

Population ecology of the demosponge *Amphimedon compressa*

by

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Abstract

The population ecology of *Amphimedon compressa* was investigated at La Parguera, Southwest coast of Puerto Rico. A preliminary survey on the distribution, abundance and population size-structure of this sponge was initially done on three inner shelf and two mid-shelf coral reefs at various depths (3m, 5m, 8m, and 12m). In addition, the population dynamics of *A. compressa* was studied for one year at Las Pelotas (LP), an inner shelf reef experiencing low water motion, and at Media Luna (ML), a mid-shelf reef exposed to high water movement. Results showed that abundance of *A. compressa* varied significantly among sites and depth zones. Colonies were absent in the shallower zone (3m) in 4 of the 5 reefs, however, there was not a clear pattern in the abundance with relation to sites or depths. Size-frequency distributions in shallow depths (5m-8m) were generally dominated by colonies less than 20cm tall, meanwhile the size-structure in the deepest zone (12m) was characterized by a combination of small (<20cm) and large (>20cm) colonies. Median colony heights increased with depth, in 4 of the 5 reefs. When comparing median colony size among reefs within depths, larger colonies were found in inner shelf sites. There was little variation in the abundances during the studied period at both sites. However, higher numbers of colonies were found in February and April as a result of higher number of sexual and asexual recruits. Sexual and asexual recruits contributed similarly to the total recruitment of new colonies. Overall, survivorships did not differ statistically between sites ($X^2_{1}=1.759$, $p=0.185$). However, survivorship at ML was size dependent with the lowest survivorships (<40%) for large colonies (>20cm) and the highest (85.7%) for small colonies (<10cm). In contrast, survivorships did not differ at LP averaging about 67% among size classes. The

high mortality of large sponges at ML may be due to fragmentation and/or detachment from drag forces caused by high water motion. Growth rates were significantly higher at LP where growth rates increase with increasing size. This size-dependent growth pattern was not observed at ML. A stage-based population matrix model predicted an increase in abundances in both populations, with the population at ML increasing more rapidly. Projected abundances at LP showed a decline unless both sexual and asexual recruits are included in the model. Conversely, abundances at ML decline only when sexual recruits are not considered. No evidence of biological interactions (predation, grazing, inter/intra specific competition, disease) affecting the growth, survivorship and recruitment, were observed in this study indicating that physical factors may play a more important role in structuring the populations of *A. compressa*.

Resumen

La ecología poblacional de *Amphimedon compressa* fue investigada en La Parguera, costa sur-oeste de Puerto Rico. Estudios preliminares sobre su distribución, abundancia y estructura poblacional de tamaño, se llevaron a cabo a varias profundidades (3m, 5m, 8m, 12m) en varios arrecifes de coral localizados en la parte interior e intermedia de la plataforma insular. Además, la dinámica poblacional de *A. compressa* se estudió por un año en Las Pelotas (LP), un arrecife interno protegido del oleaje y en Media Luna (ML), un arrecife intermedio completamente expuesto al embate de las olas. Los resultados demostraron que la abundancia de *A. compressa* varió significativamente entre sitios y zonas de profundidad. Sin embargo, no se observó un patrón definido en la abundancia. En todos los arrecifes la zona más llana (3m) se caracterizó por la ausencia o poca abundancia de colonias. La distribución de frecuencia de tamaños fue dominada por colonias pequeñas (≤ 20 cm) en las zonas llanas (5m-8m) mientras que la zona más profunda (12m) se caracterizó por la presencia tanto de colonias pequeñas (≤ 20 cm) como de colonias grandes (> 20 cm). La mediana del tamaño de las colonias aumentó con profundidad en 4 de 5 arrecifes. Por otro lado, las colonias que habitaban en arrecifes internos mostraron una mediana de tamaño mayor que aquellas colonias que se encontraban en arrecifes intermedios. La abundancia no varió considerablemente a través del año. Aún así se encontraron picos en el mes de Febrero y Abril como resultado de un mayor número de reclutas durante estos meses. El reclutamiento se dio vía reproducción sexual y asexual, ambos modos contribuyendo similarmente al número total de nuevas colonias. En general, la supervivencia no varió significativamente entre arrecifes ($\chi^2_{1}=1.759$, $p=0.185$). Pero en ML, ésta fue dependiente del tamaño donde las colonias

grandes (<20cm) mostraron una menor tasa de supervivencia, <40%, mientras que para las colonias pequeñas la misma fue de un 85.7%; mientras en LP la supervivencia fue similar entre las diferentes clases de tamaños variando entre 63-70%. Una posible explicación a la alta mortalidad de las colonias grandes en ML es la fragmentación y/o desprendimiento basal causado por las fuerzas de arrastre relacionadas al fuerte movimiento del agua. La tasa de crecimiento, por otro lado, fue significativamente más alta en LP que en ML. En LP se observó un patrón de crecimiento específico del tamaño donde las tasas de crecimiento aumentaron con el tamaño inicial, no obstante en ML dicha relación no se observó. Un modelo poblacional basado en el tamaño mostró un incremento en la abundancia total de las colonias a través del tiempo en ambos sitios, siendo esta más rápida en ML. Sin embargo, en LP la población declinaría si uno de los modos de reproducción es excluido del modelo, mientras que en ML esto ocurriría solo si los reclutas sexuales no son considerados. Durante este estudio no hubo evidencia de que factores biológicos (e.j. depredación, competencia, enfermedades) afectaran el crecimiento, la supervivencia o el reclutamiento de *A. Compressa*, lo que indica que los factores físicos deben jugar un rol más importante al estructurar las poblaciones de esta especie.

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“Que la resaca muerte no me encuentre vacío, solo, y sin haber hecho lo suficiente”

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1. INTRODUCTION

Sponges are one of the most important and diverse components of the benthic fauna of coral reefs. As a group, they play a significant role in recycling nutrients (Wilkinson and Fay, 1979; Wilkinson, 1983b; Rützler, 1990; Díaz and Ward, 1997) and cleaning the water column of bacteria, organic particles and other small plankton increasing water clarity and improving water quality (Reiswig, 1971a; Pile, 1997). In addition, they serve as a food source (Ayling, 1981) and shelter (Costello and Myers, 1987; Duffy, 1992) for several species. Sponges also play an important role in population and community structure throughout inter and intra-specific mechanisms such as competition (Aerts and van Soest, 1997; López-Victoria et. al, 2006) and mutualism (Goreau and Hartman, 1963; Wulff, 1997b; Carballo and Avila, 2004). They also influence coral reef morphology by binding pieces of coral rubble to the framework (Wulff, 1986) and degrading CaCO₃ through bioerosion (Hutchings, 1986). These processes improve coral survival (Wulff, 1986), and provide microhabitats for hundreds of species (Rützler, 1975; Hartman, 1977; Wilkinson, 1983a). Furthermore, the importance of sponges in reconstructing metazoan evolutionary relationships (Maldonado, 2004; Nichols, 2004), as a source of commercial chemicals and medicines (Munro et al., 1994; Faulkner, 2002) and in controlling phytoplankton blooms (Peterson et. al, 2006) has been recognized in the last couple of years.

Despite their multi-functional roles, sponges have received little attention in comparison to other coral reef organisms such as scleractinian corals, algae, and fishes. As an example, studies dealing with the population dynamics of sponges have been done in relatively few species (Reiswig, 1973; Wulff, 1991, 2006; Duckworth and Battershill,

2001; Duckworth, 2003), partly because their high diversity, taxonomic problems, and multiple and irregular growth forms make them difficult to quantify and identify (Wulff, 2001). Puerto Rico is not an exception. Although coral reef systems of La Parguera have been subject to intensive research in the last decades, detailed studies on the ecology of sponges has been largely limited to Vicente (1978, 1987) and McLean (2006). This represents an important gap in the general knowledge of La Parguera coral reef ecosystems given the importance of sponges as a structuring force and their influence in the dynamics of coral reef communities (Suchanek *et al.*, 1983).

Studies dealing with the population ecology of sponges may be essential because they can provide valuable insights into biological and non-biological factors that affect coral reef populations and communities. For example, characteristics such as (1) size-frequency distribution, (2) dispersion patterns, (3) population density, and (4) population dynamics, provide useful information about the structure of sponge populations, the environmental causal factors, and make possible predictions about population trends. As a consequence, in order to get a better understanding of coral reef ecology, as a whole, it is necessary to carry out comprehensive studies dealing with the biology and ecology of sponges, particularly at the population level.

This study focused on *Amphimedon compressa*, (Duchassaing and Michelotti, 1864) one of the most common shallow-water demosponges inhabiting Caribbean coral reefs (Wulff, 1997b), including Puerto Rico. *A. compressa*, formerly known as *Haliclona rubens* or *Amphimedon rubens*, belongs to the Class Demospongiae, Order Haplosclerida, Family Niphatidae. It is also found in seagrass beds and sandy bottoms attached to little pieces of rubble (pers. obs). *A. compressa* normally grows as a single erect branch,

although, repent forms and colonies with multiple branches (as a result of fusion between conspecific individuals) can be found (Wulff, 1985; pers. obs). Color varies from brilliant red to purple. Its surface is smooth with a compressible consistency, and oscules are distributed uniformly throughout the body.

Preliminary observations indicate that colony sizes of *A. compressa* tend to be larger in low water motion habitats and that maximum colony size is limited under high water motion conditions. Possible reasons for these patterns include differential growth, survival, and recruitment rates. For example, (1) growth rates may be greater in protected habitats, (2) survivorship may be lower for larger colonies in habitats exposed to wave action, and (3) recruitment rates may be higher in exposed habitats. It is possible that the water motion may be affecting these processes as it does sponge morphology and distribution (Vogel 1974; Gerrodette and Flechsig, 1979; Wilkinson and Vacelet 1979; Palumbi 1984; Denny et al. 1985). To test these hypotheses a first step may be to gather and compare baseline information on distribution, abundances, and size-frequency distributions in areas affected by different levels of water motion. A second step is to gather information on the population dynamics (growth, survivorship, and recruitment) at selected sites.

The main objectives of this research were: (i) to determine patterns of abundance and size-frequency distributions of *A. compressa* among reefs, (ii) to assess and compare growth, survival, and recruitment rates of populations of *A. compressa* in two reefs differing in water movement dynamics, and (iii) to use the collected data to develop and describe a size-based population matrix model, and carry out a simulation model to evaluate the relative importance of sexual and asexual recruitment on the population.

2. LITERATURE REVIEW

Sponges are a highly diverse group with more than 7, 000 known species (Wörheide et al., 2005) widely distributed throughout the world's oceans and freshwaters. They can be found from the intertidal zones to the deepest ocean basins (Hopper and van Soest, 2002) and from tropical (Rützler, 1970) to polar waters (Dayton, 1979). Sponges can display a broad range of growth forms ranging from thin, encrusting, sheet-like morphologies to massive globular shapes. Their morphology as well as their life history traits (e.g. growth, survivorship and recruitment) can vary in response to different environmental pressures. For example, Wilkinson and Vacelet (1979) showed that sponge morphology and size differed between and within individuals of several species when grown under different light and flow regimes. This morphological plasticity, in part, allows them to adapt and survive under different environmental conditions. Among the several physical and biological factors affecting and controlling sponge ecology, distribution, and life history traits, the most important are (1) water movement (Bell and Barnes, 2000b), (2) light (Wilkinson and Vacelet, 1979), (3) sedimentation (Könnecker, 1973), (4) substrate (Wilkinson, 1978) and (5) predation (Wulff, 2006).

2.1 Factors affecting sponge distributions

2.1.1 Water motion

Water motion is one of the main physical aspects structuring sponge communities (Bell and Barnes, 2000b). Water movements can affect abundances, species richness, and diversity of sponges (Monteiro and Muricy, 2004). At the same time it can regulate population structure (1) by increasing the food supply per unit time by entraining

water flow (Vogel, 1974) and removing waste (Bell, 2002), hence, facilitating the growth of sponges (Watson, 1976, Hiscock, 1983), (2) by reducing growth rates because of greater metabolic investment in skeletal and basal structures (Palumbi, 1986), and (3) by limiting the maximum growth of colonies by fragmentation and detachment due to storm action (Wulff, 1995) and drag-related forces (pers. obs.). In the study of Wilkinson and Vacelet (1979) growth and survival of all species tested was greatly reduced for sponges grown in low flow relative to high flow areas. However, high wave energy related to storms can increase sponge mortality rates, in particular for small individuals, by means of fragmentation, detachment, and partial mortality (Wulff, 1995b). Water movement can also negatively affect recruitment by reducing post-settlement survivorship and re-attachment of fragments, although it seems to be irrelevant for larval settlement (Maldonado and Young, 1996).

2.1.2 Light

Availability of light is especially important for phototrophic species such as *Cymbastela concentrica* (Cheshire et al., 1995; Roberts et al., 1999), which rely on light and cyanobacterial symbionts for energy uptake (Wilkinson and Vacelet, J., 1979, 1983a). Roberts et al. (2006) experimentally tested the effect of shade on growth of *C. concentrica* and found that under reduced light regimes rates of growth decreased significantly. Similar results were reported for the sponge *Lamellodysidea chlorea* by Thacker (2005). However, he did not find any effect of shading on growth (expressed in biomass) of the sponge *Xetospongia exigua*, which hosts a symbiont. Similarly, Rosell

and Uriz (1992) did not find any relationship between survivorship and light availability for the phototrophic species *Cliona viridis*.

