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Rapid diversity and abundance decline in a Caribbean coral reef sponge community

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ABSTRACT

Sponges are abundant and diverse on coral reefs, and play key functional roles; but virtually nothing is known of their dynamics. This is the first report of coral reef sponge community dynamics documented by a series of censuses in which volume and species of every individual were recorded. At the start of the 14 year study, there were 1395 sponge individuals, representing 39 species in nine orders, and a total sponge volume of 33,721 cm^3 in the censused area of a shallow Caribbean reef in San Blas, Panama. The most striking results of the 5 censuses were steady disappearance of species (51.3%) throughout the study period, and a steep drop in total sponge volume (42.6%). Species in keratose orders and with massive growth forms were lost disproportionately. Sponge losses could not be attributed to predators, physical disturbance (including a hurricane), extreme episodes of other abiotic factors, or disproportionately great loss of rare species due to random fluctuations. Disease may have played a role.

High loss rates documented at this and nearby sites could be a local phenomenon, but scattered reports of disease and mass mortality of sponges from other sites suggest these data may reflect region-wide losses. Monitoring programs designed for corals and mobile unitary organisms can miss changes in sponges because very high sponge species diversity, facile fragmentation and fusion, and quick and complete disappearance of dead sponges, impedes perception of changes if there are no prior censuses. Whether or not sponge declines are extensive will remain unknown until repeat censuses have been accomplished at additional sites. Sponges can increase water clarity, bind live corals to the reef frame, and facilitate reef regeneration, suggesting that loss of sponges could accelerate declines of coral reefs.

1. Introduction

Loss of species from communities is occurring at an accelerating rate with increasing physical, thermal, and chemical disruption of natural environments by human activities (e.g., Luck et al., 2003; Root et al., 2003); and coral reefs are particularly threatened (e.g., Harvell et al., 1999; Bellwood and Hughes, 2001; Lang, 2003; Gardner et al., 2003; Wilkinson, 2004; Pandolfi et al., 2005). Declines of coral reef ecosystems have been ascribed to climate change, nutrients, sediment, overfishing, physical damage by human activities, disease, and herbivore loss, in various mixtures (e.g., Hughes and Connell, 1999; Rogers, 2000; Aronson et al., 2002; Knowlton, 2001; Jackson et al., 2001; Zakai and Chadwick-Furman, 2002; Hughes et al., 2003; Kelmo et al., 2004; Sutherland et al., 2004; Pandolfi et al., 2005).

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Monitoring programs designed to document dynamics, and causes of declines, in reef fishes, sea urchins, and reef-building corals are being implemented as quickly as funding is in place (e.g., Lang, 2003; Wilkinson, 2004); and the resulting data are essential for management and conservation decision-making.

Time constraints on underwater research preclude inclusion of all functional groups in reef monitoring programs. Groups are added as compelling reasons are discovered. For example, inclusion of sea urchins in Caribbean monitoring was mandated by dramatic increases in algae following the near elimination of the sea urchin *Diadema antillarum* in the early 1980s (e.g., Hughes et al., 1987; Shulman and Robertson, 1996; Lang, 2003). Some groups are neglected in monitoring because they are not suspected of playing key roles, but other groups are just plain difficult. Sponges are known to play diverse functional roles that directly affect coral survival and reef health, but taxonomic and quantification challenges have stymied inclusion of sponges in reef monitoring (Rützler, 1978; Wulff, 2001). It may be time to overcome these challenges.

Coral reef sponges are far more diverse than corals (e.g., 640 Caribbean sponge species, van Soest, 1994, and 2324 sponge species from tropical and warm temperate Australia, Hooper et al., 2002), more abundant than corals in many areas (e.g., Diaz and Rützler, 2001), and play key functional roles (Diaz and Rützler, 2001; Wulff, 2001). Excavating sponges weaken solid carbonate and generate sediment, strongly influencing both coral survival and reef geology (e.g., Rützler, 2002). The great majority of sponge species do not excavate burrows, but play positive roles with respect to coral survival and carbonate balance. Sponges are particularly efficient at clearing bacteria (at least 95% removed) and other small plankton from the water column (e.g., Reiswig, 1971; Pile, 1997), with increased water clarity an obvious advantage, and the possibility that pathogens may be filtered out as well. Sponges contribute to primary productivity and nutrient regeneration by harboring diverse microbial symbionts (Wilkinson and Fay, 1979; Wilkinson, 1992; Wilkinson, 1983b; Diaz and Ward, 1997). Sponges also shelter juvenile spiny lobsters (Butler et al., 1995) and numerous invertebrate and algal symbionts (e.g., Beebe, 1928; Ribeiro et al., 2003; Cerrano et al., in press). Sponges can increase coral survival by binding live corals to the reef frame. Corals from which sponges were removed suffered 40% mortality in 6 mo, vs. 4% mortality of corals that retained sponges (Wulff and Buss, 1979). Sponges can also facilitate reef regeneration. Rubble piles seeded with sponges were consolidated within 7 mo and corals had recruited by 10 mo, whereas rubble without sponges never stabilized and had no successful coral recruits (Wulff, 1984). Loss of these functional roles at which sponges excel has direct negative consequences for corals and coral reefs.

