Gambierdiscus and Fukuyoa Species in the Greater Caribbean: Regional Growth Projections for Ciguatera-Associated Dinoflagellates.

Steven R. Kibler[a*], Eric D. Davenport[b], Patricia A. Tester[c], D. Ransom Hardison[a], William C. Holland[a], R. Wayne Litaker[a]

[a]National Oceanic and Atmospheric Administration, National Ocean Service, National Centers for Coastal Ocean Science, Center for Coastal Fisheries and Habitat Research, 101 Pivers Island Road, Beaufort, NC 28516, USA

[b]National Oceanic and Atmospheric Administration, National Ocean Service, Center for Coastal Monitoring and Assessment, 1305 East West Highway, Bldg. SSMC4, Silver Spring, MD 20910, USA

[c]Ocean Tester, LLC, 381 Gillikin Road, Beaufort, NC 28516, USA

* Corresponding Author. Email: Steve.Kibler@noaa.gov, Tel: +1.252.728.8737

Abstract

Satellite-derived sea surface temperature data from the MODIS Aqua instrument were used to project rates of growth for four *Gambierdiscus* and one *Fukuyoa* species, dinoflagellates associated with ciguatera fish poisoning. Dinoflagellate growth rates were modelled using experimental temperature vs. growth equations and projected bottom temperatures with light penetration and bathymetry masks. Daily projected growth rates for each species were used to calculate monthly, yearly and multiyear averages between 2003-2013. The resulting projections were then used to characterize patterns of regional *Gambierdiscus/Fukuyoa* abundance and compare these to ciguatera fish poisoning incidences in the Greater Caribbean Region. Model output indicated the highest growth potential was in the shelf waters of the Caribbean Sea, with moderate growth in the Bahamas, southern Florida and Gulf of Mexico; the lowest growth potential was in the northern Gulf of Mexico and along the U.S. south Atlantic coast. Mean projected growth rates generally coincided with distribution of ciguatera fish poisoning incidences in the region, with some exceptions in the southwestern Caribbean. The results of this study indicate spatial differences in *Gambierdiscus* and *Fukuyoa* growth play a prominent role in in governing the occurrence of ciguatera fish poisoning in the greater Caribbean. Growth and distribution models may be an effective tool for ciguatera risk assessment.

Keywords. Ciguatera, Ciguatera fish poisoning, benthic dinoflagellate, ciguatoxin, model, harmful algal bloom (HAB)

Abbreviations. CFP, ciguatera fish poisoning; CTXs, ciguatoxins; GCR, FGBNMS, Flower Garden Banks National Marine Sanctuary; Greater Caribbean Region; MTXs, maitotoxins; MODIS, Moderate Resolution Imaging Spectroradiometer; NSC Shelf, North and South Carolina Shelf; SST, sea surface temperatures; VI, Virgin Islands.

1. Introduction

Ciguatera fish poisoning (CFP) is the most common nonbacterial cause of human illness associated with seafood consumption and is a growing concern in coastal management as well as the seafood and tourism industries. The illness is caused by of a group of lipophyllic neurotoxins (ciguatoxins, CTXs) produced by dinoflagellates in the genera *Gambierdiscus* and *Fukuyoa* (henceforth termed CFP-associated dinoflagellates). Ciguatera fish poisoning is caused by consumption of fish containing relatively high concentrations of ciguatoxins. While CFP is predominant in tropical and lower subtropical latitudes, it is reported occasionally from temperate locations as well. In the Atlantic, CFP is most common in the Greater Caribbean Region (GCR), which includes the Greater and Lesser Antilles, the Bahamas, the Florida Keys and the Gulf of Mexico, the Caribbean Sea, and the southeast continental U.S. as far north as Cape Hatteras, North Carolina (after Kibler et al., 2015). Historically, the number of CFP incidences tends to be highest in the Greater and Lesser Antilles, Bahamas and Southern Florida, with occasional outbreaks in the Gulf of Mexico, the Yucatan Peninsula, and Central America (Fig. 1; Olsen et al., 1983; Arcila-Herrera et al., 1998; Alvarez, 1999; CDC, 2006; Tester et al., 2010; Sebastián Celis and Mancera Pineda, 2015). In recent years, rising ocean temperatures have prompted concerns that CFP incidences may increase at higher latitudes as the distribution of *Gambierdiscus* and *Fukuyoa* species moves poleward (Heimann et al.; 2011; Tester et al., 2013; Mattei et al., 2014; Kibler et al., 2015).

Unlike most other harmful dinoflagellates that bloom in the water column, CFP-associated species are primarily benthic, and found associated with substrates including macroalgae, microalgal turfs, dead coral, sand, and other materials. CFP-associated dinoflagellates are comprised of at least 15 *Gambierdiscus* and 3 *Fukuyoa* species, many of which co-occur (Vandersea et al., 2012; Gómez et al., 2015; Nascimento et al., 2015; Fraga et al., 2016; Kretzschmar et al., 2017; Smith et al., 2016; Tawong et al., 2016). Competition for space, light and other resources is intense on benthic substrates, but *Gambierdiscus/Fukuyoa* cells can reach high levels of abundance despite having low growth rates (0.1 – 0.3 d^{-1} or 0.14 – 0.43 div d^{-1}) relative to many other microalgae (0.24 – 1.06 d^{-1} or 0.35 – 1.5 div d^{-1}) (Eppley, 1972; Kibler et al., 2012; Marañón et al., 2013; Xu et al., 2016). In this context, it is likely that lipid soluble CTXs and/or water soluble maitotoxins (MTXs) produced by *Gambierdiscus* and *Fukuyoa* species serve as anti-grazing and/or allelopathic compounds (Holland et al., 2013). Although the pathways by which CTXs bioaccumulate in fish have not been fully elucidated, the flux of toxins into the food web is largely proportional to the overall abundance of CFP-associated dinoflagellates (Lehane and Lewis, 2000; Yang et al., 2016). Therefore, the highest CFP risk is expected to follow *Gambierdiscus*/*Fukuyoa* bloom events, albeit with a lag necessary for transfer and accumulation of CTXs in the food web (Chinain et al., 1999; Chateau-Degat et al., 2005; Llewellyn, 2010).

Blooms of CFP-associated dinoflagellates are well recognized in the Caribbean, where water temperatures are favorable for growth year round. Annually, Caribbean surface water temperatures typically vary from ~24 – 30 °C, temperatures yielding high *Gambierdiscus* abundance (Gillespie et al., 1985; Chinain et al., 1999; Tosteson, 2004). Field data from the GCR show *Gambierdiscus* blooms typically occur in shallow, protected bays, back reef and lagoon environments (Taylor and Gustavson, 1986; Tindall and Morton, 1998; Tester et al., 2013), where cell concentrations can exceed 50,000 cells g^{-1} macroalgae (Carlson and Tindall, 1985; Faust et al., 2005; Okolodkov et al., 2014; Tester et al., 2014). The favorability of Caribbean water temperatures is also supported by experimental data, which show optimal *Gambierdiscus*/*Fukuyoa* growth at 25 - 30 °C, gradually decreasing growth $\leq$ 24 °C, and a precipitous decline in growth at temperatures $\geq$ 31 °C (Morton et al., 1992; Kibler et al., 2012; Xu et al., 2016). This pattern is similar in the Pacific, where CFP incidence is positively correlated with water temperature, but the relationship weakens at temperatures >30 °C (Hales et al., 1999; Chateau-Degat et al., 2005; Llewellyn, 2010).

If the flux of CTXs into the food web, and resulting CFP outbreaks, are a function of relative cell abundance of *Gambierdiscus/Fukuyoa* species, it follows that regional differences in fish toxicity and/or CFP incidence rates are driven by variances in cell abundance. The prediction of Caribbean-wide differences in *Gambierdiscus/Fukuyoa* growth is an important step toward assessing CFP risks, especially considering the lack of abundance data for these species in the GCR. The few data available for Caribbean *Gambierdiscus/Fukuyoa* species characterize only local scale patterns, and are not sufficient for regional predictions. Here, we present a predictive growth model using satellite-derived water temperature data and experimentally derived temperature-growth relationships developed previously to project potential growth rates of four *Gambierdiscus* and one *Fukuyoa* species endemic to the Caribbean. This effort represents the first attempt to characterize the regional effect of temperature, the primary environmental driver governing growth (and abundance) of CFP-associated dinoflagellates (Kibler et al., 2012; 2015; Xu et al., 2016). The model only considers dinoflagellate growth due to changes in bottom temperature, depth and mean light penetration, and ignores all other factors. The resulting projections represent the first attempt to quantify large scale spatial differences in CFP occurrence based on regional patterns of *Gambierdiscus* and *Fukuyoa* growth (see following discussion). This work focuses largely on regional scale patterns, in part because of the data limitations for smaller scale analyses; but also because of the region's complex geography and rapidly changing climatic, economic and demographic character (NU. CEPAL, 2008; Nugent and Seligman, 2008). It is intended that this effort will provide the basis for development of a CFP risk assessment model for the Greater Caribbean Region to include other factors in addition to temperature.

2. Methods

2.1 Surface temperature data

Temperature data used in this study included satellite-derived sea surface temperature (SST) from the Moderate Resolution Imaging Spectroradiometer (MODIS) administered by the U.S. National Aeronautics and Space Administration (NASA). MODIS Aqua 4 km, level 3 daily sea surface temperature (SST) data acquired between 2003 and 2013 were downloaded from the NASA Ocean Color website (http://oceancolor.gsfc.nasa.gov). Data from missing and erroneous pixels were replaced with a randomly selected value using a normal distribution function (*rnorm* function in R), where the mean and standard deviation parameters were calculated from a composite of all available observations at that pixel within a three-week period.

To verify the simulated temperatures approximated observed SST values, corrected pixel data were compared with *in situ* temperatures measured at four buoys in the GCR. Buoys were located in the western Gulf of Mexico (NDBC Station 42002; 26.086 °N, 93.777 °W), the Yucatan Basin (NDBC Station 42056; 19.802 °N, 84.857 °W), the eastern Caribbean Sea (NDBC Station 42059; 15.179 °N, 67.563 °W) and the western tropical Atlantic (NDBC Station 41040; 14.516 °N, 53.024 °W) (Table 1). Temperature data were downloaded from the National Data Buoy Center website (www.ndbc.noaa.gov) maintained by the National Oceanic and Atmospheric Administration (NOAA) and hourly data were utilized to calculate daily averages and standard deviations for comparison with corrected SST temperatures. Differences among corrected temperatures, adjacent satellite-derived temperatures, and *in situ* temperatures were assessed with a non-parametric Kruskal-Wallis ANOVA.

2.2 Projected bottom temperatures

The bottom temperatures at each pixel were projected using temperature profile data from the Global Temperature-Salinity Profile Program (GTSPP; http://www.nodc.noaa.gov/GTSPP/index.html) fitted to a sigmoid equation adapted from Alvera-Azcárate et al. (2011). To represent regional differences in vertical temperature gradients, 2003-2013 GTSPP profile data were collated from seven sub-regions in the Greater Caribbean Region (GCR). These sub-regions included the eastern and western Gulf of Mexico (EGOM, WGOM, respectively), the south Atlantic Bight (SAB) and the western tropical Atlantic (WTA). The Caribbean Sea was divided into three sub-regions: the Yucatan Basin (YUC), the Colombian Basin (COL) and the Venezuelan Basin (VEN) (Fig. 1B, Table 2). The number of available temperature profiles varied widely across the sub-regions, with >21,000 profiles available from EGOM, but only 90 and 144 profiles from COL and VEN, respectively (Table 2). Data from each profile were binned into standard depths and the means and standard deviations were calculated for each bin. Temperature differences between adjacent bins were then fitted to a sigmoid equation of the form

$$s(z) = T_u + \frac{T_b - T_u}{1 + e^{((z-D)/2W)}} \qquad (1)$$

where $s(z)$ is the sigmoid function, z is the depth (m), T_u and T_b are temperatures at the surface and bottom (°C), D is the depth of the thermocline (m), and W is the width of this layer in meters (Alvera-Azcárate et al., 2011). Bottom temperatures were then estimated using the expression

$$T_{Bottom} = T_{SST} - \Delta T_z \qquad (2)$$

where T_{SST} is the satellite-derived surface temperature and ΔT_z denotes the numerator in Eq. 1 ($T_b - T_u$).

2.3 Bathymetry

Bathymetric data for the model were accessed via the ETOPO1 Global Relief Model produced by NOAA's National Geophysical Data Center (https://www.ngdc.noaa.gov/mgg/global/seltopo.html). The Coastal Relief Model was used to create a customized 2-minute bathymetry grid bound by 90 °N, 0 °S, 0 °E, and 180 °W for the region of interest. The gridded bathymetric data were then interpolated to the same pixel dimensions as the SST imagery. A depth mask ($Mask_{Bath}$) was created to remove SST pixels at locations where depths were < 0 m and > 100 m according to

$$Mask_{Bath} = 1, \quad -100 \geq D_{Bath} < 0 \qquad (3)$$

$$Mask_{Bath} = 0, \quad -100 < D_{Bath} > 0 \qquad (4)$$

where D_{Bath} is the maximum depth at each pixel.

