

Effects of competition on sexual and clonal reproduction of a tunicate: the importance of competitor identity

Gustavo Muniz Dias^{1,2,*}, Cynthia Grazielle Martins Delboni³,
Luiz Francisco Lembo Duarte¹

¹Departamento de Zoologia, Instituto de Biologia, and ²Programa de Pós-Graduação em Ecologia, Universidade Estadual de Campinas, CP 6109, CEP 13083-970 Campinas, São Paulo, Brazil

³Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão - Travessa 14 Cidade Universitária, CEP 05508-900 São Paulo, São Paulo, Brazil

ABSTRACT: Individual fitness and the structure of marine communities are strongly affected by spatial competition. Among the most common space holders are the colonial ascidians, which have the ability to monopolize large areas of hard substrate, overgrowing most other competitors. The effects of competition on colony growth and on gonad production of the ascidian *Didemnum perlucidum* were studied in southeastern Brazil by experimentally removing surrounding competitors. Colonies of *D. perlucidum* competing for space exhibited a growth rate 9 times less than that of colonies that were competitor free. Among the colonies subject to competition, growth rates were unrelated to the percentage of colony border that was free of competitors. However, the identity of the competitor was important in the outcome of border contacts. At the beginning of the experiment, most border encounters of *D. perlucidum* were with solitary organisms, which in most cases were overgrown. These were progressively replaced by colonial ascidians and bryozoans, resulting mostly in stand-off interactions. Besides reducing asexual growth, spatial competition also affected female gonad production. Colonies free of competitors had a significantly higher proportion of zooids with ovaries. Thus, our findings show that spatial competition reduces both ascidian colony size and gonad production.

KEY WORDS: Space competition · Tunicate · Reproduction

—Resale or republication not permitted without written consent of the publisher—

INTRODUCTION

For encrusting species on marine rocky shores, space is often the most important limiting resource because it provides a site for obtaining food and mating opportunities (Connell 1961, Kay & Keough 1981, Konar & Iken 2005). The mechanisms for acquiring and holding space depend on both the growth form and the particular species (Kay & Keough 1981, Keough 1984, Buss 1990, Karlson et al. 1996, Bell & Barnes 2003). Solitary and colonial species differ in many aspects of growth, reproduction and susceptibil-

ity to fouling (Jackson 1977, Buss 1979, Greene et al. 1983, Santelices 2004). Solitary species can select habitat only during the larval phase, whereas colonial species also can grow directionally toward refuges during the benthic stage (Buss 1979). In addition, colonial species are much less subject to fouling, and often outcompete solitary organisms by overgrowing them (Jackson 1977).

For colonial species, fecundity increases exponentially with colony size (Harvell & Grosberg 1988). The resulting loss of space from overgrowth and consequent death of part of the colony affects both asexual

*Email: gmunizdias@gmail.com

and sexual reproduction. Alternative strategies of growth in the face of competition also affect how species occupy space, and appear to result in a 3-way tradeoff in resource allocation between asexual reproduction and male and female function (Williams 1975, Stocker & Underwood 1991, Yund et al. 1997, Newlon et al. 2003, Pemberton et al. 2004, Tarjuelo & Turon 2004, López-Legentil et al. 2005). For example, the soft coral, *Efflatounaria* sp., has a variable life-cycle strategy: at low densities, stolons facilitate rapid directional growth, whereas at high densities, stolons are inhibited, but mortality rates are greatly reduced (Karlson et al. 1996). The ascidian, *Botryllus schlosseri*, has 2 morphs with different reproductive strategies: the semelparous morph grows indeterminately and reproduces at a fixed size, whereas the iteroparous morph reproduces sexually when extrinsic factors, such as substratum limitation, intervene (Harvell & Grosberg 1988). The bryozoans, *Celleporella patagonica* and *C. yagana*, have different growth forms; the first is a runner and the second is a sheet-like colony. *C. patagonica* compensates for its poor competitive performance by reaching maturity earlier and producing more ovicells than does *C. yagana* (López-Gappa 1989).