In most of the few cases in which entire sponge communities have been studied, community dynamics have given no cause for concern. On shallow and deep hard substrata in the Mediterranean (Sarà, 1970; Pansini and Pronzato, 1990), on Caribbean mangrove roots (Sutherland, 1980), and on a deep Caribbean reef wall (Hughes, 1996), sponges remained relatively constant, even when other faunal elements changed. However, a few reports of precipitous declines in one or a few species (e.g., Smith, 1941; Dayton, 1978; Wilkinson, 1978; Rützler, 1988; Butler et al., 1995; Cervino et al., 2000; Pronzato et al., 1999) alert that they are not immune to losses.

Loss of sponges is difficult to quantify without a prior census. Dead corals leave behind solid carbonate skeletons in which clues about their lives and deaths are embedded. But sponges quickly fall apart after dying, leaving no trace. High diversity of sponge assemblages renders loss of any particular species less perceptible, and difficult to document with the random transect data utilized in many monitoring programs. With the sole exception of 12 photo quadrats (each 1 m^2) on a reef wall in Jamaica, in which sponge dynamics were analyzed with respect to number of individuals and percent cover over a 16-year period (Hughes, 1996), sponge censuses in time series have not been made on coral reefs. The one study in which tropical sponge dynamics have been followed in terms of sponge volumes (and thus filtering and sheltering capacity) documented declines of as much as 90% following a cyanobacterial bloom in Florida Bay (Butler et al., 1995; Stevely, 1996; Stevely and Sweat, 2001).

Five complete censuses of 16 1 m^2 quadrats in a coral reef sponge community, over a 14-year period, are reported on here. A large number of sponge individuals (1395) were tracked, with volume and signs of damage recorded at each census. High diversity of species (39), representing nine orders of demosponges and the full range of growth forms, provided the initial variety needed to analyze patterns of community change. Interpretation of community dynamics was aided by data accumulated on the responses of individual sponge species to the specific physical and biological hazards at this site, including disease, sponge-feeding fishes (Wulff, 1994) and starfish (Wulff, 1995b), and a hurricane (Wulff, 1995a).

2. Methods

A coral reef sponge community on a shallow reef on the leeward side of the small island Guigalatupo, in the San Blas Province of Panama (map in Wulff, 1995b), was censused five times between 1984 and 1998. The plan was to continue censusing at intervals, but new inhabitants of the island discouraged further study after 1999. The area censused was at a depth of 2.5–2.8 m and uniformly covered with small to medium-sized massive and foliose corals, and coral rubble. The area is typical of shallow leeward reefs of San Blas and elsewhere in the Caribbean. Direct human interference was minimal during the 14 years. People of the Kuna Nation deploy fishing nets over sea-grass beds, but not the reef; and they do not use anchors while line fishing, but tie their dugout canoes up to stakes. They excavate branching coral from some very shallow reefs (e.g., Guzmán et al., 2003), but this site was deeper and branching corals were uncommon.

At each census, volume of every sponge within 16 permanently marked 1-m^2 quadrats arrayed within an 8 × 8 m area was measured by approximation to an assortment of geometric solids, with linear dimensions taken to the nearest 1 mm (methods details in Wulff, 2001). Records were kept of damage, including bite marks, breakage, and disease. Signs of disease included discoloration, bared skeleton, necrotic tissue, and abnormally fuzzy or glazed surfaces.

At least 80 sponge species inhabited this reef, but many are characteristic of microhabitats not represented in the study area. Excavating sponges were not included due to the impossibility of defining individuals and measuring volume. The amount of time it took to measure volume of every individual prohibited censusing a larger area at this intensity (Wulff, 2001); but qualitative surveys were made on 41 other reefs within a 5 km by 2.5 km area around San Blas Point in 1979, and again in 1999; and one nearby (0.8 km) reef, Ulagsukun, was surveyed in more detail in 1988 and 1999.

Corals in the census plot were identified to species, and abundance was measured at each census in terms of surface area of live coral tissue for each colony.

3. Results

3.1. Loss of species and sponge volume – summary

Initially, there were 1395 individual sponges in 39 species, and a total sponge volume of 33,721 cm^3 (2107.6 cm^3 per m^2), in the 16 m^2. The most striking result was the steady loss of species throughout the 14 years census period (Table 1, Fig. 1(a)). Half of the original species (20/39 species) disappeared from the censused community during the study. Only three additional species colonized; and one species dwindled to zero, but recolonized by the last census.

Re-surveys of nearby reefs confirmed that losses from the census plot were not unique. Sponge species that were lost from the census plot, and also from reefs where they had been noted in 1979, included (in parentheses are number of reefs from which they were missing in 1999/number of reefs on which they were noted in 1979): *Ircinia campana* (3/16), *I.* sp. 1 (1/7), *I. strobilina* (2/7), *Verongula rigida* (1/7), and *Lissodendoyx colombiensis* (1/5). One species that did not disappear from the census plot, *Xestospongia rosariensis*, could no longer be found on 3/9 of the qualitatively surveyed reefs. Two sponge species typical of sea-grass beds adjacent to coral reefs also vanished from sites where they had been noted in 1979: *Spheciospongia vesparium* was missing from 2/11 sites, and *Cervicornia cuspidifera* was missing from all 4/4 sites.