2.4 Light penetration depth

The maximum depths where *Gambierdiscus* and *Fukuyoa* cells could occur across the GCR were estimated using the diffuse attenuation coefficient for downwelling irradiance at 490 nm (K_{d490}), measured by the MODIS sensor and available from NASA's Ocean Color website (http://oceancolor.gsfc.nasa.gov/). K_{d490} is a direct level-2 output product created using an empirical algorithm (see Mueller and Fargion, 2002; Werdell and Bailey, 2005; Wang et al.,

2009) and was used to estimate average subsurface photosynthetically available radiation (I_{PAR}). From these parameters, the maximum depth (D_{max}) at which *Gambierdiscus* and *Fukuyoa* growth were possible was estimated using the Beer-Lambert law after Ryther (1956) (Eq. 5).

$$D_{max} = \frac{Log(I_{PAR}) - Log(I_c)}{K_{d490}} \tag{5}$$

A previous study by Kibler et al. (2012) indicated ~10 µmol photons m^{-2} s^{-1} was the minimum light intensity (I_c) supporting growth of *Gambierdiscus* and *Fukuyoa* species (< 1% of typical surface irradiance). Using this information, a light penetration depth mask (D_{PAR}) was created used to remove pixels where light penetration was greater than or equal to D_{max} (Eqs. 6 & 7). After depth and light masks were applied, remaining pixel values represented locations within the 200 m isobath where irradiance is sufficient to support photosynthesis.

$$Mask_{Light} = 1, \quad D_{PAR} \leq D_{max} \tag{6}$$

$$Mask_{Light} = 0, \quad D_{PAR} > D_{max} \tag{7}$$

2.5 Bottom temperature validation

Bottom temperature projections were validated by comparison with *in situ* temperature profile data collected at seven representative locations in the GCR. Validation sites were selected to include some of largest expanses of continental shelf, areas with a history of CFP, and sites where previous field data confirmed *Gambierdiscus/Fukuyoa* species are common. These validation sites included the NSC Shelf (coasts of North and South Carolina, USA), reef platforms in the Flower Garden Banks National Marine Sanctuary (FGBNMS, NW Gulf of Mexico), the shelf surrounding southern Florida (E and W coasts, Florida Keys), Campeche Bank (N Yucatan Peninsula), the Virgin Islands shelf (VI Shelf, U.S. and British), the southeastern Antilles shelf (SE Antilles; St. Lucia, St. Vincent and the Grenadines, Grenada), and the Nicaragua Rise (W Caribbean Sea; Fig. 1C, Table 3). For each location, temperature data from the World Ocean Database 2013 (WOD13, http://www.nodc.noaa.gov/OC5/WOD/pr_wod.html; Boyer et al., 2013) were collated and included profiles collected via CTD (conductivity, temperature, depth), XBT (expendable bathythermograph), PFL (ARGO profiling float), and OSD (ocean station data). Data from a total of 2,014 discrete profiles were used for bottom temperature validation, with 480 profiles available from S Florida, but only 24 from the Nicaragua Rise. Because adequate temperature profiles were not available for some of the narrow shelf locations during the 2003-2013 study period, profile data were also obtained from deeper areas around each validation site (Fig. 1C) and from earlier years. For example, of the 93 profiles collected in the FGBNMS validation area (Table 3), only 24 were collected over the shallow reef platforms themselves (≤ 70 m), with the remaining 69 from the deeper surrounding waters. Data were even more limited from the Nicaragua rise, necessitating inclusion of 6 temperature profiles data from 1980-1992

2.6 Projected growth rate

Potential growth rate of four *Gambierdiscus* and one *Fukuyoa* species endemic to the Atlantic (*G. belizeanus*, *G. caribaeus*, *G. carolinianus*, *Gambierdiscus* ribotype 2, *F. ruetzleri*) were calculated at pixels in the GCR using projected bottom temperatures with light and depth masks. The relationship between water temperature and growth rate for each species was determined previously and reported in Kibler et al. (2012) and Kibler et al. (2015). Briefly, experimental temperature vs. growth data from multiple strains of each species were fitted to a series of 3rd and 4^{th} order polynomial equations (Table S1, Fig. S1), and the resulting curves were used to calculate daily growth rate from the projected bottom temperature data at each pixel. Daily potential growth rates for each species were calculated using Eq. 8, where μ is the daily growth rate (d^{-1}) as a function of temperature, t is the time point (d), and $Mask_{Bath}$ and $Mask_{Light}$ represent the depth and light masks, respectively.

$$Growth_{t+1} = (\mu * MaskBath * MaskLight) + Growth_t \qquad (8)$$

Depth and light masks were used to exclude pixels that were beyond the depth and light limits for *Gambierdiscus* and *Fukuyoa* species as described above. Daily potential growth rates were summed to calculate monthly growth rates (mo^{-1}) and average yearly and 2003-2013 multiyear growth rates were calculated using the monthly data. Growth rates were converted to monthly division rates (div mo^{-1}) by dividing by $ln2$. Growth data were then visualized using MATLAB R2016a (The Mathworks, Inc., Natick, Massachusetts).

To simplify comparison of *Gambierdiscus* and *Fukuyoa* growth potential with geographic occurrence of CFP, a *Gambierdiscus* species composite growth model was employed. This composite was created using combined growth vs. temperature data from all strains of each of the five dinoflagellate species. The data were then fitted to a 4^{th} order polynomial equation and growth rate was calculated as described in Kibler et al. (2015) (Fig. S1).

3. Results

3.1 SST data correction The compositing and correction processes yielded monthly SST imagery with very high coverage across the GCR, despite small data gaps from pixels directly adjacent to landmass coastlines. Comparison of random model-generated data points with satellite-derived temperatures from adjacent pixels revealed that corrected values were relatively good approximates of SSTs at each location. The differences between mean satellite-derived and randomly-generated temperatures were 0.02 °C (27.57 vs. 27.59 °C) at station 41040, 0.05 °C (27.70 vs. 27.75 °C) at station 42059, 0.08 °C (27.98 vs. 28.06 °C) at 42056, and 0.28 °C (26.26 vs. 25.98 °C) at 42002 (Table 4). One-way ANOVA results showed no significant differences between satellite-derived and randomly-generated temperature data as a whole ($p > 0.05$). When the data were parsed by location (data not normally distributed), Dunn's multiple comparison results showed satellite-derived temperatures and random-generated values were significantly different at station 42002 (Table 4). At that location, the median randomly-generated estimate was slightly lower (25.74 °C) than the median temperature measured via satellite (26.48 °C), likely due to the high number of missing values (53%) in the satellite data at that location.

Not surprisingly, *in situ* temperatures measured at each buoy station showed more substantial variation from the corrected SST data. There was a significant difference between median *in situ* and corrected SST temperatures at station 41040 (W Gulf of Mexico), where corrected satellite-derived SST overestimated in situ temperatures by an average of 1.24 °C (Table 4). Median corrected satellite temperatures were significantly lower than in situ measurements by 0.65 °C at 42059 (western tropical Atlantic) and by 1.32 °C at station 42002 (eastern Caribbean Sea). Median i*n situ* and satellite estimates were not significantly different at station 42056 (Yucatan Basin) (Table 4). Such differences between *in situ* and satellite-derived SSTs are well recognized (e.g., Reynolds et al., 2005; Castro et al., 2012; Gentemann, 2014), but their correction is beyond the scope of this work.

3.2 Projected bottom temperatures

Comparison between projected bottom temperatures and *in situ* profile data showed relatively good agreement, despite scarcity of profile data from some areas. Yearly mean projected bottom temperatures were generally within one standard deviation (±1.3 °C, gray dots in Fig. 3) of mean *in situ* temperatures at all validation sites to depths of at least 50 m, and well beyond the average maximum growth depth at each site (1% surface PAR, blue dashed line, Fig. 3). Departure between in situ and projected temperatures was greater at 100 m, averaging 1.8 – 2.6 °C at the NSC Shelf, Campeche, VI Shelf, SE Antilles and Nicaragua Rise, and 4.2 - 4.8 °C in S Florida and the FGBNMS. The greater deviation with depth was partly attributable to a steep thermocline during some months that is not well represented by the sigmoid model. Deviation at depth is also attributable by relatively large spatial variability in the vertical temperature gradient at different locations in each sub-region. Fortunately, growth rates of *Gambierdiscus* and *Fukuyoa* species are likely to be very limited at depths beyond 40 or 50 m where light levels are much reduced, a characteristic borne out by field observations (Taylor and Gustavson, 1986; Grzebyk et al. 1994; Litaker et al., 2009; Richlen and Lobel 2011). So the net effect of bottom temperature errors on growth and abundance (and flux of CTXs into the food web) at these pixels is expected to be small.

3.3 Projected growth rates

The distribution of potential growth rates in the GCR illustrate how favorable water temperatures in the Caribbean Sea and southern portions of the Gulf of Mexico and the Bahamas can promote the growth of CFP-associated dinoflagellates. All five dinoflagellate species were projected to have their highest growth potential in the Caribbean Sea, where growth rates were expected to exceed 90% of μ_{max} for four out the five species (Figs. 4, S1; Table S1). The highest potential growth rates were projected for *G. caribaeus* and *F. ruetzleri*, consistent with their higher temperature optima (T_{max}) and higher maximum growth rates (μ_{max}, Table S1). Both species were estimated to reach average potential growth rates of 10-12 div mo^{-1} in shelf regions surrounding the Caribbean Sea, Yucatan Peninsula and southern Gulf of Mexico, the Florida Keys and southern Bahamas (Figs. 4B, E). The species with moderate growth rates, *G. carolinianus* and *G. belizeanus*, were projected to follow a similar pattern, but with division rates of 7-9 div mo^{-1} (Figs. 4A, C). With a greater tolerance for low wintertime water temperatures (Kibler et al., 2015), *G. carolinianus* was projected to exhibit division rates slightly higher than those of *G. belizeanus* (~7 vs. 5-6 div mo^{-1}) along the outer shelves of the northern Gulf of Mexico and South Atlantic Bight. The lowest overall growth potential was evident for *Gambierdiscus* ribotype 2, which was projected to have maximum division rates of ~6 div mo^{-1} in portions of the Caribbean Sea, lower rates in the southern Gulf of Mexico and Bahamas (4-5 div mo^{-1}), and the lowest division rates of only 2-3 div mo^{-1} in the northernmost latitudes (Fig. 4D).

Variations in interspecific vs. interannual growth were compared using the standard deviation of annual average division rates. Interspecific variation was characterized using the deviation among division rates of all five species; for clarity, data from only one representative year (2010) are shown (Fig. 5A). The largest amount of variation among species is evident around the periphery of the Caribbean Sea, where the standard deviation reached ±8-9 div mo^{-1} during 2010. This relatively high degree of variation is attributable to differences in thermal tolerance indices (T_{max}, T_0, T_u) among the five species, where some species are more tolerant of sustained high summertime temperatures in the (Table S1; see also Kibler et al., 2015). There was less interspecific variation at high latitudes where all five species are limited by winter water temperatures. Standard deviations were approximately 5 to 6 div mo^{-1} in the northern Gulf of Mexico and fell to 3-4 div mo^{-1} in the South Atlantic Bight (Fig. 5A).

In comparison, there was relatively little interannual variation in division rates within each species. The representative species *Gambierdiscus caribaeus*, for instance, exhibited standard deviation from mean annual division rates of less than ±1 div mo^{-1} over most of the GCR during the 2003-2013 period (Fig. 5B). Most of the interannual variability was evident in the Bahama Banks and the Nicaragua rise, where division rates varied by ±0.5 to 2.3 div mo^{-1}. Very similar levels of interannual variation were evident for the remaining four dinoflagellate species. More detailed spatial differences in growth variability at these locations will be examined in a later study.

To assess how year to year changes in water temperature affected potential growth of CFP-associated dinoflagellates, average annual bottom temperatures at the seven validation sites were compared with average division rate of the *Gambierdiscus* species composite. In general, average annual bottom temperatures across the GCR ranged between 25.68 and 26.58 °C. Among the sites (Fig. 1C), the highest bottom water temperatures were projected on the Nicaragua Rise (27.03 - 28.31 °C; Fig. 6A) and the lowest temperatures were projected on the NSC Shelf (20.88 – 21.85 °C) and Flower Garden Banks (23.91 – 24.88 °C; Fig. 6A). In general, average bottom temperatures varied no more than ~1 °C at each location during the 11-year study period, with a pronounced decline in temperature evident at sites bounding the Caribbean Sea during 2004, 2008, and 2012 (South Florida, VI Shelf, SE Antilles, Nicaragua Rise). The lower water temperatures are consistent with similar interannual patterns in both satellite-derived and buoy-derived SST data.

