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Bathymetric patterns of sponge distribution on the Bahamian slope

MANUEL MALDONADO*† and CRAIG M. YOUNG*

Abstract—Using a manned submersible equipped with a high-resolution video camera, we documented vertical patterns of species abundance, substratum usage, color, and body form of sponges living on the Bahamian slope. Sponge abundance is not linearly related to depth, but has a bimodal distribution, with peaks located on the upper slope (100 m depth) and between 400 and 500 m. Sponge fauna decreases dramatically between 100 and 230 m and remains rather depauperated to 320 m. The deep-water mode of the vertical distribution is dominated by abundant lithistids and astrophorids, whereas the shallow mode includes a wide assortment of species belonging to most of the sponge orders. The observed bimodal pattern is not explained by the temperature/salinity profile of the water column. Sponges are much more abundant on vertical surfaces than horizontal ones, indicating that surface angle is a major source of patchiness on the slope. Diversity both in body form and color have bimodal bathymetric distributions similar to that of the species richness, mirroring an important faunal transition along the slope. Most of the morphs and colors occur at all depths, but erect whip-like forms as well as black and purple–pink colors are found only at the shallowest sites. Above 200 m, encrusting morphs and red–orange colors dominate sponge assemblages, whereas in the deepest stations cup-like morphs as well as yellow and white–grey colors are predominant. The shift from brightly colored sponges to white sponges with increasing depth may be explained by the fact that most of the organisms from which sponge pigments are derived, including both food and symbionts, are associated with the euphotic zone. Copyright © 1996 Elsevier Science Ltd

INTRODUCTION

Most taxa of benthic marine invertebrates display distinct patterns of vertical zonation. The causes of these patterns have been extensively studied in intertidal and shallow subtidal habitats, but few studies on zonation have been done beyond scuba depths. Indeed, zonation patterns of particular phyla have been characterized in deep water for only a few taxa (e.g. echinoderms; see Carney and Carey, 1977; Gage, 1986) and community-wide zonation studies are even more rare (Grassle, 1980; Chave and Jones, 1991).

From a distributional standpoint, continental slopes are important transition zones between shallow and deep-sea environments. Very steep slopes are particularly interesting because physical gradients change so rapidly that ecological patterns are compressed into short distances, making the patterns more obvious to the observer and more tractable to the experimentalist. Slopes often have unique faunal assemblages and high species diversity

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(Gage and Tyler, 1991). Many taxonomic studies indicate that sponges are very important members of the slope fauna (Schmidt, 1879, 1880; Sollas, 1888; Topsent, 1892, 1928; Hentschel, 1929; Vacelet, 1969; Lévi, 1964, 1991, 1993; Lévi and Lévi, 1988, 1989; Uriz, 1988; van Soest and Stentoft, 1988; van Soest, 1993). In the West Indies region, it has been estimated that about 252 species of sponges inhabit the bathyal depths between 55 and 2000 m depths (van Soest and Stentoft, 1988).

Some authors have compiled bathymetric data contained in a wide assortment of local taxonomic studies, offering a comprehensive picture of the general trends in the vertical distribution of sponges (Reid, 1968; Vacelet, 1988; Tabachnick, 1994). However, since major collecting efforts in the deep-sea have generally been based on trawling, the biology of living bathyal, abyssal and hadal sponges remains poorly understood (Vacelet and Boury-Esnault, 1995). Moreover, quantitative ecological approaches have been rare, especially on rocky slopes where complex topography makes remote sampling difficult at best. Submersibles have opened the slope habitats to observation and experimentation within the last two decades, but to date, no detailed submersible-based distributional studies have been undertaken on bathyal sponges. In this study we used high-resolution video transects taken from a manned submersible to document vertical patterns of species abundance, substratum usage, color, and body form for sponges living on the Bahamian slope.

MATERIALS AND METHODS

Using an externally mounted Sony Hi-8 video camera on a *Johnson-Sea-Link* submersible, we recorded the distributions of sponges in a continuous vertical transect between 91 and 531 m depth off the southern side of Golding Cay, near New Providence Island, Bahamas (24°58' N, 77°34' W). Salinity, temperature and depth were recorded continuously using Sea-Bird sensors and a Pisces Design data logger that printed digital readout directly on the video image. We attempted to maintain the camera orthogonal to the substratum. Four parallel laser beams surrounding the video camera housing projected corners of a 306 × 250 cm² plot on the substratum. These points were later used for sampling quadrats of identical size even when the submersible had varied in its distance to the bottom. The video camera was kept at a constant focal length during the entire transect.

We subsampled the belt transect by stopping the video recorder after every 6 m of depth change and recording details of the sponge distribution in four adjacent 306 × 250 cm² plots (total quadrat area: 1225 cm²) in each frame sampled. In the cases when the correct quadrat was out of focus, we proceeded to the next properly focused frame. If no suitable frame was found before the next 6-m sampling point was encountered, we regarded that interval as a missing data point. The final data set consisted of 57 quadrats.

Although surfaces of all angles relative to the horizontal were found in the transect, we arbitrarily split the stations into two categories. Horizontal stations were those where silt falling from above could form a resting veneer on the bottom. Surfaces with angles between 0° and approximately 45° met our siltation criteria. Substrata with surface angle larger than 45° relative to the horizontal were regarded as vertical. In each quadrat, we recorded the number of sponge individuals (n), the number of species (S), and the body form and color of each individual. Sponge body form was classified into four categories: (1) erect, branched or whip-like; (2) cup-like; (3) massive, either spheroidal or irregular in shape; and (4) encrusting. Colors were categorized into 6 groups: (1) black; (2) purple or pink; (3) blue; (4) red or orange; (5) yellow; and (6) white to grey.