The nearby reef at Ulagsukun was surveyed in more detail in 1988, and by the 1999 re-survey had lost four of the 31 sponge species noted along a 200 m stretch of reef. Two of these species (*Ircinia* sp. 3, *Xestospongia proxima*) were among those lost from the census plot, and two were also lost from Guigalatupo, outside the census plot (*Cervicornia cuspidifera*, *Spheciospongia vesparium*). Seven species that were abundant at Ulagsukun in 1988 had become rare by 1999; and four of these were also lost from the Guigalatupo census plot (*Lissodendoryx colombiensis*, *Ircinia strobilina*, *Verongula rigida*, *Svenzea zeai*; the other three, *Xestospongia muta*, *Neofibularia nolitangere*, *Scopalina ruetzleri*, were not in the census plot). The initial surveys were qualitative (i.e., 'very abundant' vs. 'moderately abundant'), and no effort was made to record every species. However every species noted in the 1979 and 1988 surveys, and in the census plot, was searched for on the return surveys in 1999, resulting in a very conservative estimate of species loss from these reefs.

Although sponge species were steadily lost throughout the 14-year census period, total sponge volume only varied 10.6% (33,721–30,160 cm^3) during the first 11 years (Fig. 1(b)). At the final census in 1998, however, an abrupt decrease of 34% was found, resulting in total sponge volume loss of 42.6%.

3.2. Potential mortality sources

Individuals of 11 species were observed with signs of disease during at least one census (numbers indicate the number of censuses in which disease was observed): *Iotrochota birotulata* (5) *Amphimedon compressa* (5), *Aplysina fulva* (5), *Callyspongia vaginalis* (2), *Niphates erecta* (3), *Xestospongia rosariensis* (1), *X. carbonaria* (1), *Verongula rigida* (1), *Ircinia* sp. 1 (2) *I.* sp. 3 (1), *I. strobilina* (1), and *I. campana* (1). Disease was observed at every census (i.e., in February 1984, March 1998, June 1994, August 1988, and September 1995; and a post-hurricane survey in November 1988), and up to 24 sponges within the plot were observed to be diseased during a census. Disease was also observed outside the census plot in all of the above species, as well as *Xestospongia muta*, *Niphates caycedoi*, and *I. felix*. Diseased portions had characteristics suggesting cause by species-specific infectious pathogens: Lesions were observed to spread from day to day, and to infect branches of conspecific, but not of heterospecific, sponges with which they came in contact (Wulff, 1997a). Attempts to infect sponges of other species by imposing contact consistently failed (unpubl. data). Attempts to cure diseased individuals outside the censused area, by excising the diseased portion with a margin of apparently healthy tissue, were often successful, particularly with *Xestospongia* spp.

Other sources of mortality, such as predators and physical disturbance were studied extensively on this reef throughout the years of this study (Wulff, 1994, 1995a,b, 1997a; Wulff, 1997b), and will be considered in the Discussion.

3.3. Coral dynamics

Surface area of live coral tissue varied only 9.2% (from 18.5% to 16.8%) during the 14 years of the study, and the same species (a total of 11 scleractinian and 1 hydrozoan coral species) were represented throughout, with the exception that the sole *Acropora cervicornis* colony died between the 1994 and 1995 censuses. Corals in the genera *Diploria*, *Agaricia*, *Siderastrea*, *Porites*, and *Montastrea* remained the most abundant.

3.4. Loss of sponge species – relative abundance

Initial rareness was not disproportionately associated with loss from the plot (Table 1). By the last census, lost species included 7 of the 13 that were initially most abundant, 5 of the 13 species with intermediate abundance, and 8 of the 13 species that were least abundant (not different from an even distribution by the *G*-test, $P > .5$). Confining the analysis to the species that were most abundant at the start (i.e., the 19 species with total volumes of more than 100 cm^3), still shows a steady loss of half of the species (a decline from 19 to 10 species, Fig. 1(a)).

Table 1 – Total volume (cm^3) of each of the 39 species represented in the 16-m^{2}census plot at censuses in 1984, 1988, 1994, 1995, and 1998

