Coral Reefs
DOI 10.1007/s00338-014-1237-z

REPORT

# Genetic evidence supports larval retention in the Western Caribbean for an invertebrate with high dispersal capability (*Ophiothrix suensonii*: Echinodermata, Ophiuroidea)

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Received: 7 July 2014 / Accepted: 27 October 2014


**Abstract** The brittle star *Ophiothrix suensonii* is a common coral reef sponge commensal with high dispersal potential. Here, we utilize COI sequence data from 264 *O. suensonii* individuals collected from 10 locations throughout Florida and the Caribbean to investigate dispersal dynamics and demographic history. Locations separated by up to 1,700 km lacked genetic differentiation, confirming the ability for long-range dispersal. However, significant differentiation was detected among other regions. Samples from Utila, Honduras showed the greatest differentiation, suggesting that the circulation of the Mesoamerican gyre could be a significant factor restricting gene flow in this region. Demographic analyses provided strong evidence for a population expansion, possibly out of Florida, through the Caribbean, and into Honduras, which commenced in the early Pleistocene. However, the presence of a clade of rare haplotypes, which split much earlier (mid-Pliocene), indicates that *O. suensonii* persisted long before its recent expansion, suggesting a cyclic history of population contraction and expansion. Finally, patterns of gene flow are not concordant with contemporary surface currents; rather, they reflect historical movements possibly linked with changes in circulation during periods of Pleistocene climate change.

**Keywords** Brittle star · Caribbean · Cryptic species · Echinoderm · Genetic connectivity · Population demography

Communicated by Handling Editor Mark Vermeij

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## Introduction

An understanding of genetic population structure and demographic history can provide valuable insight into the evolutionary fate of a population or species (Hellberg 2009). The degree to which populations become genetically structured is governed by an equilibrium in which the diversifying forces of selection and drift are counteracted by gene flow. Thus, information on gene flow or the extent to which populations are genetically connected over both spatial and temporal scales is key to our understanding of evolutionary processes within ecosystems, and incorporation of these data into ecosystem management should ensure its long-term success (Almany et al. 2009).

Quantifying gene flow in the ocean presents a challenge, as unlike terrestrial environments, barriers to dispersal are less obvious. For species dispersing via pelagic larval phases, larval duration can have a strong influence on dispersal potential. For example, several studies have shown pelagic larval duration and genetic population structure to be correlated (Selkoe and Toonen 2011; Riginos et al. 2014). However, studies also continue to reveal

Published online: 05 November 2014

examples of high population subdivision over relatively short distances for species with extended larval duration (Cowen and Sponaugle 2009; Riginos et al. 2011). Examples include: reef fish (Taylor and Hellberg 2003; Eytan and Hellberg 2010), barnacles (Sotka et al. 2004), abalone (Gruenthal and Burton 2008), snappers (Ovenden et al. 2004), shrimps (Barcia et al. 2005), and stomatopods (Barber et al. 2002).

Failure to meet full dispersal potential is likely due to local larval retention or lack of recruitment into distant populations, and a combination of factors (biological and physical) could be responsible. For example, active larval recruitment near spawning grounds elevates retention for many species (Paris et al. 2007; Butler et al. 2011). Alternatively, if larvae are more passive, currents will play a larger role in dispersal patterns (Briones-Fourzán et al. 2008; White et al. 2010) and local retention could be due to larval entrapment in persistent eddy currents (Condie et al. 2011; Mullaney and Suthers 2013). If larvae do move away from their spawning grounds, poor recruitment into new areas may be due to mortality and diffusion (Cowen et al. 2006; Burgess et al. 2012), lack of suitable settlement habitat (Marshall et al. 2010), or oceanographic processes that transport larvae away from suitable settlement habitat (Ovenden et al. 2004; Cowen et al. 2006).

To date, there have been several studies of gene flow throughout the wider Caribbean and Florida focused on: tropical fish (Taylor and Hellberg 2006; Rocha et al. 2008; Eytan and Hellberg 2010; Salas et al. 2010), corals (Baums et al. 2005; Vollmer and Palumbi 2007; Andras et al. 2013), mollusks (Lee and Ó Foighil 2005; Paris et al. 2008; Díaz-Ferguson et al. 2010), lobsters (Silberman et al. 1994; Naro-Maciel et al. 2011), and urchins (McCartney et al. 2000; Lessios et al. 2001, 2003). Here, we provide the first data for an ophiuroid, the typically sponge-associated brittle star *Ophiothrix suensonii.* Ophiuroids are the most diverse class of echinoderms, with approximately 2,000 species and a fossil record extending back 500 million years. Ophiuroids likely play an important role in Caribbean coral reef ecosystems as densities can range from 20 to 40 per square meter and up to 100 times this in the reef sediment (Hendler et al. 1995).

*Ophiothrix suensonii* is widely distributed throughout Florida and the Caribbean [and may exist as far south as Brazil (USNM 8913)] where it associates with at least five sponge genera, fire coral, and occasionally gorgonians (Hendler et al. 1995; Henkel and Pawlik 2005). *O. suensonii* spawns throughout the year producing planktotrophic ophioplutei larvae. Larvae have been reared for up to 49 days in culture without metamorphosing (Mladenov 1985), demonstrating that *O. suensonii* has the potential for long distance dispersal.

Here, we utilize mitochondrial sequence data from the cytochrome oxidase subunit 1 (COI) gene to investigate gene flow in *O. suensonii* throughout Florida, the Bahamas, and the Caribbean. Despite its high dispersal potential, this species shows significant genetic differentiation throughout the region, with Utila, Honduras samples exhibiting the highest level of subdivision. Additionally, we explore the demographic history of this species and discuss possible mechanisms responsible for the observed phylogeographic patterns.

## Materials and methods

### Sampling sites and collections

A total of 264 individuals were collected from five locations in Florida (Ft Lauderdale = 5, Key Largo = 18, Long Key = 27, Key West = 25, the Marquesas Keys = 28), and five locations within the Caribbean (Crooked Island: Bahamas = 33, St Croix: US Virgin Islands = 32, Curacao: Dutch Antilles = 32, Grand Cayman Island = 32, Utila: Honduras = 32) (Fig. 1; Table 1). All individuals were preserved in 95 % ethanol at 4 °C.