Light also plays an important role in the settlement of sponge larvae. It is believed that larval settlement is controlled by a negative phototaxis (Bergquist et al., 1970; Sara and Vacelet, 1973; Maldonado and Young, 1996) which may explain why larval recruitment tends to be higher in shaded microhabitats (Maldonado and Young, 1996; Maldonado and Uriz, 1998).

2.1.3 Sedimentation

Sedimentation is one of the major physical processes controlling the distribution of sponges. Deposition of sediments can negatively affect sponge growth by covering the body with sediment particles, thus reducing feeding efficiency (Watson, 1976). In addition, sediments can cover the substrate preventing sponge larvae from settling (Maldonado and Young, 1996). Furthermore, high concentrations of sediments in the water column can hinder light penetration affecting growth (Wilkinson and Vancelet, 1979), recruitment (Maldonado and Young, 1996) and survival (Turon et al. 1998).

The effects of sedimentation on sponge assemblages were assessed by Bell and Smith (2004). They studied two sponge communities inhabiting reefs exposed to different levels of sedimentation in Indonesia and found lower overall species richness at the site with higher sedimentation rates. This result supports previous studies by Könnecker (1973) and Bell and Barnes (2000a) who suggested that sedimentation rates may control distribution of temperate sponges. However, Monteiro and Muricy (2004), suggest that sedimentation is of little importance controlling sponge community structure

in Palmas Island, Brazil, where sponge richness and diversity growing on the horizontal substrate is similar to those growing in vertical walls and cave ceilings which were subjected to much less sedimentation.

2.1.4 Substrate

Sponge growth, survival and recruitment can also be affected by the nature of the substratum. It has been documented that sponge larvae do not recruit well on recently cleared (Dayton et al. 1974; Karlson, 1978; Wilkinson, 1978; Ayling, 1980; Keough, 1984; Butler, 1986) and smooth (Maldonado and Uriz, 1998) surfaces. Some sponge larvae, such as the larvae of *Cliona viridis*, are able to settle either on siliceous or calcareous substratum. However, larvae can not survive long periods of time on siliceous substrate (Rosell and Uriz, 1992). Further studies have demonstrated that some sponges (e.g. *Terpios spp.*, and *Cliona orientalis*) grow more efficiently on clean calcareous substrate (Plucer-Rosario, 1987; Schönberg, 2003) than on living corals or artificial substrates, such as plexiglass plates (Plucer-Rosario, 1987). According to Schönberg (2003) availability of uncovered (clean) carbonate substrate may be the most important substrate feature for settlement, survival and growth of sponges, at least for clionid species, possibly because they are boring sponges.

2.1.5 Predation

Among the biological factors affecting the distribution of sponges and their dynamics, predation is one of the most important. There are numerous invertebrates that feed on sponges, for example nudibranchs (Faulkner and Ghiselin, 1983), starfish

(McClintock, 1987, Wulff, 2006), and sea urchins (Reiswig, 1973). In temperate waters these organisms do not consume the whole sponge; as a consequence, it is suggested that these interactions do not play a significant role in structuring sponge community (Wulff, 2006), even though, Guida (1976) suggested the contrary for sponges inhabiting oyster reefs in North Carolina. On the other hand, in Antarctic waters predator-sponge interactions are major structuring forces of sponge communities (Wulff, 2006). Despite the fact that only portions of the sponges are consumed, rather than the entire individual (Wulff, 2006), predation may have a negative effect on life history processes because resource or energy allocation may be directed to regeneration of lost tissue (healing of wounds) instead of growth, survivorship or reproduction (Rinkevich, 1996). Also, lesions could be irreversible. Dayton (1979) concluded that if 20%-30% of their total volume is consumed by predators, Antarctic sponges can not recover. Shield and Witman (1993) point out that wound can weaken branching sponges increasing susceptibility to breakage by water movement, which may have a greater impact on the total loss of biomass (volume) from the sponges than the direct loss from predation.

In tropical waters some vertebrates consume sponges (Wulff, 1994), for instance hawksbill turtles (Dam and Diez, 1997) and fishes (Hoppe, 1988; Wulff, 1994, 1997a, 2000; Hill and Hill, 2002). In the Caribbean, consumption of sponges by these predators may be limited to a few sponge species lacking physical (Chanas and Pawlik, 1995; Pawlik et al, 1997) and/or chemical protection (Pawlik et al, 1995). Randall and Hartman (1968) found traces of sponges in gut contents in just 11 out of 212 fishes studied, indicating that fishes did not control the distribution of sponge. However, Wulff (1997a, 2005) has demonstrated that fish predation can restrict sponges to refuges or to different

habitats, (e.g. coral reef or mangrove roots) and Hill and Hill (2002) found that the sponge *Anthosigmella varians* forma *varians* is restricted to shallow, lagoonal habitats due to predation by the gray angel fish, *Pomacanthus arcuatus*.

2.1.6 Competition

On coral reefs space is a limiting factor (Connell, 1961; Jackson, 1977). As a result organisms have developed different strategies to compete for space. Sponges, as sessile organisms that lack specific competitive organs (Aerts, and van Soest, 1997) such as extracoelenteric digestion and stinging nematocysts (Lang and Chornesky, 1990), produce toxic compounds (allelochemicals) which may function to reduce predation (Waddell and Pawlik, 2000) and to inhibit the growth of neighboring organisms (Turon, et. al, 1998). In addition physical characteristics such as tissue toughness, spicules and organics fibers serve as antipredatory defenses (Chanas and Pawlik, 1995, 1996). Rapid growth rates have also been proposed to be an important competitive mechanism among sponges. For example, Wulff (2005) reported that reef sponges transplanted to mangrove roots were overgrown by *Tedania ignis*, which is a mangrove species which shows relatively rapid growth (Wulff, 2005). However, it is suggested chemical defense is a more important strategy than physical (skeletal) components in competitive interactions (Waddell and Pawlik, 2000). On the other hand, sponges can outcompete corals and other reef organisms by encrusting and excavating skeletons and live tissue (López-Victoria, et al. 2006).

3. METHODS

3.1 Study sites

This research was carried out in the natural reserve of La Parguera, on the southwest coast of Puerto Rico. An initial survey (Oct-2005) of the distribution, abundance, and population size-structure of *Amphimedon compressa* were done at 3m, 5m, 8m, and 12m depth in various reefs (Fig. 3.1). Media Luna CRES (ML CRES) (17°56.093'N, 67°04.509'W) and Turrumote (TU) (17°56.097N, 67°01.130W), are mid-shelf reefs, Enrique (EN) (17°56'65.8" N, 67°02'21.3" W) and Romero (RO) (17°56.249' N, 66°59.433'W) are inner-shelf reefs. These reefs are characterized by a semi-flat platform breaking in a slope that goes down to a depth of 15 to 20m. Macrofauna is visually dominated by octocorals and hard corals at shallow and intermediate depths.

Studies on the population dynamics of *A. compressa* were done at Media Luna (ML) (17°56.096' N- 67°02.911' W) and Las Pelotas reefs (LP) (17°57.442' N- 67°04.176' W) at a depth of 8m (Fig. 3.1). ML is a mid-shelf reef exposed to wave action generated by the easterly trade winds (Yoshioka and Yoshioka, 1991). This site has a depth of 8m and is characterized by a bottom with consolidate substratum and low topographic relief. The second site, LP, approximately 3.5 km away from ML, is an inner-shelf reef protected from wave action by several emergent reefs. This site has a seagrass bed adjacent to a moderately sloping reef which descends to a depth of 15m with the substrate covered by unconsolidated sediments and pieces of loose rubble. Macrofauna at both, LP and ML, is dominated by octocorals with scleractinian corals and sponges as important components. ML and LP were selected based on preliminary

observations which determined that these sites showed the greatest differences in colony sizes at this depth zone.

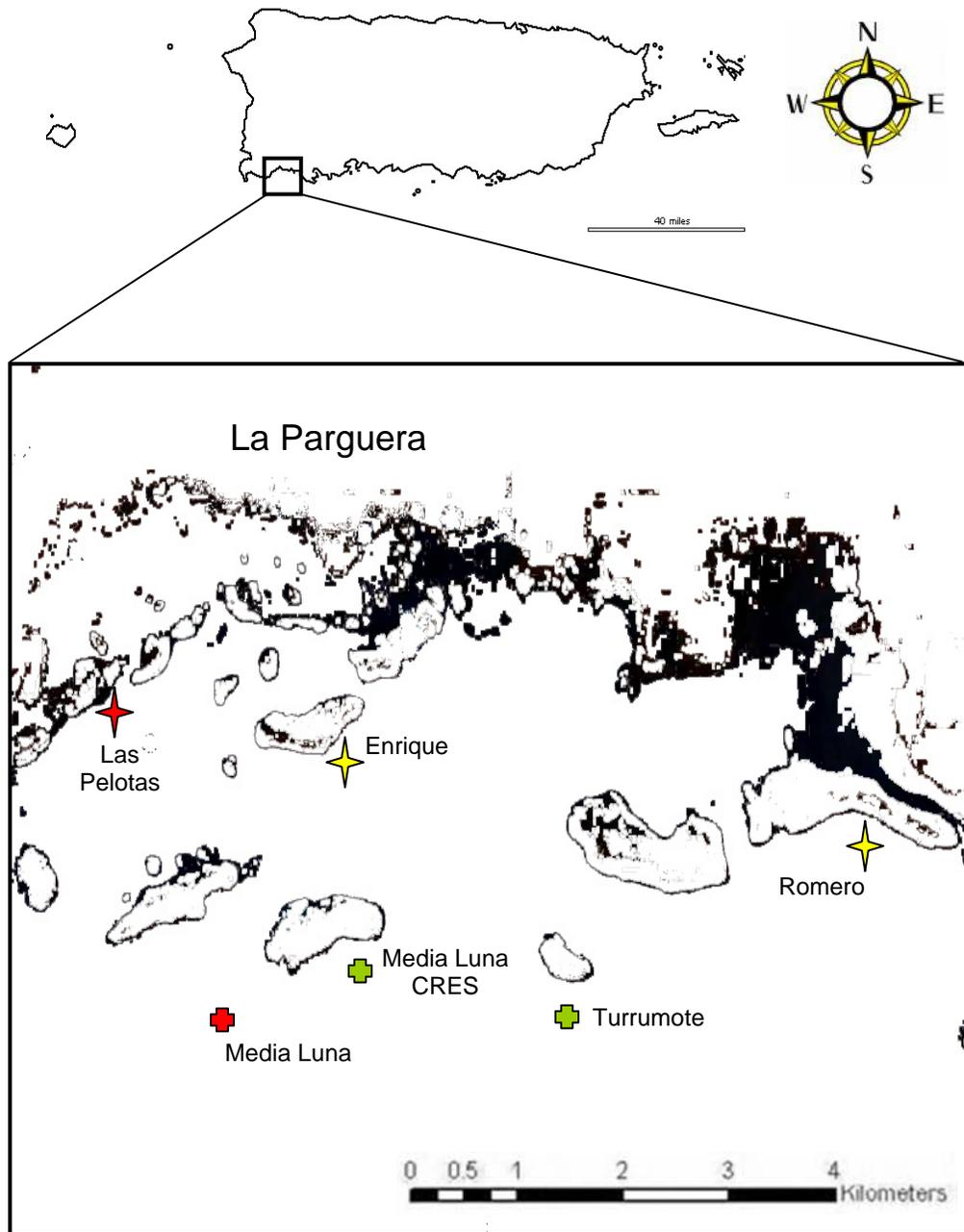


Figure 3.1 Map illustrating study sites. Stars denote inner-shelf reefs and crosses denote mild-shelf reefs. Population dynamics studies were carried out at Las Pelotas (red star) and Media Luna (red cross)

3.2 Water motion

Water movement between the two main study sites (LP & ML) was compared using the zinc-copper technique (McGehee, 1991). When these two metals are in contact under marine conditions, corrosion occurs and zinc loses weight proportional to water flow (McGehee, 1991). For this study six pairs of zinc-copper units were placed in each site at 8m depth for one month (Oct-2005). This time period of one month provides a reliable measure of water motion to characterized and differentiate water movement between sites (Muus, 1968; Doty, 1971; Vogel, 1974; McGehee, 1991; Leichter and Witman, 1997; Kaandorp, 1999; D'Amours and Scheibling, 2007; Pawlik et al., 2007; among others). Zinc was weighted before and after immersion and weight loss was compared and analyzed by a t-test.

