SYMPOSIUM

Recovery of Sponges After Extreme Mortality Events: Morphological and Taxonomic Patterns in Regeneration Versus Recruitment

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Synopsis Sponges on the Belize Barrier Reef were drastically diminished in 2 mortality events during a 6-year period. Patterns in mortality and recovery were revealed by detailed records of assemblage dynamics, in the form of 8 full censuses between June 2006 and July 2012. All sponges on a set of shallow patch reefs were mapped, identified, and measured for volume at yearly or more frequent intervals, allowing population dynamics of 54 sponge species to be quantified with respect to volume of live tissue and number of individuals. The degree to which sponges of different species suffered during each of the mortality events ranged from complete loss to no effect, resulting in immediate significant alterations in composition of the assemblage in addition to extreme losses (49% in 2008 and 71% in 2011) of the volume of living sponge. The repeated census data documented the early stages of recovery, both on the assemblage level and for every individual sponge. Groups of sponge species, defined by higher taxa or by growth form, not only experienced mortality very differently, but also recovered differently, with some showing efficient regeneration after partial mortality, others adding small individuals by recruitment, and still others not recovering at all. During the 2008 mortality event, losses of both volume and numbers of individuals were disproportionately heavy for members of the orders Aplysinida and especially Poecilosclerida, and for sponges of erect branching and semi-cryptic massive growth forms. Post-mortality recruitment was meager, resulting in no rebound in numbers of individuals; regain of volume lost was slowed by the extreme loss of many entire individual poeciloclerids. By contrast, during the 2011 mortality event, loss of volume was disproportionately heavy for members of the orders Hadromerida and Dictyoceratida, while numbers of individuals were lost from all orders in the same proportion. Among the growth forms, volume was disproportionately lost from massive and semi-cryptic massive sponges, while numbers were only disproportionately lost from the semi-cryptic massive species. During the first 7 months of recovery, a quarter of the lost volume and numbers were re-gained, by a combination of regeneration and recruitment. Relatively rapid early recovery stages reflected the high degree to which losses of volume were due to substantial partial mortality of massive sponges. Significant differences between the 2 mortality events in loss and recovery patterns among higher taxa, as well as among species within particular higher taxa, provide strong impetus for accurate identification to species of all sponges encountered in monitoring, and for continuing efforts aimed at understanding all levels of sponge systematics. In turn, patterns of mortality and recovery may be able to contribute additional characters for systematics.

Introduction

As extreme mortality events become increasingly common in coastal marine systems (e.g., Cerrano et al. 2000; Pronzato and Manconi 2008; Cebrian et al. 2011; Stevely et al. 2011), patterns of recovery, and failure to recover, are increasingly determining the course of the composition and dynamics of communities. Systems in which disturbance has been a normal feature often are populated by species that are well adapted to cycles of disturbance and recovery. By contrast, in systems in which extreme mortality is rare, and some of the current causes of mass mortality are relatively novel with respect to the evolutionary history of the organisms, recovery may be less reliable. The long course of recovery in systems lacking quick-recovering species can stymie efforts to study patterns in recovery. Accurately predicting recovery can be impossible because mortality events

can have very different recovery trajectories if the causes of mortality and the types of mortality differ, even when the same total amount of biomass is lost.

Sponges are famous for their ability to regenerate, even after substantial partial mortality and damage. Controlled experimental damage of sponges has provided some understanding of regeneration rates and of circumstances that can facilitate regeneration (e.g., Wulff 2010 and references therein), but recovery of sponges after natural damage has been less studied. Rapid healing and regeneration after partial mortality, combined with rapid disintegration and disappearance of portions of sponges or of entire sponges that have died, have caused sponge mortality events and subsequent recovery patterns to be largely invisible. Unless individual sponges have been followed over time, their loss, or partial loss, can be rendered invisible in as little as a few weeks.

Recovery of sponges has been reported for two tropical western Atlantic mortality events. Directly after a major hurricane in Jamaica, monitoring of individuals of 67 species of coral reef sponges for the first 5 weeks of recovery revealed an inverse relationship between susceptibility to damage by an intense acute physical disturbance and ability to efficiently regenerate (Wulff 2006b). Recovery of 23 species of sponges was monitored after a very different kind of mortality event in the Florida Keys, where recurrent dense cyanobacterial blooms were associated with extreme sponge mortality (Stevely and Sweat 1995; Stevely et al. 2011). Entire loss of individuals, even to the point of every individual of some species, occurred during some blooms, and thus recovery was primarily in the form of recruitment by larvae, with a lag time of 9–10 years.

Permanent census plots, in which every sponge is mapped, identified to species, and measured with respect to volume are the sole means by which such mortality events—or their absence—can be confidently evaluated, and patterns of recovery documented. In this report, 6 years of data (eight complete censuses) from a permanent plot on the Belize Barrier Reef are presented, illustrating taxonomic and morphological patterns in mortality of 54 sponge species during two extreme mortality events, as well as the early stages of recovery from each. Comparisons of loss and recovery, with respect both to numbers of individuals and total volume of sponges, demonstrate how loss of entire individuals versus partial mortality sets the stage for recovery or continued loss. Identification of every sponge to species allows exploration of the possibility that vulnerability to, and recovery from, environmental

challenges may be predictable within higher taxa. In turn, the taxonomic signatures in patterns of vulnerability and recovery may be informative additions to molecular and morphological characters used in systematics decisions.

Methods

On a shallow reef near the Carrie Bow Cay field station of the Smithsonian Institution on the Belize Barrier Reef, a permanent census plot was established in June 2006. This reef, part of a set of cays known as the Blue Ground Range (map in fig. 1 of Rützler et al. 2000), is windward-facing, with the edge of the barrier reef about 7 km to windward. Seven patch reefs were chosen as representative of the patch reefs (which ranged in area of hard substratum from approximately 1–20 m^2) within the 400-m^2 plot, and detailed maps were made of every individual sponge, coral, and gorgonian on each of those patch reefs. Every sponge was identified to species and its volume measured without disturbing it, by taking sufficient linear measurements to accurately calculate volume by reference to appropriate
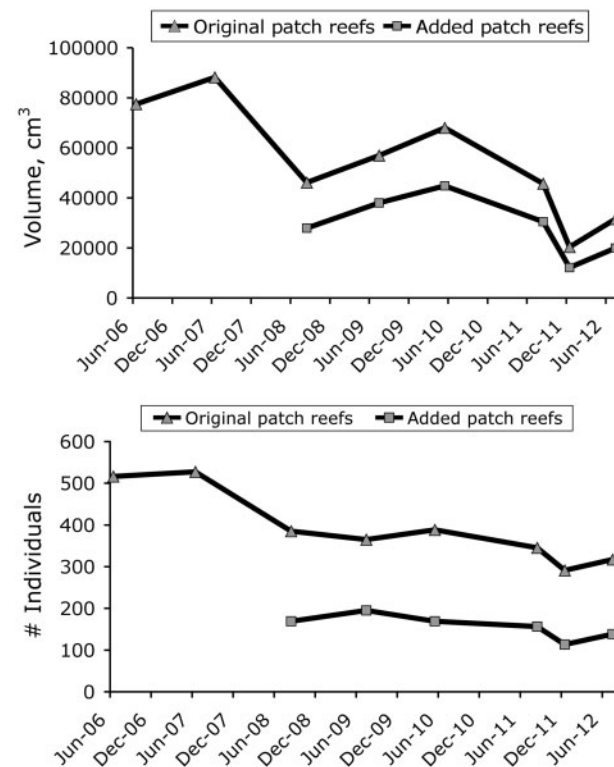