### Polymerase chain reaction and sequencing

Genomic DNA was extracted using the DNeasy Tissue Kit (Qiagen Inc.). We designed species-specific primers modified from those for *Ophiothrix lineata* by Richards et al. (2007) to amplify and sequence 708 base pairs of the 5 prime end of the COI gene in *O. suensonii*: OsuenCOIF1 (5′-AGGAACCGTAGGAACAGCCATGAGAA-3′) and OsuenCOIR1 (5′-TATCATTGTGGCTGCAGTGAAATAAGC-3′).

Total PCR volumes were 50 µL and contained 1 µL of extracted genomic DNA, 5 µL 10× PCR Buffer, 50 µM of each dNTP, 0.25 µM of each primer, and 0.75 U of HotStar Taq$^{TM}$ DNA Polymerase (Qiagen Inc.). PCR was performed in a Mastercycler Gradient (Eppendorf Inc.) thermal cycler as follows: 95 °C initial heating for 15 min to activate the hot start DNA polymerase, followed by 35 cycles of 94 °C for 1 min, 50 °C for 1 min, 72 °C for 1 min, and a 5-min final extension step at 72 °C. A negative control (no genomic DNA) was included in each PCR to check for reagent contamination. PCR products were purified using the QIAquick PCR Purification Kit (Qiagen Inc.) and sequenced in both directions using the Applied Biosystems BigDye Terminator v3.1 Cycle Sequencing Kit. Products were purified using the DyEx 2.0 Spin Kit (Qiagen Inc.) and separated using an Applied Biosystems 3130 Genetic Analyzer. Individual sequences are available

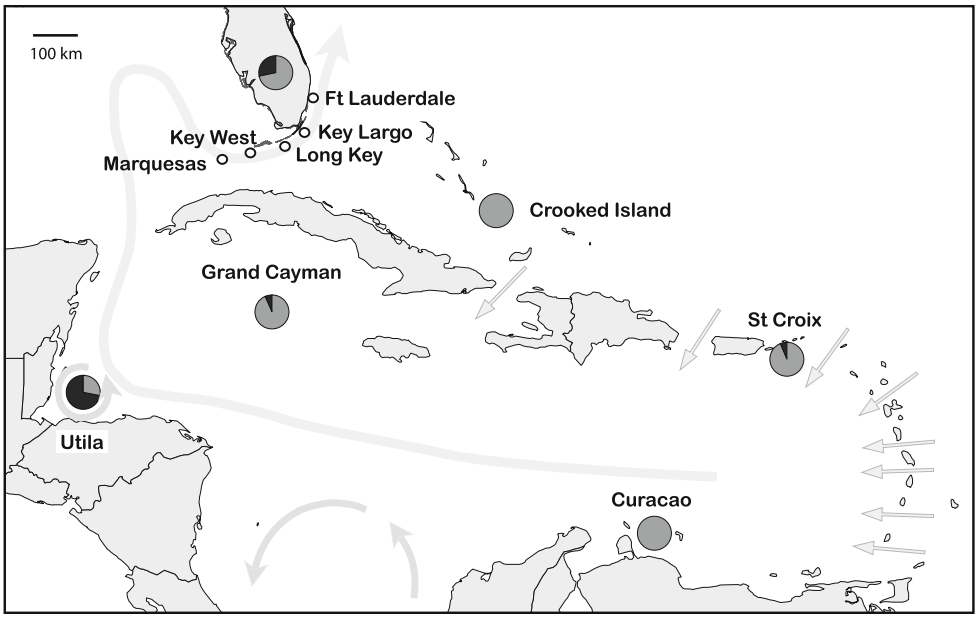


**Fig. 1** Map showing collection sites throughout Florida and the Caribbean. Pie charts show the frequency of clade 1 and clade 2 haplotypes (see Fig. 2) at each site. *Arrows* describe the general path of major surface currents and gyres

**Table 1** Genetic diversity indices for individual collection sites

| | *n* | *H* | *h* | $\pi$ |
|---|---|---|---|---|
| Key Largo (Florida) | 18 | 15 | 0.974 | 0.0054 |
| Long Key (Florida) | 27 | 18 | 0.929 | 0.0046 |
| Key West (Florida) | 24 | 21 | 0.978 | 0.0054 |
| Marquesas (Florida) | 28 | 24 | 0.984 | 0.0058 |
| Florida (including Ft Lauderdale) | 102 | 67 | 0.961 | 0.0052 |
| Cayman (Caribbean) | 31 | 22 | 0.948 | 0.0044 |
| Curacao (Caribbean) | 32 | 24 | 0.942 | 0.0045 |
| Crooked Is. (Caribbean) | 33 | 26 | 0.968 | 0.0047 |
| St Croix (Caribbean) | 31 | 21 | 0.944 | 0.0050 |
| Utila (Caribbean) | 32 | 24 | 0.972 | 0.0050 |
| All sites | 261 | 158 | 0.962 | 0.0052 |

*n* sample size, *H* number of haplotypes, *h* haplotype diversity, $\pi$ nucleotide diversity

from European Nucleotide Archive (LK026603–LK026868).

## Data analysis

Sequences were aligned and edited in MacCLADE v4.03 (Maddison and Maddison 2000). The alignment was translated using GENEDOC v2.6.02 (Nicholas et al. 1997) to check for correct invertebrate mtDNA amino acid coding and aberrant start/stop codons. The program DNASP v4.0 (Rozas et al. 2003) was used to estimate standard diversity indices, and genetic population structure was examined using an analysis of molecular variance (AMOVA) in ARLEQUIN v2.000 (Schneider et al. 2000). Pairwise $\Phi_{ST}$ values were calculated in ARLEQUIN, and the false discovery rate (FDR) procedure of Benjamini and Hochberg (1995) was used to correct for multiple hypothesis testing (FDR = 0.05).