The relationships between the presence/absence of sponges and the orientation of the substratum (horizontal/vertical) were analyzed using 2×2 chi-square contingency tables. Yates correction was applied when necessary (Sokal and Rohlf, 1981). We sought relationships between species abundance and depth by plotting the latter against the Margalef (1958) species richness index, $R = S - 1/\ln(n)$, where S and n are the mean number of species and number of individuals per quadrat, respectively. Empty quadrats were automatically given an R -value of zero. Patterns of diversity in color and shape were described with the Shannon and Weaver (1963) information function, $H' = -\sum p_i \ln p_i$. These richness and diversity patterns were all highly dependent on surface angle, a factor that was not distributed uniformly or even randomly with depth in our transect. The inclusion of different surface angles in the analysis confounded our interpretation of depth-related patterns, so in some cases we confined our analysis of richness and diversity to samples taken on vertical surfaces at all depths. Because we were seeking large-scale bathymetric patterns, we found it useful to reduce the effect of between-quadrat variance by averaging all available quadrats within 50 m depth intervals and plotting the data against the average depths of the samples taken within each interval. The number of quadrats averaged per depth interval varied from 1 to 6.

We used correspondence analysis to seek community patterns in the shape and color data and to determine if there were distinctive assemblages related to depth. Stations with no sponges were not included in these ordination analyses.

During this and preceding dives, we collected specimens of representative species for identification so we would be familiar with the fauna during video analysis. The individual sponges sampled were also videotaped *in situ*. Identification was accomplished by skeletal study using standard techniques (e.g. Rützler, 1978). In cases when we could not identify the sponges from videotapes, we made our best guess as to whether the individuals constituted species different from the other sponges in the frame, using body form, size and color as criteria.

RESULTS

Physical characteristics of the transect site

The slope at Golding Cay and elsewhere in the Bahamas Archipelago includes a mixture of surfaces having various orientations. Between approximately 200 m and 90 m, the slope is a steep vertical wall with occasional ledges. Above this depth, the contours begin to level out in a narrow shelf with well developed coral reefs. Below 200 m, the contours also become more gentle. At these depths the bedrock substratum is often covered with a thin veneer of sediment. Vertical faces are, however, common on large boulders and occasional outcroppings.

Both salinity and temperature decreased with increasing depth (Fig. 1). A thermocline was present between 180 and 230 m; above this level, the water column was virtually isothermal, temperature decreasing at a rate of only 1° for every 100 m of water depth. Small salinity anomalies were present in the region of the pycnocline. Below the thermocline both temperature and salinity decreased at a more or less constant rate to the bottom of the transect.

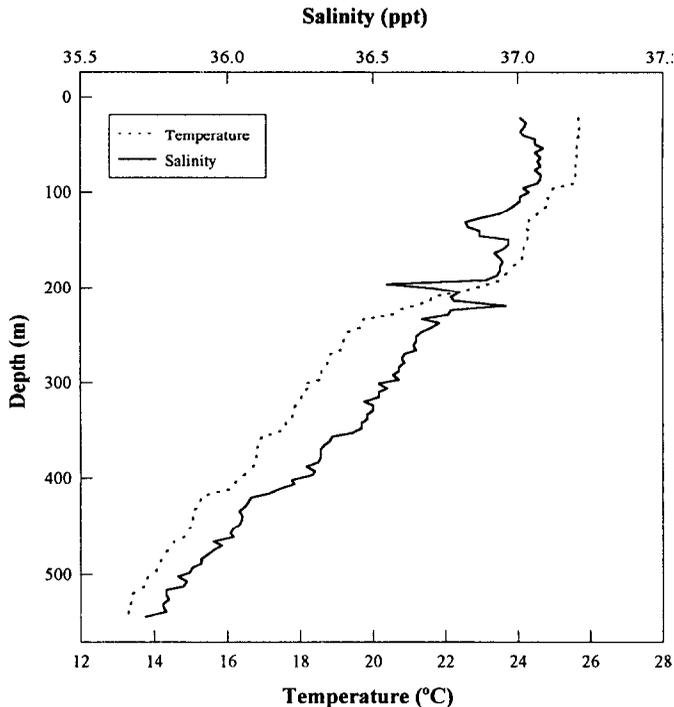


Fig. 1. Vertical profiles of temperature and salinity at the study site.

Patterns of sponge abundance

Above 200 m, where the substratum was mostly vertical, there was a general trend of increasing species and individuals with decreasing depth. Below 200 m, the number of species and individuals showed no clear bathymetric trend. Many quadrats contained no sponges (Fig. 2), and most of these were on horizontal surfaces. Only one vertical quadrat in the entire transect contained no sponges whatsoever. Chi-square analysis of a contingency table relating the presence and absence of sponges to surface angle (horizontal vs vertical) showed a highly significant association with vertical surfaces (Yates corrected $\chi^2 = 16.167$; $P = 0.001$), indicating that surface angle is a major source of patchiness.

Below 200 m there was abundant free space (> 50%) in every quadrat. Above 200 m, free space was less common; most of the primary substratum was occupied by a diverse assemblage of cnidarians and sponges. However, we found no sponges that appeared capable of dominating an entire quadrat to the exclusion of other sponge species at any depth; the largest forms (cup-like and claviform morphs) were often attached to the bottom by relatively narrow portions, and encrusting species always occurred in relatively small patches. The occurrence of species monopolizing the substratum should produce a negative relationship between the number of species and the number of individuals. Instead, there was a significant positive linear relationship ($r^2 = 0.848$, $P < 0.001$) (Fig. 3).