3.3 Preliminary study

3.3.1 Abundances, size-frequency distribution, and colony size (height)

To determine whether abundance of *A. compressa* (colonies/m²) differs significantly within reefs among depths and within depths among reefs, ten 1m² quadrats were randomly placed along two 10m long transects at four different depths (3m, 5m, 8m, and 12m, total = 40), in each reef, with the exception of ML which only has one depth (8m). Although, certainly a greater number of replicates may be desirable, 10 replicates (10 quadrats) have been found to be acceptable as a solid starting point for small scale studies (Gotelli and Ellison, 2004). All colonies within each quadrat were counted and median densities (colonies/m²) within reefs among depths and within depths among reefs were compared using a Kruskal-Wallis One-way ANOVA after data and

transformation procedures were unsuccessful in fulfilling the assumptions of normality and homoscedasticity. Student-Neuman-Keuls (SNK) test was performed for a posteriori analysis of all pair-wise comparisons. To test if there is a significant relationship between median densities and sites and between median densities and depth, patterns of abundance among depths and among reefs were analyzed with a Kendall Concordance analysis, a non-parametric test that provides an overall measure of the association between the variables (Sokal and Rohlf, 1995).

Size-frequency distributions were evaluated by measuring the height (using a ruler) of all colonies within twenty 1m² quadrats placed along two (10m x 1m) belt transects at four different depths (3m, 5m, 8m, and 12m), in each reef, with the exception of ML which only has one depth (8m). Colonies were classified into 11 size classes of 5 cm each, with the exception of the largest size class which grouped all colonies larger than 50 cm. The number of size classes was chosen to include the range of colony heights observed in the population, using the smallest class interval size without exceeding 12 classes (Sokal and Rohlf, 1995). Median colony heights within reefs among depths and within depths among reefs were compared using a Kruskal-Wallis One-way ANOVA after data and transformation procedures were unsuccessful fulfilling the assumptions of normality and homoscedasticity. Because sample size among groups was unequal, Dunn's test was performed as a posteriori analysis of all pair-wise comparisons. To test if there is a significant relationship between median colony height and sites and between colony height and depth, patterns of colony height among depths and among reefs were analyzed with a Kendall Concordance analysis.

3.3.2 Dispersion patterns

Dispersion patterns were analyzed at LP and ML by placing 16-1m² quadrats contiguously along a 16m line transect at a depth of 8 meters in each site, and counting all individuals within the quadrats. The conditions of the Poisson distribution were met in this work, (1) there is no gradient in abundance within the study area, (2) the probability of occurrence of a sponge colony within the sample area is constant ($p \rightarrow 0$), and (3) many colonies could occur in a quadrat ($k \rightarrow \infty$). Therefore, variance to mean ratio (S^2/\bar{x}) (Grieg-Smith, 1964; Dana, 1976; Yoshioka and Yoshioka, 1989) was used to determine if dispersion patterns of *A. compressa* differ from randomness. This ratio equals 1 when colonies are randomly dispersed, it is greater than 1 when colonies are aggregated, and it is less than 1 when colonies are evenly dispersed. In addition, Hill's (1973) index of patchiness (P), where $P = (\text{Variance} - \text{mean}) / \text{mean}^2$, was used to determine the pattern of spatial mortality by comparing the intensity of pattern at the beginning (December 2005) and at the end (December 2006) of the study. This index remains the same, decreases or increases when the pattern of mortality is density independent, density dependent, or inverse density independent respectively.

3.4 Population dynamics

3.4.1 Survivorship and colony growth

Estimates of survivorship were based on 106 and 120 colonies at Las Pelotas and Media Luna, respectively. Each colony was tagged (using a cable tie with a number), mapped, and monitored at three month intervals for one year. Mortality was defined as a colony observed at any given survey time that was not present at the next survey. To

determine if survivorship was size dependent, colonies were classified in three height classes: small (<10 cm), medium (10-20 cm), and large (>20 cm), in order to maintain at least twenty colonies in each size class at both sites. Survivorships among size classes and between sites were analyzed with Chi-square test.

For the analysis of growth only those individuals that survived to the end of the study period were considered. The height of each tagged sponge was measured to the nearest 0.5 cm every three months using a ruler. Colony growth was based on the change in height. A Mann-Whitney U-Test was performed to compare overall growth rates between sites after data and transformation procedures were unsuccessful fulfilling the assumptions of normality and homoscedasticity. To see if initial colony size influences colony growth, colonies were classified in the same three height classes: small (<10 cm), medium (10-20 cm), and large (>20 cm) and growth rates among size classes within sites were compare with a Kruskal-Wallis One-way ANOVA. Spearman's rank correlation was used to explore a possible relationship between initial colony size and growth rate.

3.4.2 Recruitment

Recruitment, defined as any new colony that could be seen with the naked eye, was monitored in two permanent 10m x 1m (10m²) belt transects 10m apart from each other at a depth of 8m at LP and ML. Ten 1m² quadrats were established along each transect and marked with nails to ensure and facilitate re-localization in following surveys. After an initial survey in October, 2005 (when all the existing colonies were mapped), all recruits within the quadrats, as a result of either sexual or asexual reproduction, were mapped, counted, and measured every two months for one year (i.e.

six sampling periods). New recruits as well as recruit survivorship/mortality were documented by comparing maps. Sexual and asexual recruits were differentiated following Wulff (1991), by looking at fragment orientation (horizontal vs vertical), comparing size, and by signs of fragmentation or basal detachment (Fig. 3.2 top). Since small colonies (<10cm) grew at mean growth rates of 1.75 (\pm 2.2) and 2.39 (\pm 3.35) cm/yr at ML and LP, respectively, individuals < 4 cm were considered as sexually produced (larval derived, Fig 3.2 bottom) assuming that a newly settled sponge larva can not attain a size larger than 4 cm during the 2 month monitoring interval. Chi-square analysis was performed to test for association between mode of reproduction and sites as well as for association between recruit survivorship and site. This test was also used to compare survivorships between modes of reproduction within site.

3.4.3 Size-based population matrix model

A population model was performed with the data of the survivorship and growth of colonies collected during the 1 yr study. The basic projection matrix model was $\mathbf{n}_{t+1} = \mathbf{A}\mathbf{n}_t$ where \mathbf{n}_t is a column vector representing the number of colonies in each size class at time t , \mathbf{n}_{t+1} represents the number of colonies at each class at time $t+1$, and \mathbf{A} represents the matrix describing the transition probabilities of colonies to remain in the same size class or change to a different one. In order to evaluate the relative importance of sexual and asexual reproduction in maintaining the population of *A. compressa*, a simulation model representing two different situations was performed for both sites, (1) a scenario including only sexual recruits and (2) a scenario that included only recruits from asexual fragmentation and/or detachment.

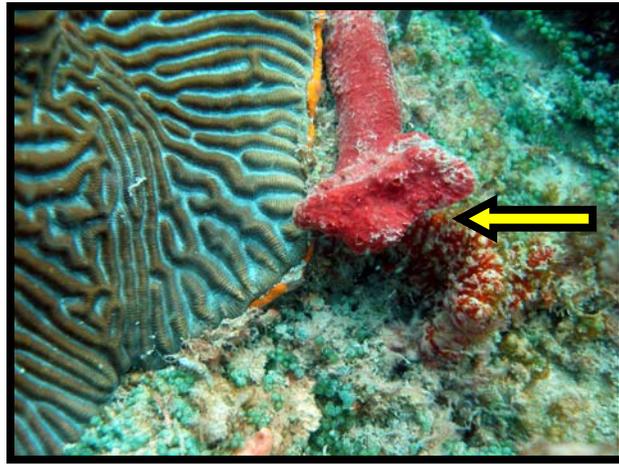


Figure 3.2 Asexual recruit with arrow showing signs of detachment) (top), circle enclosing a sexual recruit 2 cm in height (bottom).

4. RESULTS

4.1 Preliminary study

4.1.1 Water motion

Zinc mean dissolution rates were significantly higher at ML (3.05 ± 1.30 , mean \pm standard deviation) when compared to LP (0.720 ± 0.600 , mean \pm standard deviation) ($t = 4.096$ with 10 degrees of freedom, $p = 0.002$), indicating a greater water flow at ML.

4.1.2 Colony Abundances

Median densities (colony/m²) differed significantly among depths within each reef in all locations except at Turrumote (Kruskal-Wallis One-way ANOVA) (Fig. 4.1). Colonies were absent or in lowest abundance in the shallowest area (3m) in all reefs. Colony abundances were significantly lower at 3m than all other depth zones except for TU (SNK with Kruskal-Wallis One-way ANOVA). The low abundances at 3m is probably responsible for a significant overall concordance between abundances and depths among reefs (Kendall's $W=0.600$, $p < 0.001$) because no consistent relationship was observed between abundances and other (deeper) depth zones among reefs. For example, abundances did not differ significantly among the 5m, 8m, and 12m zones at LP. Alternatively, abundances were significantly greater at 5m compared to the 12m zone in ML CRES and RO (SNK with Kruskal-Wallis One-way ANOVA), whereas abundances in the 12m zone of EN were significantly greater than abundances in the 5m zone (SNK with Kruskal-Wallis One-way ANOVA).

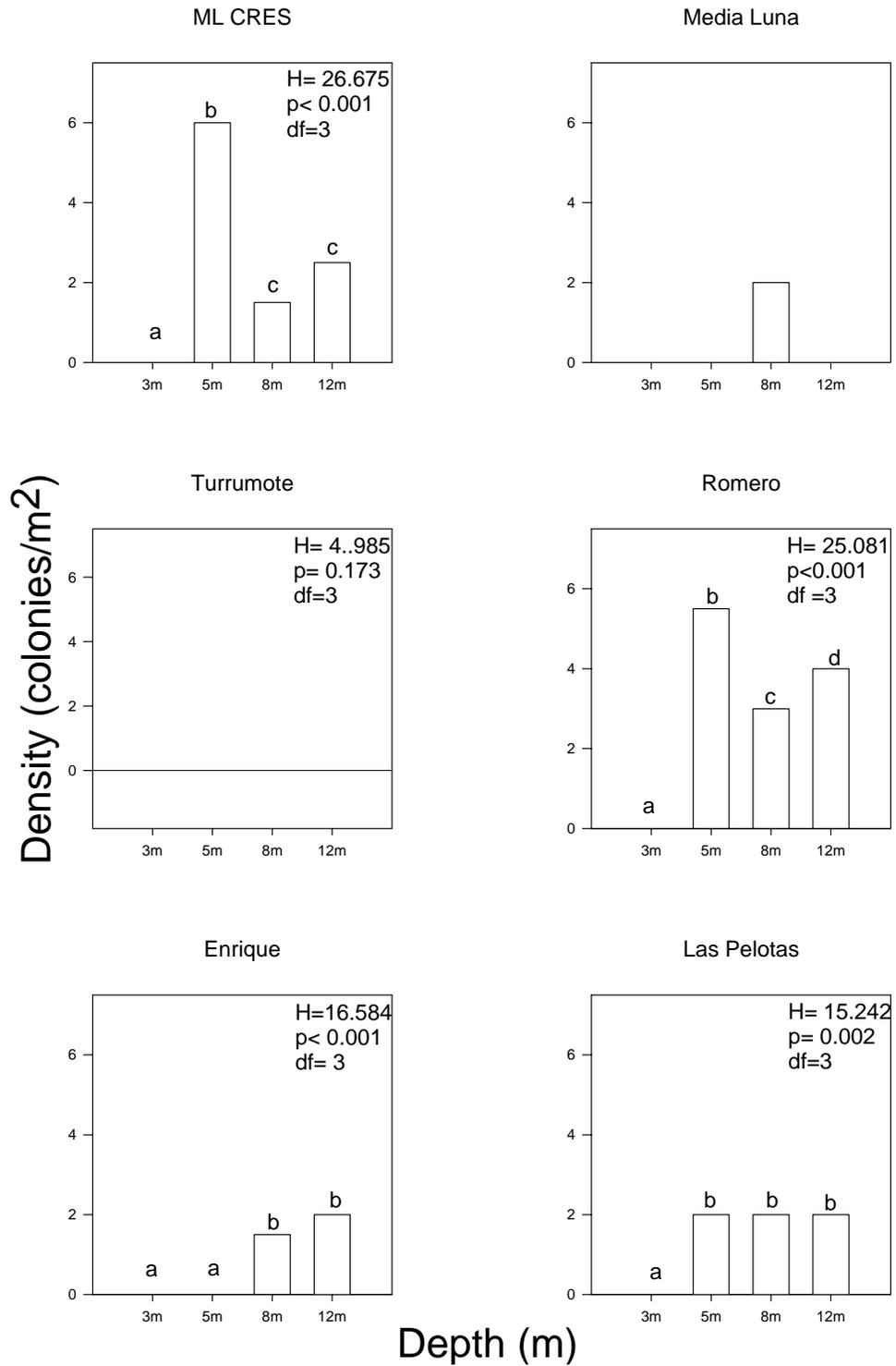


Figure 4.1 Median densities (colonies/m²) of *A. compressa* among depths within reefs. Different letters indicate significant differences between pair-wise comparisons (Student-Neuman-Keuls test). H= value of Kruskal-Wallis One-way ANOVA, df= degree of freedom.