Differences in average annual projected growth rate among the seven representative locations reflected the latitudinal temperature gradient in the region. The highest potential growth was evident at the warm Caribbean Sea locations (VI Shelf, Nicaragua Rise, SE Antilles), where growth rates averaged ~9 div mo^{-1} during the entire 11-year study period (Fig. 6B). Farther north, average composite growth rates were ~8 div mo^{-1} at Campeche Bank, ~7 div mo^{-1} in South Florida, ~6 div mo^{-1}. Commensurate with the lowest average temperatures, the FGBNMS and NSC shelf exhibited projected growth rates of 4.5 to 5 div mo^{-1} (Fig. 6).

4. Discussion

The strong dependence of dinoflagellate growth on water temperature has enabled regional-scale forecasting of growth and distribution of the dinoflagellates that cause ciguatera fish poisoning (CFP). In this study, 2003 – 2013 SST data were combined with experimental temperature-growth models to project bottom temperatures and potential growth rates of four *Gambierdiscus* and one *Fukuyoa* species, dinoflagellates associated with CFP in the Greater Caribbean Region (GCR). In accordance with year-round high water temperatures, model projections indicated the highest potential for growth of all five dinoflagellate species occurs in the shelf waters surrounding the Caribbean Sea, including the Caribbean coastlines of Central and South America (Fig. 4, 7A). Dinoflagellate growth rates are projected to be more moderate in adjacent portions of the Bahamas, southern Florida and Gulf of Mexico, commensurate with less frequent CFP occurrence in these areas. Some of the lowest dinoflagellate growth rates are projected for the northern Gulf of Mexico and the U.S. Atlantic coast north of Cape Canaveral, Florida, where wintertime conditions limit *Gambierdiscus/Fukuyoa* growth (Fig. 7A; Tester et al., 2013; Kibler et al., 2015). CFP is relatively rare at these locations, occurring only occasionally in the northern Gulf of Mexico. At higher latitudes of the U.S. south Atlantic coast, CFP outbreaks are either associated with tropical fishes from the Gulf Stream or those imported from more tropical locations (CDC, 2006; Villareal et al., 2006. Villareal et al., 2007).

Locations in the Caribbean with the highest projected growth rates are also those having the highest CFP incidence rates. Previous surveys have indicated the northeast Antilles, which include Puerto Rico, the U.S. and British Virgin Islands, the Netherlands Antilles, Monserrat, Guadeloupe and Dominica, are characterized by the highest CFP incidences in the GCR (Table 5; Tester et al., 2010; Radke, 2013; Sebastián Celis and Mancera Pineda, 2015). Summary data from these studies show the highest CFP incidence rates in the Caribbean occur in Antigua and Barbuda (219 per 100,000), the British Virgin Islands (188 per 100,000), Guadeloupe (227 per 100,000), Monserrat (417 per 100,000), Puerto Rico (486 per 100,000) and the U.S. Virgin Islands (1,258 per 100,000; Table 5, Fig. 7B). With some variation, these patterns are largely consistent with reports from earlier studies as well (Olsen et al., 1983; Taylor and Gustavson, 1986; Stinn et al., 2000). In comparison, growth projections from the current study indicated 2003-2013 average bottom temperatures in the Lesser Antilles average ~25-27 °C, with composite growth rates of 9-12 div mo^{-1} (Figs. 4, 7A). Such growth rates are equivalent to at least 70% of the maximum growth rate for each of the five dinoflagellates in this study (Table S1; Kibler et al., 2012; 2015), suggesting the Lesser Antilles are areas where *Gambierdiscus* and

Fukuyoa blooms may be most likely. Presumably, these same areas are likely to have highest transfer rates for CTXs into the food web.

Other CFP-prone locations where *Gambierdiscus*/*Fukuyoa* growth rates are projected to be relatively high include the Turks and Caicos Islands, the southern Bahamas, Cuba, southern Florida, the southern Gulf of Mexico and Campeche Bank (Figs. 5A, 7). Each of these locations have either a long a history of ciguatera incidence or recent increase in CFP risk (Taylor, 1985; Bomber, 1987; Stinn et al., 2000; Maya Entenza et al., 2007; Okolodkov et al., 2007; Morrison et al., 2008; Ley-Martínez et al., 2014; Radke et al., 2015). Although they are limited, available field data indicate *Gambierdiscus*/*Fukuyoa* cells are common in the same locations, sometimes reaching very high levels of abundance (Carlson, 1984; Bomber, 1987; Faust et al., 2005; Litaker et al., 2010; Okolodkov et al., 2014; Tester et al., 2014; Loeffler et al., 2015). Conversely, portions of the GCR exhibiting low to rare CFP incidences are generally characterized by modest rates of dinoflagellate growth. Such locations include the northern Gulf of Mexico and shelf areas along the southeast U.S. Atlantic coast, where composite *Gambierdiscus* growth rates are projected to average ≤ 6 div mo^{-1} and CFP incidences have been rare (Fig. 7; CDC, 2006; Villareal et al., 2006; 2007; Tester et al., 2013; Wenck and Moore, 2015). The relatively low projected growth rates in these locations are corroborated by low *Gambierdiscus*/*Fukuyoa* cell abundances associated with low wintertime water temperatures (Bomber et al., 1989; Vandersea et al., 2012; Tester et al., 2013; Kibler et al., 2015; Sassner, 2015).

A review of ciguatera occurrence patterns in the GCR with growth projections from this study indicate a positive association between incidence and growth potential. Average 2003-2013 monthly projected growth rates (*Gambierdiscus* composite) for the shelf areas surrounding 29 regional nations were calculated from monthly projections. Average CFP incidence rates from three recent review publications were calculated for comparison (Tester et al., 2010; Radke, 2013; Sebastián Celis and Mancera Pineda, 2015). There was a positive correlation between monthly projected growth rates and mean CFP incidence rates during July through November months ($r = 0.39$ to 0.59, $p \leq 0.05$), with the strongest correlation occurring in September ($r = 0.66$, $p \leq 0.05$; Spearman rank order correlation; Tables 5, S2). The analysis also showed a weak negative correlation between projected growth and incidence during the coldest months of February and March ($r = -0.33$, $p = 0.08$; Table S2). This pattern is consistent with high dinoflagellate growth rates driving increased flux of CTXs into the marine food web during the late summer months when abundance is likely to be highest. When the slower growth rates during the winter were averaged with those during the warmer months however, average yearly growth rates failed to correlate with CFP incidences ($r = 0.225$, $p > 0.05$). Though seasonal changes are relatively small in much of the GCR, the incidence vs. growth data suggest seasonality may play a key role in CFP outbreaks (Table 5). Taken together, the association between growth projections from this study and incidence patterns, and the spatial overlap between maximal projected growth and CFP distribution (Fig. 7) indicate the prominence of CFP in the Caribbean is largely attributable to temperature-driven growth and abundance of *Gambierdiscus/Fukuyoa* species. These data support the utility of temperature-based growth models as a potential forecasting tool for ciguatera risk in the Caribbean.

Despite the overall agreement between dinoflagellate growth projections and prevalence of CFP, some portions of the GCR are projected to support *Gambierdiscus/Fukuyoa* growth, but exhibit little CFP. For instance, average water temperatures along the most of the Caribbean coastlines of South and Central America are projected to support dinoflagellate growth rates averaging 7-9 div mo^{-1}, representing at least 80% of the maximum composite growth potential

(Fig. 7A). Reported CFP incidence rates, however, average zero to 0.02 per 100,000 in Colombia, Nicaragua, Costa Rica and Guatemala, and only slightly higher in Belize (0.15 per 100,000; Table 5). Panama is an exception, having one of the lowest projected growth rates, and a CFP incidence rate of zero.

Some of the mismatch between projected dinoflagellate growth and CFP incidence may be attributed to environmental factors other than temperature. For instance, previous studies have indicated *Gambierdiscus*/*Fukuyoa* cells are rare at highly turbid sites with direct runoff from land (Taylor and Gustavson, 1985; Litaker et al., 2010 and reference therein). Much of the Central American coast is characterized by narrow coastlines with high terrestrial runoff, conditions that worsen in the rainy season and following tropical cyclones (Hellweger and Gordon, 2002; Rodríguez-Olarte et al., 2011). These conditions have been shown to limit coral reef development along the Panama and Venezuela coasts, as well as much of the Nicaragua Rise (Woodley et al., 1997; D'Croz et al., 2005; Weil, 2003; Hallock et al., 2015). Such conditions along the continental coastlines very likely limit *Gambierdiscus/Fukuyoa* abundance as well. Most CFP outbreaks in the southwest Caribbean appear to be restricted to offshore island sites not directly impacted by runoff, such as Providencia, San Andrés, Aruba, Curaçao, Bonaire, Isla de Margarita, and Trinidad and Tobago (Tester et al., 2010; Celis Melo, 2013; Sebastián Celis and Mancera Pineda, 2015).

Low CFP incidences in areas where dinoflagellate growth rates are projected to be high may also relate to species-specific differences in growth and toxicity. There is evidence that production of CTXs varies considerably among *Gambierdiscus*/*Fukuyoa* species, with some species much more toxic than others. In the Pacific, *G. polynesiensis* appears to exhibit the highest relative toxicity, with some strains producing ~12 pg P-CTX-3C equivalents cell^{-1}

(Chinain et al., 2010). This information suggests *G. polynesiensis* may be the primary contributor to CFP in the Pacific. Similar data from the Caribbean indicate *G. excentricus* produces 2-3 orders of magnitude more CTX than other Caribbean species (Fraga et al., 2011, Litaker et al., in press). Originally described from subtropical waters of the Canary Islands, *G. excentricus* also occurs in other subtropical and temperate locations in the Atlantic and is likely distributed across the GCR (Fraga et al., 2011; Fraga and Rodriguez, 2014; Nascimento et al., 2015; Litaker et al., in press). Growth experiments are currently underway to determine the temperature-growth indices for this species so that its potential growth and abundance may be projected.

Based on the distinct differences in growth and toxicity among the Caribbean CFP-associated dinoflagellates, it is likely the distribution and abundance of individual species directly impact the flux of CFP toxins into the regional food web. Consequently, factors governing their growth likely play a critical role in the flux of ciguatoxins into local food webs. Given the paucity of abundance data for each species, and the expense associated with monitoring for CTXs in fish, modeling tools like the one developed in this study may be the only practical means for forecasting CFP risk.

4.1 A surface temperature-based model as a predictive tool

MODIS 4 km SST data were selected for this study because they offered both spatial coverage over the entire region and temporal coverage suitable for monthly dinoflagellate growth rate projections over the 2003-2013 study period. This 4 km resolution is adequate for describing regional scale and mesoscale variation in dinoflagellate growth, but does not well characterize spatial differences at smaller scales. Such limitations are evident along the western sides of the Lesser Antilles (e.g., St. Vincent and the Grenadines, St. Lucia, Martinique), which are characterized by narrow shelves smaller than the SST pixel size (Bouyesse et al., 1984). Small scale distributional patterns are also confounded by the influence of terrestrial temperatures on pixels from the land/sea margin, which were evident as missing pixels or very low water temperatures (-0.3 to 10 °C) during some months. For the purposes of small scale bottom temperature validation and calculation of mean growth rates, these errors were removed with a low-pass filter prior to mean growth rate calculation.

The utilization of water temperature as a predictive tool for CFP is not a novel concept; it has long been recognized that CFP incidence and *Gambierdiscus* distribution tend to follow large scale water temperature gradients (Halstead and Lively, 1954; Randall, 1958). The correlative relationships among SST, CFP incidence and *Gambierdiscus* growth have also been characterized at different locations in the Pacific within the context of climate change (Hales et al., 1999; Chateau-Degat et al., 2005; Llewellyn, 2010; Heimann et al., 2011). Studies in the tropical Atlantic have provided corroboration, but also underscored the sensitivity of the CFP-temperature relationship to particular locations (Radke et al., 2013; Gingold et al., 2014; Tester et al., 2010; Kibler et al., 2015).

It has long been clear that factors other than temperature also influence CFP incidence patterns. Factors such as salinity, light (quality and quantity), dissolved nutrient availability, water movement, and benthic substrate availability have the potential to affect both distribution and abundance of *Gambierdiscus/Fukuyoa* species, as well as the potential introduction of toxins into the marine food web (Morton et al., 1992; Litaker et al., 2010; Richlen and Lobel, 2011; Kibler et al., 2012, Xu et al., 2016). But the effects of these factors are difficult to gauge because of scarcity of regional data. For instance, the availability of particular benthic substrates, such as fleshy, branching macroalgae, has been shown to influence both spatial and temporal abundances of *Gambierdiscus* cells at various Caribbean sites (Ballantine et al., 1988; Lobel et al., 1988; Tester et al., 2014). But quantitative distributional data for specific types of macroalgae or other substrates have not been collected except on small scales (< 10 m to a few km), rendering assessment of substrate effects on cell abundance, growth, toxicity, or CFP incidence in the Caribbean impossible at this time.

