

## **Sponge Mortality at Marathon and Long Key, Florida: Patterns of Species Response and Population Recovery**

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### **ABSTRACT**

In the early 1990s, widespread sponge mortality events occurred in the Florida Keys, USA. These mortality events were coincidental with successive blooms of the picoplanktonic cyanobacterium *Synechococcus* sp. Although the specific cause of sponge death remains unknown, we conclude that bloom conditions caused the death of these sponges. We documented the effects of the mortality events on sponge community biomass and followed the sponge population response of 23 species for up to 15 years (1991 - 2006). In doing so, we provide an unprecedented, long-term, and detailed view of sponge population dynamics in the Florida Keys, following a set of environmental conditions that caused widespread mortality. Abundance of many sponge species following the mortality events was dynamic and contrasts with work done on deep-water sponge communities that have shown such communities to be stable over long periods of time. Recovery of the sponge community biomass in the Florida Keys was slow, taking 10 - 15 years. Some species showed consistent long-term trends but many others displayed constantly changing abundance in time and space. We conclude that sponge deaths resulting from relatively infrequent bloom conditions can chronically reduce sponge community biomass and have potentially long-term and widespread ecological consequences. Hurricane Wilma directly hit the study area in 2005, allowing us to also document the effects of a hurricane on sponge populations. Although this hurricane event significantly impacted sponge abundance, in general, massive, long-lived sponges that dominate sponge community biomass in the area tended to be more resistant. Hence, we conclude that sponge community biomass will recover more quickly than following bloom-related mortality events.

KEY WORDS: Algae bloom, cyanobacteria, hurricanes, mortality, Porifera, sponges, sponge population dynamics

## **La Mortalidad de las Esponjas en los Cayos Marathon y Long de la Florida, Estados Unidos: Patrones de la Respuesta de las Especies y de la Recuperación de la Población**

En el comienzo de los 1990s, la mortalidad de las esponjas se propago extensamente en los cayos de la Florida, Estados Unidos. Estos eventos de mortalidad coincidieron con la proliferación de cyanobacteria picoplanctónica *Synechococcus* sp. A pesar de que la causa específica de muerte de las esponjas continua siendo desconocida, concluimos que las condiciones de esta proliferación causaron la muerte de dichas esponjas. Fuimos capaces de documentar los efectos de estos eventos de mortalidad en la biomasa de la comunidad de esponjas y seguir la respuesta de la población de esponjas de 23 especies por hasta quince años (1991-2006). Al hacer esto, proveemos una vista sin precedentes, detallada, y a larga escala de la dinámica de la población de las esponjas en los cayos de la Florida, después de una serie de condiciones medioambientales que propago mortalidad. Abundancia de varias especies de esponjas siguiendo eventos de mortalidad fue dinámica y contrasta con el trabajo realizado en comunidades de esponjas de agua profunda que demuestran que tales comunidades son estables a lo largo de extensos periodos de tiempo. La recuperación de la biomasa de comunidades de esponjas en los cayos de la Florida fue lenta y tomo al menos quince años. Algunas especies demostraron tendencias consistentes a lo largo de periodos extensos de tiempo pero muchas otras demostraron una abundancia de cambios en tiempo y espacio. Concluimos que la muerte de esponjas resultando de una proliferación relativamente inconsistente puede crónicamente reducir biomasa de comunidades de esponjas y tener consecuencias ecológicas potencialmente extensas. En el 2005 el huracán Wilma afecto el área de estudio directamente, dejándonos documentar los efectos de un huracán en la población de esponjas. Aunque este huracán impacto severamente la abundancia de esponjas, en general, las esponjas más grandes y mayores que dominaban el área de la biomasa de la comunidad de esponjas perduraban más. Por lo tanto, concluimos que la biomasa de la comunidad de esponjas se recuperara más rápido en comparación a los eventos de mortalidad relacionados con las proliferaciones.

PALABRAS CLAVE: Proliferación de algas, cyanobacteria, huracanes, mortalidad, Porifera, esponjas, dinámicas de la población de esponjas

## **La Mortalité Éponge dans les Florida Keys, Etats-Unis: Les Modes de Rétablissement des Populations d'Espèces**

MOTS CLÉS: Mortalié éponge, Porifera, modes de rétablissement

## INTRODUCTION

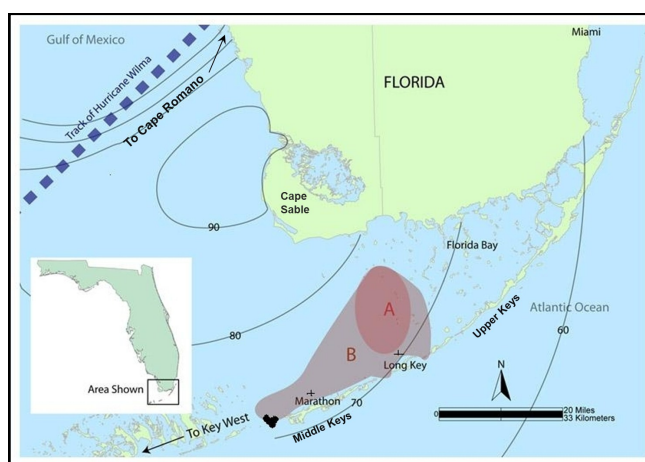
In the early 1990s, sponge populations within hundreds of square kilometers of the shallow lagoonal waters (< 3 m deep) north of the middle and upper Florida Keys were decimated (Figure 1). Circumstantial evidence implies that it was blooms of the picoplanktonic cyanobacterium *Synechococcus* sp. that caused widespread sponge mortality because sponge mortality events were coincidental with *Synechococcus* blooms that occurred sporadically between November 1991 and 1995 (Butler et al. 1995, Stevely and Sweat 1995). Two major bloom events occurred. The initial bloom extended from mid-November 1991 until February 1992, when cyanobacteria cell densities reached  $10^9$  cells/L, compared with less than  $10^4$  cells/L outside the bloom (Butler, et al. 1995). Butler et al. (1995) reported that over 80% of several sponge species and more than 40% of the loggerhead sponges (*Spherospongia vesparium*) at one study site were killed. They documented that, later, a total of 71% of sponges located near the center of the bloom were dead, whereas only 5% were damaged near the periphery of the bloom. The second, larger, more persistent bloom occurred from October 1992 until May 1993. This bloom developed in north central Florida Bay but its subsequent position was dynamic and at times extended south along the Florida Keys. Additional sponge deaths were reported at locations that were exposed to bloom waters (Butler et al. 1995). Cyanobacteria blooms were observed again in 1994 and 1995. These blooms affected the Long Key area to some degree. By this time, there were no sponges left at Butler's et al.'s (1995) experimental sites. In 1996 and 1997, repeated algal blooms again occurred in the central portion of Florida Bay (Phlips et al. 1999). These may have had some lesser effects at Long Key.

Sponges are a major component of benthic communities in many hard bottom coastal environments, are a particularly dominant structural feature in shallow lagoon hard bottom environments in the Florida Keys (Chiappone and Sullivan 1994, Field and Butler 1994), and are of ecological and economic significance. The affected Florida Keys area is recognized for its importance as a marine nursery (Holmquist et al. 1989, Thayer and Chester 1989), particularly for spiny lobster (*Panulirus argus* Latreille 1804) (Field and Butler 1994, Herrnkind and Butler 1994). Post-larval spiny lobsters often seek shelter under loggerhead sponges (Herrnkind and Butler 1994). The area also supports a significant commercial bath sponge fishery.

Although sponges frequently dominate the faunal assemblages inhabiting hard substratum habitats in tropical, temperate, and polar regions, they are rarely a major component of long-term benthic monitoring programs because accurate biodiversity estimates are difficult to obtain (Bell et al. 2006, Carbollo et al. 2008). Just prior to the first sponge mortality event, Stevely et al. (2010) completed an inventory of the sponge community

abundance and biomass in the bloom-affected area, providing the base-line data for the present study.

In response to the widespread sponge deaths subsequent to Stevely et al.'s (2010) sponge community survey, we extended the study to monitor the recovery of populations of specific species until 2006. After the 2005 survey work was completed, Hurricane Wilma brought hurricane-force winds throughout the study area. The co-occurrence of Hurricane Wilma in the study area allowed us to also provide insight into how hurricanes affect sponge population dynamics in our study area. Thus, here we provide a unique, long-term, detailed view of sponge population dynamics following a set of environmental and meteorological conditions that have caused widespread mortality in the Florida Keys.



**Figure 1.** Location of study sites, spatial extent of cyanobacteria blooms (adapted from Butler *et al.* 1995), and track of hurricane Wilma. Water mass A represents the approximate boundaries of the November 1991 to January 1992 bloom. Water mass B represents the October 1992 to May 1993 bloom. The boundaries of each bloom are approximate because the boundaries were dynamic and continually changing. The extents of maximum sustained winds of Wilma at 1030 UTC October 24, 2005 (contour lines) are from the U.S. National Oceanographic and Atmospheric Administration Hurricane Research Division.