Fig. 1 Sponge assemblage dynamics as measured by eight complete censuses in the course of 6 years: total volume of living sponges (top graph) and total number of individual sponges (bottom graph) on 10 patch reefs (seven of them censused beginning in 2006, and three patch reefs added in 2008) in the Blue Ground Range, Belize Barrier Reef.

conglomerations of geometric solids. The census was repeated at approximately yearly intervals until the seventh census in December 2011, and the eighth in July 2012, which were carried out at 4-month and 7-month intervals, respectively. At each census, all previously mapped sponges were re-measured or noted to be missing, and new recruits from larvae or fragments were added to the maps. Detailed notes were kept of the condition of each individual sponge (i.e., necrotic patches, wounds from bites, or other damage, as well as evidence of recovery from damage), and all interactions with other sessile organisms, including corals, were recorded. In 2008, three patch reefs were added to the census, for a total of 10 (and a total area of hard substratum on the censused patch reefs of $25.5\,m^2$), for the last 4 years of the study.

The compiled and analyzed data are in the form of changes in size (in terms of volume) and survival of every individual sponge on seven patch reefs over a 6-year period, and changes in size and survival of every sponge on a total of 10 patch reefs for the final 4 years of that period. Thus in the analysis, data from all 10 patch reefs are used whenever a time-series comparison began during, or after, 2008, but for comparisons involving 2006 or 2007, data from only the original seven patch reefs are used. Within these data are embedded the following data for 54 species of sponges: (1) population dynamics in terms of numbers of individuals as well as total volume, (2) survival during two different extreme mortality events, as well as during more normal years, (3) growth rates, (4) recruitment rates, and (5) ability to regenerate after partial mortality. Rates of loss and recovery can be compared on the assemblage level, as well as individually for each of the 54 species of sponge, for two mortality events. A companion report (J. Wulff, in preparation) will focus on details of assemblage change and the repercussions for coral and reef health, while this report is focused on how patterns of loss of entire individuals versus portions of individuals set the stage for recovery by recruitment versus regeneration, and how growth form and membership in a higher taxon may contribute to those patterns.

In 2011, the timing and cause of the mortality event was clear. Sponges were dying during the census in August, and a complete re-census 4 months later, in December, confirmed that sponges had continued to die, although there were no signs of mortality still in progress in December. The sponge mortality coincided with a clear environmental anomaly, an extremely dense phytoplankton bloom covering the entire southern portion of the Belize Barrier Reef for much of July–August 2011. Visibility at the census site was less than 30 cm for much of the censusing. In 2008 however, the cause and exact timing of mortality remain a mystery, because it had already occurred by the time censusing began. Dead sponges had vanished and sponges that had suffered partial mortality had completely healed their wounds.

Results

All species combined: two mortality events and two recoveries

Total volume of living sponges decreased by 49% between the summer censuses of 2007 and 2008, and by 71% between summer 2010 and December 2011 (Fig. 1). The number of individuals diminished by 27% between 2007 and 2008, and also by 27% between 2010 and 2011. Recovery in the 3 years before the mortality in 2011 was only 52% of the volume that was lost in 2008, and there was no net regain of numbers of individuals lost in 2008. Thus, the net result of the second mortality event, following after so little recovery from the first, was that these patch reefs were inhabited by 74% less sponge volume and 44% fewer individuals in December 2011 than in July 2006. Some recovery was evident only 7 months after the December 2011 census, when 24% of the volume and 27% of the numbers that had been lost in 2011 had already been re-gained. Even after that amount of recovery, however, these patch reefs were inhabited by 59% less sponge volume and 39% fewer individuals than they had been 6 years earlier. Dynamics on the three patch reefs that were added to the census in 2008 were the same as on the seven original patch reefs (Fig. 1).

Among the 54 species in the census plot were representatives of 11 recognized orders of the class Demospongiae. Three orders were meagerly represented (one species each in Chondrosida, Agelasida, and Dendroceratida, representing at their maximum abundance only 1.3%, 0.3%, and 1.2% of the total numbers and 0.1%, 0.06%, and 0.4% of the total volume), so in the following analysis the remaining 51 species are grouped in their eight orders (Hooper and van Soest 2002). Sponges' growth forms can be defined by a variety of criteria, and in this case categories that reflect functional roles played in coral reef ecosystems were chosen, because of differing repercussions on coral reef health of losses from the different categories. The categories are: erect branching, massive, semi-cryptic massive (i.e., visible from the reef surface and protruding somewhat, but with

the bulk of the massive body of the sponge tucked into crevices in the reef or under corals), and encrusting (less than 5 mm in thickness).

Loss of volume versus numbers of individuals: partial mortality versus death of whole individuals

Patterns of loss of biomass were not necessarily reflected in loss of individuals. In the 2008 mortality event, volume was significantly lost disproportionately from species representing Aplysinida and especially Poecilosclerida ($P < 0.001$, G-test of proportions lost for each order relative to the overall proportion lost). Individuals were also disproportionately lost ($P < 0.001$) from these same two orders, with poecilosclerids particularly diminished (Fig. 2), indicating the great extent to which the losses in volume were due to death of entire individuals rather than to partial mortality (Fig. 2). Patterns of loss of sponges representing different orders were very different in 2011, when volume was disproportionately lost from Hadromerida and Dictyoceratida ($P < 0.001$), but numbers of individuals were lost proportionately from all orders (Fig. 2).