We predicted that either abundance or species richness should increase in the region of the pycnocline because of increased particle density in this region and because the level of the pycnocline corresponds roughly with the depth of the chlorophyll maximum

(Young, unpublished data). The data did not support this prediction. A plot of temperature/salinity ratio against depth indicates that the pycnocline lies between 200 and 250 m (Fig. 4). Both sponge abundance and species richness of sponges (this latter averaged over 50-m depth increments) decreased dramatically from 90 to 220 m depth, remained low to 320 m, then increased to moderate values between 400 and 500 m (Figs 2 and 4) before dropping to its lowest value below 500 m. This bimodal pattern was not explained by any portion of the T/S plot.

At our site, the steep cliff on the deep reef began leveling out at about the same depth as the pycnocline, causing an increase in the number of horizontal sites between 190 and 270 m. As noted earlier, the majority of horizontal sites contained no sponges. We suspected that the abundant zero values at these horizontal sites could bias the richness data when averaged with the values for vertical stations. If depth and microhabitat are confounded covariates, we are not justified in discussing the role of depth. To test this possibility, we removed all horizontal plots from the data set and plotted average species richness by 50 m depth intervals for the vertical sites only. Using vertical sites only, there was an even stronger decrease in richness at 200 m depth. However, below the pycnocline, richness values were about twice as high on the vertical surfaces alone as on all surfaces combined (Fig. 4). This confirmed that surface angle was indeed confounded with depth below the pycnocline. Nevertheless, some patterns were similar in both plots. There was a general increase in richness caused by lithistids between 400 and 500 m depths irrespective of the data set used.

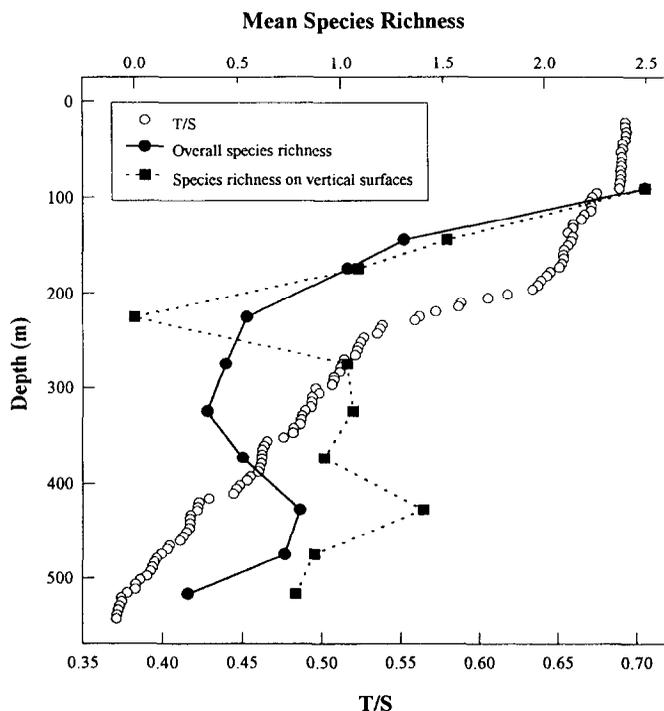


Fig. 4. Mean overall species richness and mean species richness on vertical surfaces plotted as a function of depth with the T/S curve (temperature/salinity ratio) superimposed.

Morphological patterns

For analyses of bathymetric patterns of diversity in body form and color, we used only the sites on vertical surfaces so as to eliminate confounding differences among microhabitats. Both body form and color were very diverse above 100 m depth and decreased in diversity at about the same rate as the decrease in species richness (Fig. 5). Both parameters reached their lowest level at the bottom of the cliff (200 m) then increased again between 300 and 450 m (Fig. 5). The patterns were remarkably similar to those of species richness. The parallel trends in diversity of shape and color mirrored important faunal transitions among higher sponge taxa along the slope.

The depth distributions of the four major sponge body forms are plotted in Fig. 6. Encrusting, massive and cup-like growth forms were found at all depths. Encrusting sponges represented the largest percentage of the fauna above 200 m (Figs 6(a) and 7(a), (b)). Cup-like forms reached their highest abundances near the bottom of the transect, where small cup-like lithistids were among the most common species (Fig. 7(c)). The distribution of massive forms is bimodal (Fig. 6(a)), with the deep-water mode being caused by small massive lithistids and astrophorids and the shallow mode being composed of a wide assortment of species, including astrophorids and many poecilosclerids and haplosclerids (Fig. 7(a), (c)). Erect whip-like forms (mainly species belonging to the order Dendroceratida, such as *Aplysina cauliformis* and *Aplysina fulva*) were found only at the

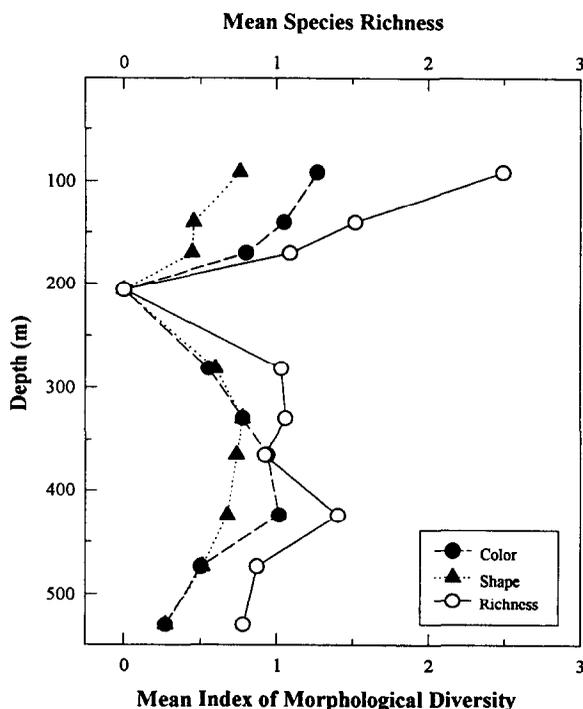


Fig. 5. Depth distributions of mean diversity values (Shannon-Weaver Index) for color and shape and mean species richness. Only data from vertical surfaces were used for the calculations.