Furthermore, it is difficult to gauge the applicability of such local characteristics to regional scale distribution and abundance patterns. An example is salinity, which may exhibit sharp local scale variability as well as some degree of regional variability, and for which regional remote sensing data are available (e.g., Grodsky et al., 2015; ESA, 2016; PO.DAAC, 2016). In the GCR, salinity changes are mainly associated with evaporation, as well as plumes from the Amazon-Orinoco, Magdalena, Mississippi-Atchafalaya, and other river systems (Hellweger and Gordon, 2002). Although lowered salinity associated with freshwater input can sometimes be traced at great distances across the Caribbean Sea and Gulf of Mexico, the river plumes typically prompt salinity changes of ≤ 2 over the width of the GCR (Sheng and Tang, 2003; Grodsky et al., 2015). Such modest shifts generally lie within the salinity optima of *Gambierdiscus* and *Fukuyoa* species (Morton et al., 1992; Kibler et al., 2012; Xu et al., 2016), and would therefore have little effect on average monthly growth rates, especially at larger spatial scales.

Projected growth rates and CFP risk forecasts that follow may also be weighed in context with a variety of socioeconomic and cultural factors potentially influencing ciguatoxicity of fishes, exposure and reporting of CFP incidence. Characteristics such as degree of dependence on seafood resources, cultural traditions among seafood consumers, local perception of CFP risks, shifts in demographics, standards of living, health care or infrastructure, and a variety of reporting biases can modify or mask incidence rates attributed to environmental signals (Nellis and Barnard, 1986; Angel-Urdinola et al., 2008; Tester et al., 2009; Branco-Araujo et al., 2011; Prado, 2013; Stevens et al., 2014; Radke et al, 2015). In one of the few attempts to quantify fisheries resource effects, Bagnis et al. (1993) reported the discard of harvested fish due to of CFP risks totaled ~3,000 tons of fish per year in Tahiti, representing an enormous economic burden on the fishing industry. A more recent fisheries study in the U.S. Caribbean showed CFP concerns over perceived high-risk species and collection sites accounted for nearly 14% of discarded fish bycatch (Trumble et al., 2006). This figure is especially disconcerting because most of the discards were high value fish species. Such complex socio-economic factors combined with the continuing lack of practical fish screening methods, underscore the critical need for CFP risk management tools in the Greater Caribbean. The SST-growth model described here represents an attempt to address this need by characterizing the regional effects of temperature on potential growth of CFP-associated dinoflagellates, and providing a tool for conceptualizing and predicting CFP risk patterns.

5. Conclusions

The model projections described in this study provide an environmental framework to help elucidate the broad patterns of CFP incidence in the Caribbean. These projections are based solely upon potential growth of the dinoflagellates involved (*Gambierdiscus* and *Fukuyoa*), and not on the pathways governing the flux of CTXs through the marine food web, and ultimately to seafood consumers. It has become increasingly clear that these pathways are complex, often involving multiple trophic levels including invertebrate fauna as well as herbivorous and piscivorous fishes (Lehane and Lewis, 2000; Arbeláez Alvarado and Ruiz Vera, 2013; Ledreux et al., 2014; Silva et al., 2015). The interplay between dinoflagellate distribution, toxin production, trophic transfer and human exposure are each subject to environmental changes associated with ocean warming and climate change. The next few decades are expected to bring latitudinal shifts in fisheries resources and poleward changes in regional *Gambierdiscus/Fukuyoa* assemblages that may affect CFP exposure and the flux of CTXs into the food web (Nurse, 2011; Kibler et al., 2015; FAO, 2016). In the context of these regional changes, predictive tools like the model developed in this study are of increasing value to guide CFP risk assessment for coastal areas in the greater Caribbean. The current effort has been limited almost exclusively to elucidation of large scale spatial patterns governing CFP occurrence, with some limited analysis of interannual effects. More information about the toxicity of individual *Gambierdiscus* and *Fukuyoa* species, as well as their abundances in the field, are needed before adequate conclusions can be drawn about the potential effect of interspecific toxicity on CFP incidences in the Caribbean. A follow-up study will focus on seasonal growth patterns across the region and the role of interspecific differences in toxicity on CFP risks.

Acknowledgements

We would like to extend out thanks to internal reviewers at the NOAA Beaufort Laboratory for helpful comments that greatly improved the manuscript. Conversations with S. Moore, M. Friedman and other collaborators, as well as questions and criticisms received from other scientists, media representatives and members of the public influenced the scope of this study.

Funding: This work was supported by the National Centers for Coastal Ocean Science, National Ocean and Atmospheric Administration (NOAA). Partial funding was also provided as an award from NOAA's Ecology and Oceanography of Harmful Algal Blooms program (ECOHAB, contribution No. ########). The views expressed herein are those of the authors and do not

necessarily reflect the views of NOAA or any of its sub agencies. Mention of trade names or commercial products does not constitute endorsement or recommendation for their use by the United States government.

References

Alvarez, P., Duval, C., Colón, T., Gonzálves, G., Martinez, E., Gómez, J., Compres, L., Piña, N., Castellanos, P.L., 1993. Ciguatera: Clinical, epidemiological and anthropoidological aspects. In: Tosteson, T.R. (Ed.), Proceedings of the Third International Conference on Ciguatera Fish Poisoning, Puerto Rico, 1990. Polyscience Publications, Quebec, pp. 169-179.

Alvarez, R., 1999. Tres brotes de ictiosarcotoxicosis por ingestion de *Sphyraena barracuda* (Walbaum) y *Seriola zonata* (Mitchill) en el Caribe de Colombia. Biomedica 19(1), 35-38.

Alvera-Azcárate, A., Barth, A., Weisberg, R.H., Castaneda, J.J., Vandenbulcke, L., Beckers, J.-M., 2011. Thermocline characterization in the Cariaco basin: A modelling study of the thermocline annual variation and its relation with winds and chlorophyll-a concentration. Cont. Shelf Res. 31, 73-84.

Angel-Urdinola, D., Cortez, R., Tanabe, K., 2008. Equity, access to health care services and expenditures on health in Nicaragua. The International Bank for Reconstruction and Development/The World Bank, Washington, D.C., 38 pp.

Arbeláez Alvarado, D., Ruiz Vera, J.M., 2013. Dinámica de la bio-acumulación de las ciguatoxinas en una cadena alimentaria. Rev. Cubana Invest. Biomed. 32, 271-283.

Arcila-Herrera, H., Castello-Navarrete, A., Mendoza-Ayora, J., Montero-Carvantes, L., González-Franco, M.F., Brito-Villanueva, W.O., 1998. Diez casos de ciguatera en Yucatán. Rev. Invest. Clin. 50, 149-152.

Armstrong, E., 2007. MODIS Sea Surface Temperature (SST) Products. NASA Jet Propulsion Laboratory http://podaac.jpl.nasa.gov:2031/DATASET_DOCS/modis_sst.html (accessed 07.09.16).

Bagnis, R., Spiegel, A., Nguyen, L., Plichart, R., 1993. Public health, epidemiological and socioeconomic patterns of ciguatera in Tahiti. In: Tosteson, T.R. (Ed.), Proceedings of the Third International Conference on Ciguatera Fish Poisoning, Puerto Rico, 1990. Polyscience Publications, Quebec, pp. 157-168.

Ballantine, D.L., Tosteson, T.R., Bardales, A.T., 1988. Population dynamics and toxicity of natural populations of benthic dinoflagellates in southwestern Puerto Rico. J. Exp. Mar. Biol. Ecol. 119, 201–212.

Barnes, B.B., Hu, C., Schaeffer, B.A., Lee, Z., Palandro, D.A., Lehrter, J.C., 2013. MODIS-derived spatiotemporal water clarity patterns in optically shallow Florida Keys waters: A new approach to remove bottom contamination. U.S. Environmental Protection Agency Papers. Paper 190, http://digitalcommons.unl.edu/usepapapers/190.

Bomber, J.W., (M.S. thesis) 1987. Ecology, Genetic Variability, and Physiology of the Ciguatera-causing Dinoflagellate *Gambierdiscus toxicus* Adachi & Fukuyo (Florida Keys, Caribbean). Florida Institute of Technology, Melbourne, FL.

Bomber, J.W., Tindall, D.R., Miller, D.M., 1989. Genetic variability in toxin potencies among seventeen clones of *Gambierdiscus toxicus* (Dinophyceae). J. Phycol. 25, 617-625.

Bouyesse, P., 1984. 7. The Lesser Antilles Island Arc: Structure and geodynamic evolution. In: Buju-Duval, B., Moore, J.C., Bergen, J.A.M., Blacklinton, G., Claypool, G.E., et al. Initial Reports of the Deep Sea Drilling Project, 78A, U.S. Government Printing Office, Washington, 83-103.

Boyer, T.P., J.I. Antonov, O.K. Baranova, C. Coleman, H.E. Garcia, A. Grodsky, D.R. Johnson, R.A. Locarnini, A.V. Mishonov, T.D. O'Brien, C.R. Paver, J.R. Reagan, D. Seidov, I.V. Smolyar, M.M. Zweng, 2013, World Ocean Database 2013. Sydney Levitus, Ed.; Alexey Mishonov, Technical Ed.; NOAA Atlas NESDIS 72, 209 pp.

Branco-Araujo, G.T., Caporale, J., Stefani, S., Pinto, D., Caso, A., 2011. Is equity of access to health care achievable in Latin America? Value. Health 14(5), Suppl., S8-S12, http://dx.doi.org/10.1016/j.jval.2011.05.037.

Carlson, R.D., (Ph.D. dissertation) 1984. Distribution, periodicity and culture of benthic/epiphytic dinoflagellates in a ciguatera endemic region of the Caribbean. Department of Botany in the Graduate School, Southern Illinois University at Carbondale, Carbondale, Illinois.

Carlson, R.D, Tindall, D.R., 1985. Distribution and periodicity of toxic dinoflagellates in the Virgin Islands. In: Anderson, D.M., White, A.W., Baden, D.G. (Eds.), Toxic Dinoflagellates. Elsevier Publishing Co. Inc., New York, pp. 171-177.

Castro, S.L., Wick, G.A., Emery W.J., 2012. Evaluation of the relative performance of sea surface temperature measurements from different types of drifting and moored buoys using satellite-derived reference products, J. Geophys. Res., 117, C02029, http://dx.doi.org/10.1029/2011JC007472.

Celis Melo, J.S., 2013. (M.S. Thesis) Evaluación del effecto de las intoxicaciones alimentarias de origen marino sobre el turismo y la salud pública en la Isla de San Andrés. Universidad Nacional de Colombia, Instituto de Estudios Caribeños, Sede Caribe, San Andrés Isla, Colombia, 117 pp.

Center for Disease Control (CDC), 2006. Ciguatera fish poisoning—Texas, 1998, and South Carolina, 2004. Morb. Mortal. Wkly. Rep. (MMWR) 55, 935-937.

Chateau-Degat, M.-L., Chinain, M., Cerf, N., Gingrass, S., Hubert, B., Dewailly, E., 2005. Seawater temperature, *Gambierdiscus spp*. variability and incidence of ciguatera poisoning in French Polynesia. Harmful Algae 4, 1053-1062, http://dx.doi.org/10.1016/j.hal.2005.03.003.

Chinain, M., Germain, M., Deparis, X., Pauillac, S., Legrand, A.M., 1999. Seasonal abundance and toxicity of the dinoflagellate *Gambierdiscus sp*. (Dinophyceae), the causative agent of ciguatera in Tahiti, French Polynesia. Mar. Biol. 135, 259-267, http://dx.doi.org/10.1007/s002270050623.

Chinain, M., Darius, H.T., Ung, A., Fouc, M.T., Revel, T., Cruchet, P., Pauillac, S., Laurent, D., 2010. Ciguatera risk management in French Polynesia: the case study of Raivavae Island (Australes Archipelago). Toxicon 56, 674-690, http://dx.doi.org/10.1016/j.toxicon.2009.05.032.

D’Croz, L., Del Rosario, J.B., Góndola, P., 2005. The effect of freshwater runoff on the distribution of dissolved inorganic nutrients and plankton in the Bocas del Toro Archipelago, Caribbean Panama. Carib. J. Sci. 41, 414-429.

Eppley, R.W. 1972. Temperature and phytoplankton growth in the sea. Fish. Bull. 70, 1063-1085.

European Space Agency (ESA), 2016. Soil Moisture Ocean Salinity mission (SMOS). Paris, France. http://www.salinityremotesensing.ifremer.fr/activities/smos (accessed 12.10.16).

Faust, M.A., Litaker, R.W., Vandersea, M.W., Kibler, S.R., Tester., P.A., 2005. Dinoflagellate diversity and abundance in two Belizean coral-reef mangrove lagoons: a test of Margalef's Mandala. Atoll Res. Bull. 534, 105-131.

Fraga, S., Rodríguez, F., Caillaud, A., Diogéne, J., Raho, N., Zapata, M., 2011. *Gambierdiscus excentricus* sp. nov. (Dinophyceae), a benthic toxic dinoflagellate from the Canary Islands (NE Atlantic Ocean). Harmful Algae 11, 10-22.