With respect to comparisons within depth zones among reefs the only significant difference in median densities were found in the 12m and 5m zones (Kruskal-Wallis One-way ANOVA). For instance, significantly lower densities occurred in the 12m zone (SNK test, $p < .005$, with Kruskal-Wallis One-way ANOVA) at TU (median density: 0.40 colony/m²) compared to all other reefs. On the other hand, significantly higher abundances at 5m were observed at RO and ML CRES compared to the other reefs. As implied by this variable pattern among reefs within depth zones, the Kendall concordance test was non significant ($W = .49$, $p > .05$). In other words no reef had consistently higher (or lower) abundances at all depths compared to other reefs. This result suggests that densities may be influenced by interactions between depths and site related factors.

4.1.3 Size-frequency distribution and colony size (height)

Size-frequency distributions of colonies are shown in Fig. 4.2 through Fig. 4.6. Shallow areas ($\leq 8\text{m}$) were dominated by small ($< 10\text{ cm}$) and mid sized colonies (10-20 cm) in all reefs. Meanwhile, the deepest zone (12m) was characterized by the presence of small and large colonies ($> 20\text{ cm}$). Median colony heights among depths differed significantly within all reefs with the exception of TU (Kruskal-Wallis One-way ANOVA, see Fig. 4.8). In all reefs (but TU) median colony height was significantly greater in the 12m zone when compared to other depths (Dunn's test $p < .005$, with Kruskal-Wallis One-way ANOVA). Kendall's concordance analysis revealed a high concordance of the median colony height among depths within reefs (Kendall's $W = .96$, $df = 2$, $p < .00$). This indicates that median colony height increases as depth increases in all reefs, with the exception of TU (Fig. 4.7).

When comparing median colony height among reefs within depths, significant differences were observed in the 8m and 5m zones but not at 12 m. At 8m median colony height was significantly lower at ML compared to all others reefs (Dunn's test $p < 0.005$). Also, median colony heights in the 5m zone were significantly greater at LP and RO when compared to ML CRES (Dunn's test $p < 0.005$), (TU and EN were excluded from the analysis because of low number of colonies found at this zone). In general, at each depth the tallest colonies were found at the less exposed inner shelf reefs (LP and RO). Nevertheless, Kendall's concordance analysis indicated that median colony heights did not show a significant pattern ($W = 0.12$, $df = 4$, $p > 0.05$) among reefs within depth zones. However, this result may reflect sampling effects of low sample sizes on median heights at TU (e.g., 4 colonies at 5 m). A significant concordance ($W = 0.85$, $df = 3$, $p < 0.05$) resulted when TU was excluded from the analysis.

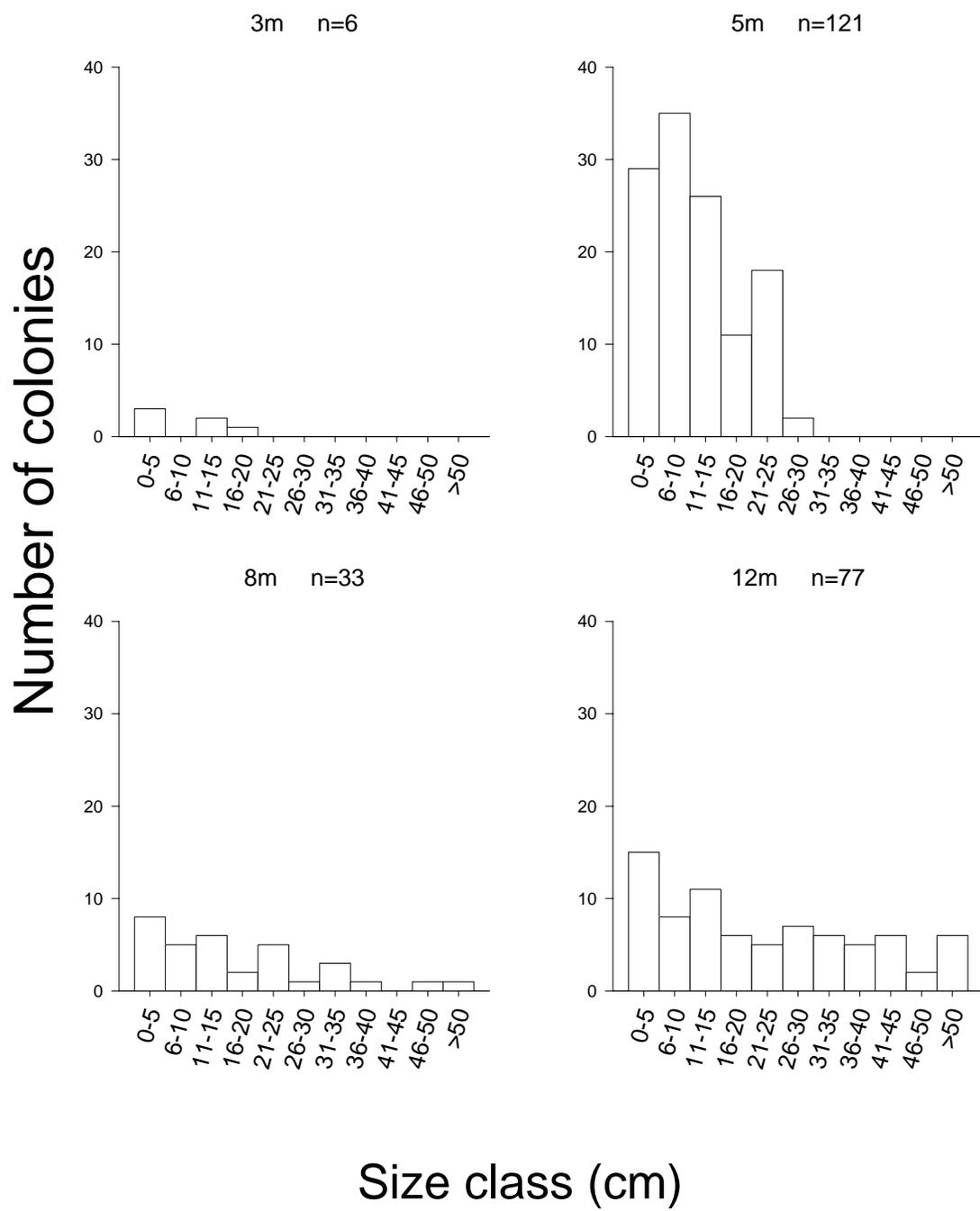


Figure 4.2 Size-frequency distributions of *A. compressa* at Romero at different depths, n=total number of colonies.

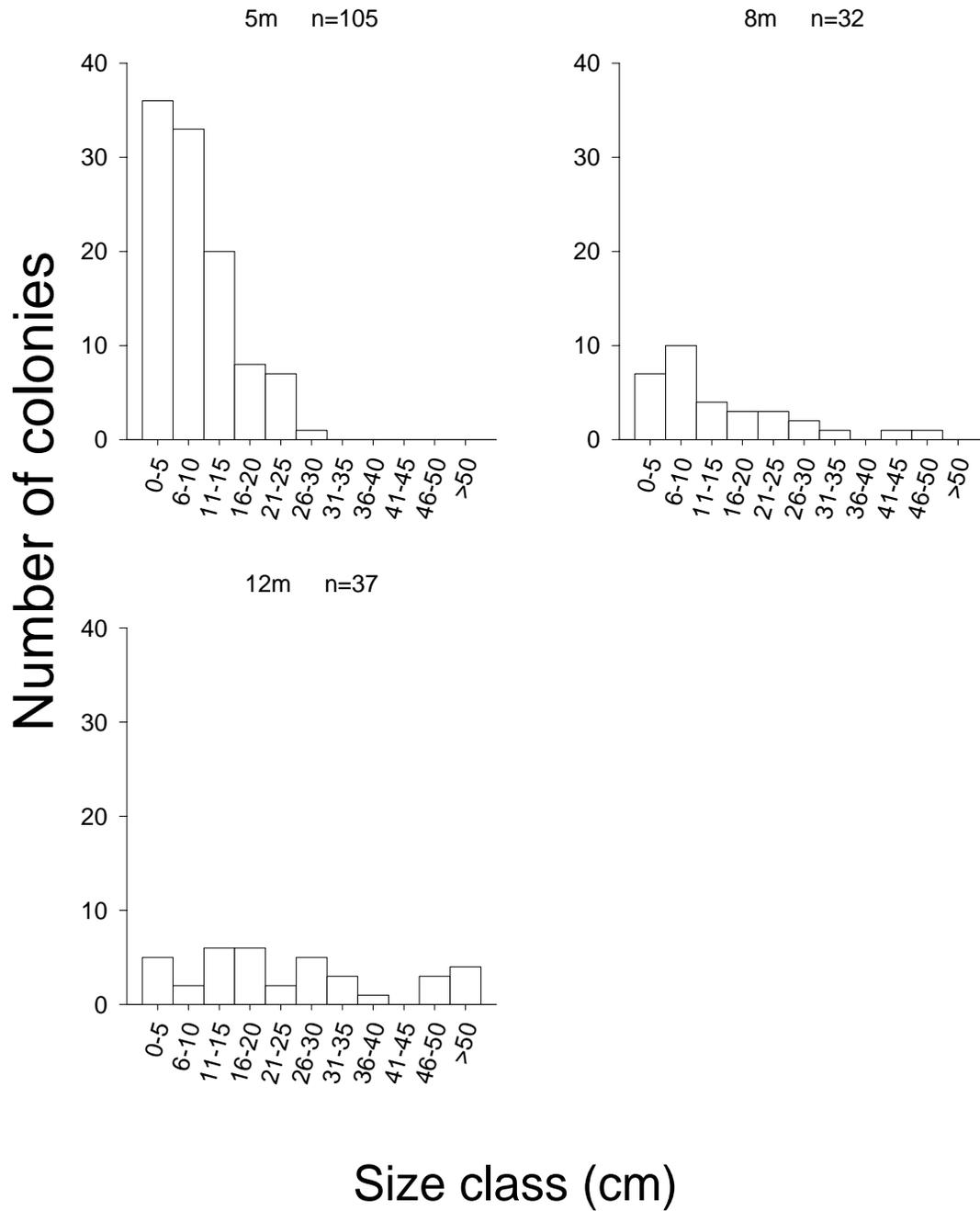


Figure 4.3 Size-frequency distributions of *A. compressa* at Media Luna CRES at different depths, n=total number of colonies. Size-frequency distribution at 3m was not represented because of the absence of colonies at this depth.

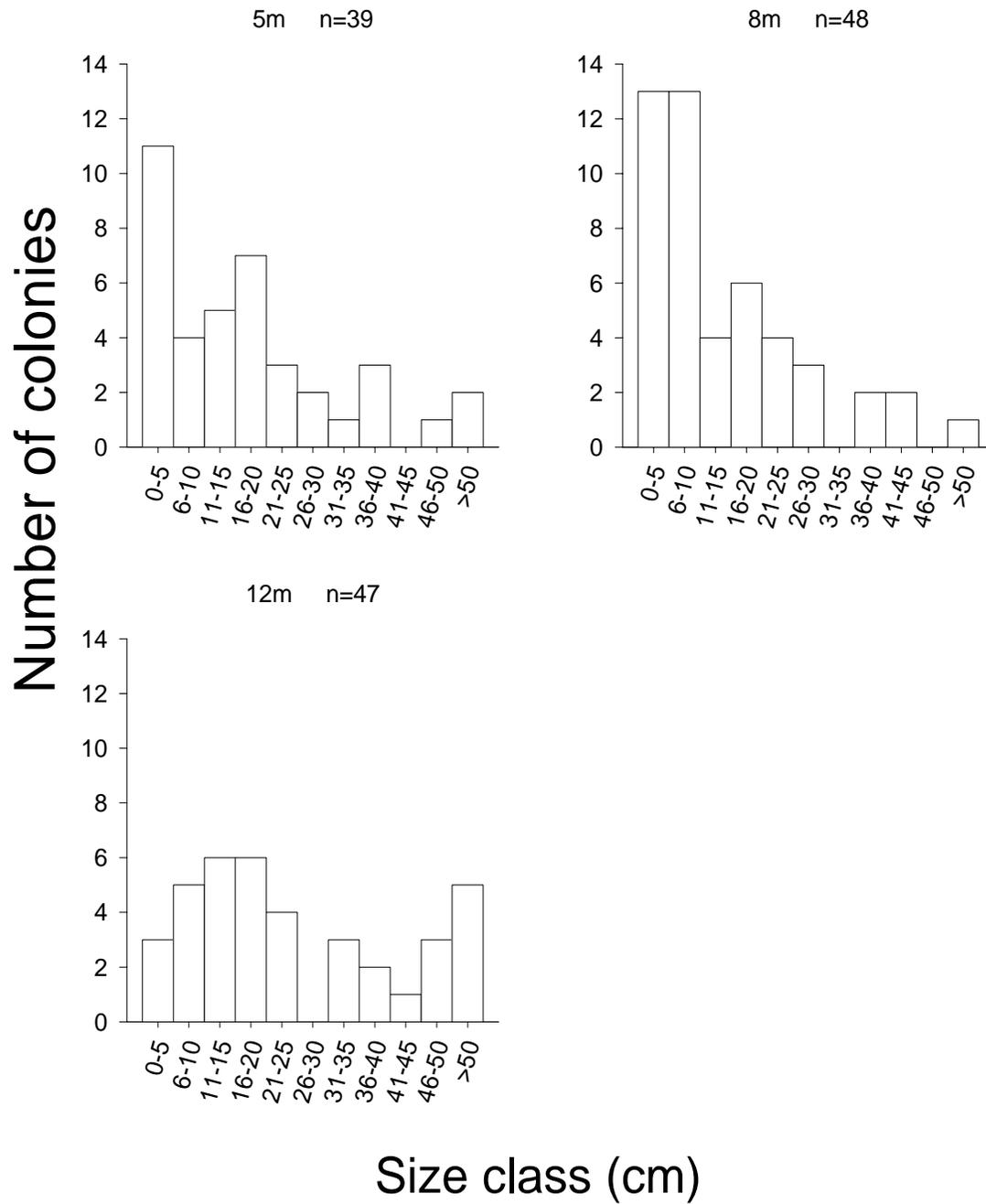


Figure 4.4 Size-frequency distributions of *A. compressa* at Las Pelotas at different depths, n=total number of colonies. Size-frequency distribution at 3m was not represented because of the absence of colonies at this depth.