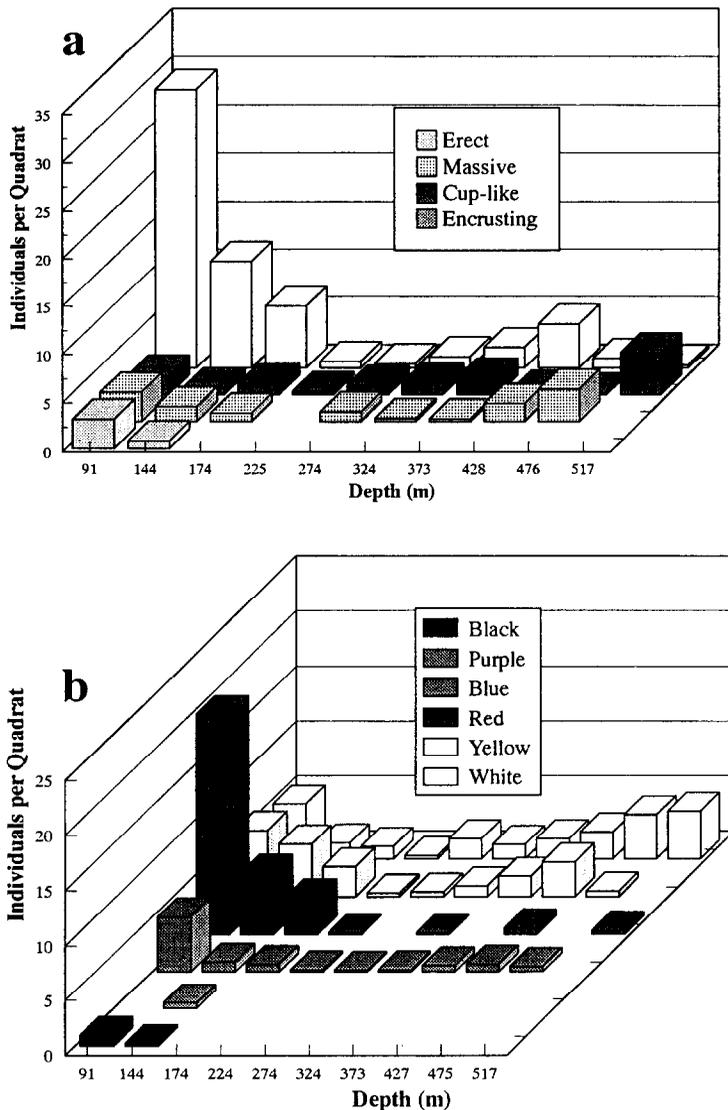


Fig. 6. The population densities of sponges having different body forms (a) and colors (b) plotted as a function of depth. Depth values are the mean of all sampling quadrats within each 50-m depth interval.

shallowest sites (Fig. 7(a)). The virtual absence of erect, branched forms below 150 m was a remarkable feature of this sponge fauna.

Most colors occurred at all depths, but black and purple-pink colors were uncommon overall and present only at the shallowest sites (Fig. 6(b)). Red-orange sponges dominated the fauna above 200 m, whereas yellow and white-grey colors were predominant at deepest stations (Fig. 7(a)-(c)). Red-orange sponges were distributed discontinuously along the depth gradient, possibly because suitable vertical sites were rare at intermediate depths.