## METHODOLOGY

### Field Methods

Stevely et al. (2010) surveyed 15 sites throughout an area north of the middle and upper Florida Keys and collected data on diversity (number of species), abundance (number of individuals in each species), and volumetric biomass of the majority of sponge species in the communities represented. Two sites on the Gulf of Mexico side of the Florida Keys--offshore from Marathon (Vaca Key) and from Long Key--were chosen for subsequent monitoring, which commenced in 1993 (Figure 1). These two sites represent the greatest degree of geographic separation of the original 15 sites, and Marathon is the most distant site

from the bloom epicenter

Initially, stations at the two sites (Table 1) were determined using LORAN C; but after 1993, the Differential Global Positioning System (DGPS) was used. Latitude/longitude coordinates of stations initially determined using LORAN C were re-recorded using DGPS. This conversion was necessary because of potential discrepancy between the two navigational systems in determining latitude and longitude. Permanent reference marker stakes and lines were established at each station in 1995 to verify that we were indeed sampling the same sites.

The typical shallow lagoonal habitat at Marathon and Long Key consists of low-relief limestone bedrock overlain with a thin veneer of sediment, interspersed with seagrass meadows growing in deeper sand. This habitat is generally populated by a complex assemblage of sponges, octocorals, corals, and macroalgae, including calcareous *Halimeda* spp. and *Penicillus* spp. and red drift algae such as *Laurencia* spp. The methodology we designed for monitoring sponge abundance at the two sites was the same as that used for the other 13 sites surveyed by Stevely et al. (2010). Briefly, at each site, sponge abundance was determined by counting all sponges within twelve 100-m by 2-m transects (200 m<sup>2</sup>). Four transects per dive were conducted and three dives were conducted at each site, so that the total area covered was 2400 m<sup>2</sup>. On one occasion, at Long Key in 1991, equipment failure prevented the completion of the full complement of 12 transects.

Other than in 1992 and 1996, surveys were conducted annually from 1991 to 2006, during a two-week interval sometime between June and August. Bloom conditions caused low visibility and prevented work in 1992 and logistical constraints prevented work in 1996. Following the widespread mortality of sponges after the 1991 survey, our initial objectives--to document commercial bath sponge and total sponge community biomass (Stevely et al. 2010)--were refocused to collect more detailed data on as many species as possible. Hence, we added additional species counts in 1994, 1995, and 1997, as funding allowed. Consequently, we present data on abundance trends of many species for which we do not have baseline pre-mortality data; but based on our personal observations, most, if not all, were present prior to the mortality. In

addition, three sponges--*Amphimedon viridis*, *Petrosia* (*Petrosia*) cf. *pellasarca*, and *Xestospongia subtriangularis*, rare or absent at Marathon between 1991 and 1998, were added later (*A. viridis* in 2002; *P. (P.)* cf. *pellasarca* and *X. subtriangularis* in 2005).

The extremely variable shape of many sponge species precluded the use of linear measurements to reliably determine sponge dimensions and hence volume. Sponge volume was thus determined by measuring the volume of water displaced by an individual, as described in Stevely et al. (2010). Sponge volumetric biomass was determined in 1991, before the sponge mortality event, and in 1993, after the event, allowing us to document both numerical and biomass declines resulting from the mortalities.

The seven sponge species we surveyed in 1991 prior to the mortality were chosen because of their conspicuous size and/or economic importance. The 13 species added to the surveys between 1994 and 1997 were included to develop a more comprehensive understanding of sponge community response following the *Synechococcus* blooms. The three sponges added in 2002 or 2005 were included because of their notable and sudden increase in abundance. These additional species were chosen because they could be easily identified in the field after initial identification in the laboratory and they, too, were conspicuous in size, or were important to the local economy. All species are listed in Table 2.

### Statistical Analysis

To determine if changes in abundance for each species were significant, statistical analyses were conducted using the software statistical package SigmaStat (version 2.0 for Windows 95, Jandel Corporation). Each data set was tested for normal distribution and equality of variance. If both these conditions were met, a T-Test was used to test for a difference between two means and a One Way Analysis of Variance (ANOVA) was used to test for differences among three or more means. When the data set failed the test for either normality of distribution or equality of variance, a Mann-Whitney Rank Sum test was used to test for differences between two medians and a Kruskal-Wallis Analysis of Variance on Ranks was used to test for differences among three or more medians. When sample sizes were equal, Tukey's Test and the less conservative Student-Newman-Kuels test were used to locate the significant differences among means. When sample sizes were unequal, Dunn's All Pairwise Multiple Comparison procedure was used. Unless otherwise noted, the results of the Tukey's Test are presented.

## RESULTS

In our previous study (Stevely et al. 2010), more than 24,000 sponges were recorded from over 3.3 ha of area surveyed. Mean abundance over the 15 sites was 7,200 sponges/hectare (range: 3,171 - 15,200), and the mean biomass for the entire area was 364 ml/m<sup>2</sup> (range: 200 -

**Table 1.** Latitude and longitude of Long Key and Marathon sampling stations in the Florida Keys. Site locations are shown in Figure 1.

Site/station	Latitude	Longitude	Depth (m)
Marathon			
Dive 1	24°46.485	81°03.789	2.7
Dive 2	24°46.465	81°03.751	2.7
Dive 3	24°46.474	81°03.742	2.7
Long Key			
Dive 1	24°51.230	80°48.805	2.5
Dive 2	24°51.241	80°48.791	2.5
Dive 3	24°51.211	80°48.820	2.5

**Table 2.** Sponge species monitored at Marathon and Long Key

Order	Family	Species	
SPIROPHORIDA Bergquist & Hogg, 1969	Tetillidae Sollas, 1886	<i>Cinachyrella alloclada</i> (Uliczka, 1929) <sup>3</sup>	
HADROMERIDA Topsent, 1894	Clionidae d'Orbigny, 1851	<i>Sphaciospongia vesparium</i> (Lamarck, 1815) <sup>1</sup> <i>Cliona varians</i> (Duchassaing and Michelet, 1864) <sup>1,2</sup>	
	Tethyidae Gray, 1848	<i>Tectitethya crypta</i> (de Laubenfels, 1949) <sup>3</sup>	
	Halichondriidae Gray, 1867	<i>Halichondria (Halichondria) melanodocia</i> de Laubenfels, 1936 <sup>3</sup>	
HALICHONDRIIDA Vosmaer, 1887	Chalinidae Gray, 1867	<i>Adocia implexiformis</i> (Hechtel, 1965) <sup>3</sup> <i>Chalinula molitba</i> (de Laubenfels, 1949) <sup>3</sup>	
	Callyspongiidae de Laubenfels, 1936	<i>Callyspongia (Cladochalina) vaginalis</i> (Lamarck, 1814) <sup>3</sup>	
	Niphatidae van Soest, 1980	<i>Amphimedon viridis</i> Duchassaing & Michelotti, 1864 <sup>4</sup> <i>Niphates erecta</i> Duchassaing & Michelotti, 1864 <sup>3</sup>	
		Petrosiidae van Soest, 1980	<i>Xestospongia subtriangularis</i> (Duchassaing, 1850) <sup>4</sup> <i>Petrosia (Petrosia) cf. pellasarca</i> (de Laubenfels, 1934) <sup>4</sup>
	POECILOSCLERIDA Topsent, 1928	Tedaniidae Ridley & Dendy, 1886	<i>Tedania (Tedania) ignis</i> (Duchassaing & Michelotti, 1864) <sup>3</sup>
		Coelosphaeridae Dendy, 1922	<i>Lissodendoryx isodictyalis</i> (Carter, 1882) <sup>3</sup>
	DICTYOCERATIDA Minchin, 1900	Spongiidae Gray, 1867	<i>Spongia (Spongia) barbara</i> Duchassaing & Michelotti, 1864 <sup>1</sup> <i>Spongia barbara dura</i> Hyatt, 1877 <sup>1</sup> <i>Spongia (Spongia) graminea</i> Hyatt, 1877 <sup>1</sup> <i>Hippospongia lachne</i> de Laubenfels, 1936 <sup>1</sup>
Irciniidae Gray, 1867			<i>Ircinia campana</i> (Lamarck, 1814) <sup>1</sup> <i>Ircinia strobilina</i> (Lamarck, 1816) <sup>1</sup> <i>Ircinia felix</i> (Duchassaing & Michelotti, 1864) <sup>1</sup>
			Thorectidae Bergquist, 1978
VERONGIDA Bergquist, 1978		Aplysinidae Carter, 1875	<i>Aplysina fulva</i> (Pallas, 1766) <sup>3</sup>

<sup>1</sup> Monitoring initiated during or prior to 1991.<sup>2</sup> Despite the absence of 1991 and 1993 abundance data for *Cliona varians*, and 1991 abundance data for *Spongia barbara dura*, field observations confirmed their presence at Marathon and Long Key in relatively high numbers, and their subsequent decimation in 1993.<sup>3</sup> Monitoring initiated between 1994 and 1997.<sup>4</sup> - Monitoring initiated 2002 or 2005.