Sponge species	ORD	Form	Year of census				
			84	88	94	95	98
Aplysina fulva (Pallas)	Vr	erbr	9767.3	8953.8	3414.2	2196.2	1243.2
Iotrochota birotulata (Higgin)	Pc	erbr	6001.3	6692.3	16442.7	11577.4	8214.4
Amphimedon compressa (Pallas)	Hp	erbr	3626.3	3153.8	6401.1	7620.4	6462.5
Ircinia sp. 1	Dc	tsh	3200.2	938.8	9		
Ircinia sp. 2	Dc	ma	1843.2	1400.8	408		
Niphates erecta Duch. & Mich.	Hp	erbr	1710.6	588.4	803.8	706.8	745.4
Ircinia sp. 3	Dc	ma	1094.6	98			
Verongula rigida (Esper)	Vr	ma	1011	354			
Ircinia campana (Lamarck)	Dc	mv	1006.9	866			
Ircinia felix (Duch. & Mich.)	Dc	ma	972	1343.3	242	260	44
Mycale laevis (Carter)	Pc	ma	656.7	3138.8	1863.5	2733.8	1593.5
Ircinia strobilina (Lamarck)	Dc	ma	651	975.6			
Xestospongia proxima (Duch. & Mich.)	Hp	tsh	465.6	92.5			
Callyspongia vaginalis (Lamarck)	Hp	brv	274.6	352.2	552.9	1151.6	49.8
Spirastrella hartmani Boury-Esnault, et al	Hd	en	233.4	333.5	109.6	78.1	60.5
Lissodendoryx colombiensis Zea & van Soest	Pc	ma	221	659	1447.8	1820.4	
Svenzea zeai Alvarez, et al.	Hl	tsh	219	24			
Callyspongia armigera (Duch. & Mich.)	Hp	en	208.5	111	52.5	3.9	1.2
Desmapsamma anchorata (Carter)	Pc	erbr	124.5	307.9	2.4		62.4
Agelas sventres Lehnert & van Soest	Ag	cm	96	130			
Niphates sp.	Hp	ma	80	19.6	6.2		
Monanchora arbuscula (Duch. & Mich.)	Pc	en	50.9	614.7	602.6	1348.8	602
Mycale microsigmatosa Arndt	Pc	en	42.4	23.3			
Xestospongia carbonaria (Lamarck)	Hp	tsh	39.4	47.2	1.5	90.6	190.5
Myrmekiodermia rea de Laubenfels	Hl	cm	38.7	14	12	3.2	0.8
Chondrilla cf. *nucula* Schmidt	Cn	en	28.7	9.6	20.4	1.8	1.8
Pachypellina podatypa (de Laubenfels)	Hp	scm	18	50.4	2.8		
Pseudaxinella reticulata (Ridley & Dendy)	Hl	en	9	11.2	2.6	3.6	17.4
Terpios belindae Ruetzler & Smith	Hd	en	6.8	8	6	5	1.8
Amphimedon erina (de Laubenfels)	Hp	ma	6	7.2	5.3		
Mycale americana (van Soest)	Pc	en	3.5	2.4	0.3		
Placospongia intermedia Sollas	Hd	en	3.2	18	33.6	1.2	74.7
Artemisina melana van Soest	Pc	en	3.1				
Amorphinopsis sp.	Hl	cm	2				
Ulosa arenosa Ruetzler	Hl	en	2	1	3.6	4.2	3.6
Tedania ignis (Duch. & Mich.)	Pc	en	1.5	0.9	2	3.1	
Clathria schoenus (de Laubenfels)	Pc	en	1.4	21.6	6.4	1.5	1.2
Dysidea etheria de Laubenfels	Dn	en	0.3	19.9	1.6	5	
Clathria venosa (Alcolado)	Pc	en	0.2	0.3	4.2	1.2	
Mycale laxissima (Duch. & Mich)	Pc	va		40.2	64	192	100
Xestospongia rosariensis Zea & van Soest	Hp	va		104	272	952	139.5
Agelas schmidti (Wilson)	Ag	va			25.1	255	195
Total volume (cm^3)			33,721	31,527	32,822	30,160	19,805
Total number of species			39	39	32	25	22
Total volume (cm^3) (only considering the original 39 species)			33,721	31,383	32,461	29,618	19,371
Total number of species (only considering the original 39 species)			39	37	29	22	18

Species are listed in order of decreasing abundance with respect to total volume at the beginning of the study. Orders in the Class Demospongiae are represented under ORD (Hd, Hadromerida; Ag, Agelasida; Pc, Poecilosclerida; Hl, Halichondrida; Hp, Haplosclerida; Dc, Dictyoceratida; Dn, Dendroceratida; Vr, Verongida; Cn, Chondrosida). Species are assigned to orders according to Systema Porifera (Hooper and van Soest, 2002). Growth forms are represented under FORM: erbr, erect branching; brv, erect branching vase (grouped with erbr); ma, massive; tsh, thick sheet; mv, massive vase; va, vase; en, encrusting; cm, massive cryptic; scm, semi-cryptic (surface visible, grouped with cm). Three species that colonized the censused area after the first census are included at the end of the table.

3.5. *Loss of sponge species – higher taxa*

Losses of species were not evenly divided among the nine orders of Demospongiae represented (Fig. 2). The keratose orders (skeletons of spongin fibers, no spicules), Dictyoceratida, Dendroceratida, and Verongida, suffered disproportionately, losing 7/9 species (i.e., 78%). The six other orders lost a total of 43% of their original species (proportion of species lost significantly different by the G-test, $P < .001$).

3.6. *Loss of sponge species – growth forms*

Sponges were divided into five growth form categories (Table 1, Fig. 3). (1) Erect branching sponges have solid or vase-shaped

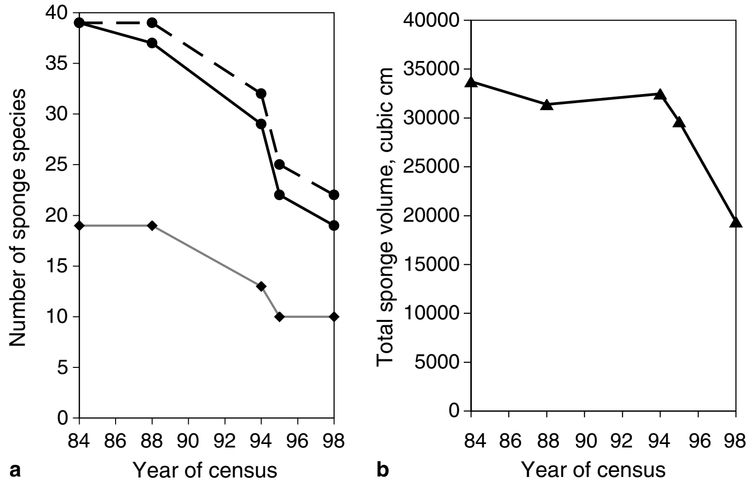

Fig. 1 – (a) Change in total number of species represented in 16 m^2 on a shallow coral reef in San Blas, Panama. Data represented by the solid line include only the original 39 species, and those represented by dashed line also include species that colonized the censused area after the first census. The grey line represents the decline of the 19 species that were most abundant (by total volume) at the start of the 14 years. (b) Change in total volume of living sponges in the same 16 m^2.

