

Population dynamics of a coral reef ascidian in a deteriorating environment

N. Shenkar*, O. Bronstein, Y. Loya

Department of Zoology, The George S. Wise Faculty of Life Sciences, Tel Aviv University, Tel Aviv 69978, Israel

ABSTRACT: In the coral reefs of Eilat, a newly described colonial ascidian, *Botryllus eilatensis*, has been observed overgrowing dead coral skeletons and rapidly colonizing artificial substrates. To study overgrowth dynamics and the relationship between coral morphology, size, and orientation and ascidian overgrowth we monitored (monthly) the interaction of 50 to 70 tagged coral colonies with *B. eilatensis*. The rate of *B. eilatensis* overgrowth on corals was influenced by the coral's morphology and orientation combined with a seasonal appearance of the ascidian. During spring, the average ascidian cover was 27 ± 4.6 % (mean \pm SE), decreasing rapidly during the summer months when sexual reproduction took place. This seasonality is linked to the vertical mixing phenomenon that occurs in Eilat every winter. Moreover, fragments of *B. eilatensis* translocated to a nutrient-rich site increased 3-fold in size and exhibited higher survivorship rates in comparison to the fragments at the original site. Increased anthropogenic activity, particularly the eutrophication occurring along the Israeli coasts, creates favorable conditions for filter-feeding organisms such as ascidians, providing them with an advantage in competition for space over reef-building corals and other organisms.

KEY WORDS: Eutrophication · Red Sea · Tunicates · Filter-feeding

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INTRODUCTION

In the past few decades coral reefs have suffered a massive, long-term decline in abundance, diversity and habitat structure due to both natural (e.g. coral bleaching, predation by crown of thorns starfish) and anthropogenic (e.g. overfishing, sedimentation, pollution) disturbances (Hughes et al. 2003, Pandolfi et al. 2003). Live coral cover is declining rapidly, with reports of up to an 80% decrease in the Caribbean and East Africa (Wilkinson 2002, Gardner et al. 2003) and ~50% decrease in the Red Sea (Loya 2007). The decline in live coral cover has a negative effect on other reef inhabitants (Pandolfi et al. 2003, Attrill et al. 2004, Feary et al. 2007). However, the conditions that are deleterious for corals (e.g. eutrophication) may create a favorable environment for filter-feeding organisms, accelerating their growth and spread (Bak et al. 1996, Aerts & van Soest 1997, Aronson et al. 2002, Ward-Paige et al. 2005). Sponges and ascidians control the removal of particulate organic nitrogen from coral reef waters (Ribes et al. 2005). Their ability to effec-

tively filter small plankton, less than 10 μ m in size (Yahel et al. 2005), plays an important role in the carbon and nutrient pathway in coral reef ecosystems (Ribes et al. 2005). It has been suggested that changes in water quality in tropical coasts, particularly pertaining to the availability of nutrients and organic matter, may result in vast changes in these benthic communities (Bak et al. 1998, Ward-Paige et al. 2005).

In general, ascidians constitute a minor benthic component on exposed surfaces of natural coral reefs. They are often found in cryptic environments such as caves, crevices and the sides or undersides of rocks and corals (Monniot et al. 1991). However, there have been recent reports of a rapid spread of several ascidian species in various tropical regions of the world (Bak et al. 1996, Lambert 2002). Bak et al. (1996) reported a 9-fold increase in the density of *Trididemnum solidum*, a colonial ascidian, along the 84 km of fringing reef in Curaçao, over a period of 15 yr. Witman & Smith (2003) reported a 3-fold increase in ascidian biomass over 1 yr in an upwelling site in the Galápagos. Whereas numerous studies have investigated the competitive relation-

*Email: levinn@post.tau.ac.il

ship between different coral species (Sheppard 1979, Abelson & Loya 1999, Connell et al. 2004), only a few studies have investigated the interactions of corals with other bottom-occupying organisms (Aerts & van Soest 1997, Aerts 1998, López-Victoria et al. 2006, Zvuloni et al. 2008), none of which have investigated coral-ascidian interactions.