Genetic isolation by distance was tested by comparing pairwise geographic distances among collection sites to their corresponding pairwise $\Phi_{ST}$ and standardized by dividing by $1 - \Phi_{ST}$ (Rousset 1997). The shortest geographic distances by sea among collection sites were calculated in Google Earth. All Florida sites were grouped, and distances were measured from their center. A Mantel test, as implemented by the Isolation by Distance Web Service (Jensen et al. 2005), was used to test for a significant correlation among the distances (1,000 randomizations).

Evolutionary relationships among haplotypes were inferred by constructing an unrooted parsimony network using the Templeton et al. (1992) method as implemented in TCS v1.13 (Clement et al. 2000). Average pairwise genetic distances among haplotypes were calculated in MEGA3 (Kumar et al. 2004) using Kimura's two-parameter model (K2P) (Kimura 1980). These distances were used to facilitate comparison with previous studies.

We explored demographic history using several approaches. First, ARLEQUIN was used to calculate the mismatch distribution, Tajima's *D* statistic (Tajima 1989), and Fu's $F_S$ statistic (Fu 1997). Assuming selective neutrality for COI, statistically significant negative values of *D* and $F_S$ indicate population expansion. Although unimodal mismatch distributions are characteristic of populations that have undergone expansion in size, they do not distinguish between a sudden increase in size (step growth) or continued exponential growth (Rogers and Harpending 1992). Therefore, our second approach was to evaluate specific demographic

hypotheses using GENIE v3.0 (Pybus and Rambaut 2002). The program requires as input a genealogy estimated under the assumption of molecular clock. It then combines two approaches: (1) a graphical nonparametric estimate of demographic history called the skyline plot and (2) a flexible maximum-likelihood (ML) framework, which allows the estimation of demographic parameters using any of seven distinct demographic models. A skyline plot is created by first dividing an ultrametric genealogy into separate internode intervals. Theta ($\theta$) is then calculated for each interval and assumed constant for the length of the interval. If the mutation rate is known, the resulting plot can trace changes in effective population size through time. The shape of the skyline plot suggests which demographic model best fits the data, and a plot of the maximum-likelihood population parameters using the suggested model should be concordant with the skyline plot. UPGMA phylogenies for these analyses were estimated in MEGA3 using K2P genetic distances. The data sets used to generate these phylogenies consisted of a large number of taxa, all displaying very limited genetic variation. Consequently, we selected the UPGMA method of ultrametric phylogenetic estimation rather than the ML method due to impractical computation demands of ML estimation under the assumption of a molecular clock.

Migration rates were estimated using LAMARC v2.1.2 (Kuhner 2006). Three Bayesian pairwise analyses were performed as follows: (1) Florida and the Caribbean (excluding Utila), (2) Florida and Utila, (3) Utila and the remaining Caribbean (see "Results" section for rationale). For analyses (1) and (2), three simultaneous chains using an adaptive heating scheme (start temperatures: 1.0 1.1 1.3) were run for 1,000,000 generations, sampling every 50 generations. Default priors and a 10 % burn-in were used. Convergence was assessed using the probability density curves for each parameter. For analysis (3), convergence was attained when the chain length was increased to 20,000,000 generations. The sampling increment was increased to 1,000, and two simultaneous chains with start temperatures of 1.0 and 1.3 were used.

## Results

### Spatial patterns of genetic subdivision

In the initial AMOVA, each collection site was defined as a distinct population (excluding Ft Lauderdale due to small sample size). The overall $\Phi_{ST}$ was low (0.053), yet significant ($P = 0.00000$), indicating significant subdivision among collection sites. All pairwise $\Phi_{ST}$ comparisons among Florida sites were very low (<0.008) and nonsignificant (Table 2). Similarly, with the exception of Utila, all pairwise comparisons among Caribbean sites were also very low (<0.009) and nonsignificant. In contrast, pairwise comparisons between Utila and all other sites showed relatively high values. Values were highest for comparisons between Utila and the Caribbean, ranging from 0.168 to 0.215 (all significant $P = 0.00000$), with values between Utila and Florida slightly lower (0.069–0.133), yet still all significant ($P < 0.005$). Comparisons between Florida and the Caribbean sites (not including Utila) gave mixed results; although most comparisons were significant ($P < 0.017$), the following pairs of comparisons between locations in close proximity: (1) Key West and the Caribbean, (2) Cayman and Florida were nonsignificant. Collectively, these results suggest two or three distinct genetically structured populations for *O. suensonii* in the sampled range.

Based on the pairwise $\Phi_{ST}$ values, we combined individuals from locations that were not significantly subdivided and tested a tentative subdivision of three groups (Utila, Florida, and the remaining Caribbean) with a hierarchical AMOVA in ARLEQUIN. The results supported this subdivision as the overall level of structuring increased ($\Phi_{CT} = 0.077$, $P < 0.007$). In addition, the results showed that the level of variation among the groups (7.65 %) was substantially higher than the variation among sites within groups (0.05 %) (Table 3). The large difference in these variance components was reflected in the accompanying $\Phi$ statistics; they showed significant variation among the groups and no significant variation among sites within groups (Table 3). However, the vast majority of variation was still within collection sites reflecting the overall low level of genetic partitioning among individual sites.

To investigate the level of relative structuring among the groups, we generated pairwise $\Phi_{ST}$ values via a third AMOVA. Results showed that the highest level of structuring was between Utila and the Caribbean ($\Phi_{ST} = 0.203$, $P = 0.00000$), followed by Utila and Florida ($\Phi_{ST} = 0.091$, $P = 0.00000$), with the Caribbean and Florida showing the lowest (yet still significant) level of structuring ($\Phi_{ST} = 0.024$, $P = 0.00000$) (Table 4).

### Migration rates

Although the default setting in LAMARC is to simultaneously estimate $\theta$ and migration (M), the statistical parsimony analyses (see below) revealed two connected star phylogenies. As a phylogeny becomes more star-like, the coalescences increasingly converge on the same point in time, and parameter estimation within LAMARC becomes less successful. Therefore, we estimated M among populations by holding $\theta$ constant for each population. Each value of $\theta$ was estimated using the ML framework in GENIE using a model of exponential expansion (see below).