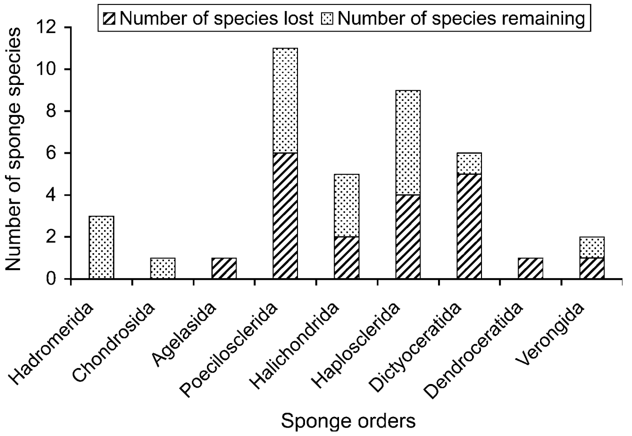

Fig. 2 – Number of the original 39 sponge species in each of the nine orders of Demospongiae represented. Cross-hatching represents species that disappeared from the censused area during the 14 years.

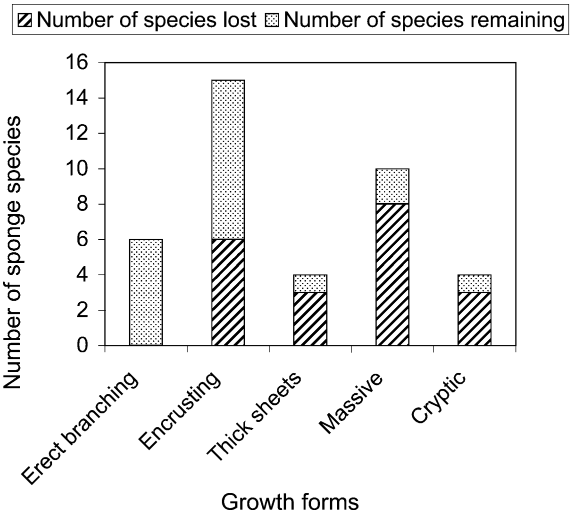

Fig. 3 – Number of the original 39 sponge species representing each of five growth form categories. Cross-hatching represents species that disappeared from the censused area during the 14 years.

branches, and a very small basal attachment:volume ratio. (2) Encrusting sponges represent the other extreme, extending in thin (generally less than 0.5 cm) two-dimensional sheets. (3) Thick sheet sponges are thicker than 1–2 cm and their surfaces are raised in low mounds. (4) Massive sponges are spherical or hemispherical. One species that is a thick-walled vase when it is large (*Ircinia campana*) was grouped with massive species because, at the smaller sizes present in the census area, it is massive. (5) Cryptic sponges are fully or mostly confined to crevices within the reef frame or under corals. All four cryptic species in this plot were massive, though constrained in shape and size by the crevices inhabited.

Sponges of different growth forms were not lost evenly (Fig. 3). No erect branching species were lost, 40% of encrusting species were lost, and 80% of massive species were lost. The proportion of massive species lost was significantly greater than those lost from the other growth forms (G-test, $P < .001$); and the proportion of erect branching species lost was significantly less (G-test, $P < .01$). Sponges of all growth forms, except erect branching, were lost throughout the 14 years, but at different rates (Fig. 4).

4. Discussion

4.1. *Rapid loss of sponge species, and how to document sponge declines*

Loss of 20 of the original 39 sponge species over a 14-year period was an unexpected and disturbing result. Loss from a small plot on one reef does not document extinction, but

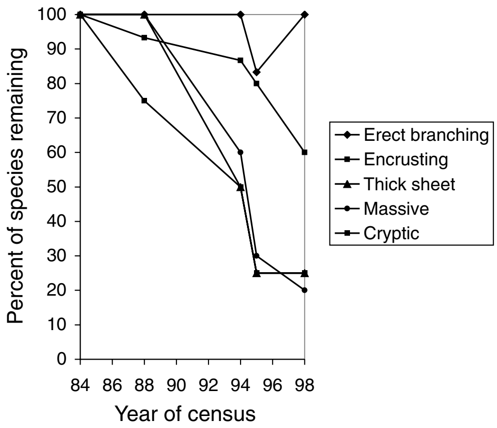

Fig. 4 – Percent of the original species in each of the five growth form categories remaining at each of the five censuses. Number of species in the plot at the start of the 14 years for each growth form were: 6 erect branching, 15 encrusting, 4 thick sheets, 10 massive, 4 cryptic.

low-intensity surveys of other reefs throughout the San Blas Point area show that these losses reflect at least a local decline in an area relatively free of direct destruction by human activities. Loss of species could not be perceived by simple observation, as the high diversity and density of sponges on Guigalatupo reef obscured the loss of any particular species until the census data were analyzed. Somewhat ironically, data analysis was delayed, and no additional census sites were established, because community stability appeared to be confirmed by the population dynamics of the three most common species, which were being studied in detail (Wulff, 1990, 1991, 1995a). However, these three are erect branching species (*Iotrochota birotulata*, *Amphimedon compressa*, *Aplysina fulva*), the sole growth form category from which no species were lost.