Ascidians have a rapid growth rate (Bak et al. 1981), reach sexual maturity when only a few weeks old and produce large numbers of short-lived, non-feeding larvae (Berrill 1950, Millar 1971). These characteristics, combined with a lack of significant predators, make ascidians very successful competitors (Lambert 2002). The rapid spread of several ascidian species in both tropical and temperate regions of the world is of growing concern (Lambert 2002, Paulay et al. 2002, Blum et al. 2007, Valentine et al. 2007).

In the coral reefs of Eilat (Red Sea) a newly described colonial ascidian *Botryllus eilatensis* (Shenkar & Monniot 2006) has been observed overgrowing dead coral skeletons and rapidly colonizing artificial substrates. This genus has a wide distribution and is a common fouling organism in estuaries and shallow water environments (Kott 1985). It is difficult to determine whether *B. eilatensis* is native or not, as it has colonized harbor structures as well as natural substrates (Shenkar & Monniot 2006). Due to a rise in anthropogenic activity, coral reefs in the northern Red Sea are experiencing increased eutrophication and the corals are severely stressed (Ben-Tzvi et al. 2004, Abelson et al. 2005, Loya 2007). Although much effort is being invested in monitoring the status of the corals and fish in this area, the possible role of other invertebrate taxa in affecting the community structure has unfortunately been overlooked. The aim of the current study was to investigate the ecology and life history of the ascidian *B. eilatensis*, focusing on its interaction with stony corals in a deteriorating coral reef environment.

MATERIALS AND METHODS

The study was conducted from 2004 to 2006 at Eilat (Red Sea coast of Israel). Observations were carried out using SCUBA diving. Ambient sea-surface temperature, chlorophyll *a* (chl *a*) levels and visibility data were obtained from the Israel National Monitoring Program (NMP, www.iui-eilat.ac.il) (see Fig. 2a).

Geographic and depth distribution. Preliminary observations showed that *Botryllus eilatensis* appears in the natural reef during April and May. In 2006, during these months, ascidian surveys were conducted on both natural and artificial surfaces in the Gulf of Eilat: the natural coral reefs at Taba (29° 29.65' N, 034° 54.345' E) and at the Inter-University Institute

marine laboratory (IUI; 29° 30.131' N, 034° 55.045' E), and on an artificial surface (composed of wood, metal and polyethylene pontoons) at the marine sport jetty at the eastern part of the North Beach (NB; 29° 32.856' N, 34° 57.265' E). The NB site is considered to be a highly disturbed site due to its proximity to the naval port area and other anthropogenic disturbances, in comparison to the Taba and IUI sites from which pollution sources are relatively distant and where recreational activities are limited (Ben-Tzvi et al. 2004). The different nature of the surveyed sites in terms of substratum availability and topography dictated the use of different survey methods. At the Taba site, due to very low densities of *B. eilatensis*, each colony observed within a defined area of 500 m² was measured and photographed. At the IUI site 4 belt-transects (50 m long, 2 m wide) were performed perpendicular to the shore at 5 to 10 m depth. At the NB sport jetty *B. eilatensis* density was estimated by counting colonies on 20 pilings (40 × 80 cm, data corrected to 1 m² density).

Seasonal appearance. To study ascidian overgrowth dynamics and seasonal appearance, a total of 70 interactions between tagged coral colonies and the colonial ascidian *Botryllus eilatensis* were photographed monthly from April 2005 to June 2006 (Fig. 1a). The monitored corals had been previously attached in May 2001 by the staff of the Underwater Observatory Marine Park to a dome-shaped steel construction with a base diameter of 10 m and a height of 3 m, at a depth of 10 to 14 m, between the IUI site and the underwater observatory (Fig. 1b). Colonies of *B. eilatensis* recruited onto the artificial structure and overgrew the corals that had been previously transplanted onto the dome structure. During the study all monitored interactions (approximately 50 to 70 mo⁻¹, except during the preliminary study, between November 2004 and February 2005, when *n* = 14 interactions) were photographed using a digital Sony T-11 and a Nikon CoolPix7900 camera, keeping a fixed angle and distance from the object. Total surface area of the coral colony and the area covered by *B. eilatensis* were measured using the Coral Point Count with Excel extensions (CPCe) (Kohler & Gill 2006) photo analysis program. Ascidian cover was calculated as the percentage of available coral area (dead and live coral tissue) covered by the ascidian. A film clip demonstrating the ascidian overgrowth at the study site is available at: www.tau.ac.il/lifesci/departments/zoology/members/loya/shenkar.html.

