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Models of habitat suitability, size, and age-class structure for the deep-sea black coral *Leiopathes glaberrima* in the Gulf of Mexico

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ABSTRACT

Deep-sea corals are important components of the benthos in the Gulf of Mexico, because they provide structural complexity to associated species of fish and invertebrates, and they serve as proxies for environmental conditions on millennial time scales. In the Gulf of Mexico, large colonies of the black coral *Leiopathes glaberrima* have been estimated to be over 2000 years old. As such, they are vulnerable to disturbance and slow to recover from adverse interactions with anchors, fishing gear, sedimentation, oil and gas extraction, and sampling. There is a growing need for non-lethal scientific collections and new information on the distribution, ecology, and population connectivity of *L. glaberrima* aggregations to support management decisions. A large number of remotely operated vehicle (ROV) surveys have been conducted in the Gulf of Mexico deep sea since 2008, including telepresence cruises that broadcast live seafloor images to shore. Visual observations from these surveys were collated and geo-referenced in a regional database with national museum records in order to: (1) map the distribution of *L. glaberrima* throughout the U.S. Gulf of Mexico, (2) predict the distribution of *L. glaberrima* based upon environmental correlates using maximum entropy (MaxEnt) modeling, and (3) correlate the size-class structure to the age-class structure using growth rate estimates from previous radiocarbon studies. We found that *L. glaberrima* has a broad distribution in the U.S. Gulf of Mexico, with suitable habitat spanning depths between 200 and 1000 m that are concentrated near the Mississippi Canyon and along the West Florida Shelf. On average, *L. glaberrima* colonies had a height of 34.2 cm and a basal diameter of 0.42 cm, which correlates to an age of ~143 yrs. Future efforts should focus on calibrating the size and growth relationships of black corals and other corals, in order to add value to telepresence-based exploration and promote non-invasive sampling techniques.

1. Introduction

Antipatharians, commonly known as black corals, are a little studied antipatharian order (Cnidaria: Anthozoa: Hexacorallia: Antipatharia) that encompasses over 235 described species (Cairns, 2007; Wagner et al., 2012; Brugler et al., 2013). Black corals occur worldwide in all oceans, and have a broad depth distribution ranging from 2 to 8600 m (reviewed by Wagner et al., 2012). Despite this wide range, black corals are typically found in deeper waters below the photic zone, with over 75% of described species being restricted to depths below 50 m (Cairns, 2007). At these depths, black corals are often abundant and

conspicuous faunal components of the benthos, occurring in many locations around the world (reviewed by Wagner et al., 2012a), including throughout the Gulf of Mexico (Brooke and Schroeder, 2007; Opresko et al., 2009; Boland et al., 2016).

A total of 29 black coral species in 15 genera have been reported from the Gulf of Mexico, including the species *Leiopathes glaberrima* (Esper, 1792) (reviewed by Opresko et al., 2009; Etnoyer and Cairns, 2016). *L. glaberrima* colonies are abundant and widespread throughout the Gulf, with some colonies reaching heights of > 1 m that provide habitat for a myriad of associated organisms (reviewed in Brooke and Schroeder, 2007). Fish species observed in association with *L.*

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glaberrima in the Gulf of Mexico include Atlantic roughy (*Hoplostethus occidentalis*), slimeheads (*Gephyroberyx darwini*), *Anthias* sp., (Aquanautix, 2010a) and Scyliorhinidae catsharks, the latter of which lay eggs on *L. glaberrima* colonies (TDI-Brooks Int, 2008). Additionally, barrelfish (*Hyperoglyphe perciformis*) have been observed schooling in the vicinity of *L. glaberrima* colonies in the Gulf (Aquanautix, 2010a). Invertebrates documented in association with *L. glaberrima* in the Gulf of Mexico include squat lobsters (*Eumunida picta*), gooseneck barnacles (Etnoyer, 2008), and the deep-sea scleractinian coral *Lophelia pertusa*, which has been observed growing on and near *L. glaberrima* colonies (Aquanautix, 2010b).

Similar to observations from the Mediterranean Sea (Bo, 2008; Mastrotoaro et al., 2010; Vertino et al., 2010; Bo et al., 2015), multiple color morphotypes of *Leiopathes* colonies have been reported throughout the Gulf of Mexico, including red, orange, light yellow-orange, pale yellow, and white (Brooke and Schroeder, 2007; Opresko et al., 2009; Ruiz-Ramos et al., 2015). However, recent morphological and molecular investigations indicate that these color morphotypes all correspond to a single species, *L. glaberrima* (Ruiz-Ramos et al., 2015), which has a wide geographic range that includes the Mediterranean Sea, the North Atlantic, the Caribbean, and the Gulf of Mexico (reviewed in Wagner and Opresko, 2015).

Recent studies of *L. glaberrima* in the Gulf of Mexico include investigations of its (1) growth rate and longevity (Prouty et al., 2011), (2) stable isotope and trace element compositions (Prouty et al., 2014), (3) dispersal potential (Cardona et al., 2016), as well as (4) morphological and genetic diversity (Ruiz-Ramos et al., 2015). Using radiocarbon dating, Prouty et al. (2011) estimated radial growth rates ranging between 8–22 $\mu\text{m}/\text{yr}$ for *L. glaberrima* from the Gulf of Mexico, corresponding to maximum longevities approaching 2100 yrs. Similar methods have been used to estimate longevities of *Leiopathes* spp. in other parts of the world, including Hawaii (Roark et al., 2006; Roark et al., 2006, 2009), the Azores (Carreiro-Silva et al., 2013) and the Southeastern United States (Williams et al., 2006; Williams et al., 2006, 2007). These studies all suggest that *Leiopathes* spp. are some of the slowest growing and longest lived organisms on the planet, with maximum longevity estimates ranging between 483 and 4265 yrs.

As a result of their extreme longevity, the skeletons of *Leiopathes* spp. corals provide important clues into past oceanographic conditions. Prouty et al. (2014) studied the skeletal composition of deep-water corals collected from the Gulf of Mexico, including *L. glaberrima*, and found evidence for nutrient enrichments in the last 150–200 yrs, likely due to increases in terrestrial runoff due to anthropogenic sources. Similarly, *L. glaberrima* specimens from the Gulf of Mexico and Southeastern United States provided evidence for recent nutrient enrichments, and also demonstrated a ^{13}C decline consistent with the anthropogenic release of CO_2 from fossil fuels (Williams et al., 2007).

Cardona et al. (2016) investigated the dispersal potential of *L. glaberrima* in the Northern Gulf of Mexico through a combination of ocean circulation models and molecular data. Their results indicate that *L. glaberrima* predominantly recruit locally in the Northern Gulf of Mexico, with long-distance dispersal across the Gulf only occurring occasionally. Consistent with these results, Ruiz-Ramos et al. (2015) found evidence for barriers to gene flow in the population genetic structure of *L. glaberrima* from nearby sites in the Gulf of Mexico (distance = 36.4 km). Furthermore, their genetic data indicated that *L. glaberrima* has a mixed reproductive strategy, including both self and cross-fertilization, which might allow this species to strike a balance between local recruitment and occasional long-distance dispersal (Ruiz-Ramos et al., 2015).

