr>
<tr>
<td>(3) ND42599F</td>
<td>GCT GCT AGT TGG TAT TGG CAT</td>
<td>–460 (5&amp;7)</td>
<td>51°C/60 s</td>
<td>72°C/45 s</td>
<td>France &amp; Hoover (2002)</td>
</tr>
<tr>
<td>(4) CO3Bam5657F</td>
<td>GGA TAA AGG TTG GAC TAT TAC AGT</td>
<td>–1000 (4&amp;7)</td>
<td>53°C/30 s</td>
<td>72°C/45 s</td>
<td>France &amp; Hoover (2002)</td>
</tr>
<tr>
<td>(5) MSH3010F</td>
<td>GCC ATT ATG GTT AAC TAT TAC</td>
<td>–870 (3&amp;7)</td>
<td>45°C/45 s</td>
<td>72°C/60 s</td>
<td>France &amp; Hoover (2002)</td>
</tr>
<tr>
<td>(6) MSH3101R</td>
<td>GAT ATC ACA TAA GAT AAT TCC</td>
<td>–840 (5&amp;7)</td>
<td>45°C/45 s</td>
<td>72°C/45 s</td>
<td>France &amp; Hoover (2002)</td>
</tr>
<tr>
<td>(7) MUT3458R</td>
<td>TAG TAT TGG CCT CTA C</td>
<td>–990 (1&amp;7)</td>
<td>51°C/20–30 s</td>
<td>72°C/50 s</td>
<td>Brugler &amp; France (2008)</td>
</tr>
<tr>
<td>cob(3’)-igr4-nad6(5’) for Acanella</td>
<td>AGG AGC CAA TCC AGT AGA GGA ACC</td>
<td>–300 (7&amp;8)</td>
<td>55°C/30 s</td>
<td>72°C/45 s</td>
<td>van der Ham et al. (in press)</td>
</tr>
<tr>
<td>(8) CytbBam1279F</td>
<td>TGG TAT TGG CCT CTA C</td>
<td>–1100 (9&amp;11)</td>
<td>55°C/30 s</td>
<td>72°C/65 s</td>
<td>Sánchez et al. (2003)</td>
</tr>
<tr>
<td>(9) Nd6Bam1648R</td>
<td>TGG TAT TGG CCT CTA C</td>
<td>–950 (10&amp;11)</td>
<td>53°C/30 s</td>
<td>72°C/60 s</td>
<td>Sánchez et al. (2003)</td>
</tr>
<tr>
<td>cox3(3’)-IGR-cox1(5’) for Antipatharia</td>
<td>CTT TGT GGC AAC TGG TTG TCA TG</td>
<td>–1100 (9&amp;11)</td>
<td>55°C/30 s</td>
<td>72°C/65 s</td>
<td>van der Ham et al. (in press)</td>
</tr>
<tr>
<td>(10) CO3gen3360F</td>
<td>TGG TAT TGG CCT CTA C</td>
<td>–950 (10&amp;11)</td>
<td>53°C/30 s</td>
<td>72°C/60 s</td>
<td>van der Ham et al. (in press)</td>
</tr>
<tr>
<td>(11) CO3anti3509F</td>
<td>TGG TAT TGG CCT CTA C</td>
<td>–1150 (12&amp;13)</td>
<td>55°C/30 s</td>
<td>72°C/65 s</td>
<td>van der Ham et al. (in press)</td>
</tr>
<tr>
<td>(12) CO1gen4446R</td>
<td>GAT AAC ATT GCA TAA ACC ATC CTT</td>
<td>–550 (12&amp;13)</td>
<td>55°C/30 s</td>
<td>72°C/65 s</td>
<td>van der Ham et al. (in press)</td>
</tr>
<tr>
<td>nad5-5’(3’)-IGR-nad4(5’) for Antipatharia</td>
<td>CAC ACT TGG TGG CCG GAT GCT ATG</td>
<td>–550 (12&amp;13)</td>
<td>55°C/30 s</td>
<td>72°C/65 s</td>
<td>van der Ham et al. (in press)</td>
</tr>
<tr>
<td>(13) ND5-5’anti10725F</td>
<td>CCA AAT ACC TTN CGT TCR GCT AAA GGT</td>
<td>–700 (14&amp;15)</td>
<td>55°C/30 s</td>
<td>72°C/45 s</td>
<td>van der Ham et al. (in press)</td>
</tr>
<tr>
<td>(14) ND1anti11217R</td>
<td>CCA AAT ACC TTN CGT TCR GCT AAA GGT</td>
<td>–700 (14&amp;15)</td>
<td>55°C/30 s</td>
<td>72°C/45 s</td>
<td>van der Ham et al. (in press)</td>
</tr>
</tbody>
</table>