**Table 2** Pairwise $\Phi_{ST}$ values between individual collection sites in the lower diagonal

Corrected $P$ values in the upper diagonal

Significant values ($P < 0.05$) are indicated in bold. Overall $\Phi_{ST} = 0.053$ ($P = 0.00000$)

| | Key Largo | Long Key | Key West | Marquesas | Cayman | Curacao | Crooked Is. | St. Croix | Utila |
|---|---|---|---|---|---|---|---|---|---|
| Key Largo | | 0.531 | 0.426 | 0.583 | 0.105 | **0.019** | **0.004** | **0.004** | **0.008** |
| Long Key | 0.001 | | 0.303 | 0.790 | 0.107 | **0.000** | **0.004** | **0.015** | **0.006** |
| Key West | 0.007 | 0.007 | | 0.727 | 0.971 | 0.587 | 0.583 | 0.790 | **0.000** |
| Marquesas | −0.003 | −0.008 | −0.005 | | 0.174 | **0.026** | **0.004** | **0.027** | **0.004** |
| Cayman | 0.026 | 0.020 | −0.015 | 0.013 | | 0.291 | 0.231 | 0.475 | **0.000** |
| Curacao | **0.042** | **0.050** | 0.000 | **0.022** | 0.006 | | 0.816 | 0.468 | **0.000** |
| Crooked Is. | **0.055** | **0.052** | 0.000 | **0.029** | 0.008 | −0.005 | | 0.816 | **0.000** |
| St. Croix | **0.050** | **0.039** | −0.007 | **0.026** | 0.003 | 0.003 | −0.006 | | **0.000** |
| Utila | **0.082** | **0.069** | **0.133** | **0.084** | **0.168** | **0.213** | **0.215** | **0.195** | |

**Table 3** Hierarchical analysis of molecular variance (AMOVA)

| Hierarchy | Variance component | % variance | $\Phi$ statistic |
|---|---|---|---|
| Florida, Utila, Remaining Caribbean | Among groups | 7.65 | $\Phi_{CT} =$ **0.077** |
| | Among sites within groups | 0.05 | $\Phi_{SC} = 0.001$ |
| | Within sites | 92.30 | $\Phi_{ST} =$ **0.077** |

Significant values ($P < 0.05$) are indicated in bold

**Table 4** Pairwise $\Phi_{ST}$ values between groups

| | Florida | Remaining Caribbean |
|---|---|---|
| Remaining Caribbean | **0.024** | |
| Utila | **0.091** | **0.203** |

Significant values ($P < 0.05$) are indicated in bold. Overall $\Phi_{ST} = 0.077$ ($P = 0.00000$)

**Table 5** Pairwise estimates of migration among three groups

| Comparison | Number of immigrants/generation into receiving population | | |
|---|---|---|---|
| | 2.5 % percentile | Mean | 97.5 % percentile |
| From Florida into Utila | 6.8 | 14.3 | 21.9 |
| From Utila into Florida | 4.9 | 10.4 | 16.4 |
| From Florida into the Caribbean | 58.0 | 77.8 | 87.0 |
| From the Caribbean into Florida | 55.3 | 74.6 | 86.8 |
| From Utila into the Caribbean | 1.3 | 3.6 | 7.1 |
| From the Caribbean into Utila | 1.1 | 3.8 | 9.1 |

Although population parameters are most robust when determined from multiple loci (Edwards and Beerli 2000), based on a single marker, levels of migration among the three groups were concordant with AMOVA results as they showed the lowest level of migration between Utila and the Caribbean (average number of migrants per generation = 3.7), followed by Utila and Florida (12.4), and lastly the highest rates of migration were between the Caribbean and Florida (76.2) (Table 5). For each pairwise comparison, LAMARC provides migration rates into both populations; consequently, any bias in the direction of migration between population pairs can be detected. Our results showed a slight bias south from Florida into both Utila and the Caribbean.

## Haplotype diversity and genealogy

From 264 *O. suensonii* individuals, we detected 161 distinct haplotypes (Table 1). Haplotype diversity ($H$) was high (0.962), and nucleotide diversity ($\pi$) was low (0.0052) compared to values $\pi$ reported for other ophiuroids ($\pi = 0.079$–$0.15$, $H = 0.933$–$1.0$, Muths et al. 2009; $\pi = 0.0039$–$0.035$, $H = 0.706$–$1.0$, Boissin et al. 2011; $\pi = 0.005$–$0.029$, $H = 0.987$–$1.0$, Pérez-Portela et al. 2013). This pattern of high $H$ and low $\pi$ is characteristic of rapid growth from a small ancestral population (Avise 2000).

With the exception of three divergent haplotypes, statistical parsimony joined all remaining haplotypes in an 11-step network at the 95 % probability level (Fig. 2). Two major haplotypes dominated the network, each showing a star phylogeny, characteristic of population expansions. Each major haplotype and its descendant haplotypes formed a group (clades 1 and 2), the distribution of which is shown in Fig. 1. The Mantel test did not detect a significant correlation between geographic and genetic distance ($P = 0.0680$). This result is expected from a population expanding in size, as the growth will shift the population out of drift-gene flow equilibrium, thereby preventing a signal of isolation by distance (Slatkin 1993).