Patterns of loss of sponges representing different growth forms also differed between mortality events. In 2008, volume was disproportionately lost from sponges of erect branching and semi-cryptic massive species ($P < 0.001$), and losses of individuals also followed the same pattern ($P < 0.001$). In 2011, volume was disproportionately lost from massive ($P < 0.001$) and semi-cryptic massive sponges ($P < 0.001$). Numbers of individuals were lost disproportionately from semi-cryptic massive sponges ($P < 0.001$), but individuals of sponges in the other growth-form categories were not lost at significantly different proportions from overall losses of individuals (Fig. 2).

Recovery after the 2008 mortality event

During the year after discovery of the 2008 mortality event, not only was there no regain of lost numbers of individuals, but number of individuals was diminished by an additional 3.8%. The relatively small change in the number of individuals was a result of further small decreases in numbers of Halichondrida, Dictyoceratida, and Aplysinida, balancing very modest increases in the other orders (Fig. 3). Volume increased in every order, with a total regain of 25.6% of the volume lost, but members of the Poecilosclerida re-gained disproportionately little of what had been lost (only 12.7%, $P < 0.001$, G-test comparison with the proportion of lost volume that was re-gained overall) and species in Aplysinida re-gained only 5.9% of what had been lost (significantly lower

proportion by the G-test, $P < 0.001$). By contrast, the Dictyoceratida re-gained a significantly greater proportion of the volume that had been lost, 27.5% ($P < 0.001$), as did the Haplosclerida (75.2%, $P < 0.001$).

Recovery varied among categories of growth form, with both massive and semi-cryptic massive sponges re-gaining disproportionately more (nearly a third) of the volume that was lost ($P < 0.001$ for both orders), but branching sponges only re-gaining 6.5% of what was lost. Encrusting sponges dramatically increased in volume, although the volume that members of this category add to the total is trivial (0.4% in 2007, and even after their disproportionately large post-mortality increase in 2009 only 1.8%). The semi-cryptic massive sponges re-gained 28.3% of the numbers of individuals lost ($P < 0.001$, G-test comparison of proportion of numbers of individuals lost that were re-gained relative to the overall proportion re-gained), but numbers of individuals continued to dwindle from all of the other three categories of growth form in 2008–2009 (Fig. 3).

Recovery after the 2011 mortality event

Recovery after the 2011 mortality event was in many respects a mirror image of recovery after that of 2008. By July 2012, total number of sponges had increased by 26.8% of the number lost, with disproportionate regains of lost numbers in members of the Poecilosclerida and Aplysinida ($P < 0.001$ for both; Fig. 4). Total sponge volume was also re-gained, by 24.5% of the amount lost, with disproportionately greater proportions of the lost volume re-gained by Poecilosclerida and Aplysinida ($P < 0.001$). Sponges in the orders Spirophorida and Hadromerida also re-gained a significantly greater proportion of the volume lost in the mortality event ($P < 0.001$), but these orders were represented by low volume and low numbers of individuals throughout the 6 years of the study. Members of the Haplosclerida continued to diminish with respect to numbers, and failed to regain volume lost.