Studies testing hypotheses on the ecology of competition have been mostly point-in-time studies that focus on the community hierarchy among species and how this transitivity affects aspects of local diversity (Karlson & Jackson 1981, Kay & Keough 1981, Kay & Butler 1983). Although this temporal restriction has been criticized, the strong differences observed among taxonomic groups are robust over ecological timescales, allowing the characterization of an inter-phyletic hierarchy (Bruno & Witman 1996, Bell & Barnes 2003, Konar & Iken 2005). Among the groups of colonial organisms competing for space, ascidians are extremely common; they can dominate large areas of rock in protected cryptic environments and usually form sheet-like colonies (Monniot et al. 1991). Although colonial tunicates have only short-lived larvae with low dispersal potential (Ayre et al. 1997), they are capable of overgrowing a clonal species, bryozoans and sponges (Bell & Barnes 2003), thus, reinforcing the importance of asexual reproduction for acquiring space.

We assessed effects of competition for space in the ascidian, *Didemnum perlucidum*, in southeastern Brazil for 6 months. The growth rate and fecundity were compared between colonies competing for space and colonies artificially free of competitors. For competing colonies, the results of interactions between *D. perlucidum* and barnacles, mussels, algae, bryozoans and ascidians were evaluated.

MATERIAL AND METHODS

Study organism. *Didemnum perlucidum* is a colonial didemnid ascidian with a tropical and subtropical distribution, and it is common in southeastern Brazil. The species ranges from the intertidal to shallow subtidal (5 m depth) zones, where it is found frequently on artificial substrata (Rocha & Monniot 1995). Like most didemnids, it has small zooids, fast growth, high fecundity and a short life span. *D. perlucidum* is classified as a pioneer in ecological succession (Lotufo 1997), and also as a potentially invasive species on the Brazilian coast (Rocha & Kremer 2005). When growing on under-surfaces, *D. perlucidum* frequently forms long thick strands that could act as a secondary dispersal mechanism because the ends of broken strands may drift to new substrates and start new colonies. In this study, *D. perlucidum* did not show this type of morphological modification, and we observed only bidirectional growth.

Field experiments. This study was performed at Praia do Segredo (23° 49' 44" S, 45° 25' 24" W) along the coast near the Centro de Biologia Marinha da Universidade de São Paulo (CEBIMar-USP), in the municipality of São Sebastião, on the north coast of São Paulo State, southeastern Brazil. In July 2004, 30 ceramic plates (330 × 330 × 5 mm) were placed horizontally at 2 depths, 1.7 and 2 m, below the sea surface. This setup was fixed to an artificial structure consisting of iron tubes. After 40 d, recruitment of *Didemnum perlucidum* colonies was observed on the bottoms of the plates and the experiment was initiated. For each plate, the most central colony of *D. perlucidum* was selected to test the effect of spatial competition on growth rate and on sexual reproduction in this species. The plates were assigned randomly to control and removal treatments. The control plates were maintained intact; on removal-treatment plates, the organisms closest to the central colony of *D. perlucidum* were removed by scraping the plate. Colonies of *D. perlucidum* that died were replaced by others that were growing on the same plate, outside the central area. The mortality in treatment and control colonies was assessed by the number of dead colonies per number of colonies analysed.

From September 3, 2004 to February 8, 2005, sampling was carried out every 2 wk. During sampling, colonies were photographed with a scale bar and recently recruited organisms were removed from the treatment plates. The areas and the perimeters of the colonies were measured from the photographs using the program Scion Image Beta 4.0.2. Growth rates between samples were calculated as the difference in colony area per number of days. To minimize manipulation artifacts, only colonies that survived for at least 3

samples were used in the growth analysis. Interactions between the colonies and competitors along the contact borders on control plates were recorded and categorized as: (1) *Didemnum perlucidum* overgrows competitor, (2) *D. perlucidum* is overgrown by competitor, or (3) stand off between competitors. This analysis was performed for each of the most abundant taxonomic groups of competitors: encrusting algae, barnacles, mussels, encrusting bryozoans and ascidians. When the outcome of interactions did not change between sampling periods, they were recorded only once to avoid pseudoreplication.