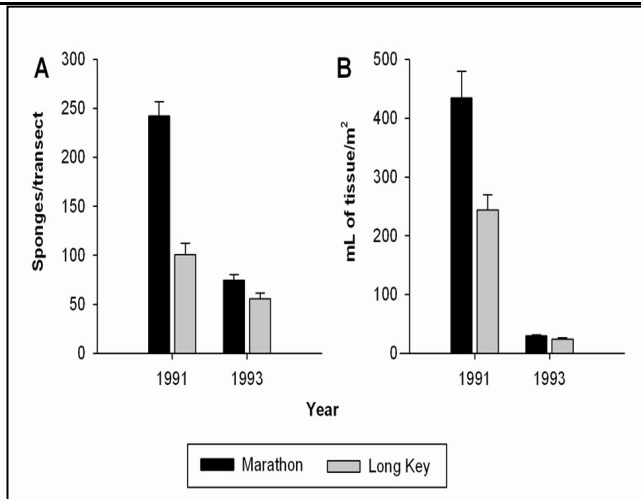
700). The sponge community biomass in the area included in that study was dominated by two large sponge species: *S. vesparium* and *Ircinia campana* (vase sponge).

Two years later, as documented herein, sponge abundance at Marathon and Long Key had declined by 69% and 45%, respectively (Figure 2A). Sponge biomass at Marathon and Long Key had declined remarkably, by 93% and 88%, respectively (Figure 2B). With few exceptions, all of the largest sponges were completely decimated. Together, *S. vesparium* and *I. campana* accounted for 68% of the total sponge community biomass loss between 1991 and 1993.

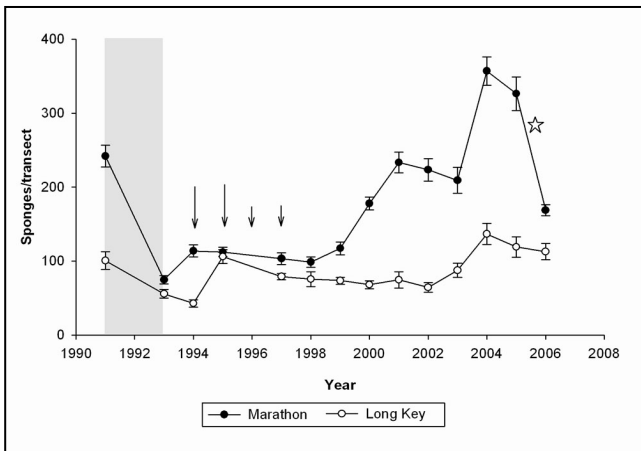
Throughout the present study, total numerical sponge abundance was greater at Marathon than at Long Key (Figure 3). Total abundance at Marathon significantly ( $p < 0.05$ ) decreased between 1991 and 1993. Recovery was

slow; and it was not until 2001 that abundance had increased to the point that it was statistically indistinguishable from the 1991 abundance. Sponge abundance at Marathon peaked in 2004; but then significantly ( $p < 0.05$ ) declined in 2006, following the 2005 hurricane season.

The pattern of sponge mortality and recovery at Long Key was different and less pronounced than the pattern observed at Marathon. Significant declines for several important species, in terms of their contribution to sponge community biomass, were observed. However, overall abundance in 1993 and 1994 did not differ significantly from the 1991 pre-mortality abundance, nor did the hurricanes greatly affect overall abundance. Evidently, the effects of the bloom-induced mortalities were less at Long Key, even though it was closer to the bloom epicenter.



**Figure 2.** Effects of sponge mortality on abundance (A) and biomass (B) at Marathon and Long Key ( $\pm$ S.E. bars).



**Figure 3.** Total sponge abundance at Marathon and Long Key, 1991–2006 (average number/transect  $\pm$  S. E. bars). The shaded area depicts timing of 1991–1993 bloom events at both sites. Large arrows represent timing of bloom events in 1994 and 1995 in the vicinity of Long Key. Smaller arrows represent timing of blooms in Florida Bay that might have affected Long Key area. The star represents the timing of Hurricane Wilma.

**Patterns of Sponge Population Response to Environmental Perturbation**

Five clear patterns of change in abundance were apparent over the study period (Table 3):

- i) Rapid decline in 1993 followed by gradual recovery;
- ii) Fluctuating abundance;
- iii) Gradual decline;
- iv) Low abundance, no change; and
- v) Abrupt increase in abundance after Hurricane Wilma.

The individual pattern of response for each species surveyed is described below. The statistical significances of the observed changes in abundance are summarized in Table 3.

**Table 3.** General patterns of response of sponge species at Marathon and Long Key. SNK:  $P < 0.05$ ; Tukey's:  $P < 0.05$ ; Dunn's:  $P < 0.05$ ; T-Test:  $P < 0.05$ . ns; not significant. Dash: not present in transects at this study site.

General patterns of response	Marathon	Long Key
Rapid decline in 1993 with recovery to 1991 levels		
<i>Spheciospongia vesparium</i>	SNK, Tukey's	Dunn's
<i>Cliona varians</i>	SNK, Tukey's	SNK, Tukey's
<i>Ircinia campana</i>	SNK, Tukey's	Dunn's
<i>Ircinia felix</i>	SNK, Tukey's	SNK, Tukey's
<i>Ircinia strobilina</i>	Tukey's	SNK, Tukey's
<i>Hippospongia lachne</i>	SNK <sup>1</sup>	ns <sup>2</sup>
<i>Spongia (Spongia.)</i>	–	ns <sup>2</sup>
<i>Spongia barbara dura</i>	SNK, Tukey's	SNK, Tukey's
<i>Spongia (Spongia)</i>	SNK, Tukey's	–
Fluctuating abundance		
<i>Cinachyrella alloclada</i>	SNK, Tukey's	SNK, Tukey's
<i>Halichondria (Halichondria) mela-</i>	SNK, Tukey's	SNK, Tukey's
<i>Adocia implexiformis</i>	SNK, Tukey's	ns
<i>Lissodendoryx isodictyalis</i>	SNK, Tukey's	SNK, Tukey's
<i>Chalinula molitba</i>	SNK, Tukey's	Dunn's
<i>Niphates erecta</i>	SNK, Tukey's	SNK, Tukey's
<i>Hyrtios proteus</i>	SNK, Tukey's	ns
<i>Amphimedon viridis</i>	ns <sup>2</sup>	–
<i>Petrosia (Petrosia) cf pellarca</i>	T-test	–
Gradual decline		
<i>Hyrtios proteus</i>	ns	SNK, Tukey's
<i>Adocia implexiformis</i>	–	SNK, Tukey's
<i>Tedania ignis</i>	ns	SNK, Tukey's
Low abundance, no change		
<i>Tectitethya crypta</i>	ns <sup>3</sup>	ns <sup>3</sup>
<i>Tedania ignis</i>	ns <sup>3</sup>	–
<i>Callyspongia vaginalis</i>	ns <sup>2</sup>	–
Abrupt increase after Hurricane Wilma in 2005		
<i>Aplysina fulva</i>	SNK, Tukey's	SNK, Tukey's
<i>Xestospongia subtrian-</i>	T-test	–

<sup>1</sup> Non-significant under Tukey's test.

<sup>2</sup> Kruskal-Wallis test indicated a highly significant difference in the medians but SNK, Tukey's, or Dunn's could not differentiate between the means.

<sup>3</sup> Kruskal-Wallis test did not detect a significant difference among medians.

*Sphaciospongia vesparium* — The loggerhead sponge (Figure 4A, Table 3) is a massive purple to brownish-black, hemispherical sponge that is extremely common in shallow lagoonal hard-bottom communities in and around the Florida Keys (Donahue 2008) and the greater Caribbean region (Wiedenmayer 1977). The aquiferous system of this species provides habitat for a myriad of invertebrates (Pearse 1950; Erdman and Blake 1987), including juvenile spiny lobsters. In 1991, Stevely et al. (2010) found *S. vesparium* to be the most important component of the sponge community in terms of biomass (58%).

In 1993, *S. vesparium* was eliminated from the Marathon site. Recovery was slow until 2000, when significant ( $p < 0.05$ ) recruitment was recorded at Marathon. By 2001, population abundance had statistically recovered to pre-1991 levels. However, the mean diameter of the sponges in 2003 was only 12 cm (range: 4 cm – 23 cm), significantly (T-Test,  $p < 0.001$ ) less than the mean diameter of 27 cm (range: 9 cm – 42 cm) in 1991. Thus, although abundance had recovered by 2003, the biomass still had not recovered, confirming that this species is relatively long-lived and slow growing.

Recovery of *S. vesparium* at Long Key was slower and less pronounced than at Marathon. The principal mode of recovery may have differed between the two study areas. In 1993, the population of *S. vesparium* at Long Key was decimated but not eliminated; two large, irregularly shaped specimens were found within the survey transects area, and several specimens were observed outside the survey transects. [Butler et al. (1995) also observed that localized necrosis in *S. vesparium* resulted in irregularly shaped specimens.] Recovery was very slow and it was not until 13 years later, in 2006, that the mean abundance was significantly (Dunn's method,  $p < 0.05$ ) greater than mean abundance in 1993; but it was still less than that of 1991. Field observations at Long Key suggest that recruitment in the years 1993 through 1999 was via asexual regeneration of remaining specimens, rather than new recruitment via sexual reproduction and larval dispersion. *Sphaciospongia vesparium* can bore into calcareous material, creating chambers and canals (Wiedenmayer 1977) that act as refugia during adverse conditions (Kelly 1986, Kelly-Borges and Bergquist 1988). In 2000, Long Key individuals were, on average, significantly ( $p < 0.001$ ) larger (mean diameter 21.4 cm) than those at Marathon (mean diameter 10.0 cm), suggesting that they had grown from remnant individuals rather than from larvae recruited over time.