Reproduction. During 2006, monthly samples (ca. 2 × 2 cm) from 5 different *Botryllus eilatensis* colonies (separated from each other by at least 1 m) were taken from the NB site. The samples were nar-

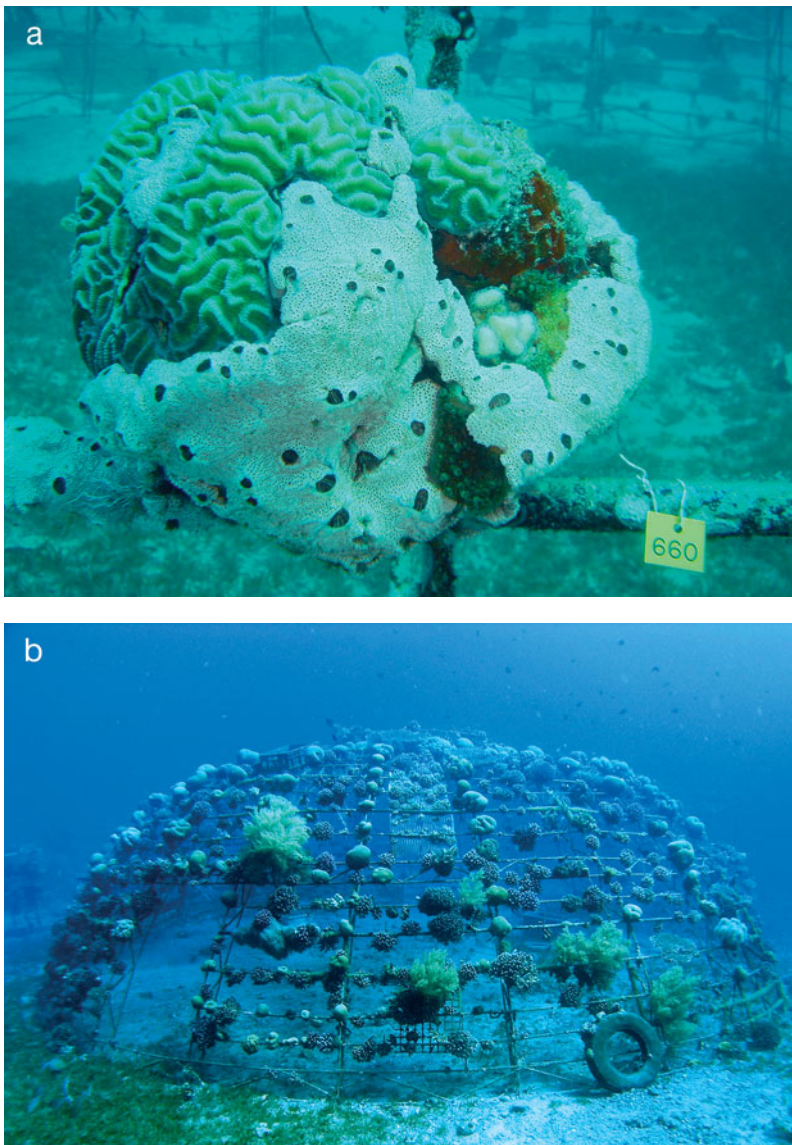


Fig. 1. (a) *Botryllus eilatensis*. Monitored interaction with the massive coral *Platygyra* sp. during March 2005. (b) Dome construction serving as substrate for monitored corals

cotized with menthol crystals for up to 3 h and fixed in 4% formalin buffer in filtered seawater. Twenty zooids from each sample were dissected under a stereomicroscope, and the presence or absence of testes and oocytes was recorded. The gonad index (GI) was calculated as the percent ratio of zooids containing gonads (testis/oocytes) to the total number of zooids examined.