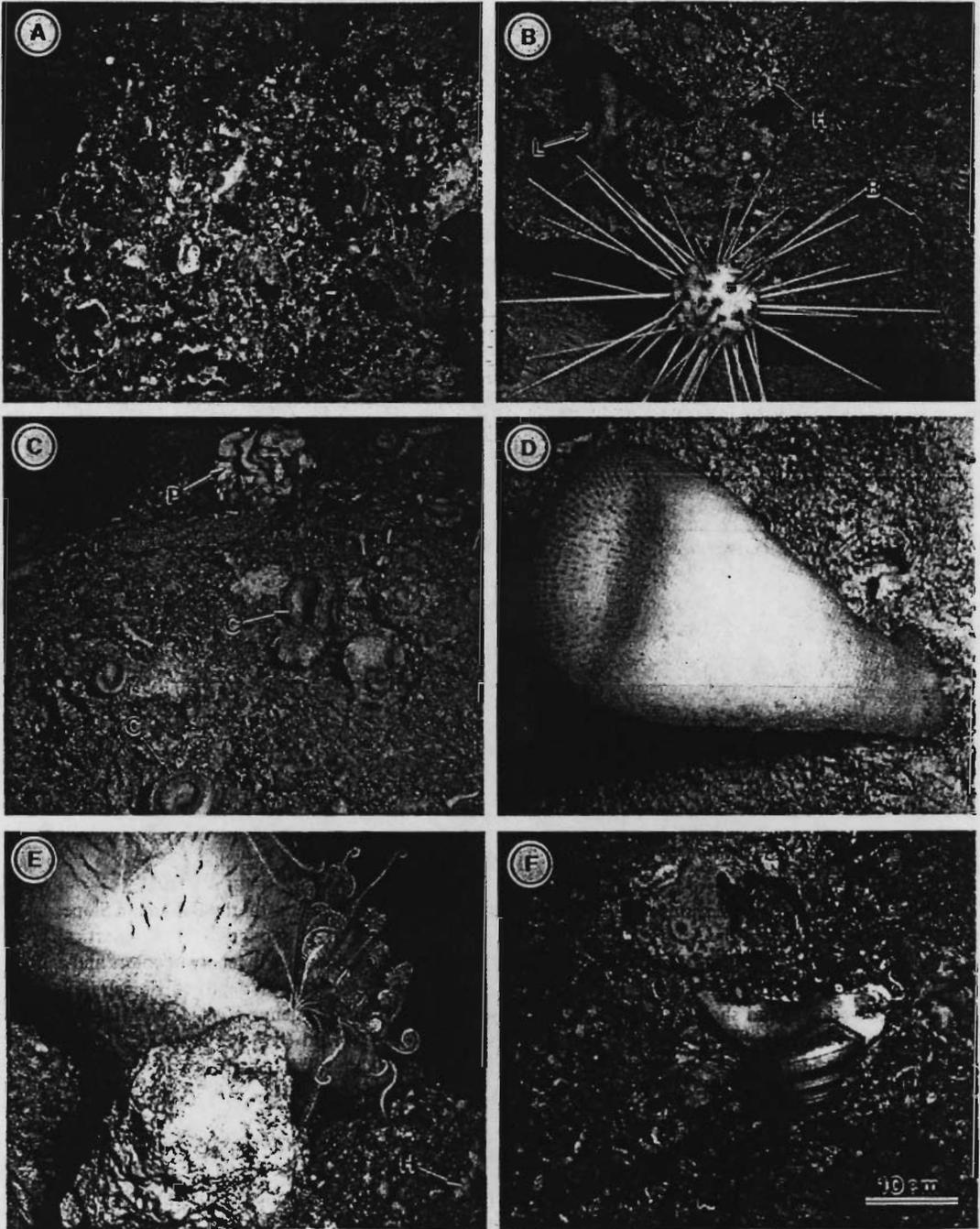


Fig. 7. See over for caption.

Fig. 7. Representative sponges from deep reef and bathyal environments on the Bahamian Slope. All photographs are the same magnification (see scale bar in F). (A) Sponge-dominated vertical surface at 34 m depth near Cable Beach, New Providence Island, showing a diversity of colors and a mixture of encrusting and upright forms. (B) Overhanging boulder at 492 m depth off French Bay, San Salvador Island showing predominance of yellow sponges in the genus *Hymedesmia* (H) and presence of an unidentified blue sponge (B) and a cup-like lithistid (L). The large sea urchin, *Calocidaris micans*, is a potential sponge predator. (C) A typical lithistid-dominated sponge community at a depth of 631 m off Tartar Bank, near the southern end of Cat Island. The cup-shaped lithistids, *Corallistes typus* (C), are aggregated at small spatial scales. In the background is an unidentified massive sponge (P), with a yellowish-brown individual of *Desmacella vestibularis* living epizooically. (D) *Dactylocalyx pumiceus*, a common hexactinellid sponge living at approximately 600 m depth off Egg Island in Northeast Providence Channel. (E) A large, unidentified hexactinellid sponge at approximately 475 m depth off French Bay, San Salvador Island. The sponge provides shelter for a small fish and serves as a perch for filter-feeders, including yellow comatulid crinoids and a white ophiacanthid ophiuroid. Surrounding rocks support patches of *Hymedesmia* sp. (F) The pleurotomariid (slit-shell) gastropod *Perotrochus midas* shown with sponges at a depth of 650 m off Chub Cay. This predatory snail is a sponge specialist, which occurs between 500 and 900 m.

The faunal transitions producing shape and color changes along the depth gradient were also obvious when the data were plotted in ordination space (Fig. 8). Deeper stations, regardless of their orientation, mostly had white–grey sponges (Fig. 8(a)) with either massive or cup-like shapes (Fig. 8(b)). Note, however, that massive and cup-like individuals