In general, *S. vesparium* had greater resistance to the algal blooms than most sponge species. At some locations, *S. vesparium* did not decline after the bloom events, whereas other species such as *I. campana* were eliminated (J. Stevely Unpubl. data). One location was less than 2 km from the Long Key survey site.

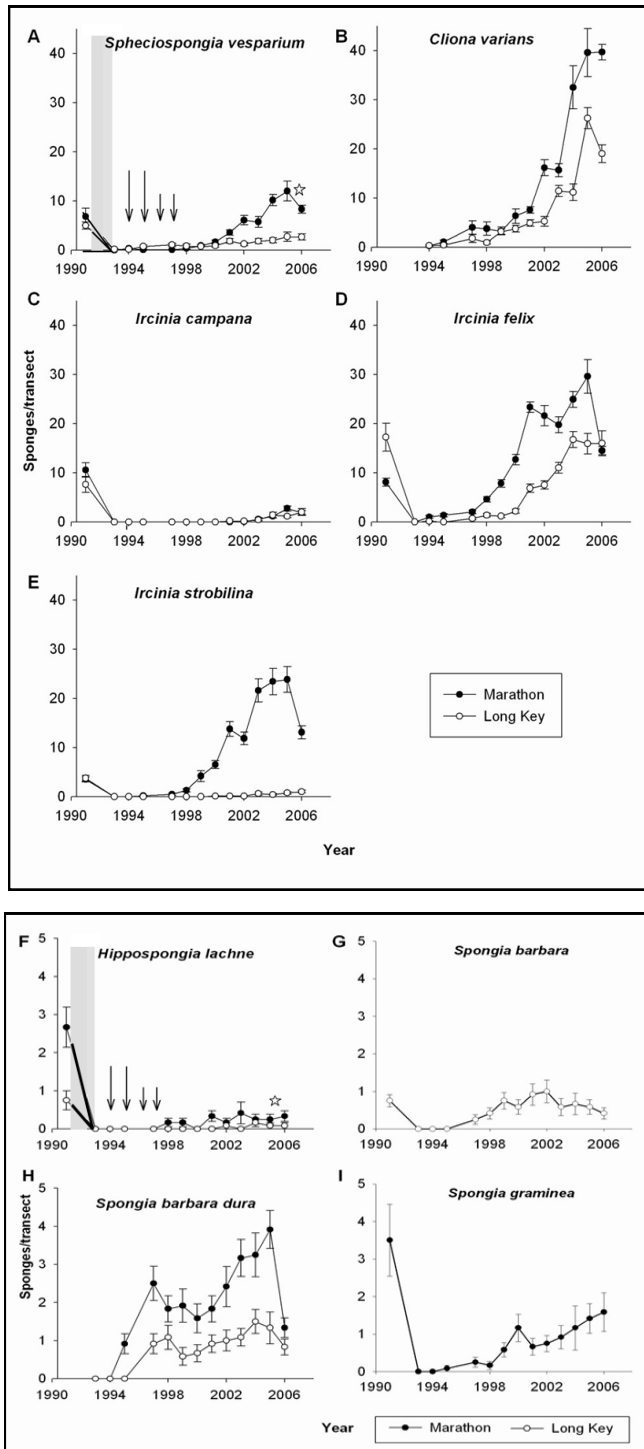
*Cliona varians* — The brown variable sponge previously known as *Anthosigmella varians* (Figure 4B, Table 3), is common throughout Florida and the general Caribbean region. It has a tough consistency that allows it to prevail in shallow habitats with coarse sediment and strong wave action (Rützler 2004). It occurs as very large encrustations in high-energy environments and as a smaller massive form that may be digitate or globular in lower-energy environments (Wiedenmayer 1977, Vincente 1978). Like *S. vesparium*, this species also bores basally into calcareous substrate. It is considered to be an aggressive competitor for substrate (Vincente 1978). *Cliona varians* significantly ( $p < 0.05$ ) increased in abundance throughout the study at both sites from 1994, when its abundance was first recorded.

*Ircinia campana* — (Figure 4C, Table 3) is common in the Florida Keys and is typically a large and easily recognizable, yellowish-brown sponge with a distinctive vase-shaped morphology. It was eliminated at both Marathon and Long Key in 1993. There was no evidence of recruitment at Marathon or Long Key until 2002 and 2003, respectively. Abundance had significantly ( $p < 0.05$ ) increased at Marathon by 2005, but abundance at both sites remained far below levels found in 1991. Mean diameter in 2004 (12.5 cm) was still significantly ( $p < 0.05$ ) smaller than the mean size found in the study area in 1991 (18.2 cm).

*Ircinia felix* — The branching stinker sponge (Figure 4D, Table 3) is a massive, lobate sponge that is typically yellowish-brown with darker oscular linings. In the low-energy environments of the Gulf of Mexico side of the middle to upper Florida Keys, this sponge branches extensively to form a mat. *Ircinia felix* was eliminated at both Marathon and Long Key by 1993, but recovered quickly and significantly ( $P < 0.05$ ) to 1991 levels at both sites. As with the other sponges previously described, recruitment at Long Key lagged behind that at Marathon.

*Ircinia strobilina* — The stinker sponge (Figure 4E, Table 3) is a massive, spherical sponge common throughout the Florida Keys and general Caribbean region. *Ircinia strobilina* was decimated in 1993 at both Marathon and Long Key. Although not very abundant in 1991, recruitment at Marathon was rapid and pronounced; abundance eventually exceeded 1991 levels by almost 7 times. In contrast, at Long Key, recruitment was limited; abundance in 2006 was still significantly ( $p < 0.05$ ) lower than in 1991.

*Hippospongia lachne* — is known locally as the sheepswool or wool sponge (Figure 4F, Table 3). The softness and durability of the fiber skeleton, when prepared as a bath sponge, makes it by far the most valuable Caribbean commercial bath sponge (Storr 1964). *Hippospongia lachne* was eliminated at both sites by 1993.



**Figure 4.** Sponge species exhibiting rapid decline followed by consistent, statistically significant recovery (average number/transsect  $\pm$  S.E. bars). The shaded area (shown on Figures 4A and 4F) depicts timing of 1991 – 1993 bloom events at both sites; large arrows represent timing of bloom events in 1994 and 1995 in the vicinity of Long Key and smaller arrows represent timing of blooms in Florida Bay that might have affected Long Key area. The star represents the timing of Hurricane Wilma.

Recovery of the population was limited; the first appearance of specimens occurred in 1998 and 2002 at Marathon and Long Key, respectively. Due to low abundance and limited recovery, statistical confirmation of recovery was not clearly established (Table 3). We know, however, that wool sponges were being harvested at Channel Key Bank and other locations that had been decimated, thus indicating successful recovery at some locations. Recovery of *H. lachne* to 1991 levels at these other sites was verified by further survey work (J. Stevely Unpubl. data).

*Spongia (S.) barbara* — The yellow sponge (Figure 4G, Table 3), another commercially important bath sponge in the Caribbean region, is characterized by a symmetrical columnar shape and smooth surface. *Spongia (S.) barbara* was not present at Marathon, but was found at Long Key in 1991 at an abundance that could support commercial harvest. It was eliminated from Long Key by 1993. By 1997, recruitment was evident, and between 1999 and 2006 abundance was comparable to that of 1991.

*Spongia barbara dura* — (Figure 4H, Table 3) It is important to note here that differentiation of *Spongia* species can be difficult in the field (Cook and Berquest 2002) and there is confusion regarding the proper taxonomic status of this sponge (Van Soest 1978). However, we were able to differentiate it from other *Spongia* (Stevely et al. 2010). There are no recorded landings of the commercial bath sponge *S. barbara dura* (hardhead sponge) in Florida, because the sponge rarely reaches the minimum legal size in these waters. However, it is occasionally harvested in the Bahamas (J. Stevely Pers. observation). Abundance data for *S. barbara dura* was not collected at Marathon or Long Key in 1991 because it was not considered to be a commercially valuable species (Stevely et al. 2010). Following the mortality events, *S. barbara dura* exhibited rapid recruitment with significant ( $p < 0.05$ ) increase in abundance at both areas. Although the pattern of recruitment at Long Key was very similar to that at Marathon, overall abundance was consistently lower.

*Spongia (S.) graminea* — The glove sponge (Figure 4I, Table 3) is characterized by its massive columnar to sub-conical shape with distinctive ridges on the sides. Although *S. (S.) graminea* is a commercial bath sponge, it is considered to be of inferior quality because of its weak spongin fiber skeleton; and it is infrequently harvested in Florida. *Spongia (S.) graminea* was only present in the Marathon and was eliminated by 1993. Between 1995 and 2006 the population gradually recovered, but abundance in 2006 was still lower than abundance in 1991. Both the decline and the recovery were significant ( $p < 0.05$ ).

*Cinachyrella alloclada* — Orange ball sponge (Figure 5A, Table 3) is a relatively small globular bright orange or yellow sponge, usually covered with sediment. It is characterized by the presence of sunken incurrent porefields (porocalices) and a hairy surface, and is very common in the study area. This sponge exhibited significant ( $p < 0.05$ ) fluctuations in abundance at both Marathon and Long Key over the duration of the study.