Fraga, S., Rodríguez, F. 2014. Genus *Gambierdiscus* in the Canary Islands (NE Atlantic Ocean) with description of *Gambierdiscus silvae* sp. nov., a new potentially toxic epiphytic benthic dinoflagellate. Protist 165, 839-853.

Fraga, S., Rodríguez, F., Riobó, P., Bravo, I., 2016. *Gambierdiscus balechii* sp. nov. (Dinophyceae), a new benthic toxic dinoflagellate from the Celebes Sea (SE Pacific Ocean). Harmful Algae 58, 93-105.

Friedman, M.A., Fernandez, M., Backer, L.C., Dickey, R.L., Bernstein, J., et al., 2017. An updated review of ciguatera fish poisoning: Clinical, epidemiological, environmental, and public health management. Mar. Drugs 15(72), http://dx.doi.org/10.3390/md15030072.

Gentemann, C.L., 2014. Three way validation of MODIS and AMSR-E sea surface temperatures, J. Geophys. Res. Oceans, 119, 2583-2598, http://dx.doi.org/10.1002/2013JC009716.

Gillespie, N., Holmes, M.J., Burke, J.B., Doley, J., 1985. Distribution and periodicity of *Gambierdiscus toxicus* in Queensland Australia. In: Anderson, D.M., White, A.W., Baden, D.G. (Eds.), Toxic Dinoflagellates. Elsevier, New York, pp. 183-188.

Gingold, D.B., Strickland, M.J., Hess, J.J., 2014. Ciguatera fish poisoning and climate change: analysis of National Poison Control Center data in the United States,2001-2011. Environ. Health Perspect. 122, 580-586, http://dx.doi.org/10.1289/ehp.1307196.

Gómez, F., Qiu, D., Lopes, R.M., Lin, S., 2015. *Fukuyoa paulensis* gen. et sp. nov., a new genus for the globular species of the dinoflagellate *Gambierdiscus* (Dinophyceae). PLoS ONE 10(4), e0119676, http://dx.doi.org/10.1371/journal.pone.0119676.

Grodsky, S.A., Johnson, B.K., Carton, J.A., Bryan, F.O., 2015. Interannual Caribbean salinity in satellite data and model simulations. J. Geophys. Res. Oceans 120, 1375-1387, http://dx.doi.org/10.1002/2014JC010625.

Grzebyk, D., Berland, B., Thomassin, B.A., Bosi, C., Arnoux, A., 1994. Ecology of ciguateric dinoflagellates in the coral reef complex of Mayotte Island (S. W. Indian Ocean). J. Exp. Mar. Biol. Ecol. 178, 51–66.

Hales, S., Weinstein, P., Woodward, A., 1999. Ciguatera (fish poisoning), el niño, and Pacific sea surface temperatures. Ecosys. Health 5, 20-25, http://dx.doi.org/10.1046/j.1526-0992.1999.09903.x.

Hallock, P., Hine, A.C., Vargo, G.A., Elrod, J.A., Jaap, W.C., 2015. Platforms of the Nicaraguan Rise: Examples of the sensitivity of carbonate sedimentation to excess trophic resources. Geology 16, 1104-1107.

Halstead, B.W., Lively Jr., W.M., 1954. Poisonous fishes and ichthyosarcotoxism. U.S. Armed Forces Med. J. 5, 157-175.

Heimann, K., Capper, A., Sparrow, L., 2011. Ocean surface warming: Impact on toxic benthic dinoflagellates causing ciguatera. eLS, http://dx.doi.org/10.1002/9780470015902.a0023373.

Hellweger, F.L., Gordon, A.L., 2002. Tracing Amazon River water into the Caribbean Sea, J. Mar. Res., 60, 537-549, http://dx.doi.org/10.1357/002224002762324202.

Holland, W.C., Litaker, R.W., Tomas, C.R., Kibler, S.R., Place, A.R., Davenport, E.D., Tester, P.A., 2013. Differences in the toxicity of six *Gambierdiscus* (Dinophyceae) species measured using an in vitro human erythrocyte lysis assay. Toxicon 65, 15-33.

Intergovernmental Oceanographic Commission (IOC), 1998. First Meeting of the IOC Working Group on Harmful Algae in the Caribbean and Adjacent Region (IOCARIBE-ANCA) Havana, Cuba 29 June-1 July 1998. Workshop Report No. 150, 70 p.

Kibler, S.R., Litaker, R.W., Holland, W.C., Vandersea, M.W., Tester, P.A., 2012. Growth of eight *Gambierdiscus* (Dinophyceae) species: effects of temperature, salinity and irradiance. Harmful Algae 19, 1-14, http://dx.doi.org/10.1016/j.hal.2012.04.007.

Kibler, S.R., Tester, P.A., Kunkel, K.E., Moore, S.K., Litaker, R.W., 2015. Effects of ocean warming on growth and distribution of dinoflagellates associated with ciguatera fish poisoning in the Caribbean. Ecol. Model. 316, 194-210.

Kretzschmar, A.L., Verma, A., Harwood, D.T., Hoppenrath, M., Murray, S. 2017. Characterization of *Gambierdiscus lapillus* sp. nov. (Gonyaulacales, Dinophyceae): a new toxic dinoflagellate from the Great Barrier Reef (Australia). J. Phycol. http://dx.doi.org/10.1111/jpy.12496 [Epub].

Ledreux, A., Brand, H., Chinain, M., Dechraoui Bottein, M.-Y., Ramsdell, J.S., 2014. Dynamics of ciguatoxins from *Gambierdiscus polynesiensis* in the benthic herbivore *Mugil cephalus*: Trophic transfer implications. Harmful Algae 39, 165-174.

Lee, Z.P., 2010. Global shallow-water bathymetry from satellite ocean color data. Eos, Vol. 91, No. 46.

Lehane, L., Lewis, R.J., 2000. Ciguatera: recent advances but the risk remains. Int. J. Food Microbiol. 61, 91-125.

Ley-Martínez, T.C., Núnez-Vázquez, E.J., Almazán-Becerril, A., Baron-Campis, S., Ramírez-Camarena, C., Cabellero-Vázquez, J.A., Balart, E.F., 2014. Bioprospección de toxinas tipo ciguatoxinas en peces carnívoros del Caribe Mexicano y aguas adyacentes. Recursos y Medio Ambiente, XXI National Congress of Science and Technology of the Sea, Cozumel.

Litaker, R.W., Vandersea, M.W., Faust, M.A., Kibler, S.R., Chinain, M., Holmes, M.J., Holland, W.C., Tester, P.A., 2009. Taxonomy of *Gambierdiscus* including four new species, Gambierdiscus caribaeus sp. nov., *Gambierdiscus carolinianus* sp. nov., *Gambierdiscus carpenteri* sp. nov. and *Gambierdiscus ruetzleri* sp. nov. (Gonyaulacales, Dinophyceae). Phycologia 48, 344–390.

Litaker, R.W., Vandersea, M.W., Faust, M.A., Kibler, S.R., Nau, A.W., Holland, W.C., Chinain, M., Holmes, M.J., Tester, P.A., 2010. Global distribution of ciguatera causing dinoflagellates in the genus *Gambierdiscus*. Toxicon 56, 711-730, http://dx.doi.org/10.1016/j.toxicon.2010.05.017.

Litaker, R.W., Holland, W.C., Hardison, D. R., Pisapia, F., Hess, P., Kibler, S.R., Tester, P.A. 2017. Ciguatoxicity of *Gambierdiscus* and *Fukuyoa* species from the Caribbean and Gulf of Mexico. Phycologia, In press.

Llewellyn, L.E., 2010. Revisiting the association between sea surface temperature and the epidemiology of fish poisoning in the South Pacific: reassessing the link between ciguatera and climate change. Toxicon 56, 691-697, http://dx.doi.org/10.1016/j.toxicon.2009.08.011.

Lobel, P.S., Anderson, D.M., Durand-Clement, M., 1988. Assessment of ciguatera dinoflagellate populations – sample variability and algal substrate selection. Biol. Bull. 175, 94–101.

Loeffler, C.R., Richlen, M.L., Brandt, M.E., Smith, T.S., 2015. Effects of grazing, nutrients, and depth on the ciguatera-causing dinoflagellate *Gambierdiscus* in the US Virgin Islands. Mar. Ecol. Prog. Ser. 531, 91-104.

Marañón, E., Cermeño, P., López-Sandoval, D.C., Rodríguez-Ramos, T., Sobrino, C., Huete-Ortega, M., María Blanco, J., Rodríguez, J. 2013. Unimodal size scaling of phytoplankton growth and the size dependence of nutrient uptake and use. Ecol. Lett. 16, 371-379.

Mattei, C., Vetter, I., Eisenblätter, A., Krock, B., Ebbecke, M., Desel, H., Zimmermann, K., 2014. Ciguatera fish poisoning: A first epidemic in Germany highlights an increasing risk for European countries. Toxicon 91, 76-83.

Maya Entenza, C.M., Labrador, M.M., Torres, M.M., 2007. Intoxicación por ciguatera. Estudio de 227 pacientes durante el period 1999 al 2005. Rev. Cubana Hig. Epidemiol. 42(2).

Morrison, K., Prieto, P.A., Domínguez, A.S., Waltner-Toews, D., FitzGibbon, J., 2008. Ciguatera fish poisoning in La Habana, Cuba: A study of local social–ecological resilience. Ecohealth 5, 346-359, http://dx.doi.org/10.1007/s10393-008-0188-7.

Morton, S.L., Norris, D.R., Bomber, J.W., 1992. Effect of temperature, salinity and light intensity on the growth and seasonality of toxic dinoflagellates associated with ciguatera. J. Exp. Mar. Biol. Ecol. 157, 79-90, http://dx.doi.org/10.1016/0022-0981(92)90076-M.

Mueller, J.L., Fargion, G.S., 2002. Ocean optics protocols for satellite ocean color sensor validation. SeaWiFS technical report series, Revision 3. Part II, pp. 171-179.

Nascimento, S.M., Melo, G., Salgueiro, F., Dos Santos Diniz, B., Fraga, S., 2015. Morphology of *Gambierdiscus excentricus* (Dinophyceae) with emphasis on sulcal plates. Phycologia 54, 628-639.

Nellis, D.W., Barnard, G.W., 1986. Ciguatera: A legal and social overview. Mar. Fisheries Rev. 48, 1-5.

NU. CEPAL, 2008. Demographic change and its influence on development in Latin America and the Caribbean. United Nations. In: Jaspers-Faijer, D., Schkolnik, S., Saad, P., Miller, T., huenchuan, S. (Eds.), 32nd session of ECLAC, Santo Domingo, Dominican Republic, 09-13 June 2008, Economic Commission for Latin America and the Caribbean (ECLAC), 107 p.

Nugent, R., Seligman, B. 2008. How demographic change affects development. Technical background paper. Demographics and development in the 21st Century initiative. Center for Global Development, Washington, D.C., 24 p. http://www.cgdev.org/doc/Demographic_and_Development/DD_background_12_10_08.PDF (accessed 10 July 2017).

Nurse, L.A., 2011. The implications of global climate change for fisheries management in the Caribbean. Climate and Development 3, 228-241.

Okolodkov, Y.B, Campos-Bautista, G., Gárate-Lizárraga, I., González-González, J.A.G., Hoppenrath, M., Arenas, V., 2007. Seasonal changes of benthic and epiphytic dinoflagellates in the Veracruz reef zone, Gulf of Mexico. Aquat. Microb. Ecol. 47, 223-237.

Okolodkov, Y.B., del Carmen Merino-Virgilio, F., Antolín Aké-Castillo, J., Concepción Aguilar-Trujillo, A., Espinosa-Matías, S., Herrera-Silveira, A., 2014. Seasonal changes in epiphytic dinoflagellate assemblages near the northern coast of the Yucatan Peninsula, Gulf of Mexico. Acta Bot. Mex. 107, 121-151.

Olsen, D.A., Nellis, D.W., Wood, R.S., 1983. Ciguatera in the eastern Caribbean. Mar. Fisheries Rev. 46, 13-18.

PO.DAAC, 2016. Sea surface Salinity. The Physical Oceanography Distributed Active Archive Center (PO.DAAC), NASA Jet Propulsion Laboratory, California Institute of Technology, Paseadena, California. https://podaac.jpl.nasa.gov/SeaSurfaceSalinity (accessed 12.10.16).

Prado, A., 2013. Economic and social overview of Latin America and Caribbean. Meeting of the Regional Coordination Mechanism for Latin America and the Caribbean - Santiago, 24 January 2013.

Radke, E.G., (Ph.D. dissertation) 2013. Incidence and risk factors of ciguatera fish poisoning in the Caribbean and Florida. University of Florida, Gainesville, FL.