Given the extreme longevity (Prouty et al., 2011; Prouty et al., 2011, 2014), abundance, and ecological role as an important habitat-forming species (Brooke and Schroeder, 2007; Boland et al., 2016), there is considerable interest to include *L. glaberrima* in management and conservation plans for the Gulf of Mexico (ONMS, 2016). Along with the closely related scleractinian coral *Lophelia pertusa*, *L.*

glaberrima is being considered as a species of concern by the Gulf of Mexico Fishery Management Council. However, management and conservation plans are complicated by the limited information that is currently available on the spatial distribution and demographic structure of this species.

In order to address this knowledge gap, we combined in situ observations from remotely operated vehicles (ROVs) conducted since 2008, with museum specimens to generate habitat suitability and population demographic models for *L. glaberrima*. Many of the in situ observations used as part of this study were obtained using ROVs equipped with telepresence technology, which allowed for remote observations from shoreside facilities. We combined these telepresence observations with traditional field observations in order to provide a comprehensive overview of the spatial and colony size-class distribution of *L. glaberrima* in the Gulf of Mexico. Furthermore, we used previous growth rate estimates of *L. glaberrima* to derive the age-class structure in the Gulf.

2. Data and methods

2.1. Study area

The biogeographic range of *L. glaberrima* includes the Mediterranean, the North Atlantic, the Caribbean, and the Gulf of Mexico, however, our study was limited to the U.S. Exclusive Economic Zone in the Gulf of Mexico, which includes the continental shelf and slope, and extends to a depth of 3500 m. The primary focal area was the Viosca Knoll region in the Northwest Gulf of Mexico, where current oil and gas extraction activities are concentrated (Boland et al., 2016). This region is of primary interest to the Bureau of Ocean and Energy Management (BOEM), the National Oceanic and Atmospheric Administration (NOAA) and the United States Geological Survey (USGS) due to the presence of substantial oil and gas reserves and fisheries resources. Two secondary focal areas included the western Gulf of Mexico off Texas, and the eastern Gulf of Mexico off Florida. These secondary areas have received less survey effort over the last decades, because management concerns are lower, but these regions are increasingly recognized as important habitats for deep-sea corals (Ross et al., 2017).

2.2. ROV surveys

Data analyzed as part of this study consisted primarily of videos and photo observations collected using ROVs, supplemented by metadata associated with museum specimens curated at Smithsonian Institution's National Museum of Natural History. The bulk of the samples and observations were collected on ROV expeditions aboard the NOAA ships *Nancy Foster*, *Ronald Brown*, and *Okeanos Explorer*, as well as the R/V *Falkor* operated by the Schmidt Ocean Institute. The majority of the observations reviewed as part of this study were collected during the following expeditions: (1) *Lophelia* II: Reefs, Rigs, and Wrecks (2008–2011), (2) NOAA Ship *Okeanos Explorer* cruises EX1202L3 (2012) and EX1402L2 (2014), and (3) R/V *Falkor* ROV Shakedown expeditions FK-004e and FK-006c (2012). A comprehensive table of the research expeditions contributing to the study is provided in Table 1.

Previously published studies by Georgian et al. (2014) and Cardona et al. (2016) summarized many of the ROV observations focusing primarily on the Northwest Gulf of Mexico region near Mississippi Canyon. Geo-referenced observations from those studies were uploaded to the NOAA National Database of Deep-Sea Corals and Sponges (Hourigan et al., 2015; NOAA, 2016), and combined with observations from *Lophelia* II, NOAA Ship *Okeanos Explorer*, and R/V *Falkor* expeditions along the West Florida Shelf, in order to give a comprehensive overview of the spatial distribution of *L. glaberrima* in the Gulf of Mexico (Fig. 1).

Table 1

Table of surveys in the U.S. Gulf of Mexico that contributed observations to the present study. Surveys indicated with an asterisk (*) were used for size class analyses. NOAA Ship Okeanos Explorer expeditions in 2012 and 2014 were equipped with telepresence technology. ‘Survey ID’ shows the NOAA Office of Marine and Aviation Operations assignment, or the expedition name. ‘Count’ represents the number of records of *Leiopathes glaberrima* to NOAA’s National Database of Deep-Sea Corals and Sponges.

Vessel	Vehicle	Year	Survey ID	Count
NOAA Ship <i>Okeanos Explorer</i>	ROV <i>Deep Discoverer</i>	2014	EX1402L3	21
NOAA Ship <i>Okeanos Explorer</i>	ROV <i>Little Hercules</i>	2012	EX1202L2	11
RV <i>Falkor</i>	ROV <i>Global Explorer</i>	2012	FK006c*	8
RV <i>Falkor</i>	ROV <i>Global Explorer</i>	2012	FK004e*	7
MV <i>Holiday Chouest</i>	ROV <i>Schilling UHD</i>	2011	HC-11-10	37
NOAA Ship <i>Ron Brown</i>	ROV <i>Jason II</i>	2010	RB-10-07	485
NOAA Ship <i>Nancy Foster</i>	ROV <i>Global Explorer</i>	2010	NF-10-07	80
RV <i>Seward Johnson</i>	HOV <i>Johnson Sea Link</i>	2010	FLoSEE 2010	12
NOAA Ship <i>Ron Brown</i>	ROV <i>Jason II</i>	2010	RB-10-08	4
NOAA Ship <i>Ron Brown</i>	ROV <i>Jason II</i>	2009	RB-09-05*	734
NOAA Ship <i>Nancy Foster</i>	ROV <i>Saab Falcon DR</i>	2008	USGS-NF-08	996
RV <i>Seward Johnson</i>	HOV <i>Johnson Sea Link</i>	2004-05	<i>Lophelia I</i>	6
RV <i>Pelican</i>	dredge	2004	na	2
NOAA Ship <i>Ron Brown</i>	ROV <i>Sonsub Innovator</i>	2003	RB-03-07	1
RV <i>Citation</i>	trawl	1985	NGOMCS V	1
RV <i>Seward Johnson</i>	HOV <i>Johnson Sea Link</i>	1987–2009	na	7
RV <i>Oregon</i>	trawl	1955	na	1

2.3. Image analyses

Image analyses were conducted using non-invasive visual sampling techniques. Still images and video from ROV surveys were reviewed in the laboratory using VLC software. For this purpose, technicians used in situ images from the *Lophelia II* and R/V *Falkor* expeditions as a reference. *Lophelia II* images corresponded to vouchered sample collections that were previously identified by a taxonomic expert (D. Opresko, National Museum of Natural History, Smithsonian Institution) as *L. glaberrima*. Frame grabs were collected from the video using VLC, with particular attention to images that included the presence of lasers for scale (typically projected 10 cm apart). PhotoQuad software was used to determine colony area, height, and width. ImageJ software was used for size measurements of the basal holdfast using the paired lasers as a size reference (Fowle, 2013; Fig. 2).