Populations of some species may fluctuate randomly to zero within a small census plot, but if this were the key process causing species loss, disproportionately great loss of rare species would be expected, and that was not the case. As well, if no net change is occurring in the surrounding community, an equal rate of fluctuation into the censused area would be expected, but only three species were added, while 20 were lost.

Previous reports of precipitous sponge declines have focused on a single or a few commercially important or large-bodied species (e.g., Smith, 1941; Dayton, 1978; Rützler, 1988; Butler et al., 1995; Pronzato et al., 1999; Cervino et al., 2000). In the Caribbean, where over 640 sponge species have been described (van Soest, 1994), a few very large-bodied species, e.g., *Xestospongia muta* and *Spheciospongia vesparium*, appear disproportionately often in reports of dying sponges (e.g., Goreau et al., 1998; Nagelkerken, 2000; Williams and Bunkley-Williams, 2000; and pers. comm. from E. Peters, D. Akob, T.J. Goreau, E.R. Gammill). The census data reported here suggest that, rather than being more vulnerable to mortality sources, individual large sponges may simply take longer to die (e.g., a couple of months for a large *Xestospongia muta* to die completely, Nagelkerken, 2000) and be more conspicuous while dying, boosting report rates.

The few reports of mass mortality of multiple sponge species in the wider Caribbean region have been associated with localized acute environmental disturbances, e.g., two cyanobacterial blooms in Florida Bay between 1991 and 1993 (Butler et al., 1995; Stevely and Sweat, 2001), unusual masses of cold water at Morrocoy National Park, Venezuela, in January 1996 (Laboy-Nieves et al., 2001), and a "black water event" in spring 2002, and an inversion in summer 2004, in the Florida Keys (B. Keller, pers. comm.). Losses of sponges were documented by observing the sponges as they were dying on Florida Keys reefs (B. Keller, pers. comm.) and in Venezuela (Laboy-Nieves et al., 2001). In Florida Bay, dramatic sponge losses, up to 90%, which have had profound effects on the entire ecosystem, would have never been known if Stevely (1996) had not collected prior census data on the sponge community.

Steady loss of sponge species and biomass over years is more insidious, because it can only be documented by repeated censuses. Documented loss of 20/39 species and 42.6% of the sponge biomass in 14 years, from the sole reef site in which individuals (recorded by volume) of every species have been tracked through time, raises the disturbing possibility that sponges have already been lost from other sites for which no baseline data exist. Measures of percent cover, or numbers of individuals, along randomly positioned transects, though appropriate for corals and sea urchins, do not accurately document community dynamics for a group with such (1) high morphological, size, and species diversity, (2) facility at fragmentation and fusion, (3) three-dimensional bodies, and (4) rapid disappearance after death (Wulff, 2001). To know if the losses reported here are unique or reflect large-scale sponge declines requires censuses in time series at additional sites, with volume measured, and species identified, for every individual. Ideal monitoring of coral reef sponges would include less intensive but geographically broad surveys, as well as detailed censuses of small permanent plots.

The power of data from repeated community-wide censuses has been well demonstrated. Surprising and profound conclusions from long-term studies based on photo quadrats on Australian and Jamaican reefs (Connell, 1997; Connell et al., 1997; Hughes, 1996; Hughes and Jackson, 1985; Hughes and Connell, 1999) demonstrate that there is no quick and easy substitute for tracking all of the individual organisms in a community through long periods. Unfortunately, photo quadrats are inadequate for coral reef sponges, as sponge abundance is most meaningfully measured by volume, and photos miss sponges living under and on the sides of corals (Wulff, 2001). Every individual must be measured in the field at each census. Although the time involved may seem daunting, the worthiness of such an investment is well illustrated by the recent compilation of results, many of which are relevant to conservation, from the world-wide network of 50 ha census plots in tropical forests (Losos and Leigh, 2005; reviewed by Knapp, 2005). Lives and deaths of the individuals that constitute a community cannot be documented by any other means.

4.2. What caused the loss of sponge species?

Patterns in the types of species lost from a community can sometimes provide clues about the causes of loss. In a terrestrial example, re-censuses of Wisconsin prairie remnants, after 32–52 years, revealed losses of 8–60% of the plant species. The disproportionate loss of short, small-seeded, nitrogen-fixing, and wet habitat-dwelling species directed attention towards fire suppression, due to habitat fragmentation, as a cause of species loss (Leach and Givnish, 1999). Likewise, small mammals lost from Brazilian forests were of species that are less able to cope with grassy vegetation between forest fragments (Viveiros de Castro and Fernandez, 2004); and birds with specific habitat requirements, such as nectivores that must move among habitats according to phenologies of nectar plants, have been disproportionately lost from Southern Australia woodlands (Ford et al., 2001). With the caution that the ecology of individual species of terrestrial plants and animals is generally better understood than ecology of marine sponges, it is possible to apply this approach to these sponge census data. High overlap in species lost from the census plot and those that declined on nearby reefs suggests that declines were not random, but that particular species were especially vulnerable to whatever caused the declines.