Growth and survivorship. To quantify differences in the growth and survivorship of *Botryllus eilatensis* in high nutrient versus low nutrient sites a transplantation experiment was conducted during June 2006 at the NB (high nutrient levels) and IUI (low nutrient lev-

els) sites. Five large colonies (>20 cm in diameter) of *B. eilatensis* were sampled at the IUI site, separated into similar sizes and attached using sewing thread to a PVC plate (7 × 7 cm). The plates were placed in unfiltered, running seawater containers at the IUI Marine Laboratory. Two days following successful attachment, 28 fragments were placed at the IUI jetty and 37 fragments were attached to the marine sport jetty (NB), both at 1 m depth. Each plate was photographed weekly and the ascidian surface area was measured using the CPCe (Kohler & Gill 2006) photo analysis program.

Statistical analysis. All statistical analyses were carried out using Statistica 7. Analysis of ascidian percentage cover and gonad index data were performed after arcsine \sqrt{p} transformation and tested for normality with Shapiro-Wilk's test and homogeneity of variance with Cochran's test (Zar 1999). Analysis of possible differences in percent ascidian overgrowth as a function of coral morph (branching corals versus massive corals), orientation (north-facing corals versus south-facing corals) and size (coral surface smaller or larger than 100 cm²) was investigated during the peak of the ascidian overgrowth (April to June 2005) using student's *t*-tests. Only the maximal ascidian percentage cover scored per coral during this period was included. We were not able to perform a factorial design ANOVA since there were not enough data for the south-facing-small-branching coral group. Linear regression analysis was used to examine whether the monthly average of the ascidian

percentage cover was associated with ambient sea-surface temperature, chl *a* levels and visibility data. A 1-way ANOVA was performed in order to investigate possible differences in gonad index throughout the study. Fisher's LSD (least significant differences) tests were used as post-hoc comparisons when significant differences were detected. Separate *t*-tests were performed in order to test differences in fragment size measurements between the sites for each week and a comparison between the survivorship curves at each site was made using the log-rank test. Results are presented as mean ±SE throughout the text unless denoted otherwise.

RESULTS

Geographic and depth distribution

During April and May 2006 *Botryllus eilatensis* was common along the entire coast on artificial substrates (piers, artificial reefs) and in the natural environment, overgrowing coral skeletons and rock pebbles from shallow depth (1 m at the NB site) to 10 to 15 m depth at the IUI and Taba sites. The number of *B. eilatensis* colonies at the IUI site was 5.5 ± 0.8 per 100 m² transect (n = 4) during April and 3.8 ± 1.1 during May (n = 4). At the Taba site the number of colonies observed increased from 7 to 15 per 500 m² from April to May. At the NB site the number of colonies increased from 5 ± 1.8 per 1 m² during April to 12 ± 5 per 1 m² during May (n = 20).

Seasonal appearance

The percentage of *Botryllus eilatensis* cover over the monitored corals fluctuated throughout the year (Fig. 2b). The highest cover was measured during April and May 2005 (mean $27.0 \pm 4.6\%$), decreasing rapidly in the following months to a minimum of $0.18 \pm 0.11\%$ in September. By April 2006 *B. eilatensis* had disappeared from the monitored area and reappeared the following month with an average cover of $2.8 \pm 1.3\%$. No significant association was found between monthly average of ascidian percentage cover and sea-surface temperature ($r^2 < 0.01$, $p = 0.75$) or chl *a* measurements

($r^2 = 0.01$, $p = 0.7$). A weak but significant association was found between visibility (measured as secchi disk depth) and ascidian percentage cover ($r^2 = 0.42$, $y = -2.43x + 69$, $p < 0.01$) from November 2004 to June 2006. During the peak of the ascidian overgrowth on corals (April to June 2005) a strong and significant association was found between visibility and ascidian percentage cover ($r^2 = 0.89$, $y = -1.53x + 65$, $p < 0.01$). During this period higher percentage cover was observed over massive corals (*Platygyra* sp., *Porites* sp., *Favia* sp., *Favites* sp.) in comparison to branching corals (*Stylophora* sp., *Acropora* sp.) ($t = 2.38$, $df = 81$, $p < 0.05$); north-facing corals in comparison to south-facing corals ($t = 2.37$, $df = 81$, $p < 0.05$); and small corals (< 100 cm²) in comparison to large corals ($t = 2.56$, $df = 81$, $p < 0.01$) (Fig. 3).