A linear regression was performed on a subset of the observed *L.*

glaberrima colonies for which both basal diameter and colony height was available. The slope of this linear regression was then used to estimate the basal diameter of *L. glaberrima* colonies for which only height data was available. Colony age was estimated using the basal diameter and the midpoint of the range of radial growth rates (8–22 μm/yr = 15 μm/yr) determined for *L. glaberrima* from the Gulf of Mexico during previous radiocarbon studies (Prouty et al., 2011).

2.4. Habitat suitability models

2.4.1. Overview

Areas in the Gulf of Mexico that were most likely to contain suitable habitat for *L. glaberrima* were identified using a Maximum Entropy modeling framework (MaxEnt; Phillips et al., 2004, 2006) that related known *L. glaberrima* records (latitude, longitude) to a set of spatially explicit environmental predictor variables (Table 2). MaxEnt is a

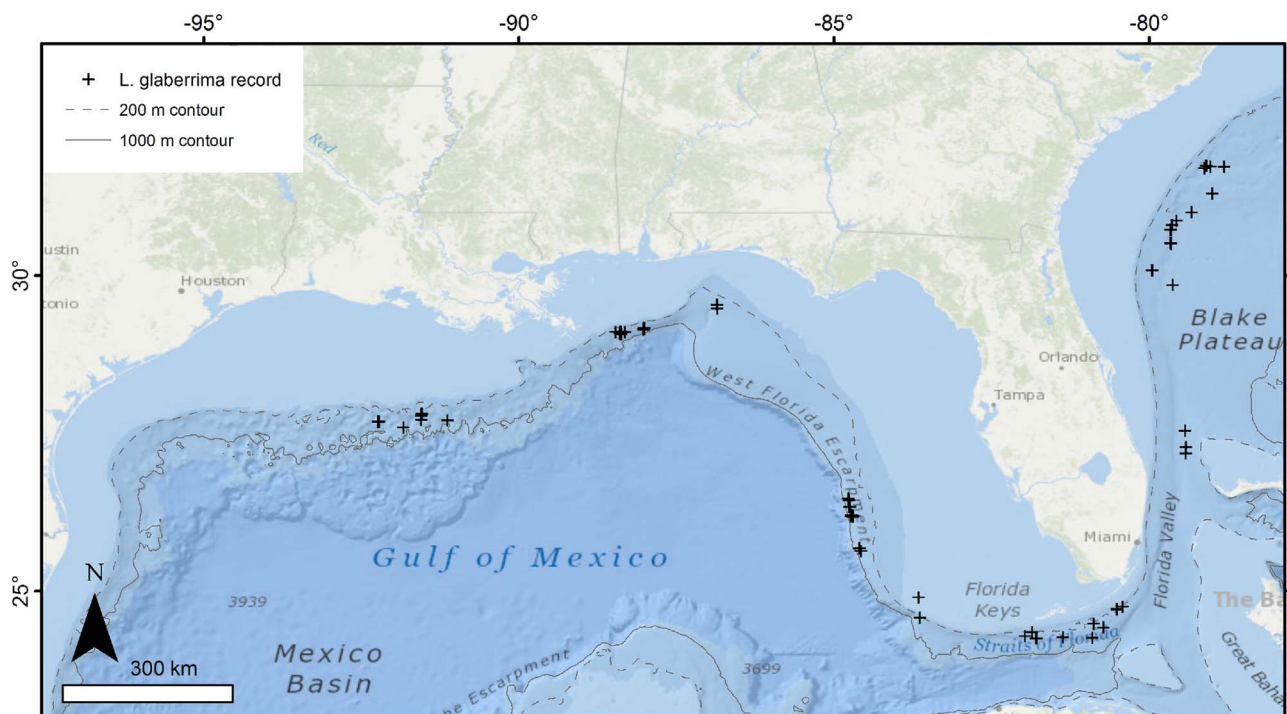


Fig. 1. Map showing *Leiopathes glaberrima* records from NOAA’s national database of deep-sea corals and sponges (NOAA, 2016).