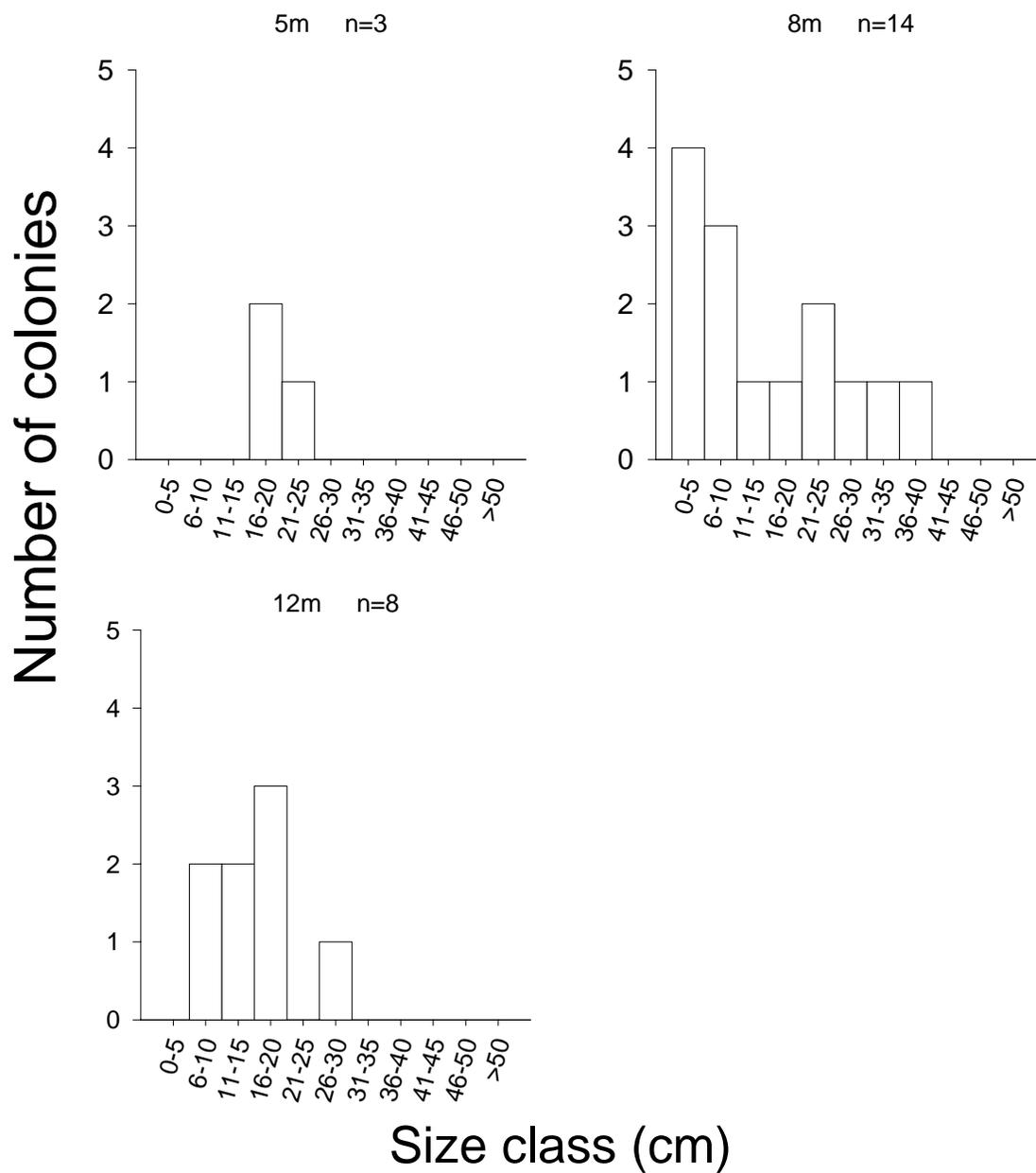


Figure 4.5 Size-frequency distributions of *A. compressa* at Turrumote at different depths, n=total number of colonies. Size-frequency distribution at 3m was not represented because of the absence of colonies at this depth.

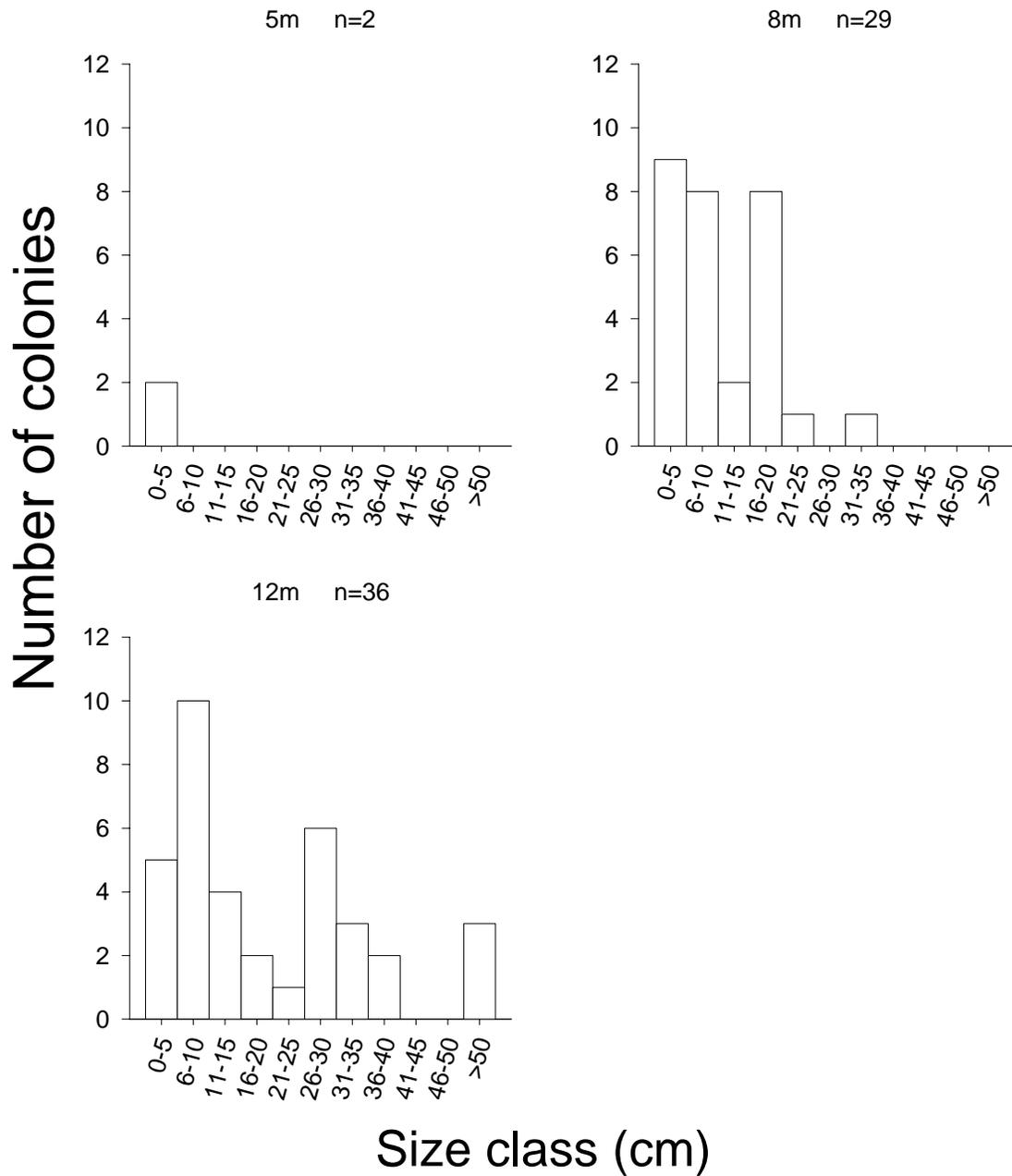


Figure 4.6 Size-frequency distributions of *A. compressa* at Enrique at different depths, n=total number of colonies. Size-frequency distribution at 3m was not represented because of the absence of colonies at this depth.

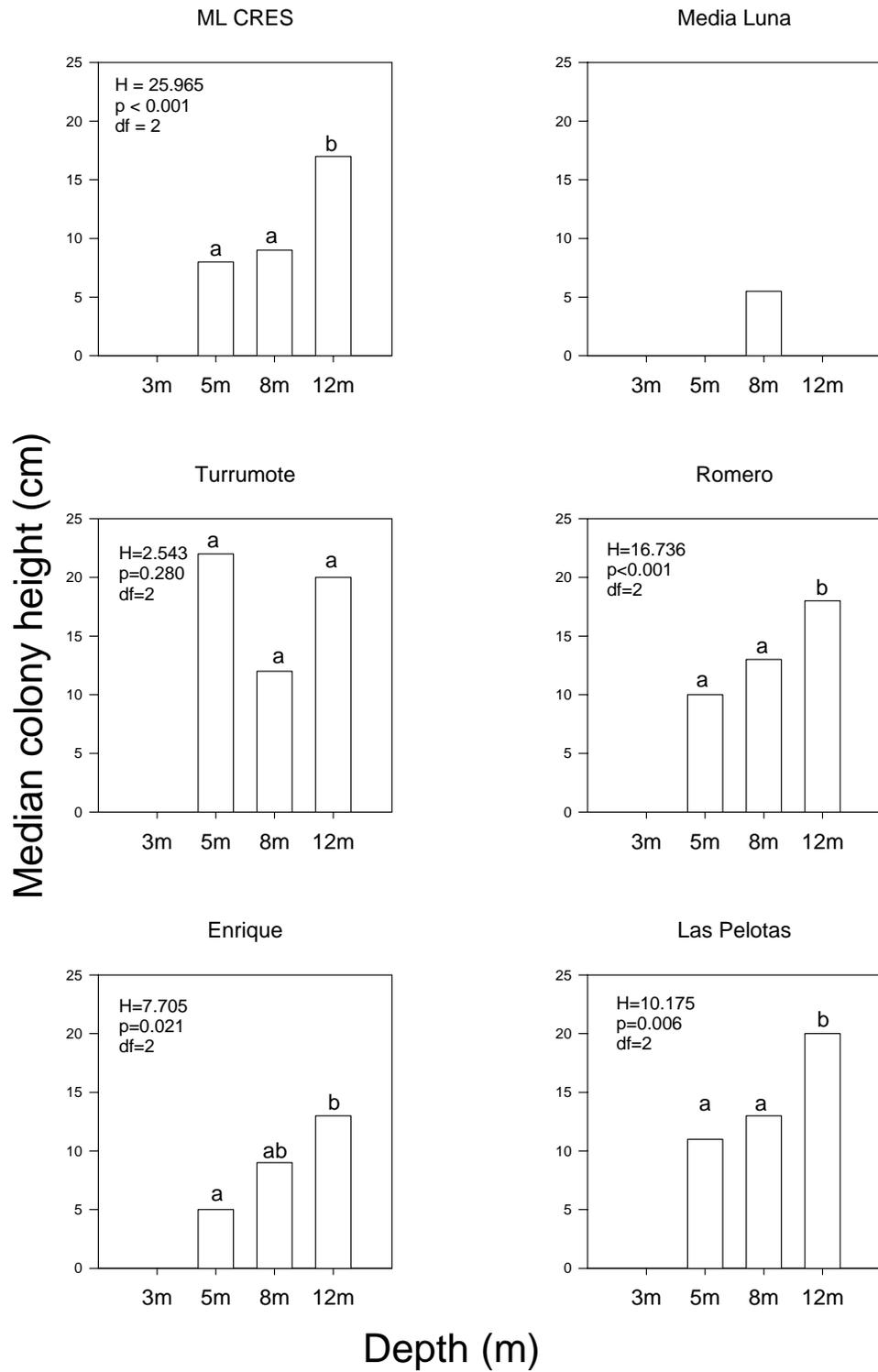


Figure 4.7 Median colony height of *A. compressa* among depths within reefs. Different letters indicate significant differences between pair-wise comparisons (Dunn's test). H= value of Kruskal-Wallis One-way ANOVA, df= degree of freedom.