At the end of the experiment, the colonies were fixed in 10% formalin for subsequent analysis of density, sexual reproduction and budding rate of zooids. The density of zooids was measured by counting the number of zooids in a 0.36 cm² area of colony, using stereomicroscopy. Density was measured at the center and at the border of each colony. In the same way, 20 zooids (10 at the center and 10 at the border of the colony) were randomly selected and assessed for the presence of testes, ovaries and buds. In these cases, data are presented as percentages. In control (competing) colonies, the area in the border analysed was randomly selected, independent of whether the border was competitor-free or with competitors. This was done to evaluate the systemic effect of competition on the entire growing edge of the colony.

Statistical analysis. The growth rate per day was compared between the control and removal-treatment colonies and between the 2 depths using a 2-way ANOVA (Zar 1999). Mathematical models were fitted to the data on the gain in area of both removal-treatment and control colonies, and the best mathematical model was selected based on the smallest number of parameters and largest R² as estimated by the program Curve Expert 1.3. Mortality variation between removal-treatment and control colonies was compared by a chi-square test on arcsine-transformed proportions (Zar 1999). Because depth did not affect growth rate or other analyses (data not shown) and was of no biological interest in this study, data from different depths were pooled and the analyses were re-run.

To test the effect of spatial restriction on the growth rate of *Didemnum perlucidum*, a linear regression test was performed on growth rates for each sampling interval versus the percentage of border free of competitors at the beginning of the interval (Zar 1999). To evaluate change over time in the composition of organisms with which *D. perlucidum* competed, regression tests were also applied using the percentage of border of *D. perlucidum* that was free of competitors or in contact with mussels, barnacles, algae, bryozoans and ascidians versus sampling days.

To evaluate the competitive ability of *Didemnum perlucidum* against each taxon (mussels, barnacles, algae, bryozoans and ascidians), the proportion of interactions in which *D. perlucidum* overgrew the competitor, was overgrown by competitors, or engaged in a stand off was assessed using a chi-square test on arcsine-transformed proportions for each taxonomic group (Zar 1999).

To assess effects of competition on sexual reproduction, the number of zooids with ovaries and with testes were compared between the 2 treatments (control versus removal) and between the 2 sampled locations on each colony (center versus border). For each gonad assessment, a 2-way ANOVA (Zar 1999) was used. Two-way ANOVA was also used to assess the effects of competition on budding rate and density of zooids, since spatially limited colonies can reduce their budding rates or produce more zooids per colony area.

RESULTS

Colony growth rates were greatly enhanced by the removal of competitors. Colonies competing for space showed a daily growth rate ($n = 20$, mean = 0.10 cm² d⁻¹, SE = 0.09) 9 times less than that exhibited by colonies with borders free of competitors ($n = 16$, mean = 0.90 cm² d⁻¹, SE = 0.22) (ANOVA, $F_{[0.05] 1,32} = 11.42$, $p < 0.01$). Dead colonies were found mainly in the first 3 samplings and the mortality rate did not differ between control (25%) and removal-treatment (29%) colonies ($\chi^2 = 62.31$, $df = 1$, $p = 0.77$).

Colonies competing and those free of competitors differed in terms of the mathematical models describing the increase of colony size through time. The size of colonies without spatial limitation (removal treatment) exhibited exponential growth described by the equation $y = 2.54e^{0.02x}$ (R² = 0.98); the growth of competing colonies (control) was described by the logistic model: $y = 22.66/(1 + 86.68e^{-0.09x})$ (R² = 0.88) (Fig. 1).

Colonies of *Didemnum perlucidum* showed a growth rate per sampling period that was unrelated to the percentage of free border at the beginning of the sampling period ($F_{[0.05] 1,99} = 0.04$, $p = 0.95$, R² = 0.002, data not shown). The percentage of free border also did not vary significantly over the sampling period ($F_{[0.05] 1,11} = 0.94$, $p = 0.64$, R² = 0.09, data not shown), so this variable cannot have been primarily responsible for the reduction in colony growth rate.