Clade 1 contained haplotype A, which is likely the most ancestral haplotype due to its high frequency (46) and central position in the network (Castelloe and Templeton 1994). Haplotype B (clade 2) had a frequency of 18 and was the only other haplotype with high frequency in the network. Although Florida haplotypes were common to

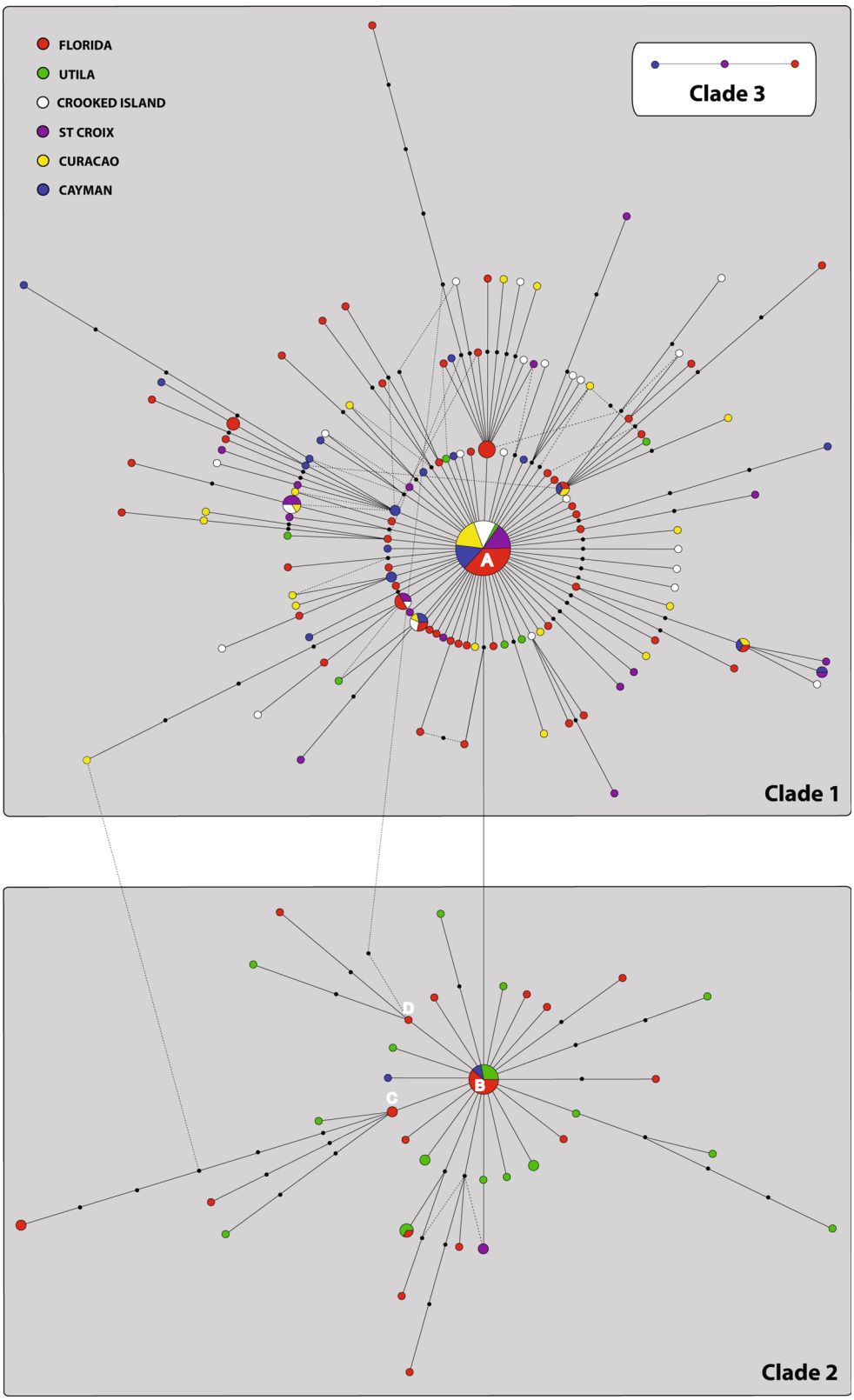


**Fig. 2** Statistical parsimony network depicting relationship among haplotypes. *Circle* size is proportional to haplotype frequency, *lines* represent single mutational steps, and *small black circles* represent hypothetical haplotypes types not sampled. *Colors* indicate sampling site. *Dashed lines* represent alternative haplotype connections

both clades, the network showed genetic partitioning between Utila and Caribbean haplotypes, as with few exceptions, all Caribbean haplotypes were restricted to clade 1, and the majority of Utila haplotypes were restricted to clade 2. Although rare in clade 1, nine Utila haplotypes were present. Haplotype A was observed just

once in Utila, with the remaining eight haplotypes separated by no more than two mutational steps.

There were three possible haplotype connections between clades 1 and 2. However, predictions from neutral coalescent theory (Crandall and Templeton 1993) suggest that haplotypes are more likely to be connected to haplotypes with higher frequency than to singletons, and haplotypes are more likely to be connected to interior haplotypes than to tip haplotypes. Therefore, the most likely connection between clades 1 and 2 is via haplotypes A and B, with one intermediate step. By establishing haplotype A as the most ancestral, the network gains temporal polarity, and all remaining haplotypes are considered more derived as they approach the tips. Consequently, the network suggests that the majority of Utila haplotypes are derived from haplotype B, which is in turn derived from haplotype A.

Clade 3 contained three divergent haplotypes (each separated by one mutational step) that did not connect to the main network at the 95 % probability level. It required an 18-step network to connect all haplotypes (87 % probability). The divergent haplotypes were distributed throughout Florida and the Caribbean (Key West, Cayman Island, St Croix), and the average pairwise K2P genetic distance between them and all remaining haplotypes was 3.24 %. This distance is greater than that observed among COI lineages in the *Ophioderma longicauda* species complex (K2P distance = 2 %, Boissin et al. 2011) but less than distances observed among COI lineages in the *Ophiothrix fragilis* species complex (K2P distance = 18.2 %, Muths et al. 2009; K2P distance = 17 %, Pérez-Portela et al. 2013). We conservatively excluded these divergent individuals from all population level analyses.

## Demographic history

Demographic analyses were performed on the three populations identified by the AMOVA: Florida, Utila, and the Caribbean. The unimodal shape of the mismatch distributions (Fig. 3), and significantly negative $F_S$ and $D$ statistics for each population (Fig. 3) strongly suggest population growth for the regions.