Reproduction

Botryllus eilatensis in the coral reefs of Eilat demonstrates seasonal reproduction (Fig. 4). Zooids with gonads were present throughout the year, but the sequence of reproductive stages exhibited a clear temporal trend. While zooids with testes were found throughout the entire research period, zooids containing testes and ovaries (with 1 or 2 oocytes) appeared only from May to October when sea-surface temperature fluctuated between 23 to 27°C. During this time a significantly higher gonad index was measured, excluding August (1-way ANOVA, followed by Fisher's

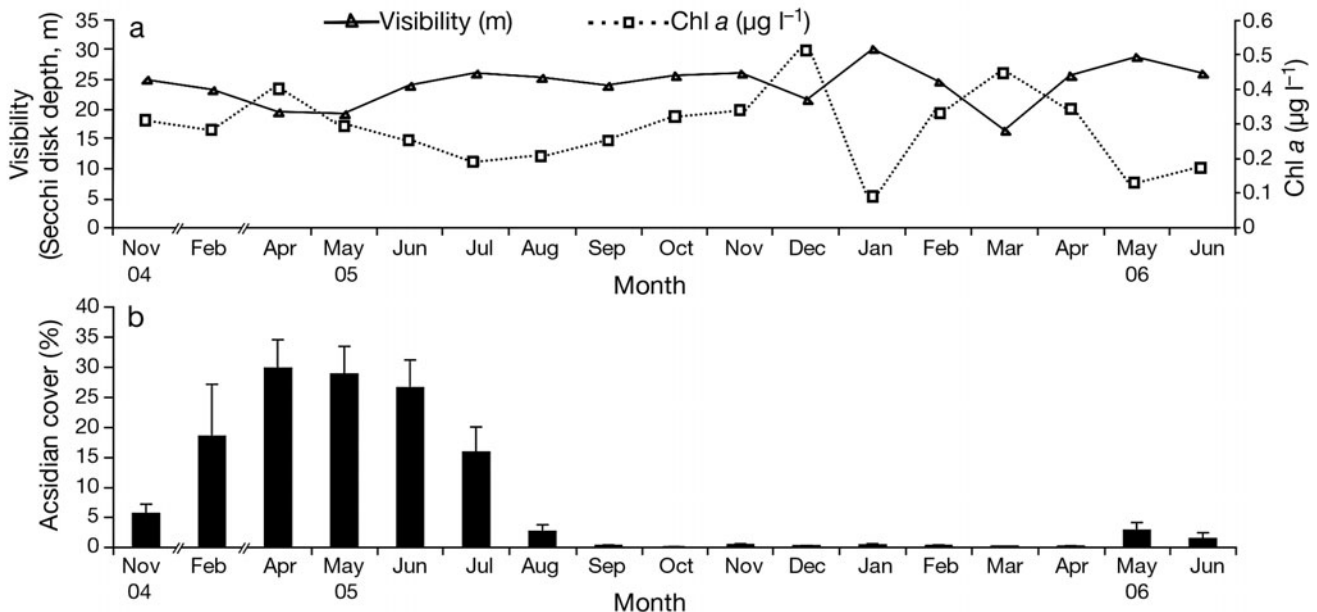


Fig. 2. (a) Chl *a* and visibility data at the monitored site during the study. Data courtesy of the Israel National Monitoring Program at the Gulf of Eilat. (b) *Botryllus eilatensis*. Seasonal variation of mean percentages of ascidian cover (\pm SE) relative to available coral area

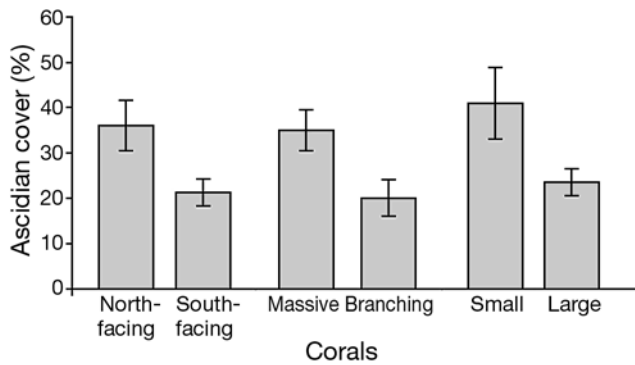


Fig. 3. *Botryllus eilatensis*. Mean ascidian percentage cover (\pm SE) measured between April and June 2005 for: overgrowing north-facing corals ($n = 41$) versus south-facing corals ($n = 42$); massive corals ($n = 47$) versus branching corals ($n = 36$); and small ($<100 \text{ cm}^2$, $n = 24$) versus large corals ($>100 \text{ cm}^2$, $n = 59$)

LSD, $F_{10,43} = 7.48$, $p < 0.01$), reaching a maximum of $82 \pm 15\%$ during June and July ($n = 10$). No embryos and no larvae were found in any of the samples.