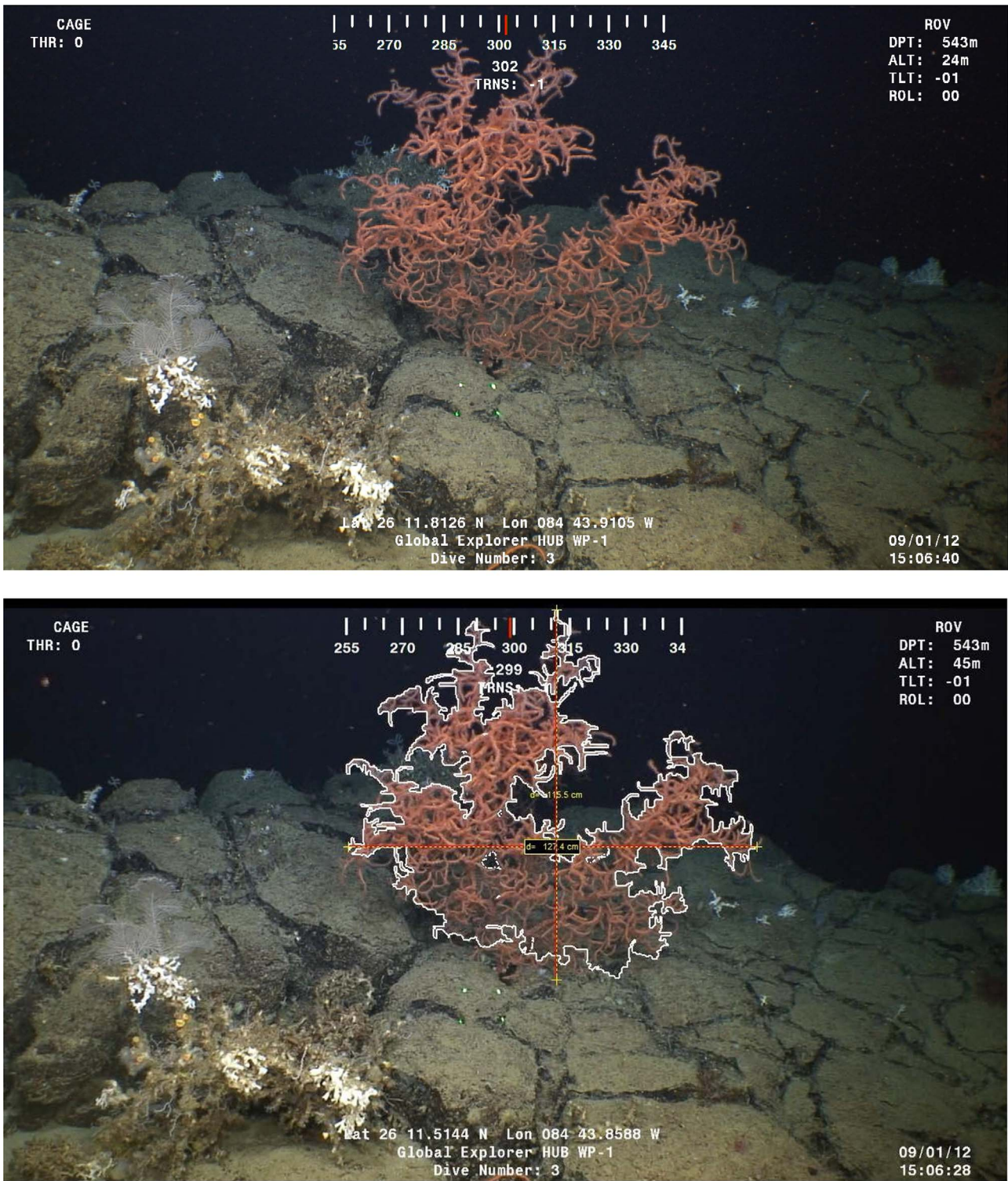


Fig. 2. Images showing a *Leiopathes glaberrima* black coral colony at 544 m depth in the Gulf of Mexico. The green colored lasers are 10 cm apart, positioned below center, near the base of the colony. The top image shows the whole colony in situ, the bottom image shows the outline used to measure height and width. (For interpretation of the references to color in this figure, the reader is referred to the web version of this article.)

statistical machine-learning algorithm that has been used widely to model species distributions (Elith et al., 2011; Merow et al., 2013) and that generally outperforms other methods for modeling habitat suitability from presence-only data (Tittensor et al., 2009; Tong et al., 2013).

A stepwise model-selection procedure was implemented to choose a model that balanced predictive performance with complexity. At each

step of this procedure, ten replicate models were fit using MaxEnt software (<http://www.cs.princeton.edu/~schapire/maxent>). Model predictive performance was calculated as the area under the receiver operating characteristic curve (AUC; Fielding and Bell, 1997) using data withheld from model fitting. Model complexity was measured using Akaike's information criterion corrected for small sample size (AICc; Akaike, 1974; Burnham and Anderson, 2002). The least important

Table 2

List of environmental predictor variables used to produce the habitat suitability model for *Leiopathes glaberrima* black corals in the U.S. Gulf of Mexico. Asterisks (*) indicate the variables included in the final model for *L. glaberrima* habitat suitability.

Environmental variables	Data Source
Depth*	NOAA CRM, GEBCO
Slope (1500 m scale)	NOAA CRM, GEBCO
Slope (10 km scale)*	NOAA CRM, GEBCO
Slope of slope (1500 m scale)	NOAA CRM, GEBCO
Slope of slope (5 km scale)*	NOAA CRM, GEBCO
Slope of slope (10 km scale)*	NOAA CRM, GEBCO
Slope of slope (20 km scale)*	NOAA CRM, GEBCO
Aspect (1500 m scale)	NOAA CRM, GEBCO
Aspect (5 km scale)*	NOAA CRM, GEBCO
Aspect (20 km scale)*	NOAA CRM, GEBCO
Rugosity (370 m scale)	NOAA CRM, GEBCO
Rugosity (5 km scale)	NOAA CRM, GEBCO
Planar curvature/slope index (1500 m scale)	NOAA CRM, GEBCO
Planar curvature/slope index (5 km scale)	NOAA CRM, GEBCO
Planar curvature/slope index (10 km scale)	NOAA CRM, GEBCO
Planar curvature/slope index (20 km scale)	NOAA CRM, GEBCO
Profile curvature/slope index (1500 m scale)	NOAA CRM, GEBCO
Profile curvature/slope index (5 km scale)	NOAA CRM, GEBCO
Profile curvature/slope index (10 km scale)	NOAA CRM, GEBCO
Profile curvature/slope index (20 km scale)*	NOAA CRM, GEBCO
BPI/slope index (20 km scale)	NOAA CRM, GEBCO
Surficial sediment mean grain size*	Chris Jenkins (University of Colorado)
Surficial sediment percent sand*	Chris Jenkins (University of Colorado)
Annual bottom dissolved oxygen*	SEAMAP, WOD 2009
Annual bottom salinity	SEAMAP, WOD 2009
Annual bottom temperature*	SEAMAP, WOD 2009
Annual sea surface chlorophyll-a concentration*	NOAA CoastWatch

environmental predictor variable in terms of model predictive performance was dropped after each step. The estimated relationships between *L. glaberrima* presence and the environmental predictor variables for the chosen final model were used to predict the relative likelihood of suitable habitat for *L. glaberrima* across the Gulf of Mexico. Detailed descriptions of environmental predictor variable development and screening, model fitting, model selection, and predicting habitat suitability can be found in [Appendix A](#).

2.4.2. Coral presence data

Data describing locations of *L. glaberrima* observations in the Gulf of Mexico were retrieved from the NOAA National Database of Deep-Sea Corals and Sponges (NOAA, 2016). This database contains geo-referenced records of coral presence from NOAA and other government and academic institutions, including museum records. Data were quality controlled by plotting their position and removing those records with 1) reported depths that were > 1000 m deeper than those derived from the NOAA Coastal Relief Model (National Geophysical Data Center, 2001 a-c2001a, 2001b, 2001c) at the same location, 2) reported locations that were > 10 km from other observations on the same dive, and 3) locations that were inconsistent with the reported place name (e.g. VK826).

In the Gulf of Mexico there were 2413 verifiable and unique records of *L. glaberrima* presence (see [Table 1](#)). The records were placed into 370×370 m grid cells, and duplicate records were removed from within each grid cell in order to reduce the effect of sampling bias in heavily sampled areas. The 370×370 m grid cell size was selected because of the spatial uncertainty in depth values from the NOAA Coastal Relief (CRM) model in deeper waters (> 50 m; See [Appendix A](#)) and the scale of topographic variables derived from the CRM 90 m grid. Following removal of duplicate records within the 370 m grid cells, 85 unique records of *L. glaberrima* remained (i.e., 85 model grid cells contained *L. glaberrima* records).

2.4.3. Environmental predictor variables

A set of 50 environmental predictor variables was compiled for potential use in the habitat suitability model. These variables included measures of seafloor topography, seafloor substrate, and physical and biological oceanography. A total of 27 environmental predictors were ultimately retained for use in the predictive model ([Table 2](#)).

3. Results

3.1. Distribution of *L. glaberrima* ROV observations

L. glaberrima colonies were observed using ROVs on hard-bottom patches in a depth range of 367–596 m. Observations spanned across the entire U.S. Gulf of Mexico, but were most common in three regions including the Louisiana shelf break west of the Mississippi Canyon, the Viosca Knoll region south of Mississippi and Alabama, and the West Florida Shelf ([Fig. 1](#)).

3.2. Habitat suitability model

The model predicted that areas with the highest likelihood of suitable habitat for *L. glaberrima* were restricted to a depth range of approximately 200–1000 m across the U.S. Gulf of Mexico ([Fig. 3](#)). Areas of highest suitability included the Flower Garden Banks region off the coast of Texas, the Viosca Knolls region near the Mississippi Canyon, and along the West Florida Shelf region to the Pulley Ridge region west of the Florida Keys ([Fig. 3](#)).