The organisms competing for space with *Didemnum perlucidum* changed throughout the succession process. At the beginning of the study, the competitors that most frequently contacted *D. perlucidum* were algae, barnacles and mussels. After 68 d, we observed a change in the composition of spatial competitors, in

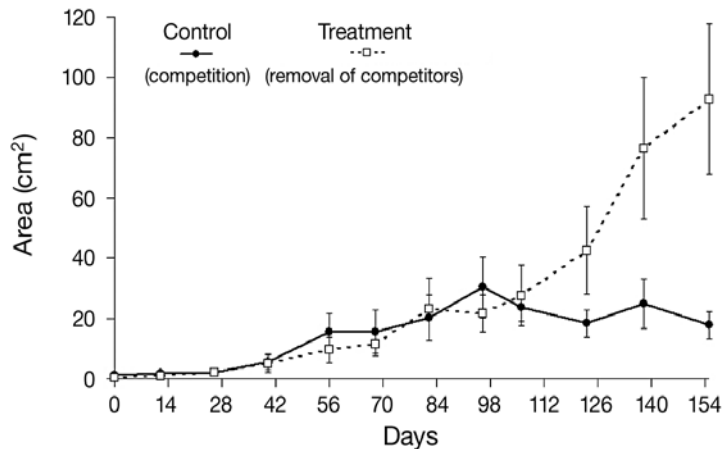


Fig. 1. *Didemnum perlucidum*. Area in cm^2 of treatment and control colonies throughout the sampling period of 154 d. Data are mean \pm SE

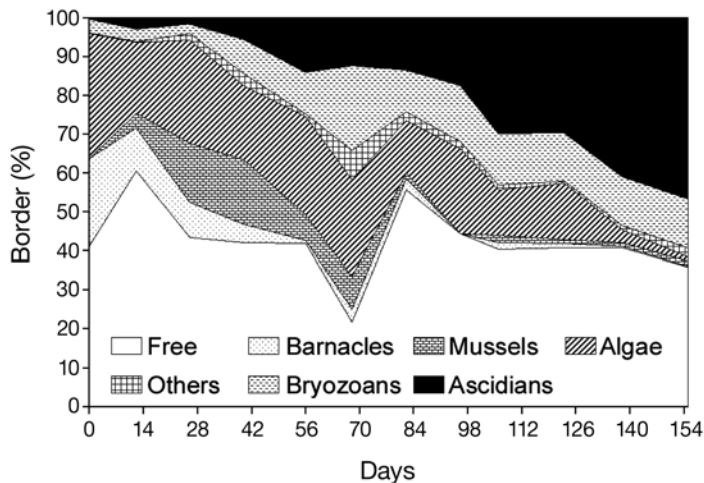


Fig. 2. *Didemnum perlucidum*. Mean percentage of colony border either free of competitors or in contact with the major taxonomic group of competitors versus time (d)

which solitary organisms were replaced by colonial animals such as bryozoans and especially ascidians. The increase in ascidians as competitors was consistent throughout the experiment (Fig. 2) and was strongly linear when regressed against sampling time (Table 1).

The results of interactions along the border of *Didemnum perlucidum* differed according to competitor identity. *D. perlucidum* overgrew mussels ($\chi^2 = 36.84$, $df = 2$, $p < 0.0001$) and barnacles ($\chi^2 = 65.86$, $df = 2$, $p < 0.0001$) in $>70\%$ of encounters. Interactions with algae ($\chi^2 = 2.41$, $df = 2$, $p = 0.30$) and bryozoans ($\chi^2 = 1.06$, $df = 2$, $p = 0.59$) resulted equally in stand offs, *D. perlucidum* overgrowing, and *D. per-*

lucidum being overgrown by the competitor. Border contacts of *D. perlucidum* with other ascidians resulted in stand offs in almost 65% of cases ($\chi^2 = 15.70$, $df = 2$, $p = 0.0004$) (Fig. 3).

The spatial restriction caused by competitors did not influence asexual reproduction and male and female gonad production in the same way. Competition for space did not affect the density of zooids (Fig. 4a), the percentage of zooids exhibiting buds (Fig. 4b), or the percentage of zooids with testes (Fig. 4c). The density of zooids and the percentage of zooids with testes in both control and removal-treatment colonies were higher in the center of the colony. The only attribute of sexual reproduction affected by spatial limitation was the percentage of zooids with ovaries, which was higher in colonies free from competitors than in those with competition (Table 2, Fig. 4d).