Growth and survivorship

Weekly monitoring of the transplanted fragments revealed a significant difference in fragment size between the sites after 2 w of transplantation ($t = 2.2$, $df = 62$, $p < 0.01$) (Fig. 5a). Whereas the fragments transplanted to the NB site increased 3-fold in size reaching an average size of $15 \pm 8 \text{ cm}^2$ (mean \pm SD) after 1 mo, the fragments at the IUI site remained at the same size throughout the experiment. In addition, higher survivorship rates were observed at the NB site of 50% by the end of the experiment ($n = 37$), in comparison to only 30% at the IUI site ($n = 28$) but these differences were not significant (log-rank test, $p = 0.25$) (Fig. 5b).

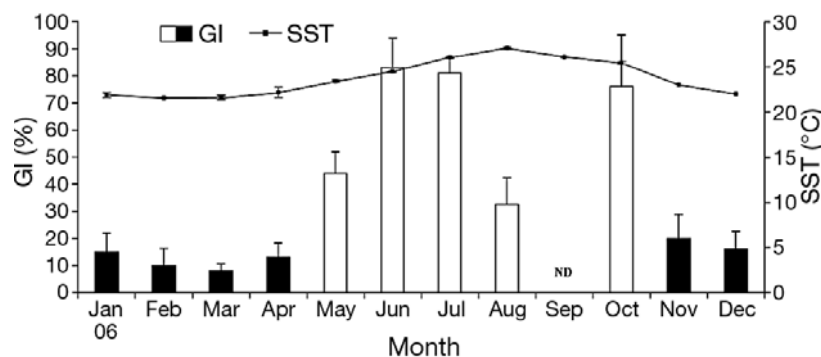


Fig. 4. *Botryllus eilatensis*. Relationship between gonad development (average gonad index, GI \pm SE) and sea-surface temperature (SST \pm SD). Gonad state is denoted by black bars for zooids containing testes and white bars for zooids with testes and ovaries ($n = 5$ colonies). ND = no data

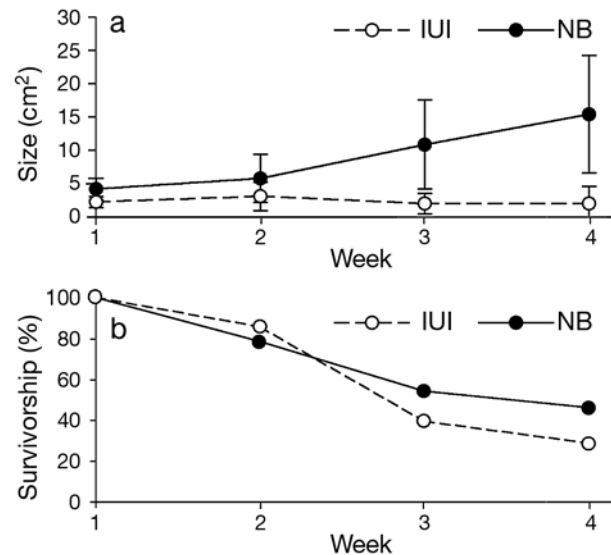


Fig. 5. *Botryllus eilatensis*. (a) Average size (\pm SD) and (b) survivorship percentage of fragments transplanted to the NB site (black circles) ($n = 37$) in comparison to the IUI site (blank circles) ($n = 28$)

DISCUSSION

One of the major questions faced by coral reef researchers is that of the ongoing change to reef community assemblages. While phase-shifts from coral to macroalgal dominance have been a major focus in many studies (reviewed in McManus & Polsenberg 2004) only a few studies have discussed the role of filter-feeding organisms in deteriorating reef environments (Birkeland 1987, Bak et al. 1996). In deteriorating coral reefs hermatypic corals and filter-feeding organism biomass are negatively correlated (Aerts & van Soest 1997), with sponge and ascidian biomass increasing as coral biomass decreases (Bak et al. 1996, Aerts 1998, Ward-Paige et al. 2005). In the present study we found that in the coral reefs of Eilat, the newly described colonial ascidian *Botryllus eilatensis* (Shenkar & Monniot 2006) may rapidly overgrow corals during periods of nutrient enrichment and become a potentially important competitor for space with the reef building corals.