Encrusting sponges not only re-gained all the numbers and volume lost in the 2011 mortality event, but increased in numbers and volume to greater levels than in 2010 (Fig. 4). Even so, they constitute a very small proportion of the total volume, only 1.4% in 2012. Erect branching sponges also re-gained, both in numbers and in volume, more than was lost during the 2011 mortality event. These rapid rebounds were balanced by regains in massive sponges of only 20.8% of the
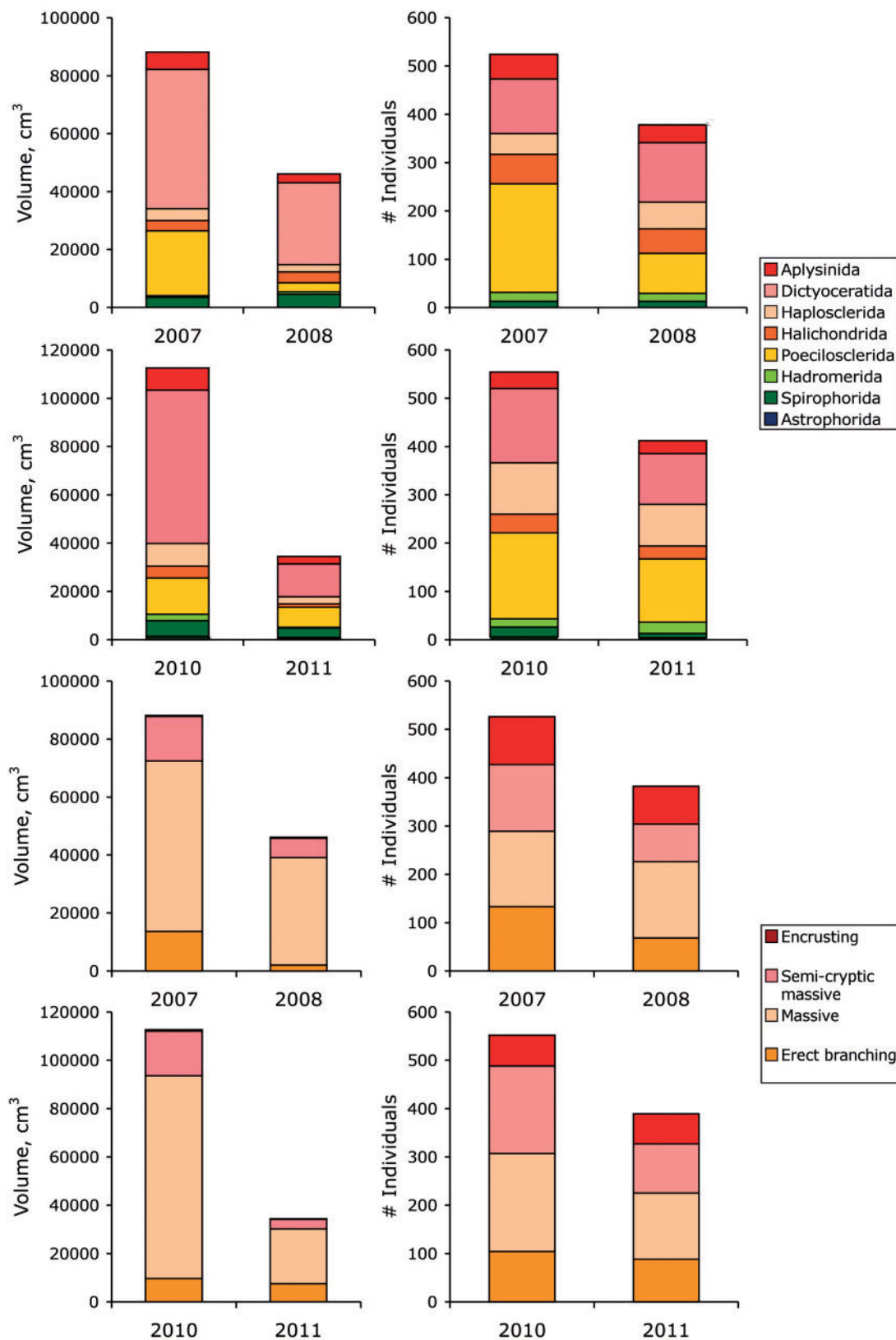
Fig. 2 Comparison of patterns in loss of volume versus loss of numbers of individuals among higher taxa and growth forms—top set of four graphs: total volume of living sponges, and total numbers of individuals, representing eight orders of the class Demospongiae before and after mortality events in 2008 and 2011. Bottom set of four graphs: total volume of living sponges, and total number of individuals, representing four growth-form categories based on functional roles of sponges in coral reef ecosystems, before and after mortality events in 2008 and 2011.
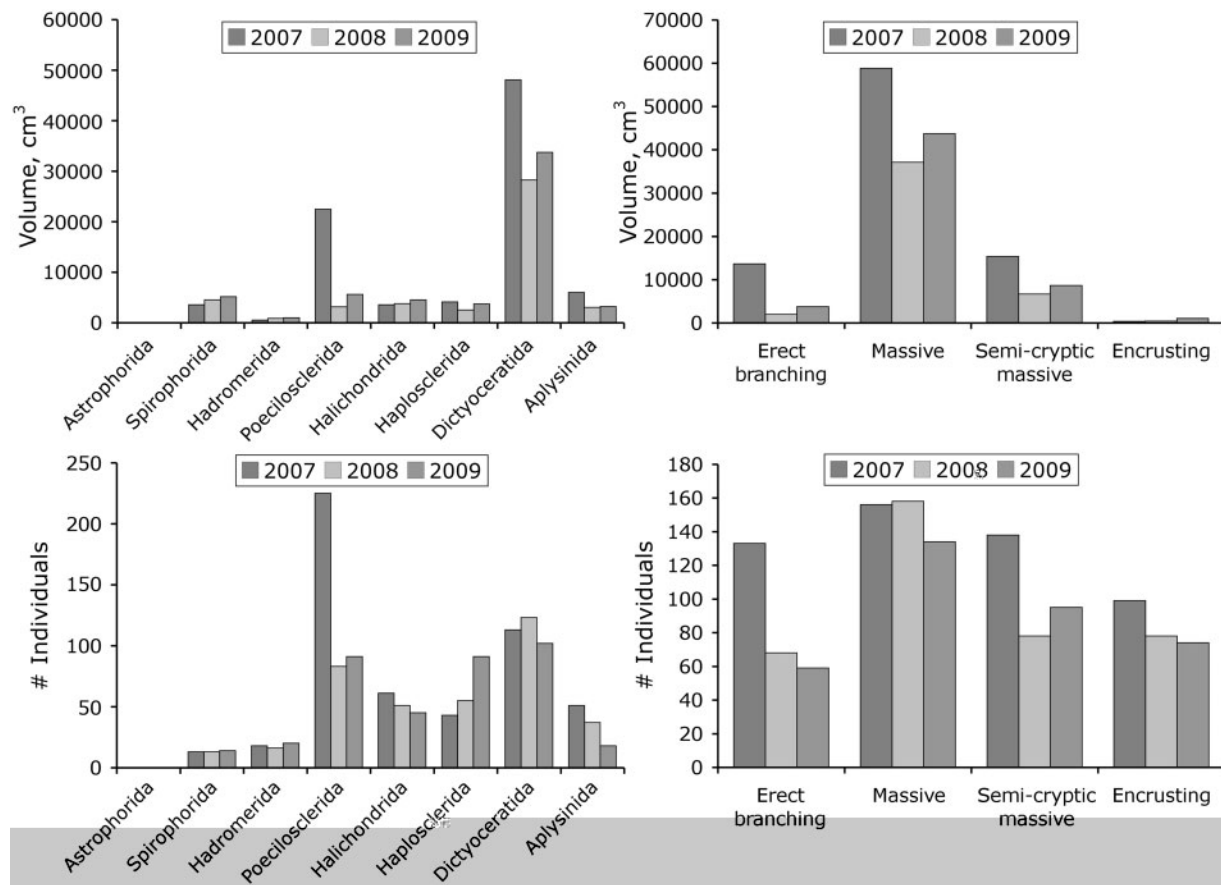
Fig. 3 Recovery of volume and numbers of individuals lost in the 2008 mortality event: volume lost and re-gained in eight demosponge orders and four functionally-defined growth forms (top graphs), and numbers of individuals lost and re-gained in eight demosponge orders and four functionally-defined growth forms (bottom graphs).

lost volume and 34.8% of the lost number of individuals, and the semi-cryptic massive sponges re-gained even less, only 2.9% by volume and 17.7% by numbers (Fig. 4).

Individual species

Population dynamics over the 6 years (eight full censuses) are compared with respect to volume and to numbers of individuals, for 11 of the most abundant species, chosen to highlight both the common characteristics imposed by higher taxon and growth form, as well as the differences imparted by idiosyncrasies of individual species. The comparisons include: four species within the order Poecilosclerida, representing three categories of growth form; four species within the genus *Iricinia*, representing two growth-form subcategories; and three species within the family Aplysinidae, representing two growth-form categories.

Poecilosclerida as a whole were strikingly diminished (86% by volume, 63% by numbers; Figs. 2 and 3) in the 2008 mortality event, and this overall pattern reflects drastic losses in all of the common

poeciilosclerid species (Fig. 5). *Mycale laevis*, initially one of the most conspicuous species, virtually disappeared, and species that initially were abundant, *Iotrochota birotulata* and *Lissodendoryx colombiensis*, also plummeted in volume, although a greater proportion of mortality in those species consisted of partial mortality rather than losses of entire individuals. Recovery for both *M. laevis* and *L. colombiensis* involved addition of new individuals by larval recruitment, whereas *I. birotulata*, representative of the erect branching sponges, showed barely any increase in numbers and little in volume, and *Desmapsamma anchorata*, also a branching species, increased rapidly in volume.