Table 1. PCR primers used in the present study to amplify targeted gene regions, predicted fragment sizes (bp) using specified primer pairs and PCR cycle profiles

*Primer used for Acanella only; bprimer used for Bathypathes only, cprimer used for Parantipathes only*
MgCl₂, 0.24 µM of each primer (Operon Biotechnologies; Table 1), 2.5 µg of acetylated BSA (Promega), 0.5 U TaKaRa Ex Taq polymerase and 40 to 80 ng of genomic DNA, and was brought to a final volume of 25 µl with dH₂O. PCRs were run using the following cycle profile: initial denaturation at 94°C for 2 min followed by 30 to 40 cycles of denaturation at 94°C for 20 to 30 s, variable annealing and extension temperatures and times based on targeted gene region (Table 1) and a final extension at 72°C for 6 min. PCR products were purified by enzymatic digestion (2 U of ExoI and 0.2 U of shrimp alkaline phosphatase [Fermentas] per 1 µl of PCR product; Werle et al. 1994) or from low melting point (LMP) agarose by digestion with agarase (5 U per 100 µl melted 1% LMP agarose; Sigma-Aldrich).

Purified PCR reactions were cycle-sequenced using the ABI BigDye® Terminator v1.1 Cycle Sequencing Kit (1/4 reactions) and purified using either an EtOH/EDTA precipitation or Sephadex G-50 columns (Sigma-Aldrich). Purified products were electrophoresed on a gel containing 3% agarose for 40 min. Purified PCR products were electrophoresed on an ABI PRISM® 3100 or 3130 xl Genetic Analyzer and sequence traces were edited using Sequencher™ v4.7 (Gene Codes). DNA sequences of specimens representing each haplotype, for each seamount, were submitted to GenBank (Table S1).

**Genetic analysis.** Representative haplotypes of *Paramuricea* were aligned using CLUSTAL-W (Thompson et al. 1994). This alignment was submitted to DnaSP v5.00.07 (Librado & Rozas 2009) to generate a haplotype sequence file; sites with missing data were excluded. A median-joining network was constructed using the DnaSP output file in Network 4.5.1.0 (Bandelt et al. 1999, www.fluxus-engineering.com).

**RESULTS**

**Haplotype distribution and abundance on the NES and CS**

Multiple haplotypes were found for 6 of the 8 genera analyzed; no haplotype diversity was observed among *Metallogorgia* and *Acanella* from our NW Atlantic col-

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Fig. 3. Geographic distribution of haplotypes in the NW Atlantic. For each genus, sampling locations are shown by a group of 1 to 6 cells, each cell representing a haplotype (see keys). Numbers in cells are the number of colonies observed for a given haplotype. Locations are organized in a stylistic W–E and N–S orientation. GoMn: Gulf of Maine; Margin: Oceano-grapher and Gilbert Canyons, and 2 locations on the US Continental Slope; BEA: Bear Seamount; RET: Retriever Seamount; PIC: Picket Seamount; BAL: Balanus Seamount; KEL: Kelvin Seamount; MAN: Manning Seamount; REH: Rehoboth Seamount; NAS: Nashville Seamount; MU: Muir Seamount; GOO: Goode Peak; KUK: Küntenthal Peak; MIL: Milne-Edwards Peak; VER: Verrill Peak; YAK: Yakutat Seamount
lections (Fig. 3, Table 2). Nine out of 27 haplotypes were sampled only once (Chrysogorgia Types C and D, Radicipes Types A and C, Paramuricea Types E and G, Bathypathes Types B and E, and Parantipathes Type D). An additional 7 haplotypes were sampled from 4 or fewer colonies, but in only one case was a haplotype restricted to a single seamount peak (Parantipathes Type C on Kükenthal, n = 4). These 4 Parantipathes Type C colonies were collected within meters of one another during a single ROV dive. Four additional Parantipathes colonies were collected from different depths on the same peak, and corresponded to haplotype A or B, both of which were distributed across multiple seamounts (Fig. 3). Of the remaining undersampled haplotypes, 2 were found on 2 different seamounts within the NES (Chrysogorgia Type B and Bathypathes Type C), 2 were found on 3 different seamounts in the NES and CS (Chrysogorgia Type B and Paramuricea Type D) and 2 were found on 2 different seamounts in the NES and CS (Chrysogorgia Type E and Radicipes Type B). The geographic range of a haplotype was positively correlated with the number times it was sampled, and for those haplotypes restricted to an individual seamount, sample size was low and we could not differentiate between true endemism and undersampling (Fig. 2). Though analysis of the vertical distribution of haplotypes was constrained to the varying depth range sampled for each seamount (Fig. S1), most haplotypes found on both the NES and CS chains, with the exception of Parantipathes Type B, do not appear to be stratified by depth.