4.1.4 Dispersion Patterns

Variance to mean ratios were significantly higher than 1.0 ($p < 0.001$) on 1m^2 scale at LP as well as ML ($p < 0.001$) suggesting an aggregated pattern. Hill's (1973) index of patchiness was used to compare intensity of pattern between sites. Aggregations at ML were patchier than aggregations at LP (Table 4.3). At the end of the study LP showed a slight increase in patchiness of the original colonies which suggests that there is an inverse density independent effect on mortality. Meanwhile at ML, the patchiness index decreases slightly indicating density dependent effect on mortality. However, in both cases the change in patchiness was small and not significantly different from density independent mortality.

Table 4.1 Variance to mean ratios and patchiness for *A. compressa* at LP and ML at 1m^2 scale. N= num. quadrats, S/\bar{x} = Variance to mean ratio. S=variance, \bar{x} =mean.

Site	N	Time	Mean	Variance	S/\bar{x}	p value	Patchiness
LP	16	Dec-05	2.18	5.63	2.57	$p < 0.001$	0.726
LP	16	Dec-06	1.43	3.19	2.22	$p < 0.001$	0.860
ML	16	Dec-05	2.87	16.38	5.69	$p < 0.001$	1.640
ML	16	Dec-06	2.75	14.86	5.40	$p < 0.001$	1.601

4.2 Population Dynamics

4.2.1 Abundance

The average number of colonies ranged between 2.20 colonies/m² and 3.15 colonies/m² at LP and between 2.95 colonies/m² and 3.55 colonies/m² at ML (Fig. 4.8). At both sites abundances increased at the beginning of the study (Dec-05 to Apr-06) reaching the highest abundance during February and April. These peaks were partly due to the high numbers of recruits during February (see recruitment section). After this maximum, however, patterns of abundance differed between reefs. At ML abundances remained relatively stable through time, while at LP the total number of colonies slightly decreased until attaining a minimum value in December 2006.

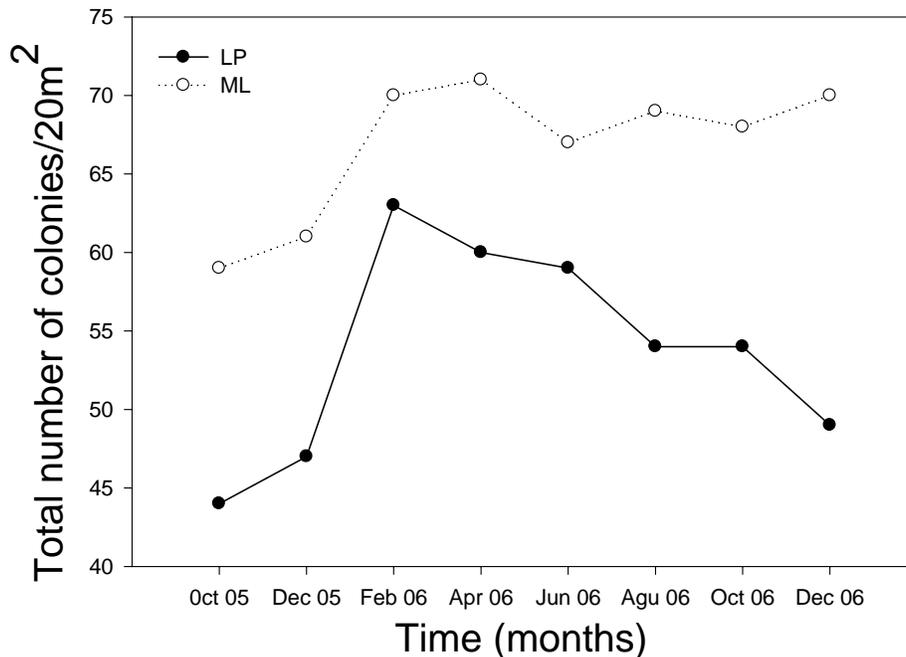


Figure 4.8 Temporal variations in the total abundances (colonies/20m²) of *A. compressa* at Las Pelotas and Media Luna.

4.2.2 Survivorship

Overall survivorship did not differ statistically between sites (LP: 67%, or 71 ex 106; ML: 76%, or 91 ex 120; $X^2_{1}=2.176$, $p>0.100$). To determine if survivorship was size dependent, sponges were classified in three height classes: small (<10 cm), medium (10-20 cm), and large (>20 cm). At LP survivorship did not differ among size classes ($X^2_2= 0.505$, $p> 0.100$) with survivorship varying from 63% for small colonies to 70% for medium and large colonies. In contrast, survivorship at ML was size-specific ($X^2_2=20.240$, $p<0.001$) with the lowest survivorship (<40%) for the largest size class and the highest survivorships (85.7%) for the smallest size class.

Table 4.2 Observed and expected number of live/dead among size classes and colony condition at LP and ML reefs. ()=expected values.

	Size class								
	Small		Medium		Large		Total		
	Live	Dead	Live	Dead	Live	Dead	Live	Dead	
LP	29(31)	17(15)	21(20)	9(10)	21(20)	9(10)	71	35	106
ML	60(53)	10(17)	23(20)	6(10)	8(20)	13(10)	91	29	120

4.2.3 Growth

The analyses of growth were based on 71 and 91 colonies that survived for one year at LP and ML, respectively. There was a significant difference in growth rates between sites (Mann-Whitney U-Test, $T = 8245.500$, $p < 0.001$). Sponges inhabiting LP showed an overall faster growth than sponges at ML. Median colony growth at LP was 4.5 cm/yr while colonies in ML grew at a median rate of 1.5 cm/yr.

There was also a significant difference in rate of growth among size-classes within site, LP (Kruskal-Wallis One-way ANOVA, $H = 27.713$ $df=2$, $p < 0.001$), ML (Kruskal-Wallis One-way ANOVA, $H = 9.920$, $df=2$, $p = 0.007$). At LP colony growth rates tended to increase with colony size (Fig. 4.9). This size-specific tendency could be confirmed by a positive, though weak, Spearman's rank correlation coefficient ($r_s = 0.584$, $p < 0.001$) (Fig. 4.10 bottom). In contrast, at ML medium-sized colonies showed higher growth rates, but the relationship between initial size and growth was non significant ($r_s = 0.103$, $p = 0.324$).

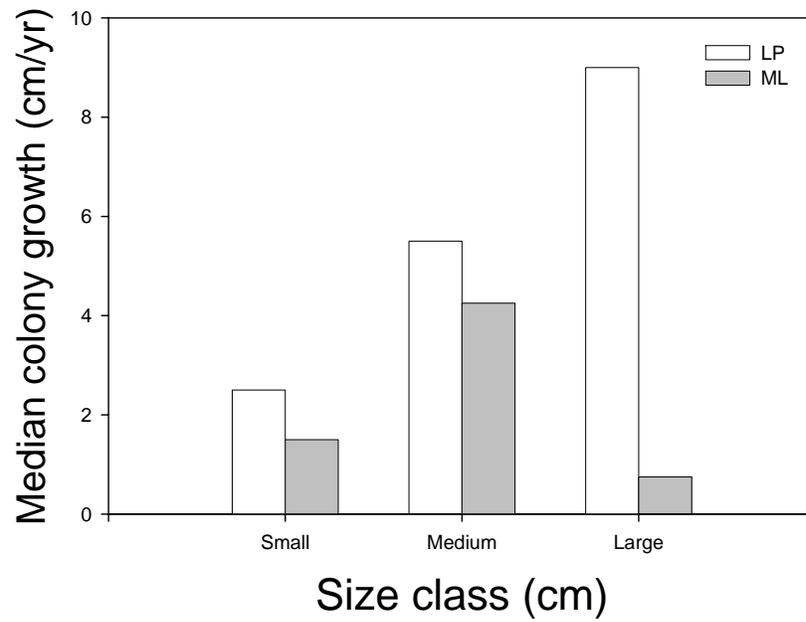


Figure 4.9 Comparisons of rates of growth among size-classes within sites. Small (<10), medium (10-20), large (>20).

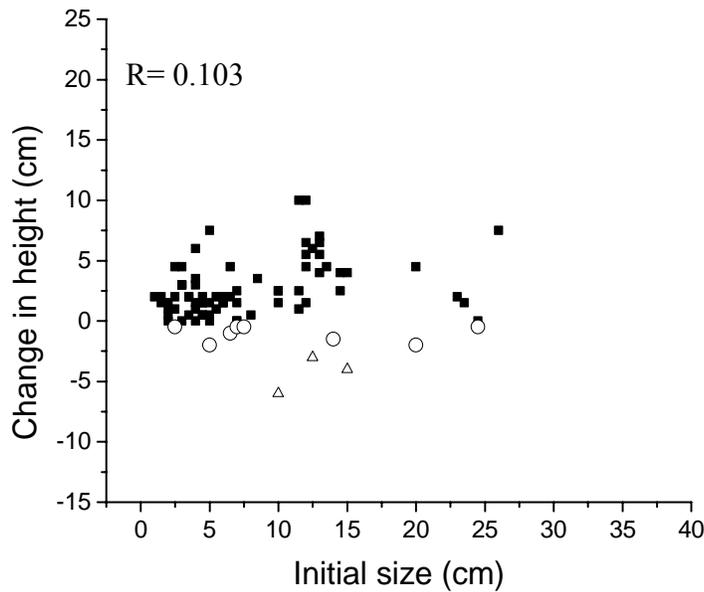
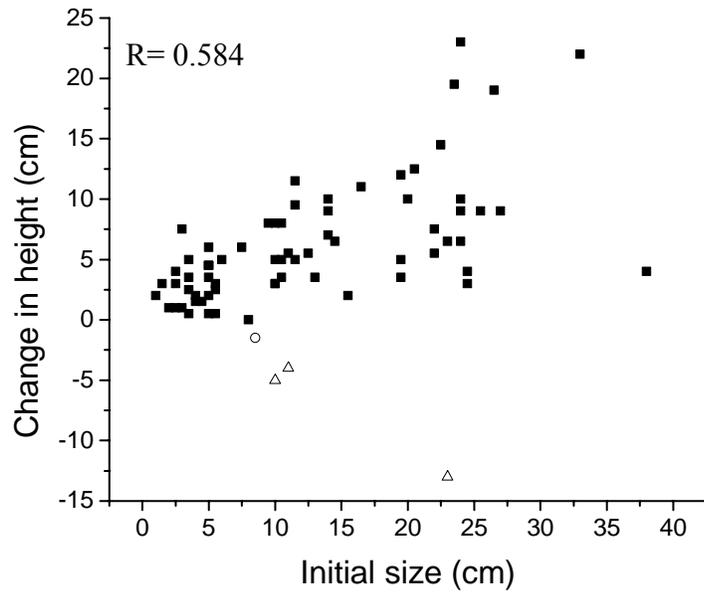


Figure 4.10 Growth rates of *A. compressa* expressed as absolute measure (change in height). Squares represent positive growth, open circles represent shrinkage, and open triangles represent sponges with signs of fragmentation. LP (Top), ML (Bottom).

4.2.4 Recruitment and recruit survivorship

Number of recruits per m² per year was 1.85 at LP and 1.80 at ML. Sexual and asexual recruitment contributed similarly to the total number of new colonies observed (Fig. 4.11) with no significant relationship between sexual or asexual recruits and sites ($X^2_{1df} = 1.082$, $p > 0.05$). At both sites recruitment followed a similar pattern peaking in the month of February due in part to the relatively high number of larva derived recruits (Fig. 4.12). Sexual recruits were higher during the first part of the study (Dec05 - Jun06) accounting for 93% and 79% of the total sexual recruitment at LP and ML, respectively. Asexual recruits were also higher during this time period when approximately 60% (at both sites) of the total asexual recruits were found.

At ML a high proportion ($\approx 67\%$) of the sexual recruits survived at least for 8 months. In contrast, at LP sexual recruits experienced relatively low survivorships with only 44% of the colonies surviving during the same period. At this site some small colonies were found totally buried by sediments or overgrown by the sponge *Chondrilla nucula*. On the other hand, rates of survivorships or re-attachment of generated fragments (asexual recruits) were relatively low with respect to sexual recruit survival at both sites. At the end of the study only 36% (7 ex 19) and 30% (4 ex 13) of the fragments remained within the study area for at least 8 months at LP and ML, respectively. No significant difference in survivorship between sexual and asexual recruits was observed at ML ($X^2_{1df} = 2.627$, $p > 0.05$) and LP ($X^2_{1df} = 0.679$, $p > 0.05$). Similarly, overall survivorship of recruits, both sexual and asexual, did not differ significantly between sites ($X^2_{1df} = 1.407$, $p > 0.05$).