Radke, E.G., Grattan, L.M., Cook, R.L., Smith, T.B., Anderson, D.M., Morris Jr., J.G., 2013.Ciguatera incidence in the U.S. Virgin Islands has not increased over a 30-yeartime period despite rising seawater temperatures. Am. J. Trop. Med. Hyg. 88, 908-913, http://dx.doi.org/10.4269/ajtmh.12-0676.

Radke, E.G., Reich, A., Morris Jr., J.G., 2015. Epidemiology of ciguatera in Florida. Am. J. Trop. Med. Hyg. 93, 425-432.

Randall, J.E., 1958. A review of ciguatera, tropical fish poisoning, with a tentative explanation of its cause. Bull. Mar. Sci. 8, 236-267.

Reynolds, R.W., Zhang, H.-M., Smith, T.M., Gentemann, C.L., Wentz, F., 2005. Impacts of *in situ* and additional satellite data on the accuracy of a sea surface temperature analysis for climate. Int. J. Climatol. 25, 857-864.

Richlen, M.L., Lobel, P.S., 2011. Effects of depth, habitat, and water motion on the abundance and distribution of ciguatera dinoflagellates at Johnston Atoll, Pacific Ocean. Mar. Ecol. Prog. Ser. 421, 51-66.

Rodríguez-Acosta, A., Girón, M.E., Aguilar, I., 1997. Ciguatera: Epidemiología y clínica en referencia a u brote de casos humanos en Venezuela. Arch. Venez. Med. Trop. 1(10), Jun 1997.

Rodríguez-Olarte, D., Mojica Corzo, J.I., Taphorn Baechle, D.C., 2011. Fifteen. Northern South America: Magdalena and Maracaibo basins. In: Albert, J.S., Reis, R. (Eds.), Historical Biogeography of Neotropical Freshwater Fishes, University of California Press, pp 243-257.

Ryther, J.H., 1956. Photosynthesis in the Ocean as a function of light intensity. Limnol. Oceanogr. 1, 61-70.

Sassner, J., 2015. Algae Patrol: Documenting a changing community. Holiday 2015 issue, North Carolina Sea Grant https://ncseagrant.ncsu.edu/coastwatch/previous-issues/2015-2/holiday-2015/algae-patrol-documenting-a-changing-community/ (accessed 04 October 2016).

Sebastián Celis, J.S., Mancera Pineda, J.E.M., 2015. Análysis histórico de la incidencia de ciguatera en las Islas del Caribe durante 31 años: 1980-2010. Biol. Invest. Mar. Cost. 44(1), 7-32.

Sheng, J., Tang, L., 2003. A numerical study of circulation in the western Caribbean. J. Geophys. Res. 33, 2049-2069.

Silva, M., Rodriguez, I., Barreiro, A., Kaufmann, M., Isabel Neto, A., Hassouani, M., Sabour, B., Alfanso, A., Botana, L.M., Vasconcelos, V., 2015. First report of ciguatoxins in two starfish species: *Ophidiaster ophidianus* and *Marthasterias glacialis*. Toxins 7, 3740-3757, http://dx.doi.org/10.3390/toxins7093740.

Smit, A.J., Roberts, M., Anderson, R.J., Dufois, F, Dudley, S.F.J., Bornman, T.G., Olbers, J., Bolton, J.J., 2013. A coastal seawater temperature dataset for biogeographical studies: Large biases between *in situ* and remotely-sensed data sets around the coast of South Africa. PLoS ONE 8(12), e81944, http://dx.doi.org/10.1371/journal.pone.0081944.

Smith, K.F., Rhodes, L., Verma, A., Curley, B.G., Harwood, D.T., Kohli, G.S., Solomona, D., Rongo, T., Munday, R., Murray, S.A. 2016. A new *Gambierdiscus* species (Dinophyceae) from Rarotonga, Cook Islands: *Gambierdiscus cheloniae* sp. Nov. Harmful Algae 60, 45-56.

Stevens, K., Irwin, B., Kramer, D., Urquhart, G., 2014. Impact of increasing market access on a tropical small-scale fishery. Mar. Policy 50, 46-52.

Stinn, J.F., de Sylva, D.P., Fleming, L.E., Hack, E., 2000. Geographic information systems and ciguatera fish poisoning in the tropical western Atlantic region. In: Williams R.C., Howie

M.M., Lee C.V., Henriques W.D. (Eds.), Proceedings of the 1998 Geographic Information Systems in Public Health, Third National Conference, San Diego, California, pp. 223-233.

Tawong, W., Yoshimatsu, T., Yamaguchi, H., Adachi, M. 2016. Temperature and salinity effects and toxicity of *Gambierdiscus caribaeus* (Dinophyceae) from Thailand. Phycologia 55, 274-278.

Taylor, F.J.R., 1985. The distribution of the dinoflagellates *Gambierdiscus toxicus* in the eastern Caribbean. In: Gabrie, C., Salvat, B. (Eds.), Proceedings of the 5thInternational Coral Reef Congress, vol. 4. Antenne Museum, EPHE, Tahiti, pp.423-428

Taylor, F.J.R., Gustavson, M.S., 1986. An underwater survey of the organism chiefly responsible for ciguatera fish poisoning in the eastern Caribbean region: the benthic dinoflagellate *Gambierdiscus toxicus*. In: Stefanon, A., Flemming, N.J. (Eds.), Proceedings of 7th International Diving Science Symposium, Padova University, Padova, Italy, pp. 95–111.

Tester, P.A., Feldman, R.L., Nau, A.W., Faust, M.A., Litaker, R.W., 2009. Ciguatera fish poisoning in the Caribbean. Smithsonian Contributions to the Marine Sciences 38, 301-311.

Tester, P.A., Feldman, R.L., Nau, A.W., Kibler, S.R., Litaker, R.W., 2010. Ciguatera fish poisoning and sea surface temperatures in the Caribbean Sea and the West Indies. Toxicon 56, 698-710, http://dx.doi.org/10.1016/j.toxicon.2010.02.026.

Tester, P.A., Vandersea, M.W., Buckel, C.A., Kibler, S.R., Holland, W.C., Davenport, E.D., Clark, R.D., Edwards, K.F., Taylor, J.C., Vander Pluym, J.L., Hickerson, E.L., Litaker, R.W., 2013. *Gambierdiscus* (Dinophyceae) species diversity in the Flower Garden Banks National Marine Sanctuary, Northern Gulf of Mexico, USA. Harmful Algae 29, 1-9, http://dx.doi.org/10.1016/j.hal.2013.07.001.

Tester, P.A., Kibler, S.R., Holland, W.C., Usup, G., Vandersea, M.W., Leaw, C.P., Teen, L.P., Larsen, J., Mohammad-Noor, N., Faust, M.A., Litaker, R.W., 2014. Sampling harmful benthic dinoflagellates: comparison of artificial and natural substrate methods. Harmful Algae 39, 8-25, http://dx.doi.org/10.1016/j.hal.2014.06.009.

Tindall, D.R., Morton, S.L., 1998. Community dynamics and physiology of epiphytic/benthic dinoflagellates associated with ciguatera. In: Anderson, D.A., Cembella, A.D., Hallegraeff, G.M. (Eds.), Physiological Ecology of Harmful Algal Blooms. Springer-Verlag, Berlin, pp. 293-313.

Tosteson, T.R., 2004. Caribbean ciguatera: a changing paradigm. Rev. Biol. Trop. 52, 109-113.

Trumble, R.J., Olsen, D., Cummings, N., 2006. A pilot program to assess methods of collecting by catch, discard, and biological data in the commercial fisheries of St. Thomas, U.S. Caribbean. CRP Contract No. NA05NMF4540042, 63 p. with appendices. http://sedarweb.org/s30rd01-pilot-program-assess-methods-collecting-bycatch-discard-and-biological-data-commercial (accessed 01.12.16).

Vandersea, M.W., Kibler, S.R., Holland, W.C., Tester, P.A., Schultz, T.F., Faust, M.A., Holmes, M.J., Chinain, M., Litaker, R.W., 2012. Development of semi-quantitative PCR assays for the detection and enumeration of *Gambierdiscus* species (Gonyaulacales, Dinophyceae). J. Phycol. 48, 902-915, http://dx.doi.org/10.1111/j.1529-8817.2012.01146.x.

Villareal, T.A., Moore, C., Stribling, P., Van Dolah, F., Luber, G., Wenck, M.A., 2006. Ciguatera fish poisoning – Texas, 1998, and South Carolina, 2004. Morb. Mortal. Wkly. Rep. (MMWR) 55(34), 935-937.

Villareal, T.A., Hanson, S., Qualia, S., Jester, E.L.E., Granade, H.R., Dickey, R.W., 2007. Petroleum production platforms as sites for the expansion of ciguatera in the northwestern Gulf of Mexico. Harmful Algae 6, 253-259.

Wang, M.H., Son, S.H., Harding Jr., L.W., 2009. Retrieval of diffuse attenuation coefficient in the Chesapeake Bay and turbid ocean regions for satellite ocean color applications. J. Geophys. Res., 114, C10011.

Weil, E., 2003. The corals and coral reefs of Venezuela. In: Cortés, E. (Ed.), Latin American Coral Reefs, Elsevier Science B.V., Amsterdam, pp. 9-52.

Wenck, M.A., Moore, C.J., 2015. Ciguatera fish poisoning from fish caught off the coast of South Carolina. EpiNotes Disease Prevention and Epidemiology Newsletter 25(6), 5-8, http://www.scdhec.gov/Health/docs/EpiNotes%20Spring%202006%20Edition.pdf (accessed 20.10.16).

Werdell, P.J., Bailey, S.W., 2005. An improved bio-optical data set for ocean color algorithm development and satellite data product variation. Remote Sens. Environ., 98, 122-140.

Woodley, J.D., De Meyer, K., Bush, P., Ebanks-Petrie, G., Garzon-Ferreira, J., Klein, E., Pors, L.P.J.J., Wilson, C.M., 1997. Status of coral reefs in the south central Caribbean. In: Lessios, H.A., Macintyre, I.G. (Eds.), Proceedings of the 8th International Coral Reef Symposium, Panama City, Panama June 24-29, 1996, Vol. 1, Smithsonian Tropical Research Institute, Panama, pp. 357-362.

Xu, Y., Richlen, M.L., Liefer, J.D., Robertson, A., Kulis, D., Smith, T.B., Parsons, M.L., Anderson, D.M., 2016. Influence of environmental variables on *Gambierdiscus* spp. (Dinophyceae) growth and distribution. PLoS ONE 11(4), e0153197, http://dx.doi.org/10.1371/journal.pone.0153197.

Yang, Z., Luo, Q., Liang, Y., Mazumder, A. 2016. Processes and pathways of ciguatoxin in aquatic foodwebs and fish poisoning of seafood consumers. Environ. Rev. 24(2), 144-150, http://dx.doi.org/10.1139/er-2015-0054.

Figure Captions

Fig. 1. Maps of A. The study area in the Greater Caribbean Region (GCR), including the southeast coast of the United States, Gulf of Mexico, Caribbean Sea, Greater and Lesser Antilles, and portions of the western tropical Atlantic. Abbreviations: NC, North Carolina, SC, South Carolina, FL, Florida, B. Sub-regions used to project bottom temperatures: South Atlantic Bight (SAB), Western Tropical Atlantic (WTA), Eastern Gulf of Mexico (EGOM), Western Gulf of Mexico (WGOM), and the Yucatan (YUC), Colombian (COL) and Venezuelan Basins (VEN) (see Table 2, section 2.2 for details), C. Representative locations where *in situ* profile data were used to validate projected bottom temperatures (see Table 3, Fig. 3, section 2.5 for details).

Fig. 2. Conceptual diagram. Model components including daily MODIS sea surface temperature data used to generate corrected monthly composites, use of fitted vertical profile date to project bottom temperatures in seven sub-regions, assembly of projections into monthly bottom temperature composites, use of experimental temperature vs. growth models to calculate projected growth rates for five species of dinoflagellates associated with ciguatera fish poisoning (CFP) in the Greater Caribbean Region (GCR). See methods for details. Abbreviations: T, Temperature, SST, Sea Surface Temperature.

Fig. 3. Projected bottom temperature validation. Mean *in situ* water temperatures vs. Mean projected bottom temperatures ± Std for seven representative locations in the Greater Caribbean Region (GCR): A. the NSC Shelf (shelf of North and South Carolina, U.S.A.), B. the Flower Garden Banks National Marine Sanctuary (FGBNMS), C. South Florida, D. Campeche Bank, E. the Virgin Islands Shelf (VI Shelf), F. the Southeast Antilles, and G. the Nicaragua Rise. Mean

depth indicates average maximum growth depth (≥1% surface PAR). See Table 3, Fig. 1C and section 2.5 for details.

Fig. 4. Projected growth rates. Average monthly potential growth rate (div mo^{-1}) for five species of dinoflagellates during 2003-2013. A. *G. belizeanus*, B. *G. caribaeus*, C. *G. carolinianus*, D. *Gambierdiscus* ribotype 2, E. *Fukuyoa ruetzleri*.