The TCS network showed a large proportion of identical or closely related haplotypes. Consequently, the UPGMA phylogenies generated for the skyline plots (not shown) contained many zero-branch lengths and short internode intervals. This type of topology creates a noisy skyline plot, which is often difficult to interpret due to an excessive number of internode intervals. This problem is resolved by use of the generalized skyline plot (Strimmer and Pybus 2001), which uses an Akaike Information Criterion correction ($AIC_c$) to reduce the number of groups. Internode intervals smaller than an optimal threshold epsilon ($\varepsilon$) established by the $AIC_c$ are pooled into a reduced number of groups.

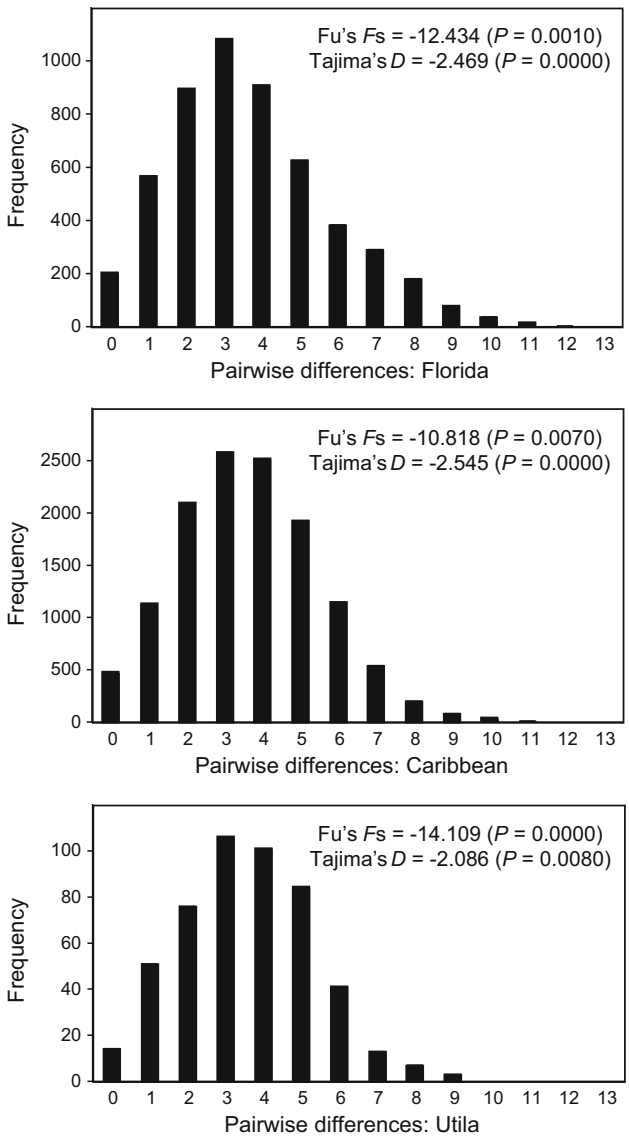


**Fig. 3** Mismatch distributions, Fu's $F_S$ statistic, and Tajima's $D$ statistic for Florida, Caribbean, and Utila populations

Generalized skyline plots for each population are shown in Fig. 4. The $y$-axis for these plots is logarithmic; therefore, the general pattern of linear increase for each plot suggests a continuous exponential increase in effective population size ($N_e$) through time for each population. Plots of ML parametric estimates of $N_e$ through time were then generated using an exponential model of population growth and superimposed on the skyline plots. The ML estimates corresponded closely with the skyline plots indicating that a model of exponential growth is a good fit for the data.

A skyline plot is scaled to time if the mutation rate per site per generation is known. The COI mutation rate for *O.*

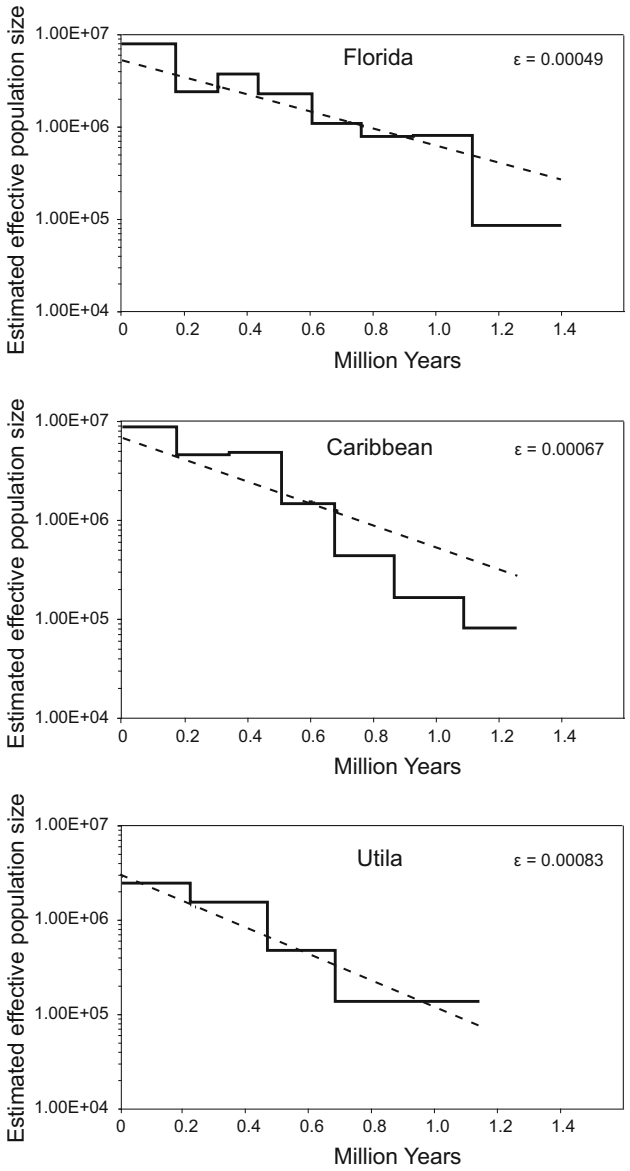


**Fig. 4** Log-linear generalized skyline plots for Florida, Caribbean, and Utila populations. *Dashed lines* are the maximum-likelihood parametric estimates generated using an exponential growth model. Epsilon ($\varepsilon$) values represent the plot smoothing parameter estimated using the Akaike Information Criterion correction procedure ($AIC_c$) (see text)