*Cinachyrella alloclada* appears to have been relatively resistant to the plankton blooms at both sites; in 1994, it had the highest recorded abundance of all species surveyed, and field observations indicated it was also abundant in 1993 prior to its inclusion in this survey. It remained abundant at Long Key throughout 1994 - 1995, a time when it was likely to have been exposed to bloom waters. However, because we do not have pre-bloom abundance records for *C. alloclada*, strong recruitment in 1993 rather than resistance to the bloom cannot be ruled out. Nevertheless, this species was reported by Peterson et al. (2006) to be a major contributor to sponge community biomass in areas of Florida Bay that were repeatedly exposed to bloom water. Butler (2008) reported that *C. alloclada* was the most resistant sponge during a more recent bloom event. The extremely hirsute surface of this species may aid in deterring the incurrent flow of *Synecococcus* by trapping a layer of sediment, which acts as an additional filtration barrier.

*Halichondria (H.) melanodocia* — (Figure 5B, Table 3) is a small amorphous sponge that is black with greenish yellow tinges. The sponge is soft and easily torn. This species rapidly increased in abundance at Long Key around 1995 but declined significantly ( $p < 0.05$ ) over the next 5 years. In contrast, abundance at Marathon did not change significantly until 2001, when it increased two-fold; after which it declined as well. This “boom and bust” pattern is characteristic of an opportunistic recruitment strategy.

*Adocia implexiformis* — (Figure 5C and 6B, Table 3) forms a lavender tubular mass that easily fragments, and is typically found growing attached to hard substrate and unattached among seagrasses. The species exhibited significant ( $p < 0.05$ ) fluctuations in abundance, exploding to an almost 20 - fold peak at Marathon in 2000. The observed changes in abundance at Marathon were among the most dramatic observed for any species during this study. At Long Key, levels of abundance were quite low compared with those at Marathon, and abundance significantly ( $p < 0.05$ ) decreased over the course of the study. Following the 2005 hurricane season, *A. implexiformis* was mostly absent from both areas.

*Lissodendoryx isodictyalis* — (Figure 5D, Table 3) is typically subspherical, and is characterized by dull yellow coloration and a translucent diaphanous surface. This sponge is frequently loosely attached to sediment in areas with a thin veneer of sediment, but may also occur in

seagrass areas. At Marathon, *L. isodictyalis* abundance increased significantly and then significantly declined ( $p < 0.05$  for both). At Long Key, this species was uncommon, and changes were not significant.

*Chalinula molitba* — (Figure 5E, Table 3) is a small, soft, fragile sponge with a distinctive pale blue to violet coloration. Although typically encrusting with lobes, it was stringy at our study sites. Abundance significantly increased and decreased at both Marathon and Long Key over the course of the study ( $p < 0.05$  for all). The most notable change in abundance was a sharp decline at Long Key between 1995 and 1997. In general, changes in abundance at Long Key were more pronounced than were changes at Marathon.

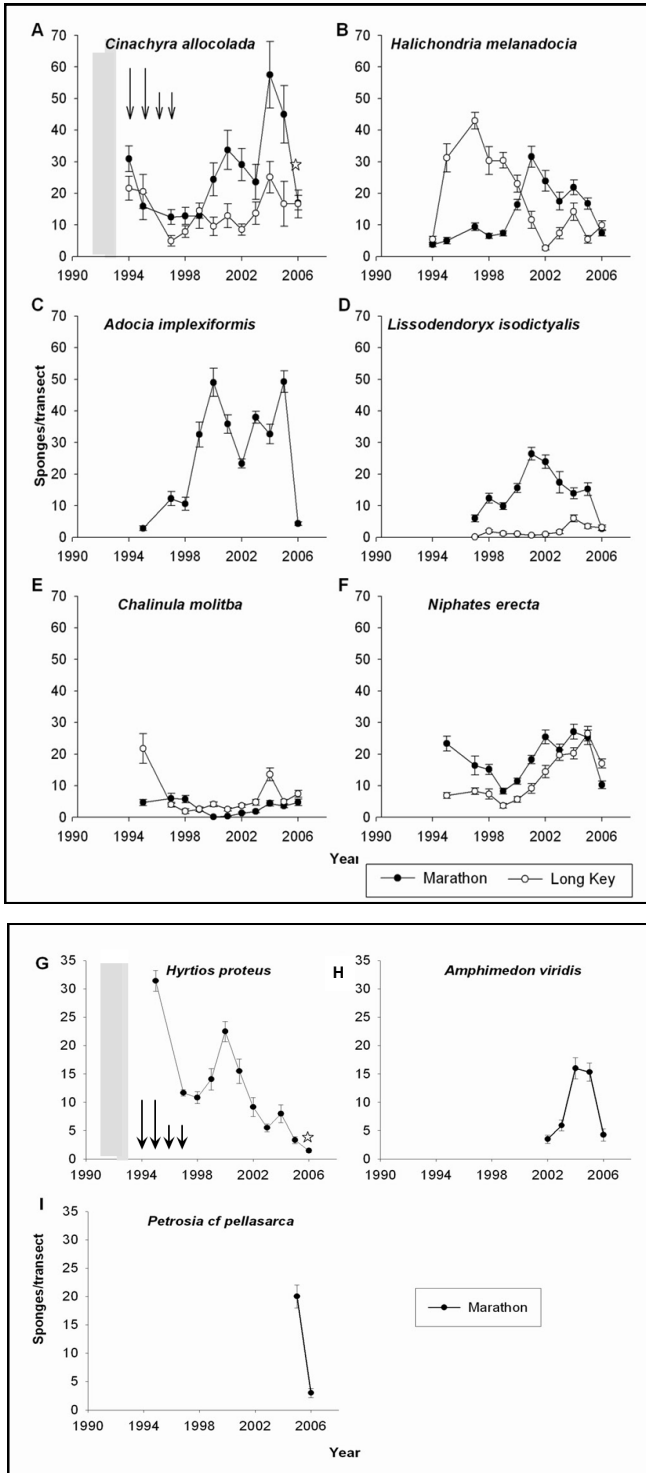
*Niphates erecta* — The lavender rope sponge (Figure 5F, Table 3) is relatively common and easily recognized by its dull gray, solid, single, ramose branches. It was relatively abundant at both Marathon and Long Key immediately after the bloom events. Patterns of abundance were similar at both Marathon and Long Key. In general, *N. erecta* exhibited significant ( $p < 0.05$ ) increases and decreases in abundance at both study areas over the course of the study.

*Hyrtios proteus* — (Figure 5G and 6A, Table 3) is a small amorphous purplish-black sponge with a distinctive conulose surface; and it is softly resilient. This sponge was much more abundant at Marathon than at Long Key. In general, this species significantly ( $p < 0.05$ ) declined at both areas. However, at Marathon, a significant ( $p < 0.05$ ) spike in abundance occurred before further decline (Figure 5G); whereas, at Long Key, abundance declined to near zero and never increased (Figure 6A). By the end of the study, *H. proteus* was uncommon at both areas.

*Amphimedon viridis* — (Figure 5H, Table 3) is easily recognized by its brilliant green coloration and branching habit. Although our abundance data for this species is limited, the data were sufficient to document that *A. viridis* had indeed recruited into the Marathon area to a significant degree. It was not found at Long Key.

*Petrosia (Petrosia) cf. pellararca* — (Figure 5I, Table 3) This sponge species is very irregularly shaped and has a characteristic chocolate brown coloration. It is considered to be a species of *Petrosia* (K. Rützler, National Museum of Natural History, Pers. communication), and is similar to the sponge recognized as *Petrosia (P.) pellararca* (de Laubenfels 1934) in the Caribbean today (Zea 1987). We began to collect abundance data for this species because it had essentially been absent for many years and was obviously a new and common recruit, at least in 2005. Abundance significantly ( $p < 0.05$ ) decreased following the hurricanes.





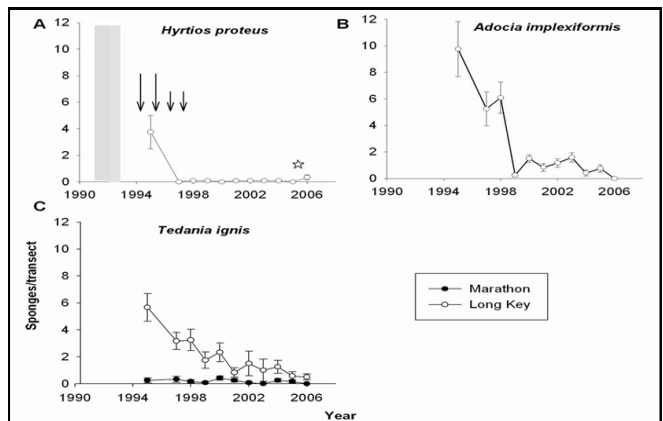
**Figure 5.** Opportunistic sponge species exhibiting rapidly increasing and decreasing abundance (average number/transect ± S.E. bars). The shaded area (shown on Figures 5A and 5G) depicts timing of 1991–1993 bloom events at both sites. Large arrows (shown on Figure 5A) represent timing of bloom events in 1994 and 1995 in the vicinity of Long Key and smaller arrows represent timing of blooms in Florida Bay that might have affected Long Key area. The star represents the timing of Hurricane Wilma.