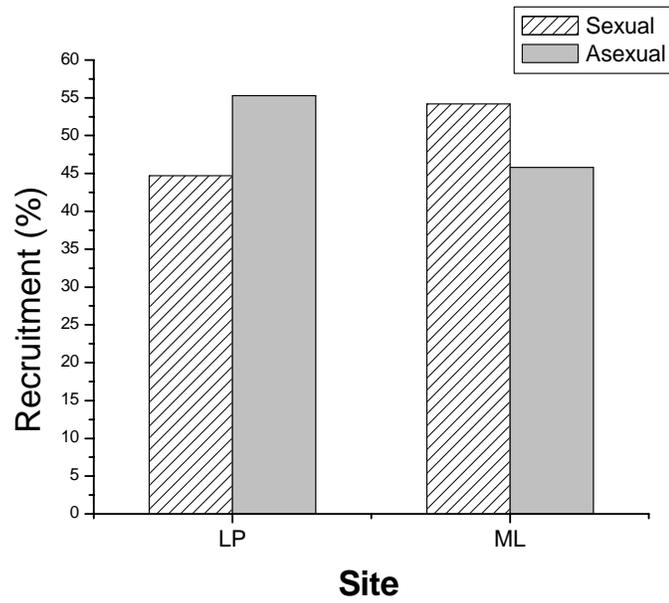


Figure 4.11 Relative contributions of sexual and asexual recruits to the total recruitment at the study sites.

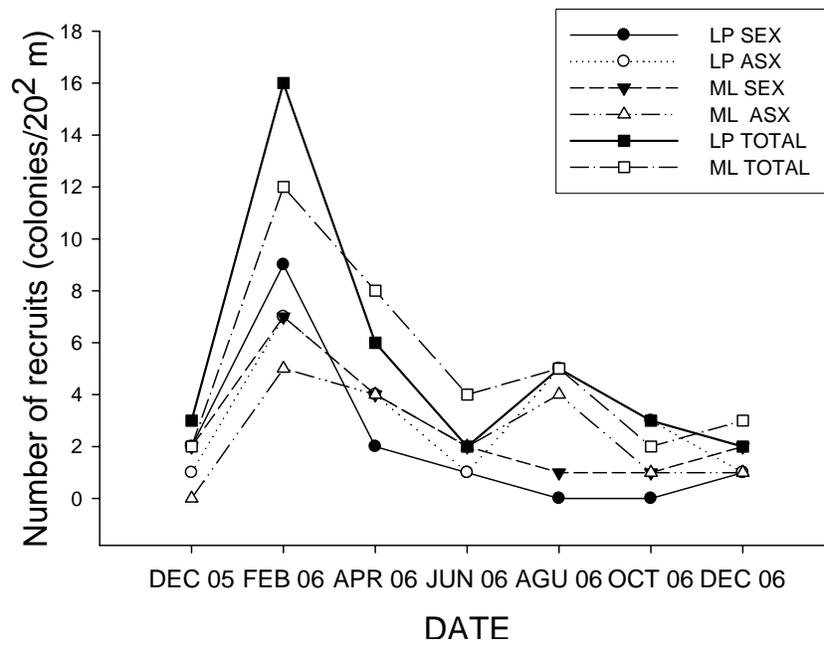


Figure 4.12 Temporal variation of sexual and asexual recruitment of *A. compressa* within the 20 m² area at LP and ML during the study period.

4.2.5 Size-based population matrix model

Projected abundances of *A. compressa* increased in the population matrix models in both reefs. The projected abundances increased more rapidly at ML at an annual rate of 15% ($r = 0.140/y$) and 5.5% at LP ($r = 0.053/y$, Fig. 4.13). The reason for the higher population increase at ML compared to LP is probably due to the higher survivorships of the recruits (0.548 vs. 0.459 respectively), and for small (0.900 vs. 0.644 respectively) and medium (0.875 vs. 0.713 respectively) size colonies (Table 4.3). The population projections also indicate that these size-specific survivorship patterns apparently have a greater effect on population growth than reproduction because higher rates of recruitment, attributed to the medium and large colonies, occurred at LP.

Table 4.3 Transition matrices estimated for *A. compressa* populations in LP and ML. Re= recruits, d_x = size-specific probability of mortality.

	LP			
	Re	Small	Medium	Large
Re	0.00	0.615	0.945	1.04
Small	0.351	0.640	0.071	0.00
Medium	0.054	0.004	0.357	0.00
Large	0.054	0	0.285	0.875
$\sum P$	0.459	0.644	0.713	0.875
d_x	0.541	0.356	0.287	0.125
	ML			
	Re	Small	Medium	Large
Re	0.00	0.688	0.203	0.296
Small	0.516	0.860	0.125	0.000
Medium	0.032	0.040	0.750	0.000
Large	0.00	0.00	0.00	0.333
$\sum P$	0.548	0.900	0.875	0.333
d_x	0.452	0.100	0.125	0.667

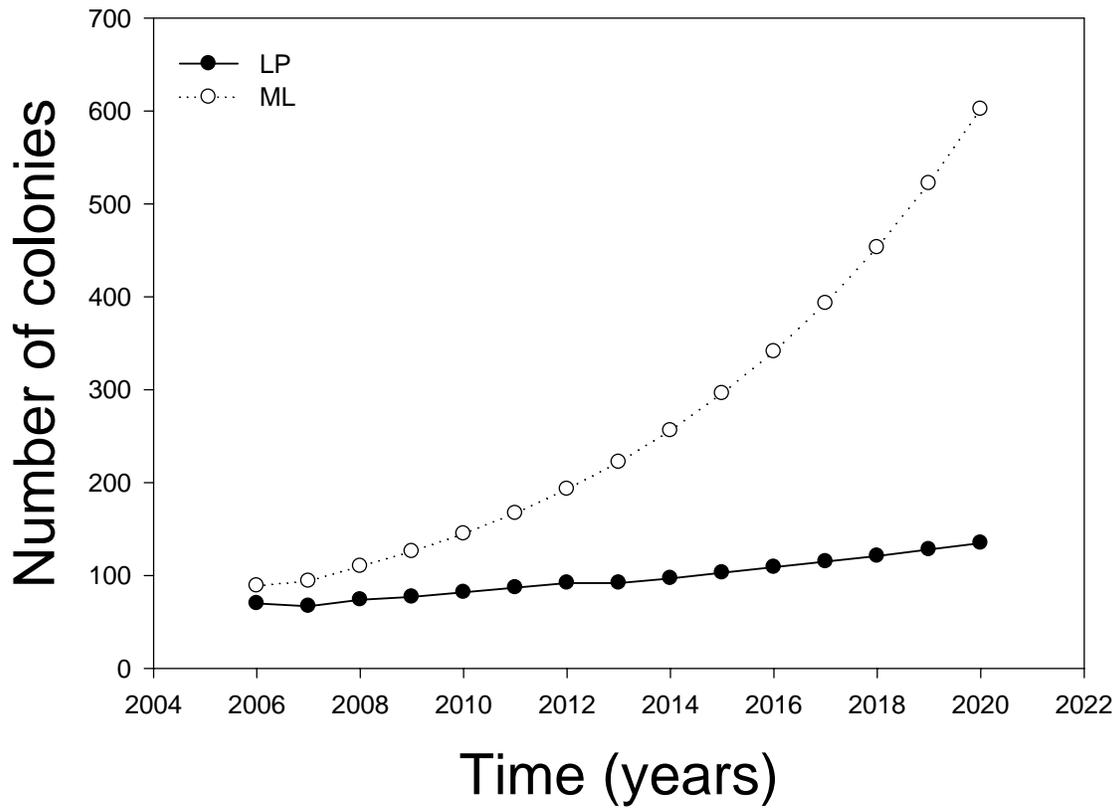


Figure 4.13 Projected abundances of *A. compressa* through time at the study sites. Model performed with data of the survivorship and growth of colonies collected during the 1 yr study.

Projected abundances of *A. compressa* decreased at LP when either sexual or asexual reproduction is excluded from the simulations (Fig. 4.14 top). This suggests that both strategies are required for the population growth at this site. In relative terms, populations declined more rapidly when asexual recruitment is excluded, partly because sexual recruits are small, and small colonies have higher mortalities than larger size classes at this site (Table 4.4).

At ML projected populations increased with sexual reproduction alone and decreased when only asexual reproduction is considered (Fig. 4.14 bottom). The decrease in abundances with asexual reproduction results from the larger sizes of asexual recruits in conjunction with the higher mortalities of these size classes. In turn, the higher mortalities of larger colonies may be due to the inability of large fragments/colonies to reattach to the substrate because of high water motion.

Therefore, the relative importance of asexual versus sexual recruitment for population growth at LP and ML may be ultimately attributed to differences in water motion and its consequent effects on colony growth and survival.

Table 4.4 Transition matrices estimated for a simulated population of *A. compressa* at LP including only sexual or asexual recruits. Re= recruits, dx = size-specific probability of mortality.

	Sexual recruits			
	Re	Small	Medium	Large
Re	0.000	0.299	0.460	0.506
Small	0.555	0.640	0.071	0.000
Medium	0.000	0.004	0.357	0.000
Large	0.000	0.000	0.285	0.875
$\sum P$	0.555	0.644	0.713	0.875
dx	0.445	0.356	0.287	0.125
	Asexual recruits			
	Re	Small	Medium	Large
Re	0.000	0.316	0.486	0.534
Small	0.157	0.640	0.071	0.000
Medium	0.105	0.004	0.357	0.000
Large	0.105	0.000	0.285	0.875
$\sum P$	0.367	0.644	0.713	0.875
dx	0.633	0.356	0.287	0.125

Table 4.5 Transition matrices estimated for a simulated population of *A. compressa* at ML including only sexual or asexual recruits. Re= recruits, dx = size-specific probability of mortality.

	Sexual recruits			
	Re	Small	Medium	Large
Re	0.000	0.354	0.105	0.152
Small	0.631	0.860	0.125	0.000
Medium	0.000	0.040	0.750	0.000
Large	0.000	0.000	0.000	0.333
$\sum P$	0.631	0.900	0.875	0.333
dx	0.369	0.100	0.125	0.667
	Asexual recruits			
	Re	Small	Medium	Large
Re	0.000	0.316	0.093	0.136
Small	0.235	0.860	0.125	0.000
Medium	0.058	0.040	0.750	0.000
Large	0.000	0.000	0.000	0.333
$\sum P$	0.293	0.900	0.875	0.333
dx	0.707	0.100	0.125	0.667

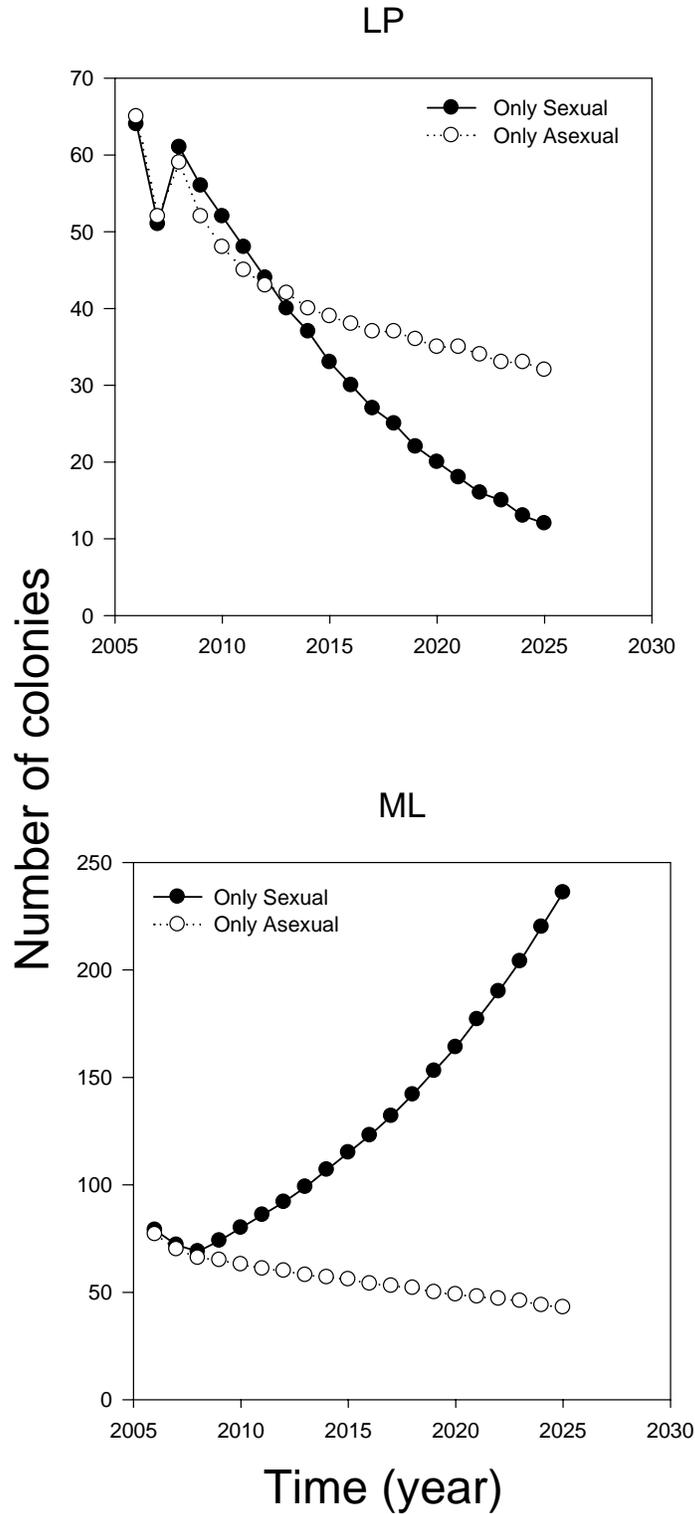


Figure 3.14 Simulation model representing two different situations performed for both sites, (1) a scenario including only sexual recruits and (2) a scenario that included only recruits from asexual fragmentation and/or detachment.