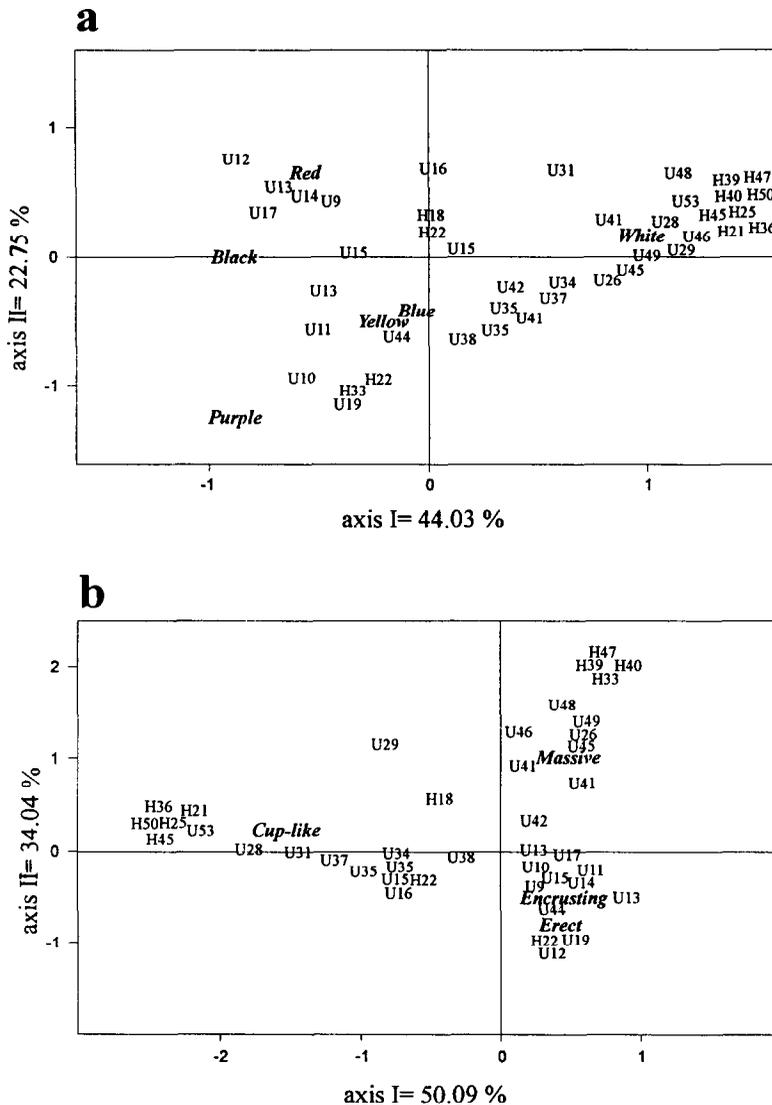


Fig. 8. (a) Correspondence analysis showing the ordination of colors (bold italics) superimposed on an ordination of sampling quadrats. The two main axes of the ordination explain 66.78% of the total variance. (b) Correspondence analysis showing the ordination of body-form categories superimposed on an ordination of sampling quadrats. The two main axes explain 84.13% of the variance. Each station is designated by a letter (H for horizontal or U for upright) and the first two digits of the depth in meters.

did not usually coexist; they occupied different sampling stations at similar depths. The extreme scores characterizing the horizontal stations in the ordination space indicate that these stations generally had low numbers of individuals in each shape or color category.

Ordination of individual sites confirmed that shallow sites were dominated by red and orange sponges (Fig. 8(a)) and by abundant sponges with encrusting and erect body forms (Fig. 8(b)). Individuals of some species of Dendroceratida occurred over a wide range of depth (from 50 to 200 m), showing a fading (loss of purple and orange tinges) with increasing depth. Black and purple colors were also characteristic of some shallow sites. However, their positions on ordination space do not overlap with any sampling stations. This fact indicates that sponges of these colors are not abundant and that they are limited to a few shallow sites. In contrast, the central positions of the blue and yellow colors in ordination space indicate that sponges of these colors are uniformly represented along the transect and also that they are not strongly associated with any particular body shape.

Faunal composition

The sponge fauna inhabiting depths from 350 to 500 m was dominated by astrophorids and lithistids (*sensu lato*). Astrophorids inhabited both horizontal and vertical surfaces whereas lithistids were almost always found on vertical or very steep surfaces lacking sediment coverage.

The astrophorids in our transect were generally more than 10 cm in diameter or height and had either a massive or cup-like shape. The most abundant astrophorids were species belonging to the genera *Pachastrella* and *Asteropus*. Lithistids s.l. were the megabenthic organisms most abundant on rocky outcrops in deeper water (Fig. 7(c)). They were generally cup-like or claviform, 1–5 cm in height. The most abundant triaenose lithistids belonged to the genera *Corallistes*, *Discodermia* and *Racodiscula*. Non-triaenose lithistids or lithistid-like sponges were also well represented by genera such as *Scleritoderma* and *Vetulina*. It is noteworthy that the blue lithistid *Scleritoderma cyanea*, recently described by van Soest and Stentoft (1988) from Barbados and thought to be rare, was relatively abundant on the deeper rocky outcrops we sampled.

On the vertical sides of deep rocky outcrops, an undescribed yellow encrusting species of the genus *Hymedesmia* (Fig. 7(b)) was very common, as it has also been reported from the Cuban slope (Alcolado, 1990). Many of the encrusting species, particularly members of the genera *Desmacella* and *Jaspis*, were epizoic on other sponges (Fig. 7(c)). The presence of ample free space on deep rocky outcroppings suggests that these sponges have not adopted an epizoic habitat because of spatial competition, as has been suggested for shallow-water sponges living in space-limited environments (Rützler, 1970).

The sponge fauna was rather depauperate between 230 and 320 m. One of the few species here was the massive yellow sponge *Spongosorites siliquaria* van Soest and Stentoft. The few scattered individuals of the genus *Agelas* at these depths had a lighter orange color and weaker body consistency than individuals living shallower. It is also noteworthy that we found one individual of the shallow-water sclerosponge *Calcifibrosporgia actinostromarioides* Hartman at a depth of 234 m harboring a dense population of epizoic zoanthideans, as described by Willenz and Hartman (1994) for shallow water specimens from Jamaica. This represents a major depth extension for this species.

Above 230 m the sponge fauna becomes gradually more diverse. At about 200 m, the most common species were members of the genus *Agelas* as well as keratose species, particularly

in the genera *Aplysina* and *Ircinia*. Sponges became the most abundant of all megabenthic organisms at about 100 m. Similar sponge dominance on the deep reef has been reported for other parts of the Caribbean as well (Suchanek *et al.*, 1983).

Only two species of hexactinellids were found along the transect: *Hexactinella* sp. and *Dactylocalyx pumiceous* Stutchbury (Fig. 7(d)). The former was represented by only one individual whereas the latter was a relatively common species with scattered individuals along the deeper parts of the transect. We also found in previous samplings the occasional presence of species of the genera *Farrea* and *Myliusia*.

DISCUSSION

Abundance patterns

Our goal in this study was to document bathymetric patterns of species replacement, species richness, and morphological diversity. However, we soon found that these factors could not be analyzed unambiguously along the depth gradient without also considering the small-scale spatial distributions. Differential occupation of vertical and horizontal surfaces coupled with differential availabilities of such surfaces with depth complicated the picture. By analyzing only vertical surfaces, the bathymetric patterns emerged more clearly. None of the parameters of interest changed linearly with depth. Although richness and morphological diversity were highest on the shallow portions of the slope, these parameters also reached moderately high levels between 400 and 500 m after declining to low levels between 200 and 400 m. The bimodal distribution reflected a change in the species composition of the fauna. The intermediate zones appeared to be depauperate because the deep reef species had dropped out and the true bathyal species such as lithistids had not yet appeared. The few species found in this intermediate zone were generally represented by only one or two individuals per site (Fig. 2), indicating that either recruitment or survival is not high.