Thirteen environmental predictor variables were included in the final habitat suitability model for *L. glaberrima*: aspect at 5 km scale, aspect at 20 km scale, depth, mean annual bottom dissolved oxygen, mean annual bottom temperature, mean annual sea surface chlorophyll-a concentration, surficial sediment mean grain size, profile curvature/slope index at 20 km scale, surficial sediment proportion sand, slope at 10 km scale, slope of slope at 5 km scale, slope of slope at 10 km scale, and slope of slope at 20 km scale (see [Table 1](#)). The most important environmental predictor variables for model fitting were depth, mean annual bottom temperature, and slope at 10 km scale. Depth also contained the most non-redundant information that explained variation in predicted likelihood of habitat suitability for *L. glaberrima*. The predicted likelihood of suitable habitat for *L. glaberrima* was greatest for depths ranging from 200 to 1000 m, for mean annual bottom temperature values ranging from 6 to 16 °C, and for large-scale (10 km) seafloor slope ranging from 1% to 7% ([Fig. 4](#)).

3.3. Size-class structure

A total of 368 *L. glaberrima* colonies were identified in ROV videos. Of these, the height of 357 colonies could be measured using scaled lasers. Only 18 colonies had both height and basal diameter measurements. There was a strong correlation between colony height and basal diameter ($R^2 = 0.6629$, p -value = 0.0000771; [Fig. 5](#)) among the 18 colonies. Using the linear correlation between height and basal diameter ([Fig. 5](#)), the basal diameter and radius was estimated for the remaining 339 colonies. On average, *L. glaberrima* colonies had a height of 34.23 cm and estimated basal diameter of 0.42 cm.

The average age was estimated for colonies larger than 18 cm ($n = 222$) using basal radius and the midpoint of known growth rates ($15 \mu\text{m}/\text{year}$, [Prouty et al., 2011](#)). The average estimated age of *L. glaberrima* colonies was 143 yrs, with an average range of 0–909 yrs. Among all measured colonies ($n = 357$), the most abundant size class ($n = 191$, or 53.5%) was 15–30 cm high ([Fig. 6](#)), and corresponded to an age range of 50–100 yrs. The next most abundant size class ($n = 68$, or 19%) was < 15 cm high ([Fig. 6](#)), which corresponded to an age less than 50 yrs. The size class of 30–45 cm ($n = 55$, or 15.4%) correlated to an age 101–250 yrs. The size class of 45–60 cm ($n = 22$, 6%) corresponded to an age > 250 yrs. The size class of 60–74 cm ($n = 12$,

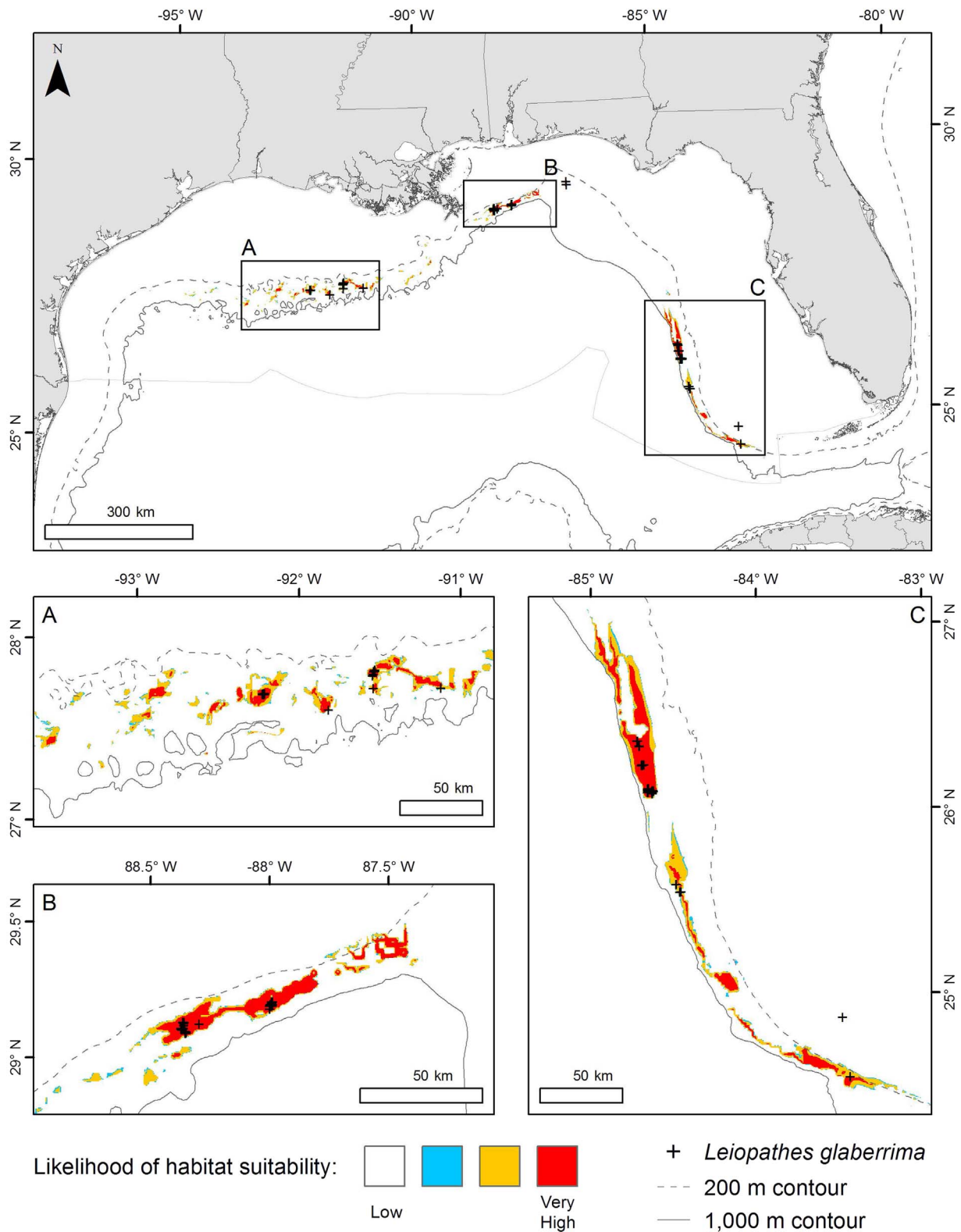


Fig. 3. Map showing records of *Leiopathes glaberrima* in the U.S. Gulf of Mexico, overlaid onto a map of predicted likelihood of habitat suitability for this species in the region. Inset maps show records and predicted likelihood of habitat suitability in a) the northwest outer continental shelf, b) the northern Gulf of Mexico, and c) the West Florida slope. The spatial extent of the model is the US Exclusive Economic Zone in the Gulf of Mexico, depicted by the horizontal light gray line.