The monitoring of the coral-ascidian interactions revealed that *Botryllus eilatensis* has a seasonal appearance. During spring (April to June) the average percentage of coral cover by the ascidian reached approximately 30% and decreased rapidly during the summer months (Fig. 2b). The rapid spring

growth may be a result of the vertical mixing phenomenon that occurs in Eilat every winter, which results in higher nutrient levels in the water column (Genin et al. 1995). Ascidians are able to filter even very small particulate matter ranging between 0.5 to 2 μm diameter (Bak et al. 1998, Bone et al. 2003). Indeed, as visibility decreased, indicating an increase in particulate matter in the water column (Udy et al. 2005), ascidian percentage cover significantly increased, most likely due to the additional food supply. Similarly, Ward-Paige et al. (2005) reported an increase in Clionid sponge cover due to increase sewage contamination at the Florida Keys. As the water column gradually becomes depleted of particulate matter, the ascidian percentage cover declines until the following winter. The discrepancies in percentage cover between 2005 and 2006 may be a result of the deep and prolonged vertical mixing event that occurred in 2005 (ca. 600 m depth), which produced more particulate matter, in comparison to the shallower (ca. 500 m depth) and shorter event during 2006 (Shaked & Genin 2007).

Botryllus eilatensis is very common on both natural substrates (IUI and Taba sites) and artificial substrates (NB) during April and May. However, while it became scarce in the natural environment during the summer, live colonies were still found in high numbers on artificial substrates at the NB site (N. Shenkar unpubl. data). Saito & Nagasawa (2003) described a similar phenomenon in another botryllid species in Japan, in which during unfavorable conditions (e.g. high SST) the blastozooids degenerate and only the vascular system remains. These colonies can live more than 1 mo and recover by vascular budding if surrounding environmental conditions improve. Indeed, following 1 mo of translocation of *B. eilatensis* fragments from the IUI site to the NB site, the fragments increased 3-fold in size while the fragments at the IUI site remained at the same size (Fig. 5a). The NB fragments also exhibited higher survivorship rates (Fig. 5b). Again, this may be a result of higher food availability, since the NB site is subjected to more human-mediated disturbance due to its proximity to a port and a tourist area, resulting in higher nutrient levels (NMP, www.iui-eilat.ac.il) and consequently deterioration of the coral reefs at this area (Ben-Tzvi et al. 2004, Abelson et al. 2005).

We found significantly higher percentages of cover of *Botryllus eilatensis* over the massive corals in comparison to the branching corals, over small coral colonies in comparison to large ones and over north-facing corals in comparison to the south-facing ones (Fig. 3). The higher ascidian percentage cover observed over the north-facing corals may be a result of the north to south currents in the monitored area (Abelson et al. 1999) which facilitate transport of food