At all depths, sponge abundance and diversity was higher on vertical surfaces than horizontal ones. This same pattern has been observed in many shallow-water sponge assemblages (e.g. Sará and Vacelet, 1973). The major exceptions to this rule are in shallow, tropical environments with a high proportion of photophilous sponges (i.e. Laubenfels, 1950) and some deep-sea habitats (e.g. Rice *et al.*, 1990) where vertical surfaces are simply not available. In shallow water, sponges may be outcompeted for horizontal living space by fast-growing macroalgae (e.g. Witman and Sebens, 1990). These algae are not important at the depths we studied. Siltation has been demonstrated to limit recruitment of sessile animals on subtidal horizontal surfaces (Young and Chia, 1984), and sedimentation and sediment mobility have been invoked to explain the impoverishment of sponge faunas (e.g. Vacelet, 1969; Sará and Vacelet, 1973; Battershill and Bergquist, 1990; Witman and Sebens, 1990).

The zone with lowest species richness and number of individuals was at 200 m, which is just below the pycnocline and coincidentally at a depth where horizontal surfaces were especially abundant. The richest sites were on vertical walls in shallow water. Because density discontinuities are generally areas of high suspended food concentration, we expected a more diverse assemblage of filter-feeding sponges at this depth. The expected effect was not seen, but the distributional pattern could be disrupted at our site because the pycnocline coincides with an abrupt increase in the number of horizontal sites. It would be

useful to characterize the faunas in the region of the pycnocline at sites where vertical surfaces predominate both above and below the pycnocline.

Ours is not the only study reporting an intermediate zone with low sponge diversity in the tropical Atlantic. Two previous studies (Lewis, 1965; van Soest and Stentoft, 1988) based on dredge and trawl samples from the Bermuda slope reported a sponge impoverishment between 150 and 250 m depths. Similar zones have also been reported in water less than 100 m (e.g. Boury-Esnault and Lopes, 1985; Schmahl, 1990; Schubauer *et al.*, 1990; Witman and Sebens, 1990; Maldonado and Uriz, 1995), and various explanations, including substratum instability and competition with macroalgae, have been used to explain these zones.

Growth form patterns

Massive, encrusting and cup-like sponges occurred along the whole slope, whereas branched, erect specimens occurred at shallow sites only. A study by Vacelet (1969) in bathyal Mediterranean bottoms reported that erect sponges (i.e. branched, cup-shaped or stalked forms) are most abundant on horizontal surfaces, whereas encrusting and massive sponges predominated on vertical surfaces. Our observations on encrusting forms agree, but we we found cup-like and massive sponges on both horizontal and upright surfaces (Fig. 8(b)).

Erect, tree-like body forms were virtually absent below 150 m, an observation that could lead to the conclusion that this growth form is not adaptive in deep-sea environments. However, most of the erect sponges were members of the order Dendroceratida. Some members of this group are massive or encrusting in shape and these were not found in deep water either. This suggests that erect sponges are absent from deep water because of some unknown constraint not necessarily related to the erect growth form. Long-stalked sponges were also conspicuously absent on the slope; this morphology, which is characteristically found on rocky slopes below 700 m and on soft abyssal bottoms (e.g. Lévi, 1993; Koltun, 1970), seems to be a special adaptation to very deep environments. Deep-sea filter-feeding ascidians occupying the same habitats have converged with sponges in this stalked growth form (Monniot and Monniot, 1975).

Our observation of abundant encrusting sponges at the shallowest slope depths agrees with previous reports in deep coral reef habitats (Suchanek *et al.*, 1983; Witman and Sebens, 1990). Encrusting species are often opportunistic, which may explain why encrusting sponges are found at all depths and represent one of the most common forms even at 400 m, where they predominate on vertical substrata. These deep-sea encrusting sponges are mostly known from collections of small rocks, shells, etc. (e.g. Sollas, 1888; Ridley and Dendy, 1887; Topsent, 1892, 1904, 1928). Many encrusting sponges in the deep sea are thin and colorless and can easily be overlooked. For example, Barthel and Tendal (1993) recently noted that the abundance of the encrusting genus *Hymedesmia* at abyssal depths off Norway has generally been underestimated.

Cup-like sponges were especially abundant on the deeper parts of the slope, mainly because of the presence of lithistids (s.l.) and astrophorids at these depths. It has been suggested that a vase-shaped body form can optimize the water circulation through the sponge body (e.g. Levinton, 1982; Gage and Tyler, 1991). This could be especially important in deep-sea sponges to compensate for increased water viscosity and scarcity of particles. It has also been suggested that a vase-shaped body reduces adverse effects of sedimentation by

confining inhalent pores to the outside (often downward-facing) side of the cup and the exhalent opening to the upper side (Sar and Vacelet, 1973).

Large, cup-like and massive sponges also play an important ecological role in the deep-sea by providing a microhabitat for many benthic animals (e.g. Ilan *et al.*, 1994). Their porous bodies provide shelter for cnidarians, polychaetes, vermetid gastropods, small crustacea and fishes. Many epifaunal organisms on sponges (e.g. sponges, barnacles, serpulids and many echinoderms) are filter-feeders that may take advantage of the water flow created by the sponges (Fig. 7(e)).

Color patterns

Sponges are known to display a remarkable interspecific and intraspecific variability in color. However, the causes of color shift in the sponge assemblages along the slope are poorly understood. Wulff (1994: 269, Fig. 1) classified sponges on a Caribbean coral reef into nine color categories, and we collapsed these into seven categories that were more appropriate for establishing a comparison with our data set. When we compare our data for the continental slope to Wulff's data from a coral reef, some major differences are seen (Fig. 9). The comparison confirms and highlights some of the bathymetric trends we noted on our transect (Fig. 6(b)). For example, black and purple sponges were found only in shallow habitats. White sponges were uncommon in shallow water but became increasingly abundant with increased depth. Finally, it is noteworthy that green sponges, which may contain algal symbionts, were not found on the slope.