3.3%) corresponded to ages > 250 yrs. Colonies that were 74 cm and taller (n = 9, or 2.5%) correlated to ages > 500 yrs. Large colonies were present in both the northwestern and eastern parts of the Gulf of Mexico. The largest *L. glaberrima* coral colonies were over 1 m tall, with an age range estimated to be a minimum of 565 and maximum of 2000

years old, depending on the growth rate. Large colonies > 1 m tall were observed at sites near Green Canyon and Viosca Knolls, located west and east of the Mississippi Canyon, and on the West Florida Shelf.

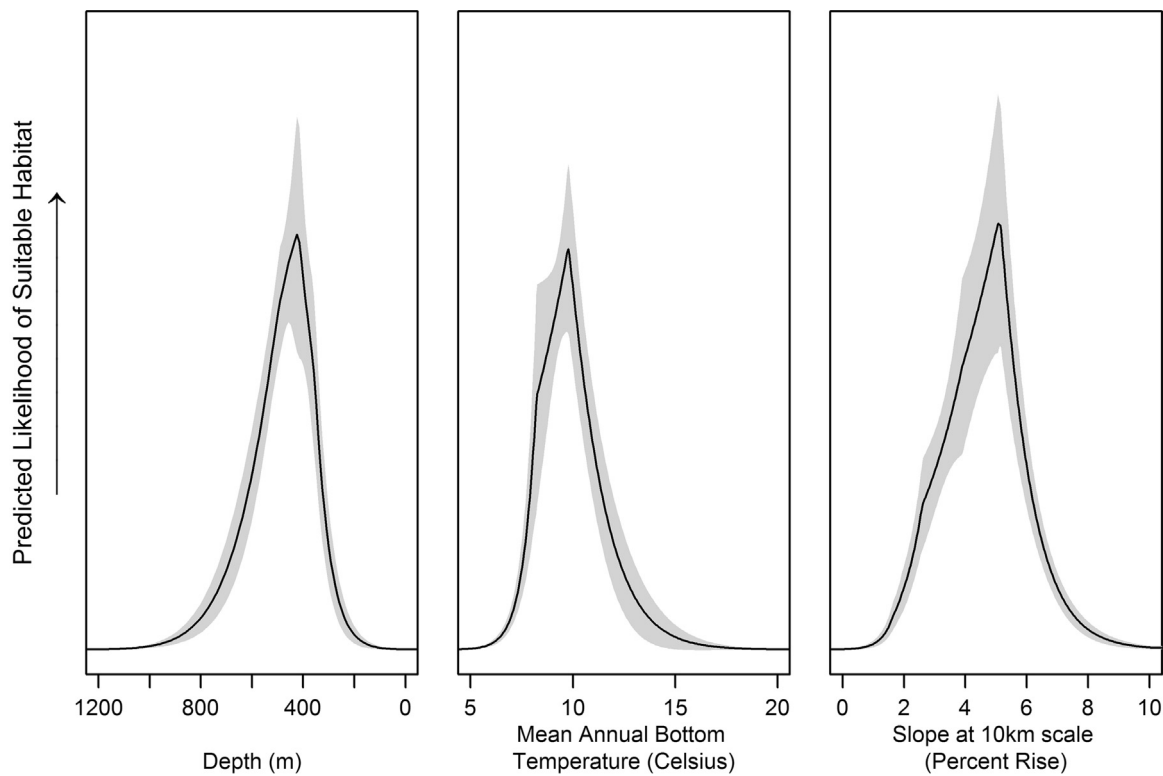


Fig. 4. Response curves depicting the relationship between predicted likelihood of habitat suitability and values for a) depth, b) mean annual bottom temperature, and c) slope at 10 km scale.

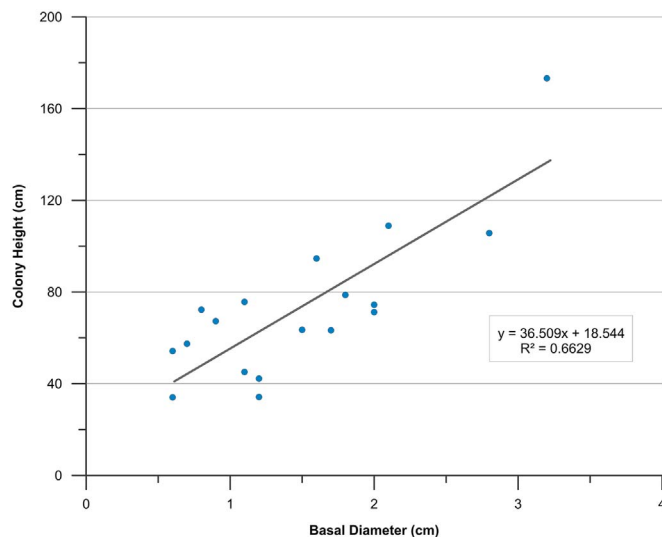


Fig. 5. Scatter plot showing the linear correlation between the basal diameter and height of *Leiopathes glaberrima* colonies (n = 18).

4. Discussion

This study documents a broad distribution of *L. glaberrima* colonies in the U.S. Gulf of Mexico, from Texas to the Southern Florida Straits (Figs. 1 and 3), and suggests that the extent of suitable habitat for *L. glaberrima* is very large (Fig. 3) where bottom temperature, surface productivity, slope and rugosity are conducive to settlement and growth. Through direct ROV observations, this study recorded *L. glaberrima* throughout the Gulf at depths between 367 and 596 m (Figs. 1 and 3). In the Gulf of Mexico, this species has previously been recorded at depths between 62 and 642 m in the NOAA national database of deep-sea corals (NOAA, 2016), and at depths of 37–450 m in the

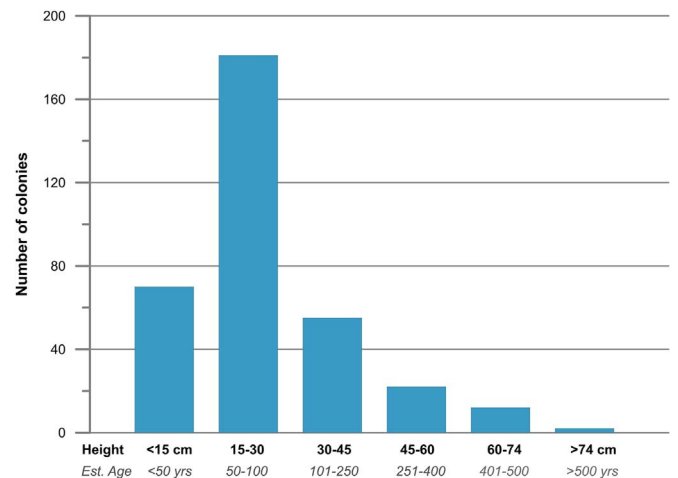


Fig. 6. Bar plot showing the number of *Leiopathes glaberrima* colonies observed in each size class (n = 357). Based on the midpoint of growth rates estimated from a previous study (15 $\mu\text{m}/\text{yr}$; Prouty et al., 2011), these size classes correspond to age classes shown in gray italics as < 50 yrs, 50–100, 101–250, 251–400, 401–500, and more than 500 yrs old.

literature (Opresko et al., 2009).