particles to the ascidians. The susceptibility of both the massive and the small coral colonies may be explained by the ascidian larval behavior and by the growth dynamics of the ascidian colony. Ascidian larvae are known to prefer dead coral skeletons for settlement (van Duyl et al. 1981, Stoner 1994) and shaded areas (Young & Chia 1984, Oren & Benayahu 1998). Although not quantified, it is possible that the massive coral growth forms on the dome construction provided more shaded area on their undersides in comparison to branching corals and therefore may be more 'attractive' to ascidian larvae for settlement. In addition, field observations reveal that *B. eilatensis* advances over the coral skeleton from the coral base (demonstrated in: www.tau.ac.il/lifesci/departments/zoology/members/loya/shenkar.html). Branching corals may thus 'escape in height' from ascidian overgrowth due to smaller colony surface area at the bottom of the colony (Meesters et al. 1996); while the small coral colonies could 'escape in size' from ascidian larvae settlement. However, the latter have a greater circumference to total surface area ratio, and are therefore more susceptible to overgrowth by benthic organisms (Meesters et al. 1996). During the peak ascidian appearance this overgrowth over the small monitored corals was 100% for a period of 2 mo. Surprisingly, once the ascidian cover had disappeared (end of summer), the coral tissue seemed healthy and unbleached. Pawlik et al. (2007) found that coral reef sponges that interact with corals are able to cause coral bleaching by producing secondary metabolites. Ascidians too are able to produce noxious secondary metabolites (Pisut & Pawlik 2002, McClintock et al. 2004), but their effect on coral tissue has not yet been examined. It seems that the rapid growth rate of colonial ascidians (up to 14 cm linear growth per month, Bak et al. 1996, ca. 10 cm² per month, current study) is the key to their ability to overgrow reef-building corals and occupy newly available surfaces.

There are a number of factors regulating sexual reproduction of ascidians, for which temperature (Millar 1971) and food availability (Sahade et al. 2004, López-Legentil et al. 2005) have been suggested as the main factors. We observed a significantly higher number of zooids containing gonads (testes and ovaries) from May to October 2006 (Fig. 4), when water temperature and solar irradiation rise. However, since no embryos or larvae were detected, it was difficult to ascertain the exact timing of larval release. Several studies have showed that the ascidian-spawning season occurs after the period of highest water temperature (Goodbody 1961, Becerro & Turon 1992); therefore, it is likely that *Botryllus eilatensis* reproduces sexually from August to October. Although year-round reproduction is typical to tropical coral reef ascidians

(Goodbody 1961, van Duyl et al. 1981), similar seasonality was observed by Hirose et al. (2005) for *Diplosoma virens* in Ryukus in Japan, which, like Eilat, is situated at the northern limit of coral reefs, and exhibits higher seasonal amplitude in water temperature than regions in low latitudes. In addition, Okuyama & Saito (2001) observed sexual reproduction in a botryllid ascidian in Japan from July to December with a peak in August. López-Legentil et al. (2005) discussed the possibility of a trade-off between resource allocation to reproduction and asexual growth in a Mediterranean colonial ascidian. During the summer months, when there is an 'energy shortage' in the Mediterranean littoral system, growth rates of *Cystodytes* sp. were at their maxima, while reproduction occurred during spring and early summer, before the season of limited food availability. We found an opposite trend; during the winter months there is investment in asexual growth, following the vertical mixing event that causes nutrient enrichment, while during the summer, as sea-surface temperature rises, there is an investment in sexual reproduction.

Birkeland (1987) suggested that along a eutrophication gradient the dominance of algae and filter feeders will increase, with filter feeders alone dominating under the most eutrophic conditions. We suggest that the rate of *Botryllus eilatensis* overgrowth on Eilat's corals is influenced by food availability in the water column. Nutrient enrichment in this region occurring either due to human activities (i.e. mariculture, tourist area development) (Loya 2007) or naturally (deep vertical mixing events) (Genin et al. 1995), may result not only in algal blooms (Lindell & Post 1995, Smith et al. 2005) but also in booming populations of filter-feeding organisms, as demonstrated in other coral reefs (Bak et al. 1996, Witman & Smith 2003, Ward-Paige et al. 2005). This is of ecological significance, because in contrast to an algal phase shift that may be controlled by herbivore pressure (Hughes et al. 1999, Szmant 2002, McManus & Polsenberg 2004) and is limited by light, in the case of *B. eilatensis* no significant predator is evident in the area nor is there an effect of light on its distribution (N. Shenkar unpubl. data). A rise in monopolization of the substrate by ahermatyphic organisms, such as ascidians, may reduce coral cover by preventing planulae from settling and decreasing the availability of the substrate for coral growth (Aronson et al. 2002). The increasing evidence of the negative effects of rapid overgrowth by ascidians (Bullard et al. 2007, Dijkstra et al. 2007, Valentine et al. 2007) and their ability to alter marine communities and economically affect commercially important activities, such as fishing and aquaculture (Bourque et al. 2007), highlights the need to include this group in coral reef monitoring programs worldwide.

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