*suensonii* is unknown; however, Roy and Sponer (2002) reported a COI genetic distance for the brittle star *Ophiactis savignyi* of 2.6 % between Pacific and Atlantic haplotypes that were likely isolated since the Isthmus of Panama closure 3.1 MYA. By dividing the genetic divergence by twice the time since separation, a mutation rate of 0.42 % per MY is obtained. Although the generation time for *O. suensonii* is also unknown, data for two other species of brittle star are available. Davoult et al. (1990) reported time to maturity for *Ophiothrix fragilis* as 6–10 months, and Hendler (1975) estimated the generation time for *Amphipholis squamatus* as approximately 1 year. Using a generation time of 1 year and the mutation rate estimated for *O. savignyi*, the skyline plots for *O. suensonii* indicate that all populations commenced expansion approximately 1.2–1.4 million years ago. Regardless of the exact timing of these events, it appears that Florida was the first population to expand, followed by the Caribbean, and lastly Utila.

## Discussion

### Population subdivision

Although *O. suensonii* has the ability for long-range dispersal, as evidenced by the low genetic differentiation seen among many Caribbean and Florida locations, significant population structure was detected. In particular, Utila showed pronounced differentiation from other regions, especially the remaining Caribbean. Current recirculation has the potential to retain echinoderm larvae (Black and Moran 1991; Black 1993) and genetic isolation of echinoderm populations due to localized oceanographic circulation has been reported for several species (Sponer and Roy 2002; Waters and Roy 2003; Perrin et al. 2004). Therefore, a possible explanation for the limited genetic exchange between Utila and other regions could be entrapment of larvae in the persistent cyclonic gyre within the Gulf of Honduras (Sheng and Tang 2003, 2004). A Lagrangian circulation model developed for fish larvae by Paris et al. (2007) has confirmed the importance of the Mesoamerican gyre in local larvae retention, and a biophysical model predicting larval reef fish dispersal across the Caribbean showed self-recruitment was higher in Belize and Honduras than other areas of the Caribbean (Cowen et al. 2006). This recirculation system was seen as the likely process responsible for retention and genetic isolation in several marine species (toadfish, Collette 1983; blennies, Johnson and Brothers 1989; gobies, Colin 2002; gobies, Taylor and Hellberg 2006; zooxanthellae, Andras et al. 2011; octocorals, Andras et al. 2013) and may also be responsible for isolating the Utila population of *O. suensonii*.

The model of Paris et al. (2007) also highlighted the importance of larval biology, i.e., larval survival and vertical movement patterns, factors that may also be involved in the process of genetic subdivision seen in Utila for *O. suensonii.* For example, if population subdivision was simply a function of ocean currents, we might also expect the strong flow of the Florida Current to be an effective barrier to gene flow into and out of Florida. However, while we detected significant structure between Florida and

the Caribbean, differentiation was low and migration rates were almost ten times that seen between Utila and the other populations. Similarly, although Palumbi et al. (1997) found *Echinometra* urchins to show low amounts of genetic exchange across the path of two major currents in the Indo-Pacific, genetic exchange was high across the third, suggesting currents do not always act as a barrier to dispersal. Furthermore, work on urchins in the Western Caribbean has shown an equivocal relationship between regional circulation patterns and population subdivision. The Mesoamerican gyre in Belize and the Columbia–Panama gyre in Panama have the potential to retain larvae in both these regions, but comparisons of connectivity in *Diadema antillarum* and *Tripneustes ventricosus*, both with larval durations in excess of 1 month, showed only *D. antillarum* populations were significantly subdivided (Lessios et al. 2001, 2003).

Considering that the process of genetic subdivision is a species-specific interplay between biological and physical factors, it is not surprising that the phylogenetic breaks for a variety of species located throughout Florida, the Gulf of Mexico, and the wider Caribbean were not concordant with the subdivision observed for *O. suensonii*. These breaks include the Mona Passage (Taylor and Hellberg 2003, 2006; Baums et al. 2005; Foster et al. 2012), the Gulf of Mexico versus wider Caribbean (Rocha et al. 2005), and Florida/Bahamas versus the Caribbean (Lee and Ó Foighil 2005; Hemond and Vollmer 2010). Although both fish and coral show a break at the Mona Passage, unique combinations of species-specific factors, rather than more general phenomena, may still be responsible for this break. For example, the subdivision in *Acropora palmata* may be linked to the specific timing of larval release and subsequent entrapment in transient eddy currents (Baums et al. 2006). For *Elacatinus* gobies, distinct color morphs are found on either side of the passage; therefore, it is possible that larvae may actually cross the passage, but environmentally driven post recruitment selection is maintaining the break (Palumbi and Warner 2003; Rocha et al. 2005).

## Migration patterns and demographic history

Despite the genetic subdivision seen in Utila, larvae appear to be moving freely throughout Florida and the remainder of the Caribbean. The assumption that length of dispersal phase is correlated with dispersal ability appears to hold for *O. suensonii*, as our results showed no significant population structure among Caribbean locations separated by as many as 1,700 km. High levels of gene flow have been detected in ophiuroid species in the Northwest Atlantic (Cho and Shank 2010), Northeast Atlantic (Muths et al. 2009; Boissin et al. 2011; Pérez-Portela et al. 2013), Southern Oceans (O'Hara et al. 2014), and throughout the wider Caribbean in other species with extended pelagic larval duration, notably, the spiny lobster (*Panulirus argus*) (Silberman et al. 1994) and queen conch (*Stombus gigas*) (Mitton et al. 1989). Major surface currents flowing through the Caribbean and Florida were seen as the likely mechanism connecting these populations, and it is plausible that these currents play a role in connecting *O. suensonii* populations in Florida and the Eastern Caribbean.