### Regional and global haplotype distributions

Of the 8 genera in the present study, 4 were collected on both the geographically isolated Muir Seamount and the NES and CS chains (Fig. 3). In only a single case did we observe a haplotype restricted to Muir Seamount: Paramuricea Type G, which was represented by one specimen. Type G is closely related to the widespread Type C, the most common haplotype found on Muir Seamount (Fig. 4).

We were able to sequence the 5’-region of *msh1* for 5 museum specimens collected in 1971 and 1993 from NE Atlantic locations. Three of the specimens had haplotypes that we identified on the NES and CS chains: Iridogorgia Type A was found on the SE side of San Jorge (Portugal), Metallogorgia Type A (n = 2) on Plato Bank, and Chrysogorgia Type B on Irving Bank. A novel Chrysogorgia haplotype was collected from Tyro Bank (Type F). Although this haplotype was not found on the NES and CS chains, we recently collected a specimen with the same haplotype on the bathyal slope of the Bahamas (E. Pante & S. C. France unpubl. data). The 3 chrysogorgiid haplotypes that were common to the NES and CS chains and NE Atlantic were also found in the Pacific (Table S1).

### Correspondence between genetic haplotypes and nominal species

Six of the 27 haplotypes correspond to nominal species. *Iridogorgia* Type A corresponds to *I. magnispiralis* Watling, 2007; *Type B = I. splendens* Watling, 2007;
**Thoma et al.: No evidence of endemism on NW Atlantic seamounts**

**Metallogorgia** Type A = *M. melanotrichos* (Wright & Studer, 1889); Radicipes Type A = *R. gracilis* (Verrill, 1884); Acanella Type A = *Acanella eburnea* (Pourtalès, 1868); Bathypathes Type D = *B. alternata* Brook, 1889.

The remaining haplotypes come from colonies that are yet to be identified or are undescribed species: all types of Chrysogorgia; Radicipes Types B and C; all types of Paramuricea; Bathypathes Types A–C and E; and Parantipathes Types A–D.

**Fig. 4.** Median-joining network depicting relatedness and geographic distribution of *msh1* haplotypes of *Paramuricea*, based on 14 variable sites. Circle size is proportional to the number of colonies with the corresponding haplotype (sample size indicated in parentheses). Hash marks and branch lengths represent the number of mutational steps between each haplotype.

**Relationships among haplotypes of *Paramuricea***

We observed 6 haplotypes among the 85 colonies of *Paramuricea* sequenced from the NW Atlantic. Although there is little overall genetic differentiation among the haplotypes, they can be divided into 3 groups (Fig. 4). Types A and E, which are the only haplotypes found on the continental margin, group together with Type D (from Balanus, Kelvin and Verrill Peak). The remaining 3 haplotypes, which were collected from seamounts only, form 2 well-separated groups (Type B versus Types C/G). Levels of divergence among haplotypes are low within the A/D/E (uncorrected *p*-distances: 0.129 to 0.268%) and C/G (0.324%) groups. Types B and C/G are more divergent from A/D/E (0.528 to 0.667% and 1.544 to 1.861%, respectively) and from one another (1.055 to 1.238%) (Fig. 4).

We obtained *msh1* sequences from congeners collected from outside the study area (i.e. Norway, Gulf of Mexico, Caribbean and Hawaii). Specimens from Norway and the Gulf of Mexico were poorly preserved, and we could recover only partial *msh1* sequences (~208 bp); for the region of overlap their sequences were identical to group A/D/E. The sequence of the Caribbean specimen *Paramuricea multispina* (GenBank accession no. AY683077) is identical, except for a single ambiguity, to Type E found in a specimen from the Gulf of Maine. The ambiguous base is at a position in the alignment that is not variable in other sequences of *Paramuricea* or holaxonians examined (i.e. *Leptogorgia chilensis*, AY268460; *Pseudopterogorgia americana*, AY683087; *Eunicea clavigera*, AY683058). A complete *msh1* sequence from an unidentified *Paramuricea* collected in Hawaii (EU293799) yielded a novel haplotype (Type F). Both haplotypes E and F differ by a single substitution from Type A.