The habitat suitability model presented herein suggests that the preferred depth range of *L. glaberrima* is 200–1000 m, including deeper depths (642–1000 m) at which this species has not yet been recorded in the Gulf of Mexico. This deeper depth range has been relatively well studied in the Gulf of Mexico, compared to other regions, but the majority of studies deeper than 642 m have mostly focused on soft bottom habitats and cold seep ecosystems (reviewed by Boland et al., 2016). Outside the Gulf, *L. glaberrima* is also known from the Mediterranean, North Atlantic and Caribbean at depths between 37 and 1532 m (reviewed in Wagner and Opresko, 2015).

Model selection was driven by model performance rather than

identification of the environmental variables that best explain the distribution of *L. glaberrima*. In this case, the environmental predictor variables in the final model were consistent with a habitat with a specific range in depth, temperature and topographic complexity. One consequence of the model selection process is that some meaningful environmental predictors may be dropped during model selection if they are correlated with other variables that result in better model performance. Even in these instances, however, the environmental predictor variables remaining in the final model can often help identify some of the environmental conditions, but not necessarily all, that are most likely to provide suitable habitat. Future studies should be undertaken in order to ground truth the habitat suitability model presented here, and to determine the environmental variables and ranges that are most important in creating suitable habitats for *L. glaberrima*.

Field surveys are not the only way to ground truth habitat suitability models. For example, ground truthing could also be accomplished by reviewing historical ROV dives that have not yet been annotated for the presence of *L. glaberrima*. While this study included a comprehensive review of ROV dives that targeted deep-sea coral habitats in the U.S. Gulf of Mexico since 2008, the total area surveyed was less than 11.63 km² (370 m × 370 m × 85 m) or 2909 acres—a very small fraction (< 1%) of the Gulf of Mexico deep-sea. There are still several earlier studies that have yet to be analyzed for the presence (and absence) of *L. glaberrima*. Reviewing those earlier dives would likely provide additional *L. glaberrima* records that would help refine the habitat suitability model. New records would also support models at higher spatial resolution. The spatial resolution of the model presented here was limited to 370 × 370 m, because of the positional uncertainty in older *L. glaberrima* presence records, errors in bathymetry data, and the coarseness of environmental predictor variables. As new records and higher resolution datasets (e.g., bathymetry and backscatter from multibeam echosounders) become more available, these should be used to increase the spatial resolution of the habitat suitability models. Absence data obtained from historical reviews and new surveys would also allow for more types of analyses.

It is important to note that the inferred age-class structure of *L. glaberrima* colonies reported here (Fig. 6) was derived using constant growth rates throughout the lifespan of this species. Prouty et al. (2011) studied the growth rate of *L. glaberrima* in the Gulf of Mexico using radiocarbon techniques, and found evidence for an inverse relationship between age and growth rate. Using similar techniques, Roark et al. (2009) studied the growth rate of *L. annosa* from Hawaii (as *L. glaberrima*), and found evidence for faster initial growth that slows throughout the lifespan of the species, indicating that size is not linearly proportional to age. Thus, as the case with many other organisms (reviewed by Metcalfe and Monaghan, 2003), growth rates are likely not constant throughout the lifespan of *L. glaberrima*. Nevertheless, the size-frequency distribution presented here exhibited distinct peaks in size classes of colonies (Fig. 6). While the ages attributed to these size classes may not be accurate, each size class still corresponds to a different age class, with larger size classes also corresponding to older age classes.

The presence of distinct classes in the size-frequency distribution of *L. glaberrima* colonies (Fig. 6), suggests that this species reproduces via periodic and episodic recruitment events. Several previous studies have examined the size-frequency distribution of other black corals species, including *Antipathella fiordensis* from New Zealand (Grange, 1985) and *Antipathes griggi* and *A. grandis* from Hawaii (Grigg, 2001; 2001, 2004). These previous studies all reported similar distinct peaks in the size-frequency distribution, which they attributed to periodic reproduction and recruitment. Very little is known about the reproductive seasonality of black corals (reviewed in Wagner et al., 2011, 2012). The few studies that have examined the reproductive seasonality of black corals have all been conducted in shallow water (< 70 m), and reported a seasonal appearance and disappearance of gametes on an annual cycle. Whether deep-water black corals, such as *L. glaberrima*, also have a seasonal

reproductive cycle is currently unknown and should be examined by future studies.

Another major assumption of the visual techniques employed in this study is that paired lasers (typically set 10 cm) can reasonably estimate the size of colonies with a base diameter less than 2 cm. It must be recognized that the ages reported here are only coarse estimates based on these assumptions. There is substantial room for improvement of fine scale colony measurements using stereo-cameras, laser line scanners or other methods. There is also a need for refinement of these methods and broader application of the visual technique to achieve some level of accuracy and reliability, as has been done for fish and mobile invertebrates targeted by commercial fisheries.

Despite the limitations of this study, the implications to marine management and conservation are important. As a first step, the areas in which habitat suitability for *L. glaberrima* is high should be mapped at a high resolution (e.g., 5 m), and then surveyed to confirm the presence of corals. If the models are supported by these surveys, resource managers should take appropriate conservation measures in order to minimize adverse impacts to these habitats from bottom fishing, oil and gas extraction, water pollution, as well as other anthropogenic impacts. In this regard, both direct observations and statistically derived habitat models should be used in tandem to improve the discovery and management of ecologically important species such as *L. glaberrima*.

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Appendix A. Detailed methods for models of *Leiopathes glaberrima* habitat suitability in the Gulf of Mexico

A1. Environmental predictor variables

A1.1. Seafloor topography

Depth data for the Gulf of Mexico were extracted from the 3 arc-second NOAA Coastal Relief Model (CRM; <https://www.ngdc.noaa.gov/mgg/coastal/crm.html>) for Florida and the East Gulf of Mexico (National Geophysical Data Center, 2001b), the Central Gulf of Mexico (National Geophysical Data Center, 2001a), and the Western Gulf of Mexico (National Geophysical Data Center, 2001c) and from the 2010 release of the 30 arc-second General Bathymetric Chart of the Oceans (GEBCO; General Bathymetric Chart of the Oceans, 2010). Datasets were projected into WGS 1984 UTM Zone 15N and bi-linearly resampled to 92.6625 m resolution.

A merged depth dataset was created from the CRM and GEBCO using depth values from the CRM where available and GEBCO outside the extent of the CRM. A depth variable at 370 m resolution was created by calculating the 4 × 4 cell block mean of the merged depth dataset.

Slope, slope of slope, and aspect were derived from the merged depth dataset using ArcGIS 10 Spatial Analyst tools (ESRI, 2011). Rugosity, total curvature, planar curvature, and profile curvature were derived using DEM Surface Tools (Jenness, 2013), and bathymetric position index (BPI) was derived using the Benthic Terrain Modeler tool (Wright et al., 2012). Seafloor topography datasets were bi-linearly resampled to 370 m resolution. In addition to the merged depth dataset, a set of smoothed depth datasets were generated at 92.66 m resolution using a Gaussian low-pass filter to remove details from the merged depth dataset at different spatial scales (370 m, 1.5 km, 5 km, 10 km, 20 km). The seafloor topography variables were also derived from the smooth depth datasets using the same tools.