*Tedania (T.) ignis* — The fire sponge (Figure 6C, Table 3) is widespread throughout the Caribbean and is characterized by its bright red coloration and irritation to the skin upon handling. This species was never common at Marathon during the study, and showed no significant trends. It was more abundant at Long Key, but it underwent a long-term gradual and significant ( $p < 0.05$ ) decline.

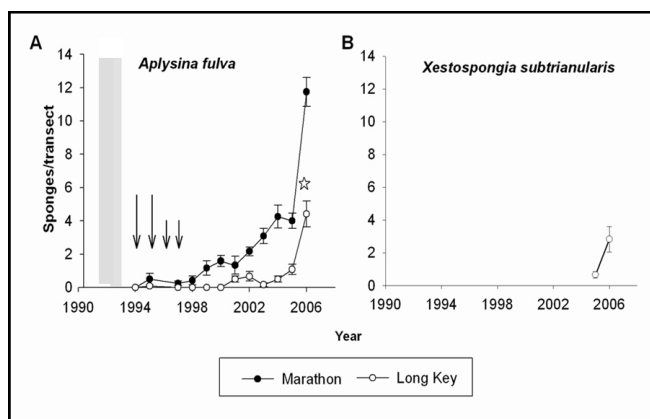
*Aplysina fulva* — The scattered-pore rope sponge (Figure 7A, Table 3) is easily recognized by its morphology (long thin elastic branches), texture (rubbery, smooth), and color (yellowish-brown with lavender tinges). Initially, it was relatively uncommon at both sites. However, abundance increased steadily and significantly ( $p < 0.05$ ) at Marathon to the point that it was ranked the fifth-most abundant species in 2006. A similar but less pronounced pattern was observed at Long Key.

*Xestospongia subtriangularis* — The sprawling sponge (Figure 7B, Table 3) is a large caramel-colored branching sponge, with a brittle texture. The limited data for this species documents that it was another species that recruited into the Marathon area long after the sponge mortality. Interestingly, it significantly ( $p < 0.05$ ) increased in abundance after the hurricanes.

*Tectitethya crypta* — is a hemispherical to conical sponge, typically covered with a thin layer of sediment (Table 3). It is recognizable by the is black with a greenish tinge. This species was relatively common at Long Key but less so at Marathon, and in both locations it was noticeably clumped in distribution. No significant change in its abundance at either Marathon or Long Key was observed during the study.



**Figure 6.** Sponges that gradually declined in abundance (average number/transect ± S.E. bars). The shaded area depicts timing of 1991–1993 bloom events at both sites. Large arrows represent timing of bloom events in 1994 and 1995 in the vicinity of Long Key. Smaller arrows represent timing of blooms in Florida Bay that might have affected Long Key area. The star represents the timing of Hurricane Wilma.



**Figure 7.** Sponges that increased in abundance after Hurricane Wilma (average number/transect  $\pm$  S.E. bars). The shaded area depicts timing of 1991–1993 bloom events at both sites. Large arrows represent timing of bloom events in 1994 and 1995 in the vicinity of Long Key. Smaller arrows represent timing of blooms in Florida Bay that might have affected Long Key area. The star represents the timing of Hurricane Wilma.

*Callyspongia (Cladochalina) vaginalis* — The branching vase sponge (Table 3) - a highly characteristic greyish-lavender, conulose, tube-shaped sponge, also typically sedimented (Alcolado 2007) - was uncommon at Marathon and extremely rare at Long Key. Because its abundance was low, no discernable abundance pattern or statistical trend was established.

#### Effects of Hurricane Wilma

The most influential of the two hurricanes that brought tropical storm-strength and hurricane-force winds throughout the study area after the 2005 survey work was completed was Hurricane Wilma, which had maximum sustained wind speeds estimated at nearly 105 knots (Category 3 intensity) when landfall occurred in southwestern Florida near Cape Romano on 24 October 2005. Table 4 describes the typical morphological characteristics of each species and our assessment of the principal agent(s) for their decline in abundance due to hurricane effects. The sponge population at Marathon was highly affected by Hurricane Wilma (Figure 3). Between 2005 and 2006, total abundance and the abundances of 13 species (Table 4) significantly decreased. In contrast, Hurricane Wilma had little effect at Long Key; only one species (*N. erecta*) declined significantly in abundance. Interestingly, two species increased significantly in abundance following Hurricane Wilma--*Aplysina fulva* at both Marathon and Long Key and *X. subtriangularis* at Marathon. Overall, species with strong attachments to the substrate, including large or massive species, were damaged the least. Sponges with weak attachments, branching growth patterns, fragile structures, or high profiles were damaged by the hurricane to the point that their abundances were significantly diminished. High-profile species with complex structures

of some type, fragile skeletons, and weak attachments were the most vulnerable.

## DISCUSSION

### Do *Synechococcus* Bloom Conditions Kill Sponges?

A direct causal link between the blooms and mode of sponge death has not been established (Butler et al. 1995, Lynch and Philips 2000, Peterson et al. 2006). Previous reports of sponge mass mortality have not been associated with blooms of planktonic cyanobacteria such as *Synechococcus* spp. Although such blooms can be toxic to marine animals (Mitsui et al. 1989), there was no noticeable mortality of fish or invertebrates during the 1991 - 1993 sponge mortality events (Butler et al. 1995).

Butler et al. (1995) suggested the possibility that the exceptionally dense and persistent blooms of *Synechococcus* spp. in the Florida Keys impaired the filtration and feeding mechanisms of sponges. In laboratory experiments (Lynch and Philips 2000), three sponge species (including *H. melanadocia*, and *S. vesparia*) present in their study area were exposed to bloom-level densities of both natural and laboratory-cultured *Synechococcus* for the relatively short duration of up to five days. They did not die; the sponges were able to filter the *Synechococcus* spp. However, clearance rates from surrounding water by sponges showed some decline over time, indicating that longer-term exposures might ultimately lead to mortality. During our study, the bloom events were persistent, some lasting for 6 - 8 months.

Many cyanobacteria, including *Synechococcus* spp., are known to excrete a sticky carbohydrate polymer in prodigious quantities (Philips et al. 1989). Although, under laboratory conditions, the production of this polymer was reduced compared with the rate of production in the natural environment, polymer production was enhanced by high-salinity conditions such as those present in the early 1990s (Swart et al. 1999) where the bloom was initiated (Lynch and Philips 2000). It seems probable that the laboratory experiments were unable to duplicate the duration and nature of the bloom conditions experienced by individual sponges in nature. It is possible that high concentrations of polymer occluded sponge canals, 'starving' the sponge mesophyl, causing stress, and leading to localized infection and subsequent necrosis of sponge tissue.

Stress that can destroy weakened sponges has been implicated in sponge viral (Vacelet and Gallissian 1978), bacterial (Vacelet et al. 1994), cyanobacterial (Rützler 1988) and fungal infections. Previous instances of mass sponge mortalities in the Caribbean, Gulf of Mexico, and the Mediterranean have been attributed to a variety of sponge infections (Lauckner 1980, Peters 1993), sometimes in response to environmental stress. Moreover, commensal bacteria that normally digest necrotic sponge tissue may become virulent and digest living tissue under unfavorable environmental conditions (Vacelet et al. 1994).

**Table 4.** Effects of hurricanes on sponge abundance at Marathon and Long Key. Tukey's:  $P < 0.05$ ; SNK:  $P < 0.05$ ; Dunn's:  $P < 0.05$ ; T-test:  $P < 0.05$ ; Mann-Whitney:  $P < 0.05$ . Significance columns indicate the test(s) that established statistically valid differences. Dash: Not present in transects at this study site.

Species	Morphological	Hurricane effect	Marathon		Long Key	
			Change in abundance	Significance	Change in abundance	Significance
<i>Spheciospongia vesparium</i>	Massive, low profile, broad base, tough, strong attachment		No change		No change	
<i>Cliona varians</i>	Thick clubs, broad base,		No change		No change	
<i>Ircinia campana</i>	Massive vase, elastic, flexible, weak attachment	Detachment, and transport off-site	Decrease	SNK	No change	
<i>Ircinia felix</i>	Branching mass, weak attachment	Detachment, and transport off-site	Decrease	SNK	No change	
<i>Ircinia strobilina</i>	Massive, narrow base, weak attachment (rollers common)	Detachment, and transport off-site	Decrease	SNK	No change	
<i>Hippospongia lachne</i>	Massive, squat, broad base, tough, strong attachment		No change		No change	
<i>Spongia barbara</i>	Massive, tough, strong attachment		—		No change	
<i>Spongia barbara dura</i>	Columnar (high profile), weak attachment	Detachment, and transport off-site	Decrease	SNK	No change	
<i>Spongia graminea</i>	Massive, tough, strong attachment		No change		—	
<i>Cinachyrella alloclada</i>	Small, low profile, broad,	Scouring and burial	Decrease	Tukey's, SNK	No change	
<i>Halichondria melanadocia</i>	Small, fragile, low profile, weak attachment	Scouring or burial and pulverization	Decrease	SNK	No change	
<i>Adocia implexiformis</i>	Stringy, fragile, relatively high profile, weak attachment	Pulverization, fragmentation, and	Decrease	Tukey's, SNK	No change	
<i>Lissodendoryx isodictyalis</i>	Small, fragile, low profile, weak attachment	Pulverization	Decrease	Tukey's, SNK	No change	
<i>Chalinula molitba</i>	Fragile, weak attachment	Pulverization	Decrease	SNK	No change	
<i>Niphates erecta</i>	Branching, firm, weak attachment	Pulverization, fragmentation, and transport off-site	Decrease	Tukey's, SNK	Decrease	SNK
<i>Hirtios proteus</i>	Small, low profile, broad base, strong attachment	Scouring and burial	Decrease	SNK	No change	
<i>Amphimedon viridis</i>	Branching, firm, weak attachment	Pulverization and transport off-site	Decrease	SNK	No change	
<i>Petrosia cf pellasarca</i>	Amorphous, fragile, weak attachment	Pulverization and transport off-site	Decrease	T-Test	—	
<i>Tedania ignis</i>	Small, soft, low profile, weak attachment		No change		No change	
<i>Aplysina fulva</i>	Thin branching, tough, elastic, multiple weak attachments	Fragmentation and re-attachment	Increase	SNK	Increase	SNK
<i>Xestospongia subtriangularis</i>	Branching mass, firm, brittle texture, multiple weak attachments	Fragmentation and re-attachment	Increase	Mann-Whitney	—	
<i>Tectitethya crypta</i> <sup>2</sup>	Large, low profile, strong attachment		No change		No change	
<i>Callyspongia vaginalis</i> <sup>2</sup>	Tube-shaped, weak attachment		No change		—	