DISCUSSION

Although larval recruitment to densely occupied regions of rocky shores can be favorable for some species (Raymundo 2001), in most cases it results in overgrowth, shading, allelopathy and, as observed for *Didemnum perlucidum*, suppression of clonal and sexual reproduction. Since the growth rate of colonies of *D. perlucidum* competing for space was almost 10 times less than that for colonies free from competitors, this would have a great effect on the fitness of the colony, as its fecundity is exponentially related to the colony's area (Harvell & Grosberg 1988). A decline of growth rate in crowded populations has been reported in stony corals (Hughes & Jackson 1985, Muko et al. 2001), soft corals (Karlson et al. 1996) and ascidians (López-Legentil et al. 2005). Although some authors have mentioned chemically mediated or aggressive behavior in the border contacts between competitors (Buss 1990, Bruno & Witman 1996, Engel & Pawlik 2000) most of the limitations to *D. perlucidum* growth seem to be physical,

Table 1. *Didemnum perlucidum*. Linear regressions of the mean percentage of border in contact with various competitors (y) versus sample time (time since start of experiment, d)

Competitor	Regression	F	df	p	R ²
Barnacles	$y = -0.105x + 12.72$	16.72	11	0.002	0.63
Mussels	$y = -0.053x + 8.71$	2.66	11	0.131	0.21
Algae	$y = -0.155x + 29.36$	22.73	11	0.001	0.69
Bryozoans	$y = 0.068x + 5.38$	6.26	11	0.030	0.39
Ascidians	$y = 0.298x - 4.53$	121.66	11	<0.001	0.92

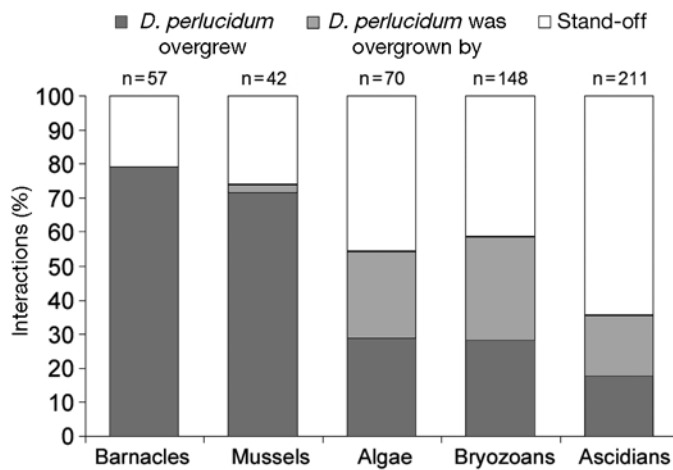


Fig. 3. *Didemnum perlucidum*. Results of border contact between *D. perlucidum* and the 5 most abundant taxonomic groups of competitors

since no tissue necrosis or retraction was observed. In addition, competition did not increase the mortality of colonies. The death of both treated and control colonies occurred near the beginning of the experiment and was probably caused by factors other than competition, such as predation by fishes. In the study area, the abundance of ascidians is reduced 5-fold by predation in the post-recruitment period (E. Vieira, G. Dias & L. Duarte unpubl. data).

Table 2. *Didemnum perlucidum*. Two-way ANOVAs on the density of zooids, percentage of budding zooids, percentage of zooids with testes and percentage of zooids with ovaries. Main effects are due to treatments (control versus removal-treatment colonies) and location of the zooids (colony border versus center)

Source of variation	df	MS	F	p
Density of zooids				
Treatment	1	462.52	0.457	0.503
Location	1	5655.02	5.586	0.023
Treatment × Location	1	0.52	0.001	0.982
Error	44	1012.35		
Zooids with buds				
Treatment	1	0.01	0.003	0.959
Location	1	8.94	2.973	0.091
Treatment × Location	1	0.30	0.098	0.755
Error	46	3.01		
Zooids with testes				
Treatment	1	4.25	1.084	0.303
Location	1	35.47	9.051	0.004
Treatment × Location	1	0.27	0.069	0.794
Error	46	3.92		
Zooids with ovaries				
Treatment	1	74.833	14.255	<0.001
Location	1	28.08	5.349	0.025
Treatment × Location	1	3.12	0.594	0.445
Error	46	5.25		