A substantial portion of the initial sponge volume on these reefs was of species representing the order Dictyoceratida, in particular the genus *Ircinia* (48% of the total volume in 2006). Population dynamics for the four *Ircinia* species fell into two distinct patterns. Although all four species are in the massive growth-form category, two of them have very large volume to footprint ratios (*Ircinia strobilina*, a sphere, and *Ircinia campana*, a very thick-walled
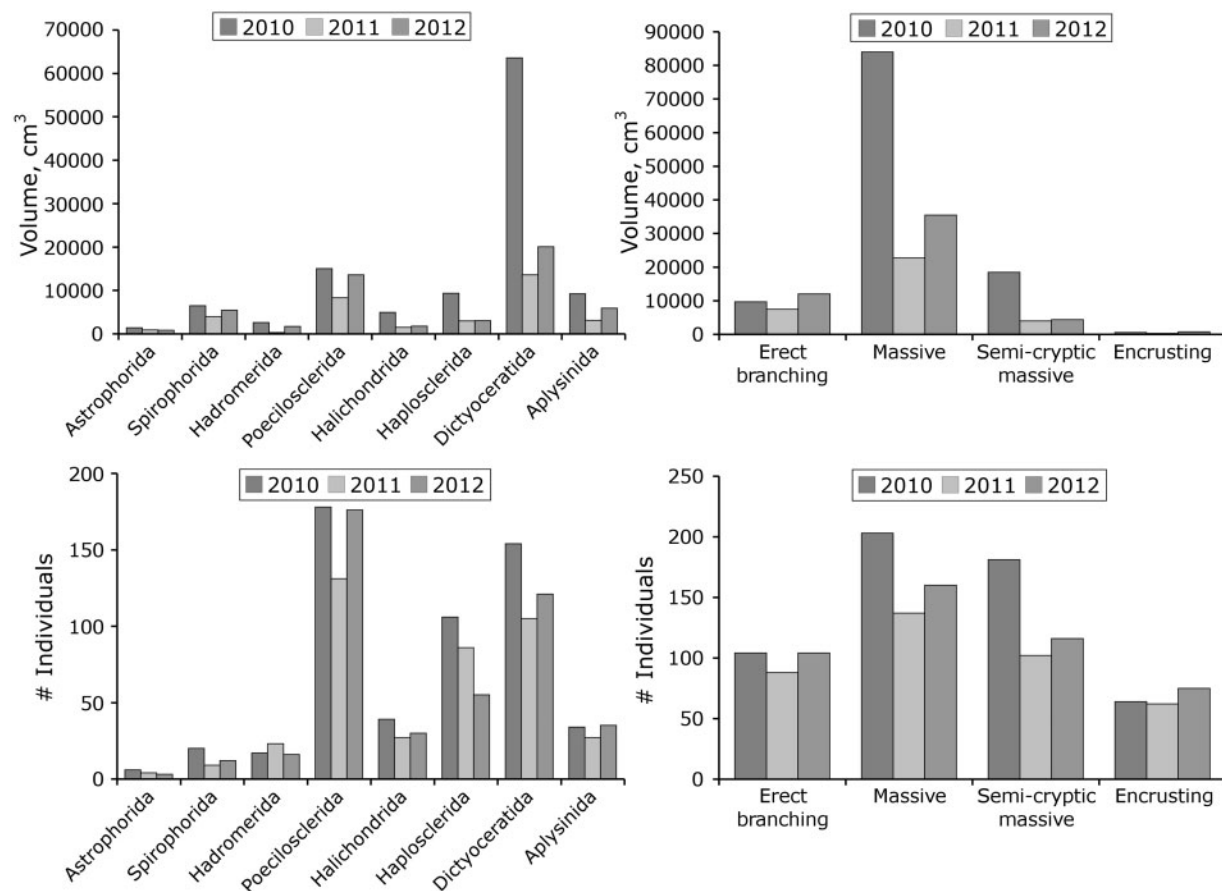
Fig. 4 Recovery of volume and numbers of individuals lost in the 2011 mortality event: volume lost and re-gained in eight demosponge orders and four functionally-defined growth forms (top graphs), and numbers of individuals lost and re-gained in eight demosponge orders and four functionally-defined growth forms (bottom graphs).

vase), and the other two typically continue to spread laterally as they grow, although they can be quite thick (up to 15 cm at this site). These laterally spreading species suffered with respect to volume during both mortality events, but rebounded readily so that both species maintained a substantial presence in the community (Fig. 6). By contrast, the two high volume:footprint species diminished both in volume and in numbers in the 2008 mortality, and although they re-gained a small portion of volume they re-gained no individuals. Continued losses in the 2011 mortality event resulted in both of these species being completely eliminated from the censused patch reefs, even though out of the 54 species they initially had ranked 2nd and 11th with respect to volume.

Three species of the family Aplysinidae, one massive and the others erect branching, were abundantly represented. The population dynamics of the massive species, *Verongula rigida*, were strikingly similar to those of the massive dictyoceratid species, with a large drop in volume in 2008, followed by a moderate increase before an even larger drop in 2011, and with number of individuals steadily diminishing throughout the 6 years (Fig. 7). By contrast, the branching species, *Aplysina fulva* and *Aplysina cauliformis*, differed from all of the other species by losing volume in 2007. As typical for erect branching sponges, dynamics in terms of numbers of individuals and of volume do not fluctuate in tandem.