The widespread disappearance of sponges in the Florida Keys and Florida Bay that we witnessed from 1991 through 1993 was dramatic. A major decline in overall abundance and biomass occurred at both Marathon and Long Key during the two major bloom events between 1991 and 1993, and sponge biomass remained at a reduced level for a considerable period—at least 10 – 15 years. Moreover, the timing of recruitment differed at both sites; recruitment of specific species at Long Key often consistently lagged that at Marathon. For most of the larger long-lived species, a significant period of time elapsed before recruitment was visible at both sites. Finally, patterns of decline in sponge abundance and the patterns of response or recovery were not necessarily the same within a species between sites.

If we compare the dynamic nature of the spatial extent and duration of the 1991 - 1993 blooms with the patterns and timing of sponge mortality we observed, it is clear that the bloom conditions were somehow the principal cause of the sponge mortality during that time. Many of our findings support this conclusion:

- i) All species surveyed over the initial bloom events (1991 - 1993) were essentially eliminated at both locations.
- ii) Recruitment of several species at Long Key lagged behind their recruitment at Marathon, a feature consistent with the continued exposure of the Long Key site to repeated bloom events after 1993.
- iii) Several opportunistic species increased explosively in abundance upon cessation of bloom conditions at both Marathon and Long Key, possibly because of reduced competition for space and food caused by the demise of large specimens that predominated in these sites.

Further supporting our conclusions, Butler (2008) reported a re-occurrence of sponge deaths in association with new bloom conditions in 2007. Again, no sponge mortality was reported outside of the bloom area.

### Patterns of Response

All species surveyed over the initial bloom period were essentially eliminated. Significant recruitment did not occur in many species until after cessation of the major blooms in 1995. Because the responses of individual species to bloom conditions followed several general patterns, recovery from the blooms produced a complex picture of sponge community dynamics in space and time.

*Rapid Decline and Gradual Recovery* — Nine large species (*S. vesparium*, *C. varians*, *I. campana*, *I. felix*, *I. strobilina*, *H. lachne*, *S. barbara*, *S. barbara dura*, and *S. graminea*) that predominated in the sponge community prior to 1991 and were monitored in this study from 1991 or 1993 recovered to some degree over the course of the study. These species are long-lived, stable components of

other tropical west-central Atlantic environments (Hechtel 1965, Wiedenmayer 1977, Van Soest 1978, 1980, 1984, Zea 1987). *Spheciospongia vesparium*, *C. varians*, *I. felix*, *I. strobilina*, and *S. barbara dura* showed consistent and pronounced increases in abundance at Marathon, but exhibited either delayed or less pronounced increases at Long Key. The differences in recovery between areas may be, in part, due to the unpredictable nature of larval dispersal and survival, the usually more adverse salinity and temperature conditions in waters of close proximity to Florida Bay [greater seasonal and interannual extremes (Swart and Price 2002), to the point of lethality to invertebrate larvae or postlarvae (e.g., Bert et al. In preparation)], the greater exposure of the Marathon area to open ocean waters, or the prolonged and repetitious bloom conditions at Long Key from 1991 through 1997. Bloom-laden water was spread to adjacent parts of the bay by strong seasonal cold fronts, which promote water outflow from Florida Bay into adjacent waters (Lee and Smith 2002). The prevalent water flow patterns during winter would have brought the intermediate-concentration bloom waters described by Philips et al. (1999) into close proximity to our Long Key site. Thus, it seems that Marathon was affected only by the two major blooms, whereas Long Key likely was affected by bloom waters over a more prolonged period of time (1991 - 1997).

The length of time required to observe recruitment of the normally conspicuous *S. vesparium* seems quite remarkable in that, at both study areas, aggregations that survived bloom conditions were located only 1 - 3 km from decimated aggregations. Moreover, recruitment at Long Key lagged that at Marathon by about five years despite the presence of large individuals that had recovered from bloom conditions within the study area, whereas all individuals had been eliminated from Marathon. Size data for *S. vesparium* at Long Key compared with that at Marathon indicates that initial recovery at Long Key was via regeneration of individuals not completely killed during the initial bloom, rather than recruitment via sexual reproduction and larval dispersal. In a recent study near Long Key, Donahue (2008) transplanted *S. vesparium* and other species into areas depopulated of sponges and into an area with a well-established sponge community unaffected by bloom conditions. He found that *S. vesparium* and some other species had significantly faster growth rates in the depopulated areas and suggested that this resulted from decreased competition for food.

Several features of *C. varians*, *I. felix*, *I. strobilina*, and *S. barbara dura* may have been conducive to their increase in abundance at Marathon. Increased availability of substrate for colonization and decreased competition for food may have allowed these species to thrive. *C. varians* is apparently very hardy; it can thrive even in polluted waters (Alcolado 2007). *I. felix* can grow rapidly and overgrow other sponge species, probably because it harbors a photosynthetic cyanobacteria symbiont

(Wilkinson and Cheshire 1988) and has chemical defenses against predation (Freeman and Gleason 2010), as does *I. strobilina* (Waddell and Pawlik 2000).

The formerly abundant *I. campana* was a major component of total sponge community biomass prior to bloom conditions (Stevely et al. 2010). However, it did not recruit to the area for a decade after it was decimated; and it was present at only a small fraction of its former abundance at both areas 13 years after the initial bloom. Of all the major long-lived species found in the study area, *I. campana* appeared to have the most limited ability to recover. *Ircinia campana* is a chemically defended sponge that heals very slowly (Walters and Pawlik 2005). If badly damaged, individuals may die rather than recover. Similarly to the situation for *I. campana*, *H. lachne* recovered only slightly in our study areas; but it was sufficiently abundant at other locations affected by the algal blooms to support commercial harvest. *Spongia graminea* also recovered only partially compared with its 1991 abundance.

**Fluctuating abundance** — After cessation of bloom conditions, and removal of the dominant food and space competitor species at both Marathon and Long Key, several species increased explosively in abundance, indicating an “opportunistic” life history strategy. Nine species (Figure 5) were observed to have population fluctuations that would suggest an opportunistic life history strategy, with significant increases and decreases in abundance during the study. *Cinachyrella alloclada*, *H. melanadocia*, *L. isodictyalis*, *C. molitba*, and *N. erecta* exhibited highly opportunistic patterns of changing abundance at both Marathon and Long Key throughout the study.

*Cinachyrella alloclada* is considered to be an opportunistic species in Cuban waters (Pedro Alcolado, Instituto de Oceanología, Pers. communication) because its principal mode of reproduction at some locations is the extrusion of numerous tiny sponge buds, which are locally dispersed, resulting in a clustered distributional pattern of small, closely clumped individuals. This mode of reproduction can lead to rapid increases in numbers of individuals and the clumped distribution (Rützler and Smith 1992) we observed in the field.

Two species, *A. implexiformis* and *H. proteus*, showed a different pattern of abundance between the two sites. At Marathon, these species widely varied in abundance during the study; whereas, at Long Key, they both showed a gradual decline in abundance. Taken as a whole, this group provides an example of the complexity of sponge community dynamics in space and time. Individually, species may not show the same pattern at different sites over the same period of time, indicating that a variety of factors other than bloom conditions can influence their life histories.

**Gradual Decline** — Three species (*H. proteus*, *A. implexiformis*, and *T. ignis*) generally exhibited a gradual decline in abundance from 1995 forward, to the point that they were uncommon at Long Key. One explanation for this general demise is that, with the increasing recruitment of other species into Marathon and Long Key over the latter part of the study period, opportunistic species such as *Tedania ignis* could no longer compete for food and space. *Tedania ignis* can reclaim bared space, is a fast grower, and can overgrow other species; but it is a poor recruiter to bare substrate and is vulnerable to predation (Wulff 2006b, 2010), which could contribute to a long-term decrease in abundance.