The ecological significance of sponge color remains unclear for most species, but three

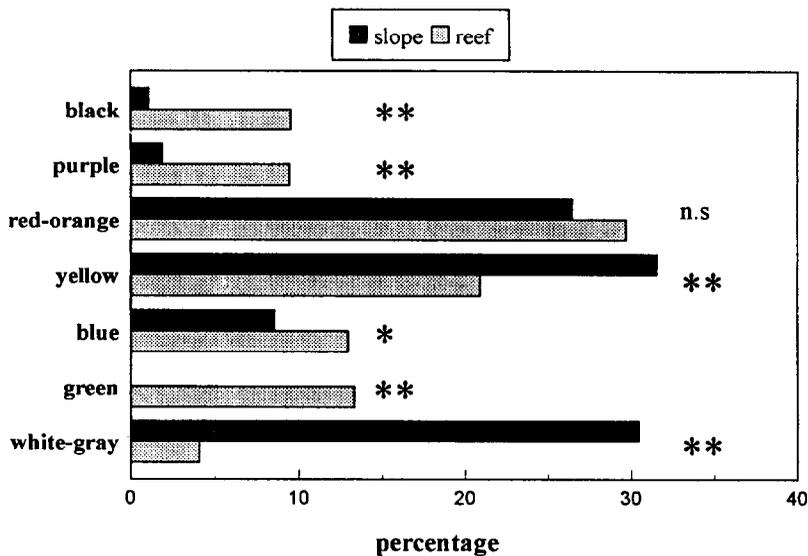


Fig. 9. Comparison of the relative percentages of the slope fauna (from this study) and reef fauna (data from Wulff, 1994) consisting of species of various colors. Significant differences in pairwise comparisons (Z-tests) are indicated as follows: one asterisk, $P < 0.05$; two asterisks, $P < 0.001$; n.s., not significant.

major hypotheses have been advanced: (1) pigments (e.g. carotenoids, melanins) filter out damaging u.v. radiation, (2) bright colors serve as an aposematic warning of toxic or unpalatable tissues to predators, and (3) color is a non-adaptive, fortuitous consequence of some metabolic product.

It has been demonstrated that u.v. radiation in sunlight can cause death of some sponge species (Jokiel, 1980). The existence of red, orange, yellow and blue sponges at the deepest slope suggests that these colors are not functioning as u.v. screens. However, the presence of black and purple sponges only on the shallowest parts of the slope is likely to be related to irradiance. Black melanin pigments are especially common in keratose sponges, which are rather limited to shallow water, whereas purple pigments, which are found in a variety of different sponge taxa are mostly derived from symbiotic Cyanobacteria (Sara and Vacelet, 1973). Transplantation of black and purple sponges into shaded habitats often leads to a fading of the pigments (e.g. Sara and Vacelet, 1973; authors pers. obs.), another piece of evidence that these colors are related to high levels of irradiance.

Red and orange were the most common sponge colors at the shallowest parts of the slope, and sponges with these colors declined rapidly with depth. Yellow sponges showed a similar pattern, though a small peak in yellow sponges was found at a depth of 475 m. This was mainly caused by a single species of yellow *Hymedesmia* in deep water. Red, orange and yellow pigments in sponges are derived from carotenoids which are either used in their original form or modified by oxidation or esterification with fatty acids (Lee and Gilchrist, 1985). Carotenoids are obtained either from food organisms (prokaryotes and phytoplankton) or from endosymbiotic bacteria and cyanobacteria. Sponges cannot synthesize carotenoids *de novo*, so the presence of red and orange sponges in complete darkness must indicate that they are receiving some pigments from food produced in the euphotic zone before the pigments have completely degraded. Carotenoid concentrations in shallow-water sponges vary spatially and temporally in ways that are not understood (Lee and Klontz, 1990).

The physiological factors resulting in blue coloration are poorly understood. In shallow water sponges, blue pigments can be derived from symbiotic bacteria or cyanobacteria (e.g. in the genus *Terpios*), and sometimes these bacterial pigments can be incorporated into sponge cells devoid of symbionts (i.e. Rutzler and Smith, 1993). We found blue sponges to be most abundant in shallow water, but a few were present at all depths (Fig. 7(b)). The major blue species on the deeper parts of our transect was *Scleritoderma cyanea*. Blue sponges of the genera *Oapsacas*, *Azorica*, are known from much greater depths elsewhere in the North Atlantic. The causes of blue pigment in these deep-sea species remain largely unknown.

As photosynthetic symbionts are responsible for pigments in many shallow-water sponges, it is not surprising that many deep-sea sponges are white or light grey in color. Inability to store pigments is probably not critical at great depths, not only because u.v. protection is not needed, but also because the absence of visual predators eliminates any need for aposematic coloration as a defense mechanism. In an extensive field study of fish visits to sponges of various colors on a Caribbean reef, Wulff (1994) found evidence that sponge color was related to predation intensity. However, most known predators on deep-sea sponges are echinoderms (De Ridder and Lawrence, 1982; Jangoux, 1982; Warner, 1982) and gastropods (Harasewych *et al.*, 1988), neither of which would be dissuaded by coloration (Fig. 7(b), (f)). Mechanical defense supplied by spicules is probably much more important (Birenheide *et al.*, 1993).

In summary, the observed shift from brightly colored sponges to white sponges with increasing depth along the slope may be explained parsimoniously by the fact that most of the organisms, including both food and symbionts, from which pigments are originally derived, are associated with the euphotic zone. In deep water, photosynthetic symbionts are replaced by colorless bacterial symbionts or by cyanobacteria. This inability to be brightly colored is not important in deep water because the selective pressures favoring coloration are not present either.

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