Fig. 5. Interspecific vs interannual variation. Comparison of interspecific and interannual variability in projected average division rates (div mo^{-1}) for ciguatera fish poisoning (CFP)-associated dinoflagellates. A. Variability in annual division rate among five *Gambierdiscus* and *Fukuyoa* species during representative year 2010. B. Interannual variability in average division rate for *Gambierdiscus caribaeus*, a representative species. Note different color scale.

Fig. 6. Yearly bottom temperature and growth rates. Variability in average annual projected bottom temperature (°C) and composite dinoflagellate growth rate (div mo^{-1}) at seven representative location in the Greater Caribbean Region (GCR). Locations correspond to validation areas in the GCR, The North and South Carolina shelf (NCS), Southern Florida (S Florida), the Flower Garden Banks National Marine Sanctuary (FGBNMS), the Virgin Islands (VI) shelf, Campeche Bank (Campeche), the Nicaragua rise (Nicaragua), and the southeast (SE) Antilles. See Table 3 for details.

Fig. 7. Projected growth of ciguatera fish poisoning (CFP)-associated dinoflagellates vs. Ciguatera incidence: A. 2003-2013 Average projected division rate (div mo^{-1}) for *Gambierdiscus*

species composite, B. CFP incidences compiled from survey data and literature reports by Tester et al. (2010), Sebastián Celis and Mancera Pineda (2015), and Radke (2013).

Table Captions

Figure S1. Growth rate (μ, d^{-1}) vs. temperature (T, °C) relationships for Caribbean *Gambierdiscus* and *Fukuyoa* species: A. *G. belizeanus*, B. *G. caribaeus*, C. *G. carolinianus*, D. *Gambierdiscus* ribotype 2, E. *Fukuyoa ruetzleri*, and F. composite growth curve constructed by combining data from all five dinoflagellates. Solid lines represent 3rd or 4th order polynomial curves fitted to the data (see Table 4) and the broken lines denote upper and lower 95% confidence intervals. The regression coefficient (r^2) and p-values are shown. Panels A through E from Kibler et al. (2015).

Table 1. Buoy locations for *in situ* data used to correct pixels in the daily SST imagery. Data from each buoy were downloaded from the National Data Buoy Center website (www.ndbc.noaa.gov) maintained by the National Oceanic and Atmospheric Administration (NOAA). See locations in Fig. 3B.

Table 2. Summary information for sub-regions used to project bottom temperature and dinoflagellate growth in the Greater Caribbean Region (GCR; Fig. 1B). Mean Growth Depth denotes the pixel depth within each region after light ($MASK_{Light}$) and depth ($MASK_{Bath}$) masks were applied (see section 2.3 and 2.4). Mean Bottom Temperatures and standard deviations (Std)

were projected by fitting *in situ* vertical profile temperature data to a sigmoid equation (see section 2.2). n denotes the number of in situ profiles for each region.

Table 3. Validation areas where *in situ* temperature profiles were collated for projection of bottom temperatures. Latitude and longitude describe boundaries of each area; n denotes the number of temperature profiles available; Mean Depth denotes the average maximum growth depth (≥1% surface PAR; see section 2.3 and 2.4); BT minimum and maximum projected bottom temperature (°C) in each area. Abbreviations: NSC Shelf, North and South Carolina Shelf; FGBNMS, Flower Garden Banks National Marine Sanctuary; VI Shelf, Virgin Islands Shelf; SE Antilles, Southeast Antilles. See Fig. 1C and Fig. 3 for details.

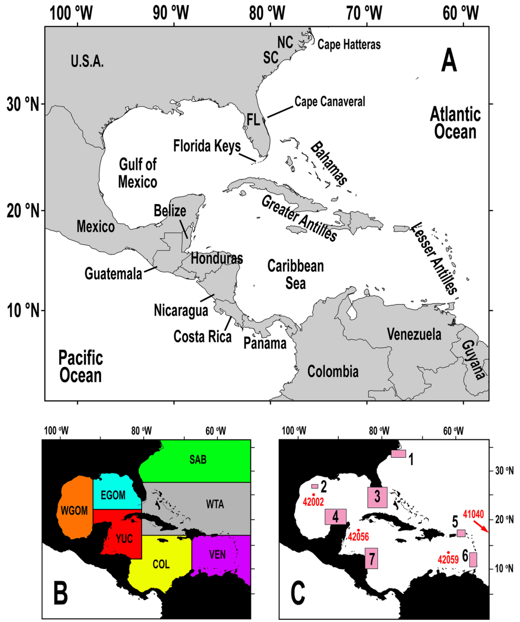
Table 4. Comparison of 2007-2013 satellite (SST), random estimate (random), and *in situ* sea surface temperature data (˚C) at four data buoy sites located in A. the western Gulf of Mexico (NDBC Station 41040), B. the western tropical Atlantic (NDBC Station 42059), C. the Yucatan Basin (NDBC Station 42056) and D. the eastern Caribbean Sea (NDBC Station 42002). Shown are the median, range and statistical test results for Mann-Whitney Rank Sum Test (T statistic) or Kruskal-Wallis nonparametric ANOVA (H statistic).*Denotes statistical significance ($\alpha = 0.05$). See Table 1, Fig. 1C and section 3.1 for details.

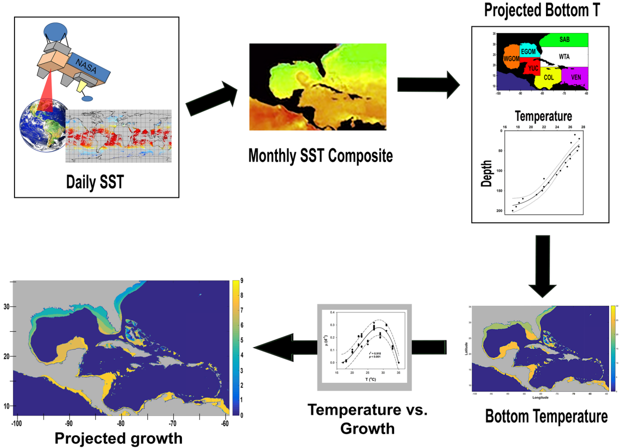
Table 5. Ciguatera fish poisoning (CFP) incidence rates (per 100,000) and mean projected growth rate (Div. mo^{-1}) for the *Gambierdiscus* species composite. Data were collated from the shelf areas (≤ 200 m) surrounding 29 nations in the Greater Caribbean Region (28 nations & S. Florida, USA) represent average incidences from data reported by: [1]Tester et al. (2010),

[2]Sebastián Celis and Mancera Pineda (2015) and [3]Radke et al. (2013). When possible, incidence data from only the most recent time periods were included. See Table S2 for all months.

Table S1. Polynomial growth vs. temperature equations for *Gambierdiscus* and *Fukuyoa* species as reported in Kibler et al. (2015). See Fig. S1 for fitted curves.

Table S2. Average monthly projected growth rates (Div. mo^{-1}) during 2003 – 2013 for shelf areas (≤ 200 m) surrounding 29 nations (28 nations + S. Florida, USA). Mean denotes 2003 - 2013 average.


100 °W
90 °W
80 °W
70 °W
60 °W
30 °N
20 °N
10 °N
A
U.S.A.
NC
SC
Cape Hatteras
Cape Canaveral
FL
Atlantic Ocean
Florida Keys
Gulf of Mexico
Bahamas
Belize
Greater Antilles
Lesser Antilles
Mexico
Honduras
Guatemala
Caribbean Sea
Nicaragua
Costa Rica
Panama
Venezuela
Guyana
Colombia
Pacific Ocean
B
100 °W
80 °W
60 °W
SAB
EGOM
WGOM
WTA
YUC
COL
VEN
C
100 °W
80 °W
60 °W
30 °N
20 °N
10 °N
1
2
42002
3
4
42056
5
41040
6
42059
7