Loss of sponge species to physical disturbance is not consistent with the patterns observed. Declines in number of species did not coincide temporally with Hurricane Joan (October 1988), which was the most dramatic disturbance during the 14 years of this study. In very shallow water, many erect branching sponge individuals were lost, but the keratose species that declined in the plot were disproportionately among the hurricane survivors (Wulff, 1995a). Sponge volume losses measured directly after Hurricane Joan were quickly recovered, and volume did not begin to plummet in the census plot until 1994.

Food preferences of the spongivores on this reef (determined by experiment and observation) cast doubt on the possibility that predators could be responsible for sponge losses. A total of 4150 bites on sponges by seven species of unmanipulated angelfishes, trunkfishes, and filefishes were observed in and near the censused area (Wulff, 1994). Fish took bites from most of the sponge species (35/39 species = 90%), but disproportionately avoided sponges in the genus *Ircinia* (Wulff, 1994), which declined. There was no evidence that the large, seagrass-dwelling starfish, *Oreaster reticulatus,* ventured onto this reef during the 14 years (parrotfishes bite them if they move onto the reef), but if they had, prey choice experiments (Wulff, 1995b) indicate that they could have consumed *Ircinia felix*, which declined, but also *Mycale laevis* and *Iotrochota birotulata*, which were among the few species that increased (Table 1).

Disproportionately great loss of sponge species that are resistant to physical disturbance and predators leaves few other possible explanations of continuous decline. Drastic episodic changes in salinity, temperature, or sedimentation are one possibility. In a study of coral and algal dynamics on the reefs in this same area of San Blas, Shulman and Robertson (1996) documented substantial declines in corals, and increases in macroalgae and microalgae, between 1983 and 1990. They considered increases in sedimentation due to deforestation as a possible factor, but temporal patterns of community changes especially implicated coral bleaching in 1983 and decreases in grazing due to the die-off of the sea urchin *Diadema antillarum* in 1983. Corals did not decline much in the Guigalatupo plot, but the first census was made after the 1983 bleaching. Although *Agaricia*, the coral genus that was most affected by bleaching, was the second most abundant coral genus by surface area of live tissue in the plot, it constituted only 14.2% of total coral area at the first census. The lack of a sponge decline concomitant with the coral decline between 1984 and 1988 may indicate that sponges were less affected than corals by loss of *Diadema*. After 1988, rapid and steady declines in sponges in the census plot, but not in corals, argue against sponge loss due to extreme episodes of any abiotic conditions that would have also influenced corals.

Disease, increasingly prevalent in reef corals (e.g., Green and Bruckner, 2000; Sutherland et al., 2004), has also been implicated in some rapid sponge declines (e.g., Smith, 1941; Reiswig, 1973; Rützler, 1988; Pansini and Pronzato, 1990; Pronzato et al., 1999; Cervino et al., 2000). Five of the species that declined on Guigalatupo and other nearby reefs were among those in which disease was observed. The possibility that at least some sponge losses from the censused plot and nearby reefs were due to disease is compatible with the observed patterns of disproportionate loss of keratose species (78% lost from the keratose orders Dictyceratida, Dendroceratida, Verongida; vs. 43% of species in the other six orders) and disproportionate survival of branching species (100% survival, vs. 40% survival of encrusting species, and 20% survival of massive species).

Keratose species, including commercially valuable sponges, have consistently dominated reports of loss of sponge species to disease in the Caribbean during the 1930s (Smith, 1941), in Florida Bay during the 1980s (Butler et al., 1995; Stevely and Sweat, 2001), in Papua New Guinea (Cervino et al., 2000), and in the Mediterranean (Pansini and Pronzato, 1990; Pronzato et al., 1999). Reiswig (1973) suggested that keratose species are more susceptible to environmental stresses because of their denser tissue; and Vicente (1989) suggested that the genera *Spongia* and *Hippospongia* are especially vulnerable to pathogen infection in warmer waters because they evolved in cooler water.

By contrast, sponges of branching growth forms (including those in keratose orders) may be less vulnerable to mortality due to disease. Adherence of erect branching sponges to heterospecific neighbors has been demonstrated to increase survival of branch fragments that have been severed by hazards (including species-specific pathogens) that differentially affect each species (Wulff, 1997a). Branching species may also experience increased genet survival when infected portions are physiologically isolated by asexual fragmentation.

Directly evaluating the importance of disease for sponge community dynamics is difficult because sponges fall apart and disappear shortly after death. Smith (1941) reported that sponges were completely rotted within a week of the first sign of disease. Adding two weeks for the bared skeleton to fall apart suggests that a medium-sized diseased sponge could disappear within 3 weeks. If this estimate of the time during which a sponge individual could be observed in a dying state is a reasonable average, and disease occurs throughout the year (as observed at this site), it is possible that only 1/17th of the annual disease incidence in these sponges would be observed in the course of 3 weeks of field work, i.e., observation of only five diseased sponges in the plot could represent a sample (in time) of a total of 85 diseased sponges in the course of a year. Whether or not disease caused species loss from this plot, these calculations suggest that disease could have a much larger impact then indicated by observed prevalence during routine monitoring.