**DISCUSSION**

**Improving geographic and taxonomic sampling**

Based on samples from 13 seamount peaks from 2 chains spanning a distance of approximately 1700 km, the isolated Muir Seamount, and the adjacent continental margin, our study provides new data on the genetic diversity and geographic distribution of octocorals and black corals from a relatively understudied biogeographic region. To date, studies of faunal endemism on seamounts have largely been conducted in the South Pacific (Wilson & Kaufmann 1987, Stocks & Hart 2007). In Wilson & Kaufmann’s (1987) comprehensive review of seamount biota, only 17% of the taxa included were from the Atlantic, among which only one specimen was collected in the vicinity of our study area (San Pablo Seamount, NES; Cairns 1982 in Wilson & Kaufmann 1987). Since 1987, several studies have characterized seamount biodiversity in the North Atlantic (Mironov & Gebruk 2006, review to mid-2005 by Stocks & Hart 2007), including Hall- Spencer et al. (2007), who estimated levels of endemism for corals in the NE Atlantic. Nonetheless, studies on seamount endemism in the NW Atlantic remain scarce (Sterrer
1998, Calder 2000, see also Mironov & Krylova 2006). This contribution, therefore, broadens the geographical breadth of the current body of research on seamount endemism.

The present study also provides data on the diversity of deep-sea corals, a relatively abundant and conspicuous, yet understudied, taxonomic group. Most studies of endemism have been conducted on fish, molluscs and crustaceans (Stocks & Hart 2007). Our study, along with Smith et al. (2004), represents one of the rare efforts to characterize the distribution of coral species across seamounts based on genetic tools (see Baco & Shank 2005 for a population-level study of Hawaiian deep-sea corals). While Smith et al. (2004) focused on a single octocoral subfamily (Keratoisidinae), the present study examines 3 families of octocorals as well as 2 antipatharian genera to provide information on distribution and diversity patterns from 2 distinct anthozoan lineages. We describe the distribution of 27 coral haplotypes, putatively corresponding to at least 27 species, only 6 of which could be identified based on published records. Two of these 6 identified species correspond to new species descriptions (Watling 2007) from specimens collected during the expeditions that underlie the present study. Taxonomic work on the remaining unidentified material is ongoing.

**Biogeography of coral haplotypes**

Seventeen of 27 coral haplotypes were not restricted to individual peaks, and 15 were not restricted to either seamount chain. For haplotypes that were restricted to individual peaks or chains, low sample size prevented us from discriminating true endemism from undersampling. In most studies that estimate endemism, the majority of taxa are not restricted to individual seamounts or seamount groups, which is evidence for successful dispersal and recruitment. In the NE Atlantic, <3% of octocorals, black corals and scleractinians are seamount specialists (Hall-Spencer et al. 2007); therefore, we expect levels of endemism on individual seamounts to be even lower. Similar results were observed in the Pacific, where no endemism was detected for bamboo corals (Smith et al. 2004). Since we frequently observed more haplotypes with increased HOV/ROV operation time (data not shown), increasing sampling effort could expand the observed geographical range of these rare haplotypes.

Three of the 27 haplotypes were also found in the Azores and in the Pacific. These wide geographic distributions could reflect high dispersal capabilities or ancient connections between ocean basins. The absence of variation among *Metallogorgia* colonies, for example, contrasts with the genetic diversity observed in other chrysogorgiid genera (i.e. *Chrysogorgia, Iridogorgia* and *Radicipes*). This pattern could reflect a relatively recent origin for the genus *Metallogorgia* (i.e. insufficient time to speciate), or superior dispersal capability relative to confamilial species. Deep-sea corals are long-lived (e.g. Roark et al. 2006, 2009) and slow-growing (Grigg 1993), and the time needed to diversify may therefore be relatively long (e.g. diversification and longevity are negatively correlated in the rockfish *Sebastes*; Bonsall 2006). Thus speciation rates may be slower and the generation of endemism through *in situ* diversification would be expected to take longer. Finally, the slow rate of evolution of the mitochondrial markers may not reflect actual species divergence. Fukami & Knowlton (2005) estimated the overall rate of mt genome evolution within the *Montastrea annularis* species complex (Scleractinia) at only 0.03 to 0.04% per million yr, and Lepard (2003) estimated the mutation rate of *msH* to range between 0.14 and 0.25% per million yr, which renders it unlikely that substitutions will be seen between lineages that have diverged less than 1 million yr ago when comparing sequences of 1000 nucleotides or less.