Daily SST

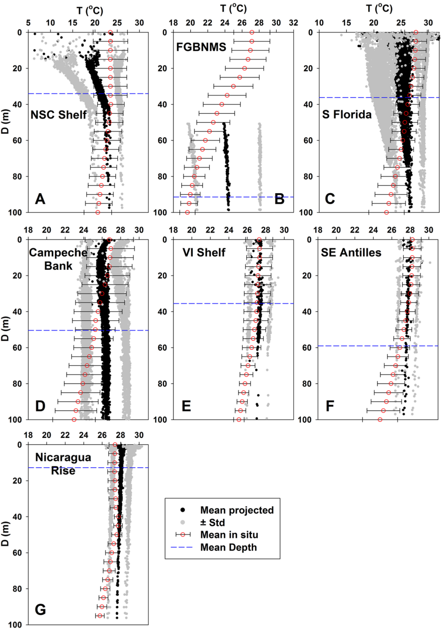
Monthly SST Composite

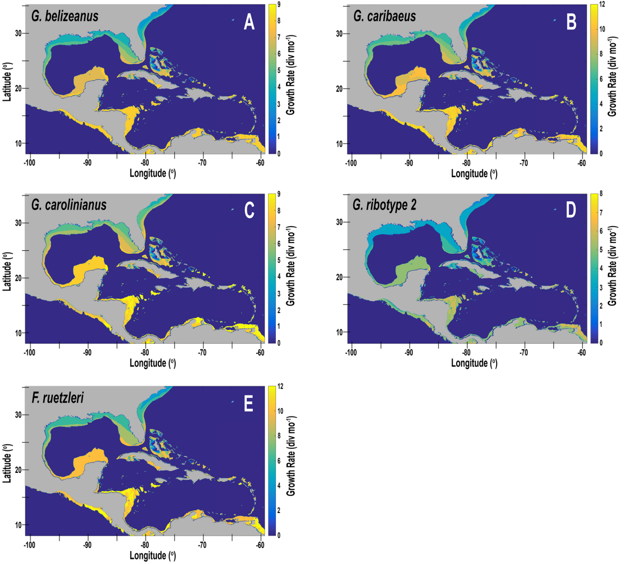
Projected Bottom T

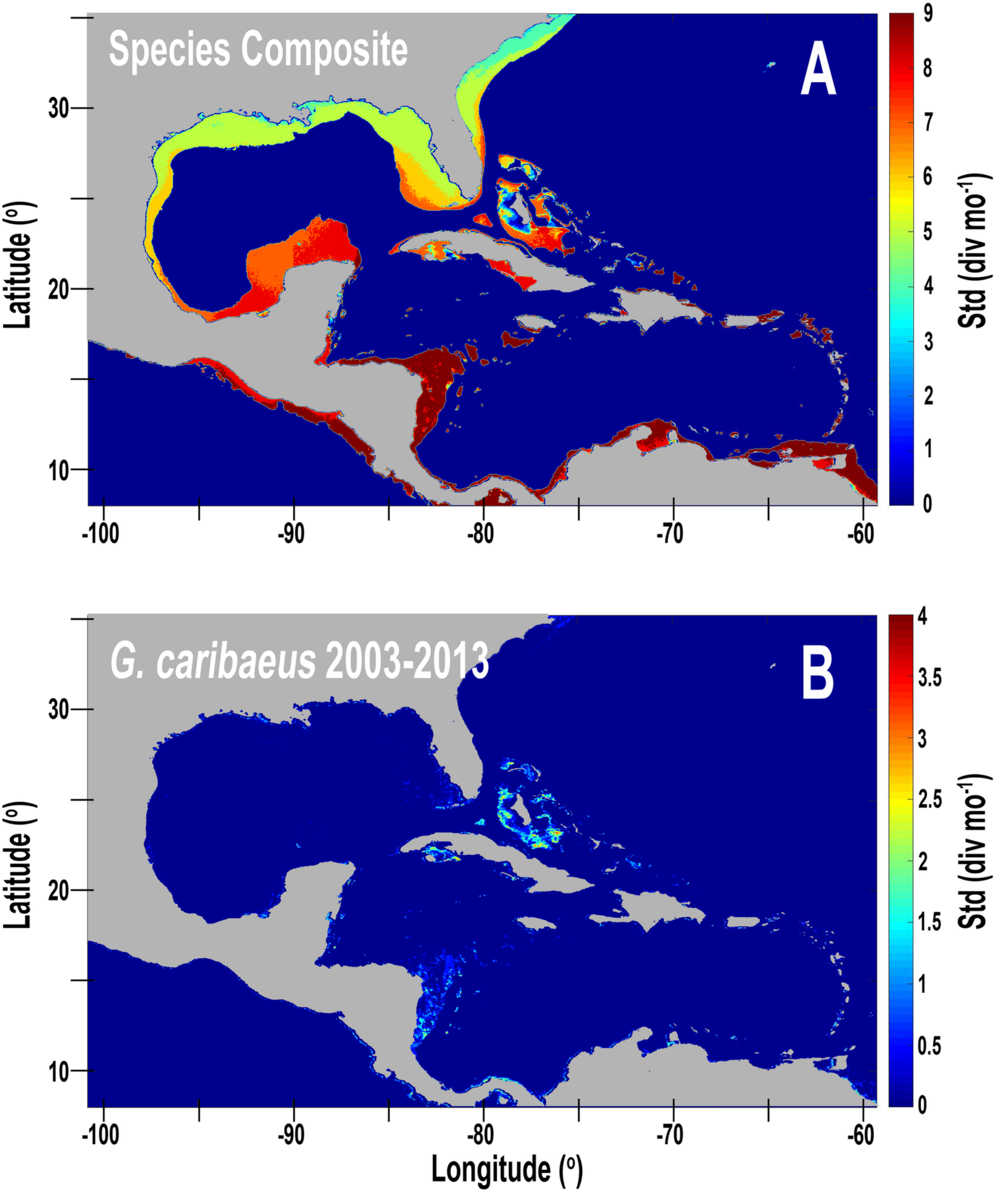
Bottom Temperature

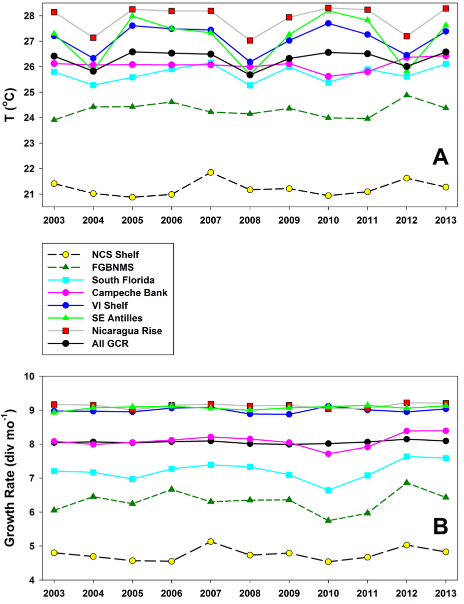
Temperature vs. Growth

Projected growth


T (^{o}C)
5 10 15 20 25 30
18 20 22 24 26 28 30 32
10 15 20 25 30
D (m)
0 20 40 60 80 100
NSC Shelf
A
FGBNMS
B
S Florida
C
18 20 22 24 26 28 30
Campeche Bank
D
VI Shelf
E
SE Antilles
F
Nicaragua Rise
G
Mean projected
± Std
Mean in situ
Mean Depth


G. belizeanus
A
G. caribaeus
B
G. carolinianus
C
G. ribotype 2
D
F. ruetzleri
E
Latitude (°)
30
20
10
Longitude (°)
-100
-90
-80
-70
-60
Growth Rate (div mo⁻¹)
0
1
2
3
4
5
6
7
8
9
10
12


Species Composite
A
Latitude (°)
30
20
10
-100
-90
-80
-70
-60
Std (div mo^{-1})
9
8
7
6
5
4
3
2
1
0
G. caribaeus 2003-2013
B
Latitude (°)
30
20
10
-100
-90
-80
-70
-60
Longitude (°)
Std (div mo^{-1})
4
3.5
3
2.5
2
1.5
1
0.5
0


T (°C)
28
27
26
25
24
23
22
21
A
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
NCS Shelf
FGBNMS
South Florida
Campeche Bank
VI Shelf
SE Antilles
Nicaragua Rise
All GCR
Growth Rate (div mo⁻¹)
10
9
8
7
6
5
4
B
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013

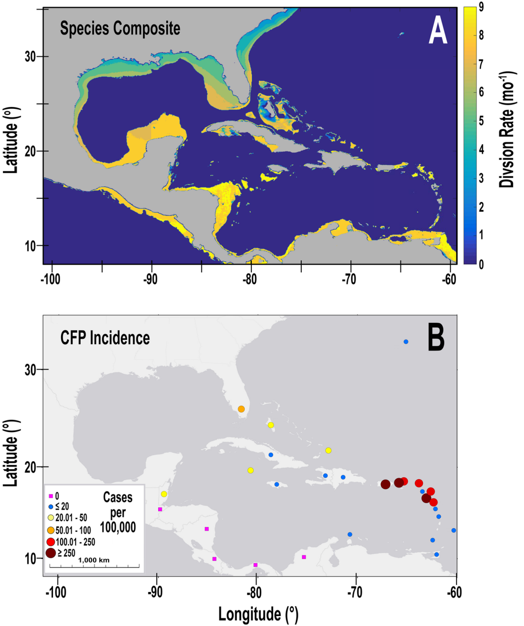

Species Composite
A
Latitude (°)
30
20
10
-100
-90
-80
-70
-60
Divsion Rate (mo⁻¹)
9
8
7
6
5
4
3
2
1
0
CFP Incidence
B
Latitude (°)
30
20
10
0
≤ 20
20.01 - 50
50.01 - 100
100.01 - 250
≥ 250
Cases per 100,000
1,000 km
-100
-90
-80
-70
-60
Longitude (°)

Table 1. Buoy locations for *in situ* data used to correct pixels in the daily SST imagery. Data from each buoy were downloaded from the National Data Buoy Center website (www.ndbc.noaa.gov) maintained by the National Oceanic and Atmospheric Administration (NOAA). See locations in Fig. 3B.

NDBC Station No.	Latitude °N	Longitude °W	Station Depth (m)	Location	Span
41040	14.516	53.024	4900	East of Martinique	2005-2013
42059	15.179	67.563	4804	Eastern Caribbean Sea	2007-2013
42056	19.802	84.857	4684	Yucatan Basin	2005-2013
42002	26.086	93.777	3125	W Gulf of Mexico	1973-2013

Table 2. Summary information for sub-regions used to project bottom temperature and dinoflagellate growth in the Greater Caribbean Region (GCR; Fig. 1B). Mean Growth Depth denotes the pixel depth within each region after light ($MASK_{Light}$) and depth ($MASK_{Bath}$) masks were applied (see section 2.3 and 2.4). Mean Bottom Temperatures and standard deviations (Std) were projected by fitting *in situ* vertical profile temperature data to a sigmoid equation (see section 2.2). n denotes the number of in situ profiles for each region.

Sub-Region	**Latitude Range (°N)**	**Longitude Range (°W)**	**n**	**Mean Growth Depth**	**Mean Bottom Temperature (°C)**
South Atlantic Bight (SAB)	28.47 - 35.22	59.22 - 100.82	844	32.36	22.68 ± 0.82
Western Tropical Atlantic (WTA)	18.51 - 28.43	59.22 - 81.02	595	29.78	26.97 ± 0.87
Eastern Gulf of Mexico (EGOM)	23.01 - 39.98	81.02 - 89.98	21,735	55.43	24.85 ± 1.16
Western Gulf of Mexico (WGOM)	18.01 - 39.98	90.02 - 100.82	2,894	44.64	24.74 ± 1.37
Yucatan Basin (YUC)	8.00 - 22.97	81.02 - 100.82	2,063	37.76	27.68 ± 1.75
Colombian Basin (COL)	8.00 - 22.97	71.52 - 81.02	89	25.49	27.07 ± 2.38
Venezuelan Basin (VEN)	8.00 - 22.97	59.22 - 71.52	143	47.90	27.40 ± 1.53

Table 3. Validation areas where *in situ* temperature profiles were collated for projection of bottom temperatures. Latitude and longitude describe boundaries of each area; n denotes the number of temperature profiles available; Mean Depth denotes the average maximum growth depth (≥1% surface PAR; see section 2.3 and 2.4); BT minimum and maximum projected bottom temperature (°C) in each area. Abbreviations: NSC Shelf, North and South Carolina Shelf; FGBNMS, Flower Garden Banks National Marine Sanctuary; VI Shelf, Virgin Islands Shelf; SE Antilles, Southeast Antilles. See Fig. 1C and Fig. 3 for details.

Location	**Latitude Range (°N) upper lower**	**Longitude Range (°W) upper lower**	**n**	**Mean Depth**	**BT (°C) min max**	**Notes**
1. NSC Shelf	33.75 34.75	75.50 78.00	147	34.1	14.91 27.99	Shelf along coasts of North and South Carolina, USA
2. FGBNMS	27.80 28.20	93.50 94.40	93	91.4	17.35 30.20	Incl. East Bank, West Bank, Stetson Bank
3. South Florida	24.00 28.00	79.50 83.50	480	36.2	16.64 30.17	Incl. Florida Keys, to Tampa Bay, east & west Florida shelves
4. Campeche Bank	21.00 23.50	87.50 91.50	19	50.4	22.43 29.55	N. Yucatan shelf incl. the Arrecife Alacranes Islands
5. VI Shelf	18.10 18.90	64.10 65.20	101	35.5	24.46 29.81	Incl. U.S. & British Virgin Is., Anegada to St. Croix, Culebra & Vieques
6. SE Antilles	11.75 14.25	60.75 62.00	150	59.0	16.64 30.17	Incl. St. Lucia, St. Vincent & the Grenadines, Grenada
7. Nicaragua Rise	13.50 16.50	82.00 84.00	24	12.8	23.55 30.16	Shelf adjacent to Honduras & Nicaragua

Table 4. Comparison of 2007-2013 satellite (SST), random estimate (random), and *in situ* sea surface temperature data (˚C) at four data buoy sites located in A. the western Gulf of Mexico (NDBC Station 41040), B. the western tropical Atlantic (NDBC Station 42059), C. the Yucatan Basin (NDBC Station 42056) and D. the eastern Caribbean Sea (NDBC Station 42002). Shown are the median, range and statistical test results for Mann-Whitney Rank Sum Test (T statistic) or Kruskal-Wallis nonparametric ANOVA (H statistic).*Denotes statistical significance (α = 0.05). See Table 1, Fig. 1C and section 3.1 for details.

Buoy Station	**Data type**	**Median (°C)**	**Range (°C)**	**Results**
41040	satellite	27.54	22.82 – 31.43	T = 2209655
	random	27.56	2.073 – 31.73	df = 2
	in situ	26.30	20.90 – 30.80	p = 0.885
42059	satellite	27.65	21.95 – 31.11	T = 2093219
	random	27.67	23.73 – 31.73	df = 2
	in situ	28.30	25.30 – 30.60	p = 0.440
42056	satellite	27.79	23.73 - 33.25	T = 2079200
	random	27.91	24.83 – 32.52	df = 2
	in situ	28.30	26.10 – 30.50	p = 0.119
42002	satellite	26.48	19.00 – 32.64	T = 2331740
	random	25.74	19.58 – 32.33	df = 2
	in situ	27.80	25.40 – 29.90	p = 0.012*
All Stations	SST	27.54	19.01 – 33.26	H = 135.03
	random	27.55	19.58 – 32.63	df = 2
	in situ	27.90	20.90 – 30.80	p < 0.001*

Table 5. Ciguatera fish poisoning (CFP) incidence rates (per 100,000) and mean projected growth rate (Div. mo^{-1}) for the *Gambierdiscus* species composite. Data were collated from the shelf areas ($\leq$ 200 m) surrounding 29 nations in the Greater Caribbean Region (28 nations & S. Florida, USA) represent average incidences from data reported by: [1]Tester et al. (2010), [2]Sebastián Celis and Mancera Pineda (2015) and [3]Radke et al. (2013). When possible, incidence data from only the most recent time periods were included. See Table S2 for all months.

Country	CFP Cases per 100,000	Mean September growth rate (Div. mo^{-1})	2003 -2013 Mean growth rate (Div. mo^{-1})
Anguilla [1,2]	99.7	9.0	9.0
Antigua & Barbuda [1,2]	219.4	9.0	9.0
Aruba [1]	16.1	9.1	9.0
Bahamas [1,2]	44.3	8.6	9.0
Barbados [1,2]	2.2	9.0	9.0
Belize [1,2]	0.15	8.2	9.0
Bermuda [1,2]	4.1	8.6	9.0
British Virgin Islands [1,2]	187.7	9.0	8.8
Cayman Islands [1,2]	33.0	8.6	8.1
Colombia (Atlantic) [1]	0.02	8.2	9.0
Costa Rica (Atlantic) [1]	0	8.6	9.1
Cuba [1]	1.7	7.9	9.0
Dominica [1,2]	3.0	9.0	8.7
Dominican Republic [1]	0.5	8.9	9.0
Grenada [1,2]	2.0	8.8	4.5
Guadeloupe [1,3]	227.2	9.0	9.1
Guatemala (Atlantic) [1]	0	7.5	8.7
Haiti [1]	2.0	8.3	9.0
Jamaica [1]	3.8	8.7	9.1
Martinique [1]	7.6	8.9	9.1
Monserrat [1,2]	417.3	9.1	9.0
Nicaragua (Atlantic) [1]	0	8.8	9.1
Panama (Atlantic) [1]	0	5.0	5.2
Puerto Rico [1,3]	485.8	8.9	8.4
S Florida[3]	56.0	6.0	7.0
St. Kitts & Nevis [1,2]	14.4	9.0	9.0
Trinidad & Tobago [1,2]	0.02	5.9	8.9
Turks & Caicos [1,2]	23.7	9.0	8.7
U.S. Virgin Islands [1,3]	1258.3	9.0	6.2