**Low Abundance, No Change** — The abundance of *T. crypta* and *C. vaginalis* at Marathon, and of *H. proteus* and *T. ignis* at Long Key were very low throughout the periods during which they were monitored. Butler (2008) reported that *T. crypta* was relatively resistant to bloom conditions, which might explain its persistence in low numbers. The observed pattern for *T. ignis* at Long Key contrasts with that seen at Marathon where it was relatively abundant when first included in the surveys.

Like other Hadromerida such as *Sphaciospongia vagabunda* (Kelly 1986, Kelly and Bergquist 1988), *S. vesparium*, and *Tethya* spp., *T. crypta* can cease pumping for considerable periods of time (Reiswig 1971), which also may provide some protection against bloom conditions. Similarly, the sediment-covered surface of *T. crypta* may act as a filtration barrier, as it does for *C. alloclada*. Reiswig (1973) concluded that *T. crypta* establishes stable local populations and has several life history adaptations to insure the longevity of individuals. However, due to less investment in large, energetically expensive larvae, they are unable to rapidly colonize newly available substrate within their local area. The persistent low abundance we observed is consistent with Reiswig’s (1973) conclusions.

*Callyspongia vaginalis* is a slow grower that is not easily fragmented. It relies on the production of many larvae for colonization (Leong and Pawlik 2009); but, despite its potential for larval dispersal, its population genetic structure indicates that most dispersal is highly localized (DeBiasse et al. 2010). Although it can be common in some communities (Waddell and Pawlik 2000), it has no chemical defenses against at least some predators (Walters and Pawlik 2005). This poor defense system and dispersal ability may limit its abundance in areas where competition for substrate is strong.

### Species Responses to Hurricane Wilma

After Hurricane Wilma, overall sponge abundance was significantly lower at Marathon but not at Long Key. Many species at Marathon were markedly reduced in abundance. Many species damaged at Marathon had low abundance at Long Key, precluding clear detection of significant changes in abundance. Conditions at Long Key

during Hurricane Wilma were slightly less severe than at Marathon (K. Kasper, National Oceanic and Atmospheric Administration, Pers. communication), and protection from open the Gulf of Mexico wave energy present at Marathon made a large difference in overall sponge survival at Long Key. Slight differences in reef orientation to storm waves can dramatically change the effect of a hurricane on sponge abundance (Wulff 1995).

Massive individuals of the long-lived species with strong attachments to the substrate (*S. vesparium*, *C. varians*, *H. lachne*, *S. barbara*, *S. graminea*) were remarkably resilient to hurricane conditions, even in shallow water. Apparently the survival strategy of these species is to resist wave action as single, stable individuals rather than to utilize wave action to divide single individuals into multiple fragments that can quickly attach to and colonize denuded substrates.

Many significant declines in abundance occurred in long-lived, massive species with weak or proportionally small attachments (*I. campana*, *I. felix*, *I. strobilina*) or branching or columnar forms (*S. barbara dura*) or in opportunistic species (*C. allocolada*, *H. melanodocia*, *A. implexiformis*, *L. isodictyalis*, *N. erecta*, *H. proteus*, *A. viridis*, *P. cf. pellasarca*). These species were either pulverized or fragmented by wave action or detached by sand scouring. These types of species are prone to hurricane damage (Wulff 2006a). They may be more adapted to recolonizing barren substrate following storms than are the massive sponges with strong attachments. Some may even generate propagules from small fragments or have the capacity to re-aggregate into elemental sponges from loose groups of cells (Maldonado and Uriz 1999). Others may rely on wave action for fragmentation as their principal method of reproduction as well as for dispersal (Leong and Pawlik 2009).

Wulff's (1995) evaluation of the impacts of Hurricane Joan (October 1988) on *A. fulva*, *Iotrochota birotulata*, and *Amphimedon rubens*, provides further insight into the pattern of mortality observed in this study. In Wulff's (1995) study, almost half of the individuals and biomasses of numerous species were lost during the hurricane. *Aplysina fulva*, one of the two species in our study to significantly increase in abundance after the hurricane, suffered less loss in abundance in Wulff's (1995) study than did the other two species, in part because *A. fulva*'s skeleton is composed of a tight mesh of spongin and the mesohyl is permeated with fibrillar collagen, conferring tremendous elasticity and flexibility to the sponge body. In contrast, *X. subtriangularis*, the other species that significantly increased in abundance after Hurricane Wilma, was fragmented because its relatively brittle, dense, spicule skeleton bound by nodal spongin is easily fragmented, but the fragments re-attach to stable substrate after they are immobilized.

The pattern of mortality resulting from the effects of Hurricane Wilma differed notably from the pattern resulting from the plankton blooms. The several massive species were resistant to the effects of Hurricane Wilma (*S. vesparium*, *C. varians*, *H. lachne*, *S. graminea*); but these species were decimated by plankton blooms. Because those species account for high percentages of total sponge community biomass, the blooms would have a greater impact on total sponge biomass than would hurricanes. Furthermore, many of the Marathon species that were affected by the hurricane tended to be species that could rapidly recolonize an area (*C. allocolada*, *H. (H.) melanodocia*, *A. implexiformis*, *L. isodictyalis*, *C. molitba*, *N. erecta*, *H. proteus*, *A. viridis*). Consequently, the impact of Hurricane Wilma on sponge community biomass would also be more short-term in nature. Although most studies of hurricane effects on sponge community diversity and biomass are limited by a lack of pre-storm population data (Rützler 2004), studies by Fenner (1991), Wulff (1995), and Cropper and DiResta (1999) have shown relatively rapid recovery (within two years) of sponge populations following hurricane conditions. Local geomorphology and hurricane intensity will significantly affect the severity of hurricane damage, but our data illustrate the tenacity of some sponges, even in shallow water subjected to full hurricane force conditions.

### Ecological Implications

The driving force behind the occurrence of repeated and sometimes widespread *Synechococcus* blooms in the middle and upper Keys is not clear. Nor is the extent of anthropogenic influences causing or exacerbating the blooms. It is clear that sponge community biomass takes more than a decade to recover to pre-mortality biomass, and species' relative abundances can change unpredictably and dramatically. Even if *Synechococcus* blooms occur relatively infrequently in the future—for example, every 15 - 20 years—our study shows that such repeated episodes will result in chronically reduced sponge community biomass and in altered, shifting species composition and relative abundance in the mid and upper Florida Keys. Chronic reduction in sponge community biomass, species abundance, and species composition in that area could have substantial ecological and fishery impacts.

In contrast to hurricanes and possibly sporadic sponge disease episodes, algal blooms severely reduce sponge biomass and thereby the overall ability of the local sponge community to filter water. Sponge diseases can also have pronounced effects on sponge biomass and species composition (Gochfeld et al. 2007, Wulff 2007), but are relatively rare in water of good quality and are typically restricted to certain species groups. For example, mortality of commercial bath sponges attributed to sponge diseases in Florida, the Caribbean, and the Mediterranean has been reported only infrequently (Brice 1898, Allemand-Martin 1914, Smith 1941, Vacelet 1994).

Sponges filter large volumes of water and are very efficient in retaining small food particles (particularly < 5  $\mu$ ) to meet their nutritional requirements (Reiswig 1971, Riisgard et al. 1993, Weisz 2006). In sponge dominated habitats, it is likely that sponges can significantly reduce picoplankton concentrations in the water column (Pile 1997, Pile et al. 1997), particularly in shallow water habitats (Riisgard et al. 1993). Lynch and Philips (2000) estimated that the loss of biomass in Florida Bay sponge community would significantly lengthen the time required for removal of plankton from the water column. Thus, chronic sponge community biomass loss, such as that we saw from the *Synechococcus* blooms, would likely affect the dynamics of plankton communities, with potentially broad ecological consequences (Lynch and Philips 2000). Moreover, the loss of sponge biomass caused by bloom conditions may have generated a feedback loop by rendered the Florida Bay ecosystem susceptible to reoccurring cyanobacteria blooms (Peterson et al. 2006).

### CONCLUSIONS

Our detailed and long-term data indicate that, for the sponge communities in the middle to upper Florida Keys, assessment of population recovery by measuring only numerical abundance can be misleading. Our results clearly showed the bloom impact on sponge community biomass was much greater than the impact indicated by numerical counts. However, the patterns of response exhibited by individual species show that there are many different patterns of change in abundance. The sponge assemblage at any one time may differ from that of another time, even on a relatively short-term basis. While other deeper-water sponge communities have been shown to be stable with little change over long periods of time (Pansini and Pronzato 1985), we saw a much different picture for a shallow-water sponge community. Species respond in different ways at different sites, and population change is dynamic, sometimes dramatic, and sometimes unpredictable. The fact that the system is dynamic is not as surprising because shallow water sponge communities of the Florida west coast are subjected to aperiodic perturbations (highly localized salinity events, hurricanes, harmful algal blooms, and disease). Indeed, in recent literature there is evidence that sponge assemblages are highly dynamic (Bell et al. 2006, Carballo, et al. 2008).

However, we can meaningfully discuss recovery, particularly from a resource management perspective, when looking at sponge community biomass. Those species that dominate sponge community biomass are large and appear to be long-lived. If these species are able to recruit and attain their former levels of abundance and size, then the ecological function of the sponge community, in terms of filter feeding capacity and providing structural habitat, will have been restored. However, after bloom events, this is not a rapid process for all species; restoration of sponge population biomass in our study area was at least a 10 - 15 year process.

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