Our collections of *Paramuricea* yielded a greater number of haplotypes (n = 6) than any other genus in our study area, and these could be divided into 3 divergent groups. One of these groups (A/D/E) was more closely related to colonies from distant locations (i.e. Norway, Gulf of Mexico, Caribbean and Hawaii) than to the other seamount haplotypes. The geographic paraphyly of NES and CS *Paramuricea* haplotypes, in combination with the observation of multiple, identical chrysogorgiid haplotypes found in both the Pacific and Atlantic, suggests that the 2 seamount chains are not discrete biogeographic units. A similar trend is observed for taxa of the Reykjanes Ridge (North Atlantic), which also occur in the Pacific and Antarctic (Mironov & Gebruik 2006).

**Study limitations and future efforts**

Reviewers of seamount endemism (McClain 2007, Stocks & Hart 2007) have identified geographically uneven sampling efforts and heavy reliance on morphology-based systematics as factors potentially preventing us from accurately estimating endemism at multiple spatial scales and reaching a synthetic understanding of the mechanisms involved in faunal isolation. For example, we observed that the divergent *Paramuricea* haplotypes come from colonies that are morphologically indistinguishable when viewed *in situ*. In the present study we provide molecular-based distributional information on an understudied taxonomic group from an underexplored area. Our results do not
support seamount-scale endemism in the NW Atlantic, as well-sampled haplotypes were not geographically restricted to individual seamounts and, in some instances, haplotypes also occurred in the Pacific. Our efforts, however, are limited by gaps in the taxonomy of the concerned groups, the scarcity of samples outside of the NES and CS chains, and the potential lack of fine systematic resolution offered by currently available molecular markers.

Future efforts should focus on determining the correspondence between haplotypes and nominal species. As previously stated, preliminary efforts suggest that msh1 is appropriate for detecting variation at the species level, but ultimately, it will be necessary to formally describe all specimens collected on the NES and CS chains to establish congruence between molecular and morphological data.

At the evolutionary time-scale considered, more intensive sampling will be necessary to establish biogeographic affinities between seamount chains. Using only a few specimens from museum collections, we were able to establish that some haplotypes occur outside of the NW Atlantic. Only with sampling efforts spanning ocean basins will we be able to establish how commonly distributed taxa are. For example, samples collected during a recent expedition to the bathyal slope of the Bahamas (Bahamas Deep Corals 2009, http://oceanexplorer.noaa.gov/explorations/09deepseacorals/) broaden the geographical distribution of 6 haplotypes belonging to the Chrysogorgiidae (E. Pante & S. C. France unpubl. data), 2 of which had particularly narrow ranges on the NES and CS (i.e. Iridogorgia Type B, Chrysogorgia Type C).

Developing molecular markers that are informative at the population level will provide a more complete understanding of the mechanisms involved in isolating taxa from different seamounts and seamount chains. Short sequences (<1000 bp) of mtDNA have not been shown to be variable at the intraspecific level in most anthozoans and therefore are not suitable for population-level studies (France & Hoover 2001, 2002, Shearer et al. 2002, McFadden et al. 2004, but see Chen et al. 2008a,b for scleractinians). Nuclear DNA, however, may be more variable than mtDNA in anthozoans (Chen et al. 2009). Low-copy nuclear markers have been used for species delineation and detection of introgression in stony corals (Hatta et al. 1999, van Oppen et al. 2000, 2001, 2004, Vollmer & Palumbi 2002, 2007) and soft corals (Concepcion et al. 2008), and could be particularly informative for those species that might have diverged less than 1 million yr ago. Microsatellites have been used to study population-level questions in deep-sea corals (e.g. Baco & Shank 2005), but they require high sample sizes. Sampling constraints in deep-sea hard-substrate communities render abundant collections of targeted taxa a difficult goal to achieve, particularly on expeditions with multiple objectives; we rarely were able to collect more than 5 colonies of a species per seamount peak.

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