5. DISCUSSION

No evidence of biological interactions (predation, grazing, inter/intra specific competition, disease) affecting this species were observed in this study. Among physical factors, water motion, light, and sedimentation could potentially affect the distribution and population dynamics of *A. compressa*. Although data on sedimentation was not collected, there is no reason to believe that sediment load from the water column will significantly affect the distribution of *A. compressa*, given the arborescent morphology of this sponge which may prevent sediment accumulation upon the sponge body (Chappel, 1980; Bell et al, 2002). However, small colonies could be buried or smothered by bedload sediment transport especially in high water motion environments, as is the case for other benthic species such as gorgonians (Yoshioka, 1996). Unfortunately, there is no information about the effect of bedload sediment upon the dynamics of sponges. The absence of colonies in the shallow (3m) well-lit zone in five of the six reefs surveyed could be attributed to a negative effect of high light intensities (Jokiel, 1980) on *A. compressa*. However, the relatively high abundances in the 3m backreef areas (pers. obs) indicate that high light levels do not have direct negative effects on this sponge. Alternatively, the 3m depth zone differs significantly in water motion between the forereef and backreef. McGehee (1998) demonstrated that backreef habitats had significantly lower water flow compared to forereef areas. She also demonstrates that water motion diminished with depth. The latter observation is consistent with higher abundances of *A. compressa* colonies in deeper (5-12m) depth zones in the forereef. Thus, the greater wave energy at the 3m depth on the forereefs (McGehee, 1998; Bell, 2007) may be preventing *A. compressa* from thriving at this depth zone, as has been

reported for other sponges of similar morphology (Bell and Barnes, 2000b). As a first approximation, drag increases proportionally with colony surface area and with the square of water velocity (Denny et al, 1988). Therefore, drag in the shallow forereef areas would increase the probability of detachment or fragmentation for *A. compressa* colonies in general, and especially for larger colonies. This mechanism would be consistent with the absence (or small sizes when present) of *A. compressa* colonies in the shallow forereef. Moreover, those few colonies present in this depth zone at Romero were found partially protected from wave action by skeletons of the scleractinian coral, *Acropora palmata*.

Although there was no statistically significant difference in overall colony survivorship at LP and ML, the results of this work suggest that the intensity of water motion plays an important role in size-specific survivorship of *A. compressa*. At LP survivorship was independent of colony size. In contrast, at ML large colonies showed significantly lower survivorship rates when compared to small and medium-sized colonies. This size-specific survivorship at ML could be a consequence of drag forces associated to water flow. In addition, because of its branching morphology, *A. compressa* may exhibit a small basal attachment area relative to their overall biomass (colony height) (Bell & Barnes 2000b) increasing the probability of colony dislodgement from the substrate (Wulff, 1995), as the colony increases in size. Therefore, drag forces may have a greater effect on detachment of large (compared to small) colonies. Detachment due to water motion has been previously suggested as an important source of mortality in other sessile marine organisms such as gorgonians (Birkeland, 1974) and algae (D'Amours and Scheibling, 2007), and could be the case for *A. compressa*. Since

the exact position of each tagged colony was known and the complete disappearance of the sponge was detected, the absence of any colony could be attributed to the detachment from the substrate. Results must be analyzed carefully given that detachment is not necessarily synonymous with mortality because sponges could have broken off and resettled somewhere else. However, fragments may require a reasonable time period of favorable water motion conditions in order to re-attach successfully to the substrate. The poor survival or re-attachment rates observed may be an indication that detachment may be an important source of mortality.

The high survivorship rate of small colonies is surprising given that small size is often associated with low survivorship for modular organisms (Reiswig, 1973; Wulff, 1991; Yoshioka, 1994; Turon et al, 1998; Duckworth and Battershill, 2001). However, if detachment, due to high water motion, is the main source of mortality then the high survivorship rate of small colonies is not unexpected. The high survivorship of small colonies also indicates that other external factors, such as predation, overgrowth, and competition which usually have greater adverse effect on small colonies, may play a minor role in the population dynamics of *A. compressa*.

Why colonies showed overall higher growth rates at LP, the site experiencing low water motion, is not clear. It is generally believed that sponges grow most successfully in high water flow environments because the removal of waste materials (Bell, 2002) and because the pumping activity (Reiswig, 1973), feeding efficiency (Vogel, 1977), as well as the availability of food per time (Watson, 1976; Hiscock, 1983; Bell, 2002) are increased. For example McDonald et al. (2002) found that the sponge *Cinachyrella australiensis* tends to grow faster under high water motion conditions. Similar results

were reported by Duckworth and Battershill (2003) for *Latrunculia wellingtonensis* and *Polymastia croceus*. However, it seems that this is not always true. For instance, Leichter and Witman (1997) reported greater growth rates for the sponge *Halichondria panicea* in areas of low ambient flow rates. For *A. compressa*, a suspension feeder that may rely on one (or a combination) of the different mechanisms of filter feeding (direct interception, motile particle deposition, gravitational deposition, and inertia impaction) for feeding, nutrition may be dependent on water flow. It is possible that the effectiveness of “food capture” rates of *A. compressa* is reduced under conditions of high water velocity (Rubenstein and Koehl, 1977). Consequently colony growth rates could be lessened, as is the case of *H. panicea* (Leichter and Witman, 1997) and for some Caribbean gorgonians species (Fabricius et al, 1995). This observation implies that there may be an “optimum range” of water flow in which sponges can feed most efficiently, and it is likely that this “optimum range” is exceeded at ML (Rubenstein and Koehl, 1977). More studies in this area are needed to better understand the relationship between water motion and feeding dynamics.

Spatial differences in food abundance could also explain the disparity in colony growth rates between sites. Food abundance, which in fact can be limited by the intensity of water flow (Patterson, 1984; Leonard et al., 1998; Kaandorp, 1999), has been previously recognized to affect growth in sponges (Duckworth and Battershill, 2001; Parra-Velandia and Zea, 2003; Lesser, 2006). In addition, differential water flow can affect the size of the suspended particles (Vogel, 1977) which may have a negative effect if the particles (e.g, bacterioplankton) reaching the colonies are larger or smaller than 1 to 5 μm (Reiswig, 1971b). Furthermore, strong water motion may be able to re-suspend a

greater amount of sediments affecting pumping rates of sponges (Gerrodette and Flechsig, 1979; Wilkinson and Vacelet 1979; Duckworth and Battershill, 2001), hence, affecting their feeding and other metabolic activities.

Growth can also be limited by high wave action if the sponge lacks strong skeletal structure (Palumbi, 1986). Because colonies inhabiting ML are subject to higher water movement compared to colonies at LP, they may invest more energy and resources for structural support (Palumbi, 1986). Allocating energy to producing components to cope with this scenario, such as thicker spicules (Palumbi, 1986) or greater proportions of spicules (McDonald et. al, 2002), may compromise energy devoted to growth or other life history processes. However, this may not be the case for *A. compressa* since the thickness and concentration of spicules in colonies at ML did not differ significantly from those colonies inhabiting LP (pers. obs.). Nevertheless, other morphological characteristics such as tissue variability not considered in this study should be investigated.

This study confirms that asexual fragmentation and/or detachment (Wulff, 1991) is an important part of the life history of *A. compressa*, since approximately half of the new colonies within the study area showed signs of basal detachment or fragmentation. However, the relatively high proportions of small size (<4cm) recruits found indicates that fragmentation is not the only means of reproduction. These new small colonies, some of them noticeable at a height of < 1 cm, might be sexually derived recruits assuming that newly settled larvae can not reach a height of 4 cm during the two month monitoring interval. However, this must be confirmed by genetic studies because other means of asexual reproduction producing small colonies, such as budding (Ayling, 1980)

or fission may be possible. Nevertheless, signs of these kinds of asexual reproduction were not observed during the study period, indicating that the small recruits were the products of sexual reproduction.

Recruitment can be influenced by physical or biological factors (Murphy, 1968). The overall similarities of sexual recruitment patterns between sites indicate that there is little spatial variation in this process. This suggests that differences in physical (e.g. sedimentation, topographic relief, water motion) and biological factors between reefs may not be a major determinant factor behind the larva settlement process. However, approximately 1% of the sexual recruits buried and suffocated by sediments at LP point to a negative effect of sedimentation on post-settlement survivorship, as suggested by Wilkinson and Vacelet (1979) and Zea (1993). Because sedimentation rates increase with decreasing water motion (Yoshioka and Yoshioka, 1989), post-settlement survivorship may be indirectly related to the intensity of water movement. On the other hand, exposure to continuous water motion, at both sites, probably decreases the re-attachment, and therefore the survival of asexual fragments, as mentioned before. Continuous water motion rather than availability of substrate may be the principal factor influencing survival or re-attachment of fragments. However, more field and experimental studies might be carried out in order to prove this claim.

The low success of fragment re-attachment (survival) and the high survivorship of sexual recruits indicate that sexual reproduction may be a greater contributor to the studied populations. Therefore, sexual reproduction should be considered to be an important strategy of reproduction for *A. compressa* especially under high water motion conditions where survivorship of sexual recruits was higher. This differs with previous

works suggesting that asexual reproduction is the most important mode of reproduction for clonal organisms (Highsmith, 1982, Jackson, 1985, Trautman et. al, 2000; Carballo and Avila, 2004). However, even when re-attachment is low the importance of asexual fragmentation can not be ignored as it may be more important in colonizing new substrate and maintaining the population at spatial scales larger than the one in this study, given the ability of fragments to disperse over long distances (Wulff, 1985; Carballo and Avila, 2004). Conversely, the aggregated pattern found at both sites may be an indication that sexual reproduction may be more significant in sustaining the population at small spatial scales, since sponge larvae are short-lived and potentially short dispersing (Ayling, 1980; Mariani et al., 2005) and there may be a tendency of the offspring to remain within parental colony habitats.

In summary, results indicate that the intensity of water motion may be the principal factor controlling the population size-structure of *A. compressa*. High water movement appears to be limiting, directly or indirectly, the maximum height that a colony can attain by reducing growth rates and increasing mortality of large sponges. In support of this argument is the observed increase in size as depth increases. It is well known that on coral reefs, deeper zones are less impacted by the turbulence or disturbance caused by wave action (Wilkinson and Evans, 1989; McGehee, 1998; Kaandorp, 1999; Bell, 2007). This may result in more calm and stable conditions which may increase survivorship rates (Hughes, 1984) allowing the colonies to reach larger sizes; as has been proposed for many coral species (Goreau, 1966; Glynn, 1973) and gorgonians (Birkeland, 1974). Furthermore, the tendency to find larger colonies in the

inner shelf reefs, which are subject to less water motion (McGehee, 1998) supports this contention.

Projections from the stage-based matrix models performed in this study revealed an increase in the abundances of the two studied populations of *A. compressa*. Because recruitment was similar between sites, the faster increase in population size at ML may be attributable to differences in size-specific colony survivorships. The higher probabilities of mortality of large colonies (>20cm) observed at this site, suggests that survivorships of small colonies (<10cm) may have a greater effect in the abundances. The projected population size declined at ML when sexual recruits were excluded. This implies that sexual recruitment and survivorship of smaller colonies may be the key factor underlying the maintenance of populations in areas with increasing levels of water motion. In contrast, at LP, population decreased when either sexual or asexual recruits were not considered, suggesting that both modes of reproduction play a significant role in the maintenance of the population at this site.

6. CONCLUSIONS

The results of this study indicate that water motion may be more important than biological factors (such as competition and grazing) and others physical factors (such as light and sedimentation) in the distribution and population dynamics of *Amphimedon compressa*. Increasing water motion influences the population structure of *A. compressa* by (1) reducing growth rates, (2) increasing mortalities of large colonies (including asexually produced fragments) by detachment due to drag forces, and (3) decreasing the probability of reattachment of colony fragments. At the same time, this work revealed the importance of sexual reproduction in the population dynamics of this sponge while confirming the important role of fragmentation and/or detachment as suggested by Wulff (1991)

This work is a contribution to the understanding of the sponge and coral reef communities of La Parguera, Puerto Rico, by providing quantitative baseline information on the population characteristics of *A. compressa* in contrasting habitats. However, further laboratory and field experiments and more field studies are needed on the specific effects of water motion on re-attachment and dispersal of generated fragments and larvae settlement and post-settlement dynamics. In addition studies on the reproductive biology and feeding ecology may provide valuable knowledge on the dynamics of *A. compressa*.

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