If the transport of *O. suensonii* larvae in surface currents plays an important part in shaping patterns of genetic connectivity, as suggested for other echinoderms (Lessios et al. 1984; Hunt 1993; Williams and Benzie 1997; Colgan et al. 2005), we should expect a general concordance between the direction of gene flow among Caribbean and Florida populations and the flow of the prevailing currents (see Fig. 1). Support for this expectation was provided by the pathogen responsible for the mass mortality of *Diamema antillarum,* which appeared to follow a path through the Caribbean dictated by surface currents (Lessios et al. 1984). Despite this expectation, direction of migration among *O. suensonii* populations throughout Florida and the Caribbean did not show a correlation with contemporary current flow, and work in the Indo-Pacific has produced similar results for other echinoderms (Palumbi et al. 1997; Lessios et al. 2003).

An additional expectation derived from current-mediated larval transport is that down stream populations should act as sinks for upstream source populations (Roberts 1997). Under this model, we would expect the highest levels of *O. suensonii* haplotype diversity in Florida and the Bahamas. However, haplotype diversity showed no obvious trend concordant with major surface currents. A previous study on eight species of Caribbean reef fish similarly showed no correlation between surface currents and gene flow and no trend of increasing downstream haplotype diversity (Shulman and Bermingham 1995).

A factor possibly contributing to these findings is that larvae may become entrapped in coastal currents before they have a chance to disperse in off shore currents. For example, collection sites for the brittle star *Ophiothrix lineata* were shown to be strongly connected by a counter current running inshore of the Florida Current in the Florida Keys (Richards et al. 2007), and a similar counter current runs south through the Yucatan Channel along the northwest coast of Cuba (Sheinbaum et al. 2002; Sheng and Tang 2003). Dispersal pathways may be further complicated by subsurface counter currents (echinoderm larvae can reach depths of at least 100 m; Bosch 1992) and eddies moving perpendicular to the prevailing direction of flow (Graber and Limouzy-Paris 1997; Lee and Williams 1999). None of these phenomena are mutually exclusive, and all could combine, perhaps with major currents, to create complex dispersal pathways.

Although the complexities of present day ocean circulation patterns may have contributed to the poor correlation between gene flow direction and major current flow, it seems likely that events throughout the demographic history of *O. suensonii* had a more significant influence on genetic structure. As in other brittle star species (Cho and Shank 2010; O'Hara et al. 2014), results for *O. suensonii* show clear patterns of population expansion from smaller ancestral populations. Results from the GENIE analyses suggest that the Florida population was the first to expand approximately 1.4 million years ago; the Caribbean population was the next to expand followed by Utila. Initiation of these range expansions spanned approximately 0.2 million years. Consequently, the Florida and Caribbean populations may have considerably expanded the extent of their ranges before the Utila population had commenced expansion. This sequence of events could have resulted in a general pattern of southerly migration through the Caribbean and into Utila. The distribution of haplotypes in the statistical parsimony network is concordant with this pattern. Haplotype B, at the center of clade 2, appears to be the haplotype that invaded Utila. This haplotype was found in Florida, Cayman, and Utila, suggesting a migratory pathway from Florida via Cayman into Utila.

The presence of ancestral haplotypes from clade 1 in Utila suggests that the earlier Utila population, which existed before the population expansion, survived in low numbers. This is supported by the GENIE analysis, which indicated that the effective population size of Utila was approximately 33,000 when the Florida population started to expand. This demographic pattern is suggestive of region wide population range contractions followed by periods of recovery and expansion, a common pattern reported for many taxa, with species likely surviving in Pleistocene refugia (Avise 2000). Clade 3 was distributed throughout Florida and the Caribbean, existing in sympatry with the other *O. suensonii* clades. Using a mitochondrial clock, we estimated that clade 3 diverged approximately 3.9 million years ago. This estimate strongly suggests that *O. suensonii* existed in Florida or the Caribbean long before it started expanding approximately 1.4 million years ago.

The migration, south through the Yucatan Channel, provides an obvious mismatch between gene flow direction and contemporary current flow (see Fig. 1), and gene flow in this direction may have occurred more than once. Florida haplotypes C and D (clade 2) are ancestral to several tip haplotypes found only in Utila, indicating gene flow from Florida to Utila over more recent time scales. Studies on clams and stomatopods in the Indo-West Pacific have also revealed no correlation between surface currents and gene flow (Benzie and Williams 1997; Barber et al. 2000). Glacial periods may have also affected historical gene flow patterns for *O. suensonii.* For example, the numerous glacial transitions throughout the Pleistocene are linked with interruptions in North Atlantic circulation (McManus et al. 2004; Gherardi et al. 2005), which, in combination with sea level fluctuations, likely affected patterns of Caribbean circulation.

Although the historical movements of *O. suensonii* are clearly not concordant with contemporary current patterns, these currents may have influenced gene flow over more recent time scales. Migration rates were obtained using information contained in the haplotype genealogy; therefore, they reflect gene flow patterns throughout the entire coalescent, and although there was a slight bias to the south, in general, migration was high in both directions. This suggests the southerly migration reflects the more historical movements of *O. suensonii* and the northerly migration is a more recent occurrence. If the major flow patterns of contemporary currents are, in fact, important in dispersal, it might explain the higher level of gene flow between Utila and Florida than between Utila and the Caribbean (Fig. 1).

This study has revealed significant population structure for an ophiuroid with high dispersal potential. The evolutionary history of *O. suensonii* may be one of cyclic expansion and decline associated with climate change throughout the Pleistocene and early Pliocene. Indeed, the detection and apparent decline of a divergent clade for *O. suensonii* serve to illustrate the hidden, fluctuating, and transient nature of biodiversity within Florida and Caribbean reefs.

**Acknowledgments** We thank Mary Kuhner for data analysis advice, Ruth Vargo for help in the laboratory, Christine and Ted Testerman, Eric Bartels, Walt DeMartini, Robbie Gibson, Adolphe Debrot and the Carmabi Foundation, Guy Harvey, Matt Potenski, Tyler Smith, and the Eco Marine Dive Shop for help with sample collection. We also appreciate the constructive comments given by three anonymous reviewers. This research was supported by a grant to MSS through the NOAA Center for Sponsored Coastal Ocean Science award # NA12NOS4260144 to the National Coral Reef Institute.

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