A1.2. Seafloor substrate

Gridded predictions of surficial sediment mean grain size, surficial sediment percent mud, surficial sediment percent sand, and surficial sediment percent gravel were obtained from Dr. Chris Jenkins at University of Colorado at Boulder (Williams et al., 2012), projected into WGS 1984 UTM Zone 15N, and bi-linearly resampled to 370 m resolution.

A1.3. Oceanography

Dissolved oxygen, salinity, and temperature measurements at the seafloor were obtained from bottom trawls and CTD casts (Southeast Area Monitoring and Assessment Program, 2012) and from World Ocean Database (WOD) ocean station data (Boyer et al., 2009). Gridded predictions for mean annual bottom dissolved oxygen, mean annual bottom salinity, and mean annual bottom temperature were generated at 370 m resolution from the point data using ordinary kriging (Cressie, 1993). Variables depicting the mean annual sea surface chlorophyll-a concentration and the mean annual sea surface turbidity (using water-leaving radiance at 667 nm as a proxy) were obtained from high resolution (0.0125 degrees arc length, ~ 1.4 km resolution) monthly composite satellite data from the Moderate Resolution Imaging Spectroradiometer (MODIS) instrument aboard the Aqua satellite (<https://oceancolor.gsfc.nasa.gov/data/aqua>). Data were downloaded from NOAA CoastWatch (<http://coastwatch.pfeg.noaa.gov/erddap/griddap/erdMEchlamday.html>), projected into WGS 1984 UTM Zone 15N, and bi-linearly resampled to 370 m resolution.

A1.4. Environmental predictor screening

A pairwise correlation analysis was performed on the set of 50 environmental predictor variables using the ENMTools software (Warren et al., 2010). Within pairs of highly correlated predictors (Spearman rank $R > 0.9$ or $R < -0.9$) the predictor that was most highly correlated with the most other predictors was excluded.

Because aspect (i.e., seafloor slope direction) is a circular variable (0–360°), these datasets were converted from a continuous variable to a categorical variable by reclassifying the values into the eight cardinal directions. Profile curvature, planar curvature, and BPI variables were also converted into categorical variables by reclassifying them using Jenk's natural breaks and combining them with reclassified slope to create categorical indices for each variable. These variables can have a zero value in two ambiguous situations (flat areas or vertical surfaces). Classifying these variables by combining them with slope resolved these ambiguities.

A2. Statistical modeling framework

A2.1. Model fitting

MaxEnt models were fit using version 3.3.3k of the MaxEnt software (<http://www.cs.princeton.edu/~schapire/maxent>). Model parameters were set to default values, except for the regularization multiplier and number of background points (2.0 and 20,000, respectively). For each model run, ten replicate MaxEnt models were fit using bootstrap samples generated by randomly sampling the *L. glaberrima* presence

records into model training subsets (each containing 70% of the records) and model test subsets (each containing 30% of the records). Model performance was measured by testing model predictions at the locations of the model test subsets. Area under the receiver operating characteristic curve (AUC; Fielding and Bell, 1997) indicated the ability of the models to predict *L. glaberrima* presence at test locations compared to a random selection of locations (termed background points in MaxEnt). The mean test AUC was calculated for the ten replicate models. Akaike's information criterion corrected for small sample size (AICc; Akaike, 1974; Burnham and Anderson, 2002) measures model fit and complexity. Mean AICc were calculated for the ten replicate models using the ENMTools software (Warren et al., 2010).

A2.2. Model selection

Model performance and interpretability can be reduced when models are overly complex or overly simple (Yost et al., 2008; Warren and Seifort, 2011). To choose a model that balanced predictive performance with complexity, a stepwise model selection procedure was developed. An initial model run was generated using the set of 27 environmental predictor variables. The most redundant environmental predictor in this model run was defined as the predictor whose omission from model fitting resulted in the smallest reduction in mean test AUC. For the next iteration of the model selection procedure, this environmental predictor variable was removed and a new model was run. The process of removing the most redundant environmental predictor and fitting a new model run was repeated until a model with a single remaining environmental predictor was produced or the mean test AUC for a model run fell below 95% of the mean test AUC of the initial model run. The model runs were ranked from best to worst in terms of model performance (highest mean test AUC = 1 to lowest mean test AUC = 27) and model complexity (lowest mean AICc = 1 to highest mean AICc = 27) and the two ranks were averaged to select the model run with the lowest average rank (1 = best, 27 = worst) as the best model run.

A2.3. Predictions of habitat suitability

A final MaxEnt model was fit using the set of environmental predictor variables in the best model run to generate a spatially explicit prediction of the relative likelihood of habitat suitability. The prediction was on a logistic scale that ranges from 0 to 1, but should not be treated as a probability since MaxEnt, by default, assigns a prevalence value of 0.5 when in fact the prevalence cannot be estimated from presence-only data (Elith et al., 2011). As a result, the MaxEnt logistic prediction should be treated only as a relative measure of the likelihood of habitat suitability among pixels in the same model domain for the same taxon.

A classified map of the likelihood of habitat suitability was created to allow direct comparisons to predictions for other deep-sea coral taxa in the Gulf of Mexico. The relative likelihood of habitat suitability (i.e., the MaxEnt logistic prediction) was converted into classes by identifying a series of breakpoints, each corresponding to a specific ratio of the cost for false positive errors versus the cost for false negative errors. Receiver operating characteristic (ROC) curves for the ten replicate models of the best model run were generated using the model test subsets. The mean optimal breakpoint for the ten ROC curves was generated for each cost ratio (1:1, 2:1, 5:1, 10:1), and these values were used to reclassify the MaxEnt logistic prediction. The procedure used the 'ROCR' package in R (Sing et al., 2005) to generate ROC curves and to calculate optimal breakpoints. In addition, grid cells in the highest class of habitat suitability likelihood for each of the ten replicate models of the best model run were identified as the robust very high likelihood class. A.3. Environmental predictor variable importance. MaxEnt provided multiple measures of the relative importance of each environmental predictor variable to model fitting (Phillips et al., 2004, 2006). Permutation importance was determined by measuring the decline in model performance (AUC) for each environmental predictor when

values at the model training subset locations and background locations were randomly scrambled and model performance was re-evaluated. Environmental predictor variables more important to model fitting would have higher permutation importance values. MaxEnt also evaluated environmental predictor variable importance using two jackknife tests. For the first test, MaxEnt re-fit models for each environmental predictor variable using only the single variable. For the second test, MaxEnt re-fit models for each environmental predictor variable using all other environmental predictors (omitting the variable being tested). For both jackknife tests, MaxEnt calculated AUC on the model test subsets. An environmental predictor variable that was both important and non-redundant would have higher test AUC for the models fit with only that variable and show a significant reduction in test AUC for models fit with that variable omitted.

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