4.3. *Sponge species diversity and community change*

High sponge species diversity makes sponge monitoring taxonomically daunting, especially because of the difficulty of sponge systematics and the paucity of experts. High sponge species diversity also inhibits perception of decline in any particular species. Functionally, however, high diversity may help to improve survival of individual sponges. High species diversity may decrease rates of infection by species-specific pathogens by decreasing the density of any particular species (Wulff, in preparation). Mutually beneficial interactions, frequently demonstrated among sponge species (Sarà, 1970; Rützler, 1970; Wulff, 1997a; Wilcox et al., 2002), may help retain species in the community. High species diversity can increase the probability that neighboring sponge individuals are of different species, satisfying a key condition for mutualistic associations that can increase survival of a variety of environmental challenges by participating individuals (Wulff, 1997a). Thus, coral reef sponges may be an example of positive, community-level, functional consequences of high species diversity. Declines in sponge species diversity on coral reefs may increase the rate at which remaining sponge species are lost.

4.4. *Implications of rapid loss of sponge species*

Loss of sponges from coral reefs eliminates important players in carbonate balance and coral reef health (reviews in Diaz and Rützler, 2001; Wulff, 2001). Loss of different types of sponges may have different effects on ecosystem function. A massive individual has water filtering capacity orders of magnitude greater than an encrusting sponge of the same footprint. Branching species stabilize coral rubble, as their asexually produced fragments reattach to solid substrata; and cryptic species grow from within the reef frame to stabilize rubble (Wulff, 1984). Encrusting and cryptic sponges protect coral skeleton surfaces that are otherwise vulnerable to excavating organisms (Goreau and Hartman, 1966), and some encrusting sponge species with photosynthetic symbionts can aggressively overgrow live corals (e.g., Rützler and Muzik, 1993) or co-opt settlement space from corals (e.g., Aronson et al., 2002). Keratose sponges are often resistant to predators and severe physical disturbance. Large massive species provide shelter for juveniles of mobile animals as well as enormous diversity and numbers of inquilines (e.g., Beebe, 1928; Butler et al., 1995; Cerrano et al., in press).

Contributions of the sponge assemblage at Guigalatupo to ecosystem function may have altered as the total sponge volume dropped by 42.6%, and the percent of the total volume consisting of massive sponges dropped from 22% to 8% (10.5% if the three thick-walled vase-shaped species that were added are included in the massive category), thick sheets from 11% to 1%, and encrusting species from 12% to 4%; while volume of erect branching species constituted 64% of the total at the beginning, and 85% fourteen years later (data in Table 1).

Sponges engage in mutually beneficial interactions with corals (Goreau and Hartman, 1966; Wulff and Buss, 1979), zoanthids (e.g., West, 1976), other sponges (Wulff, 1997a), and many other organisms. Secondary loss of species, i.e., loss of species that depend on species that have been directly diminished by environmental changes, is of particular concern for taxa engaged in mutualisms with sponges.

Throughout the Caribbean declines in corals and increases in algae, similar to those documented by Shulman and Robertson (1996) in San Blas, are being reported (e.g., Gardner et al., 2003; Lang, 2003; Wilkinson, 2004). Causes of coral reef degradation are many, some easier to measure than others. Climate change, nutrients, sediment, over-fishing, physical damage by humans, disease, and herbivore loss have all been implicated in various mixtures (e.g., Hughes and Connell, 1999; Rogers, 2000; Aronson et al., 2002; Knowlton, 2001; Zakai and Chadwick-Furman, 2002; Hughes et al., 2003; Pandolfi et al., 2005). Changes in diversity and abundance of sponges are more difficult to quantify, but loss of sponges may be an important factor in reef deterioration. It would be surprising if loss of significant ecosystem services provided by sponges, such as water column filtering, nutrient regeneration, binding of live corals to the reef, and facilitation of reef regeneration, did not significantly contribute to declines in corals and coral reefs.

5. Conclusions

The steady loss, over 14 years, of 51.3% of the sponge species, and 42.6% of the total sponge volume, at a permanent site on a shallow Panama coral reef, was documented by five censuses. Predators, physical disturbances, episodes of extreme abiotic factors, and random fluctuations of populations of rare species can be eliminated as the primary causes of species loss, but it is not certain what caused the mortality. Circumstantial evidence implicates disease in at least some of the losses, but sponges die and disappear so quickly that many censuses per year are required to determine exactly how much mortality is caused by disease. Less intensive surveys of nearby reefs corroborated that species losses were not confined to the censused area. To know if these data documenting sponge diversity decline are, or are not, indicative of a region-wide phenomenon requires more studies in which permanent sites are completely censused in time series, in conjunction with wide-ranging, less intensive, surveys. On this shallow Panamanian reef, community composition shifted as significantly greater proportions of sponge species with massive growth forms and in keratose orders were lost, while all erect branching species survived. Severe losses of corals and deterioration of coral reefs throughout the Caribbean region are causing great concern. Because loss of ecosystem services provided by sponges, such as increased coral survival, reef regeneration, and water clarity, can contribute to coral reef declines, determining if sponge declines are widespread must be a priority.

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