Discussion

It cannot be over-stressed that the reefs of the Blue Ground Range appeared to be healthy and well-decorated with abundant and diverse sponges in December 2011. Sponges did not look damaged and there were no signs of mortality in progress, although comparisons of the sizes of individual sponges with their sizes measured during the 2010 census provided incontrovertible evidence that many of them had suffered partial mortality, losing as much as 95% of their volume. There was 74% less volume of living sponge and 44% fewer individuals on the reefs than only 5.5 years earlier, and many
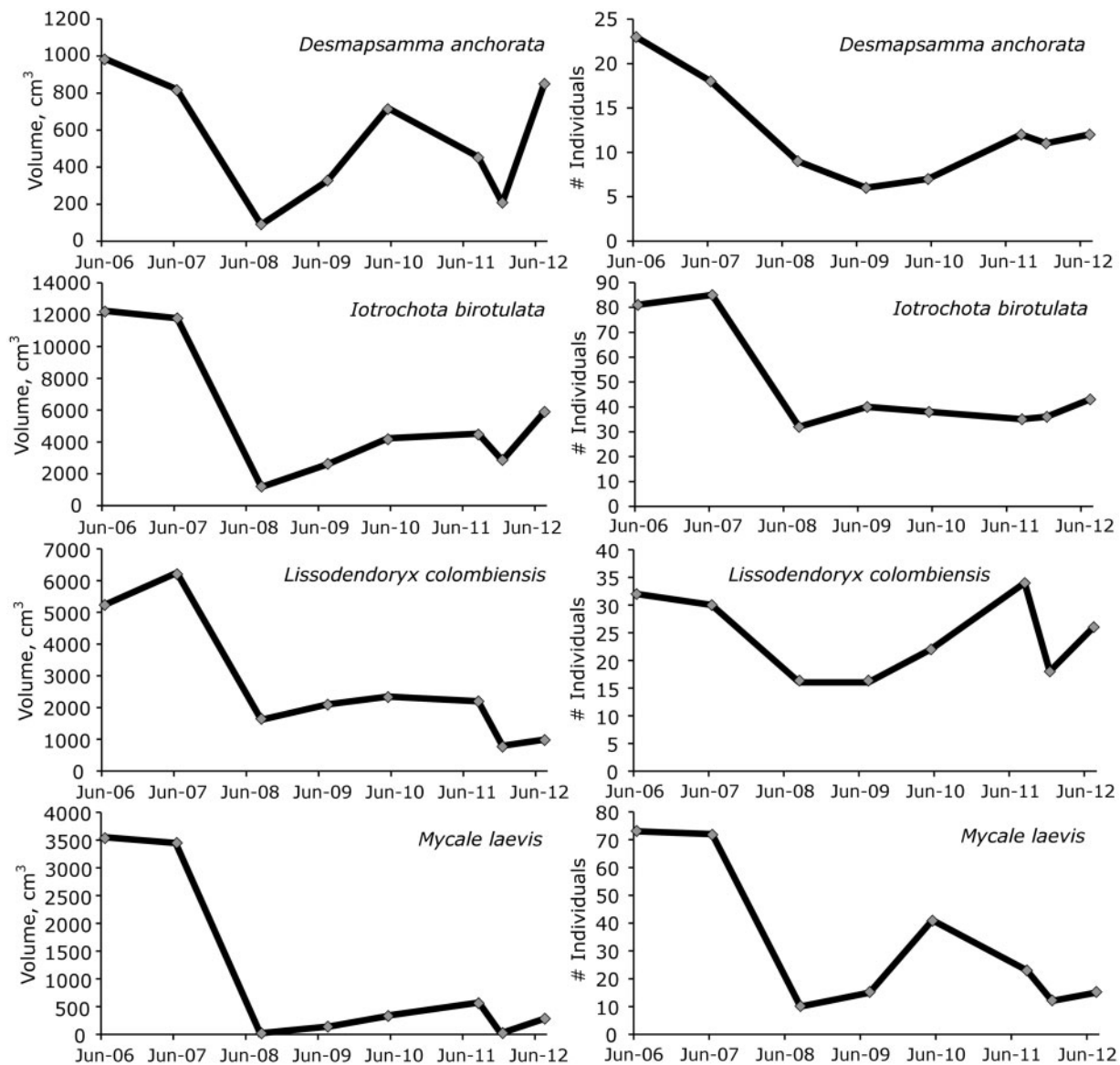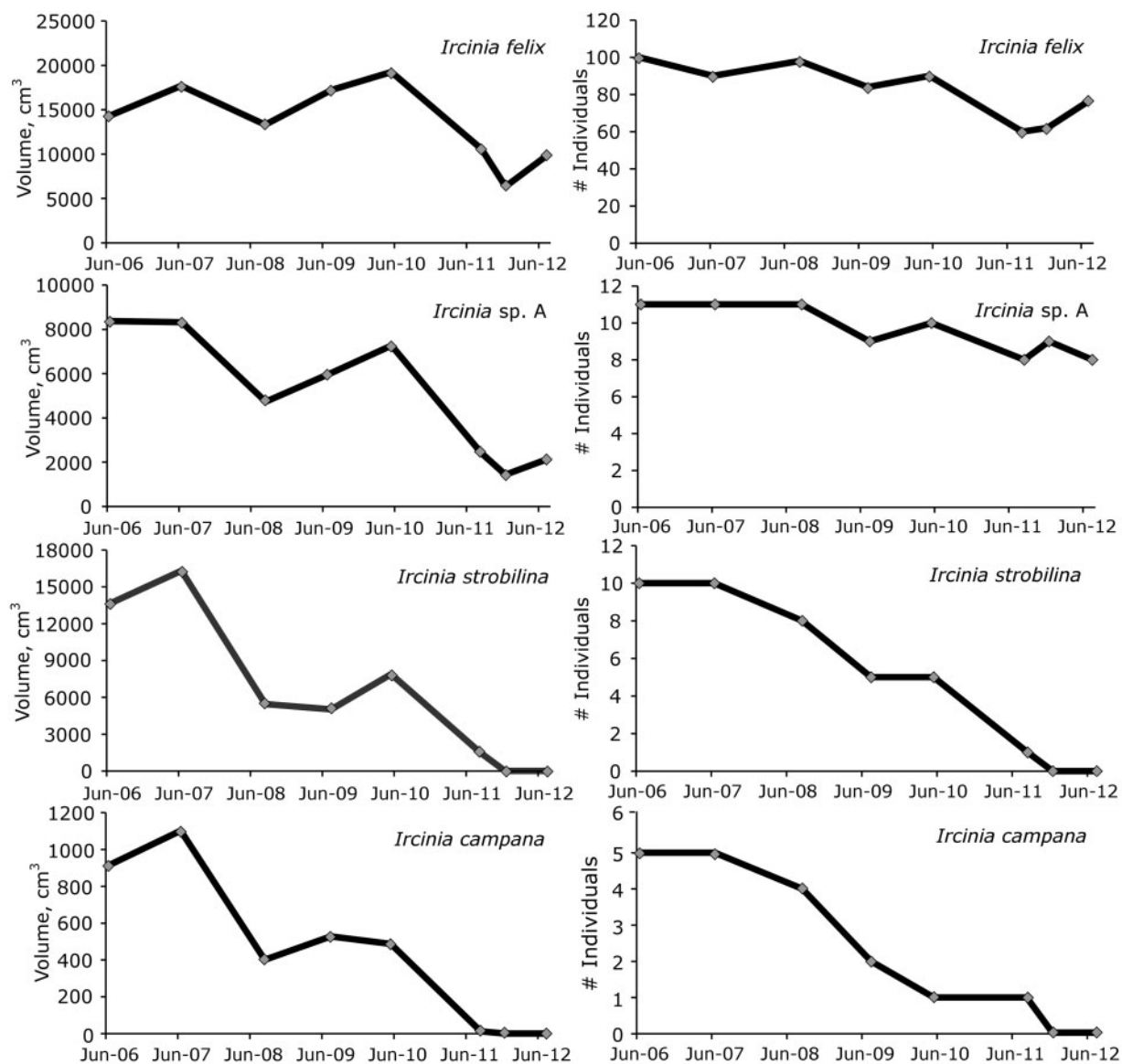
Fig. 5 Population dynamics, in terms both of volume (left) and numbers of individuals (right) of four of the initially most abundant species representing the order Poecilosclerida. Desmapsamma anchorata and I. birotulata are erect branching species, and L. colombiensis and M. laevis are semi-cryptic massive species at this site.

large sponges that had been reliable features for orienting underwater maps for 5 years were entirely missing. Some oddly shaped sponges could be interpreted as stages in regeneration only because mortality had been observed in action. For example, short stubby tubes of most individuals of *Niphates digitalis* were the result of death of the upper portions of their typical tall tubes, followed by sloughing of the necrotic material and regeneration of the rims; many individuals of *V. rigida* had deep scooped-out areas on their surfaces where necrotic areas had been sloughed and the surface tissue reconstituted. That the 52% regain of volume lost in 2008 in the 3 years before the 2011 mortality event was primarily due to

regeneration after partial mortality, as was the relatively rapid regain of volume lost in 2011, confirms the importance of the legendary regeneration capabilities of sponges in times of repeated extreme mortality events.

Phylogenetic patterns in responses to environmental challenges that were identified by analyzing patterns of mortality and recovery on the level of order include disproportionate loss of volume by species in the Hadromerida (-89.6%) and Dictyoceratida (-78.6%) during the dense phytoplankton bloom in 2011. The match with heavy mortality of species in these orders during dense phytoplankton blooms in Florida Bay (Stevely et al. 2011) suggests that their
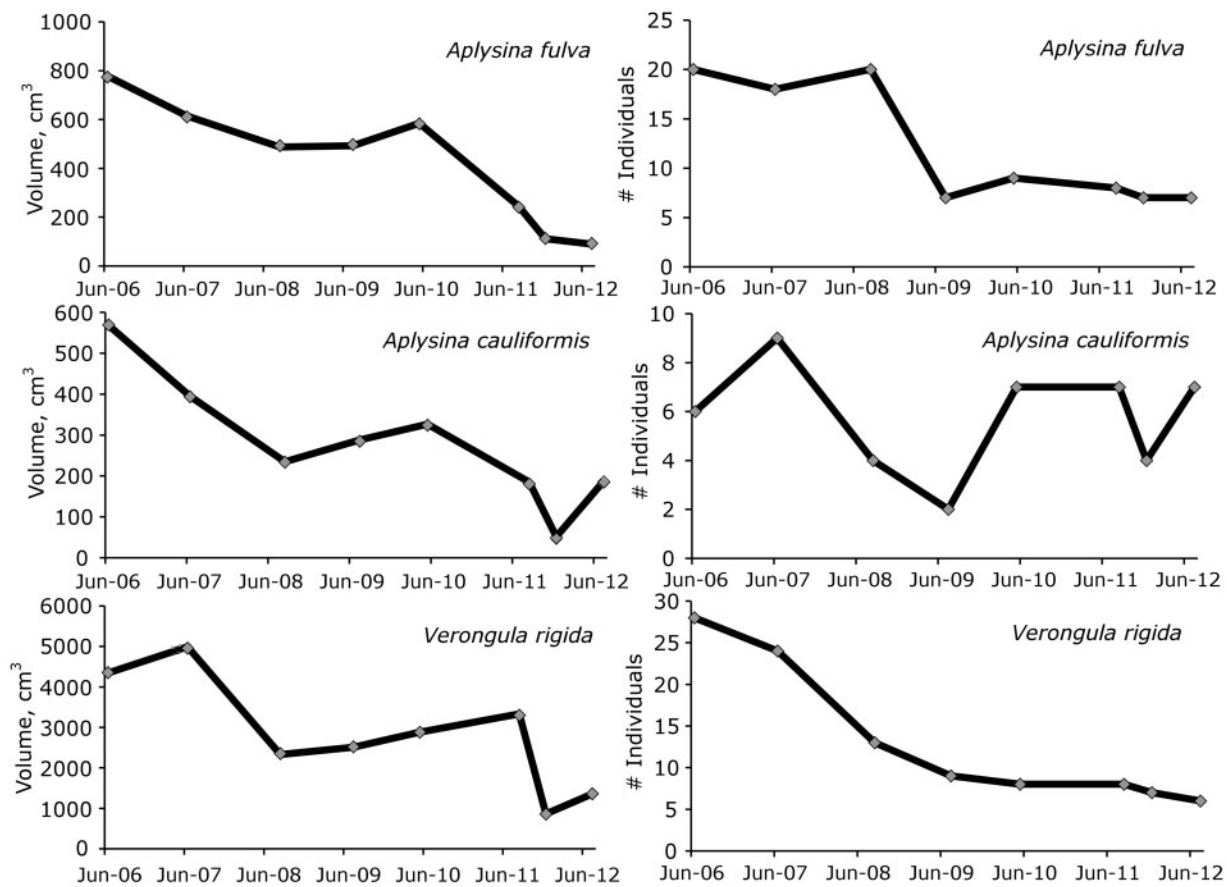
Fig. 6 Population dynamics, in terms of both volume (left) and numbers of individuals (right) of four of the initially most abundant species representing the genus Ircinia. All four species are in the massive growth-form category, but they differ in that I. strobilina and I. campana both have a very small basal attachment that anchors a large volume, whereas Ircinia felix and Ircinia sp. A continue to expand the surface area covered as they grow, resulting in thick, sprawling mounds.

vulnerability to this agent of mortality may be due to an aspect of these sponges that is conferred by their common ancestry. Stevely et al. (2011) grouped species that shared patterns of mortality and recovery into categories labeled: "rapid decline and gradual recovery," "fluctuating abundance," "gradual decline," and "low abundance, no change." All nine species in their category of "rapid decline, gradual recovery" were hadromerids or dictyoceratids. Mortality at their sites was even more severe than in Belize, and because most of the individuals representing these species at their sites were entirely killed, recovery was delayed by the vagaries of larval recruitment.

Differences among demosponge orders in the degree to which, and the ways in which, their members succumbed in the two mortality events in Belize were striking. Disproportionately heavy mortality during the 2011 phytoplankton bloom of members of the Hadromerida and Dictyoceratida strongly suggests a different cause of mortality in 2008, when Aplysinida, and especially Poecilosclerida, were dramatically diminished (respectively, 53% and 85.9%). The disproportionate loss in 2008, of both volume and numbers of individuals from members of Aplysinida and Poecilosclerida reflected heavy mortality of entire individuals rather than partial mortality. How this impeded recovery is well illustrated by

Fig. 7 Population dynamics, in terms both of volume (left) and of numbers of individuals (right) of three of the initially most abundant species representing the family Aplysinidae. Aplysina fulva and A. cauliformis are both erect branching species, and V. rigida is a massive species.

the population dynamics of individual poecilosclerid species (Fig. 5). Recruitment by larvae of *M. laevis* and *L. colombiensis* (both semi-cryptic massive species at this site) bolstered numbers of individuals in the years before the 2011 mortality, but with little increase in volume because each individual was so small. *Iotrochota birotulata*, like other branching species, has been demonstrated to recruit more by asexually generated fragments than by larvae (Wulff 1991), and this species re-gained few individuals. Population dynamics of *D. anchorata* reflect its extraordinarily rapid growth and fluid reconfigurations of biomass (Wulff 2008). Although members of the orders Dictyoceratida and Haplosclerida were also considerably diminished in volume (respectively, 41% and 39%) during the 2008 mortality event, individuals were not lost, and recovery with respect to volume in the following year was substantial (respectively, 27.5% and 72.5% of what had been lost), reflecting rapid regeneration after partial mortality (Fig. 3).

The way in which mortality is dealt can influence the ability of sponges to recover. Many of the same

(or closely related) species in the Belize census also participated in a major hurricane in Jamaica in 1980 (Wulff 2006b). Types of wounds meted out by Hurricane Allen were more varied than those from the phytoplankton bloom, which uniformly caused necrotic patches that either spread throughout an individual or were halted. Within 4 weeks after the hurricane, 41% of the 291 individual sponges that were monitored after they were damaged in the storm had completely regenerated their surfaces and were pumping. Breakage by storm waves appeared to be readily healed for massive species with breakable skeletons, and in the case of branching species breakage resulted in more individuals. Surface wounds, even deep ones, were readily patched but when debris smashed massive sponges with tough skeletons, necrotic patches often developed and spread, resulting in death. The key distinction between the growth-form categories ''massive tough'' and ''massive breakable'' is based on membership in higher taxa, with species in the Dictyoceratida (*Ircinia*, *Smenospongia*), Aplysinida (*Verongula*), Spirophorida (*Cinachyrella*), and Astrophorida

(*Geodia*) prominent in the tough category. It was sponges in this category from which the highest proportion of individuals were ultimately lost (i.e., factoring in immediate storm damage as well as post-storm continued mortality). Tough, massive sponges were diminished by 36%, while species in other categories of growth form lost 21.4–27.5% (Wulff 2006b). Curiously, 5 years later, when Wilkinson and Cheshire (1988) evaluated the sponge fauna at a reef site in Jamaica where sponges were annihilated during Hurricane Allen, the five species that had recruited most abundantly were all in the massive, tough skeleton category.

Underscoring the degree to which recovery is influenced by the type of environmental hazard as well as by phylogeny, compensation for disproportionately high rates of mortality by higher rates of larval recruitment was not observed in Belize after the 2008 mortality. The devastated Poecilosclerida only re-gained 5.6% of the individuals lost and the Aplysinida continued to lose individuals during the following year, suggesting that whatever caused the mortality also caused lingering physiological effects that inhibited reproduction. By contrast, in 2011, both Poecilosclerida and Aplysinida fully recovered their losses with respect both to volume and to numbers of individuals within the first 7 months after the mortality (Figs. 3 and 4).

As illustrated by the 11 species for which details of population dynamics are provided (Figs. 5–7), similar vulnerability and recovery patterns within higher taxa are further influenced by growth form. The difference between the vulnerability and recovery of branching versus massive (including semi-cryptic massive) species in the face of the dense phytoplankton bloom in 2011 is reminiscent of the differences in the fates of species representing these growth forms in a census plot in Kuna Yala, Panama (Wulff 2006a). During the 14 years of the study, disease was implicated in the loss of 8/10 of the massive species from the plot, but none of the six branching species was lost; a pattern predicted by a simple model of disease progression within the bodies of sponges of different growth forms (Wulff 2006c). If the necrotic portions that developed during the phytoplankton bloom progress within sponge individuals in a fashion similar to the way disease progresses, this may explain why species of branching and encrusting sponges were relatively unaffected by the phytoplankton bloom, as well as why the two *Ircinia* species with low surface:volume ratios entirely succumbed, while the two *Ircinia* species with more rambling forms primarily suffered partial mortality and were thus able to regenerate (Fig. 6).

Too few studies have been made in which all members of a sponge fauna have been monitored over time for phylogenetic patterns in responses to different agents of mortality to be clear. However, hints of consistent patterns in vulnerability and recovery of members of particular higher taxa, as well as idiosyncratic patterns of individual species within higher taxa, suggest the potential for helpful exchange between the disciplines of ecology and systematics. The utility for systematic analysis of other types of ecological characters has been demonstrated or suggested. For example, a cryptic species of *Tedania* (Poecilosclerida) was discovered by observations of starfish consuming individuals of *Tedania* spp. living on mangrove roots, but rejecting individuals inhabiting seagrass meadows. Subsequently, molecular and morphological differences were discovered; also, only one of the two species succumbed to disease at a site in Panama, and only one of the species was capable of withstanding more extreme environmental fluctuations (Wulff 2006d). At a higher level, patterns of specificity between 92 species of Caribbean sponges and six species of obligately symbiotic zoanthids may be informative with respect to placement of sponge genera within suborders of Haplosclerida (Swain and Wulff 2007). Reports on the extraordinary recent progress that has been made on familial and ordinal levels of the systematics of demosponges (e.g., Cárdenas et al. 2012; Morrow et al. 2012; Hill et al. 2013) have focused on evaluating the use of various molecular and morphological characters. It is possible that ecological characters, including symbiotic associations, susceptibility to disease, and defenses against predators, as well as vulnerability to, and ability to recover from, environmental hazards, may also be brought to bear on difficult systematic decisions.

Acknowledgments

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