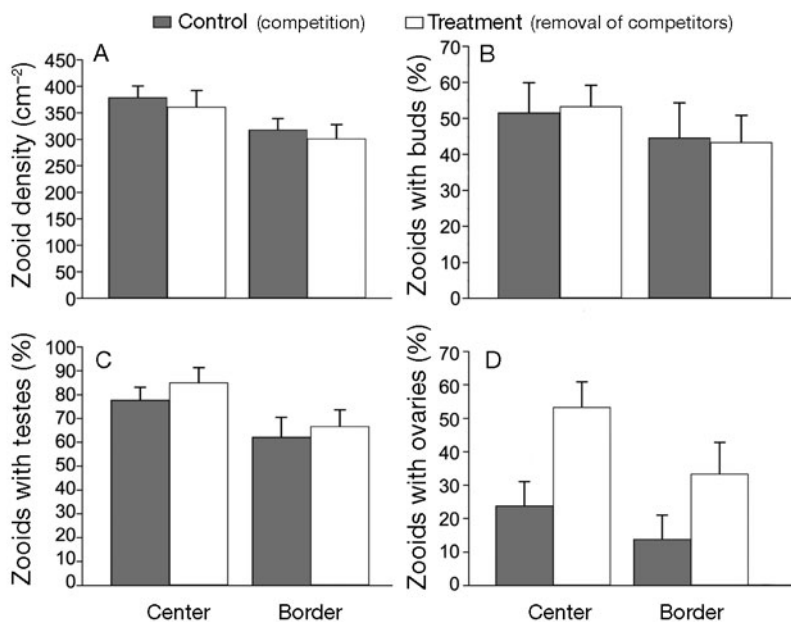


Fig. 4. *Didemnum perlucidum*. (A) Density of zooids, (B) percentage of budding zooids, (C) percentage of zooids with testes, and (D) percentage of zooids with ovaries, from control and treatment colonies (samples from the center and border of colonies). Data are mean + SE

Our long-term observations of the interactions allowed us to suggest that, as in polar regions (Barnes 2006), interactions between *Didemnum perlucidum* and other encrusting species in southeastern Brazil tended to be constant, with no reversals observed through time. Our observations began in the post-recruitment period, and thus also allow understanding of how a pioneer species acquires and holds space. The percentage of free border was similar throughout the study, but a major change in the identity of the competitors occurred. Barnacles and mussels, together with algae, are solitary organisms that show in general rapid recruitment ability and are, thus, extremely common in the first phases of succession (Jackson 1977). In contrast, bryozoans and colonial ascidians were more common in the last 3 samplings, probably because of the low ability of their larvae to recruit new substrata (Keough 1984). This change of competitors through the study period explains

better than the percentage of free border why the growth rate of competing colonies declined near the end of the experiment, since colonial animals like ascidians often overgrow solitary ones (Jackson 1977). At the beginning of the study, in most of the encounters *D. perlucidum* smothered barnacles and mussels, except for a few cases in which the barnacles elevated their feeding apertures above the substratum preventing overgrowth (escape in size) (Sebens 1982). The interactions of *D. perlucidum* with colonial organisms differed from those observed with solitary animals, and several stand-off interactions were observed, mainly in contacts with other ascidians. Thus, in addition to the complex interplay of environmental, physical and temporal factors that affects the success of competitors (Barnes & Rothery 1996), for *D. perlucidum* the identity of its competitor also had a strong influence in the outcome of border contacts.

While the most visible form of spatial competition is direct overgrowth of organisms already occupying space (Aerts 2000), stand offs are a frequent result of border interaction, mainly in intra-phyletic encounters (Karlson 1980, Schmidt & Warner 1986, Bell & Barnes 2003). This kind of interaction contributes greatly to the dynamics of spatial competition and the maintenance of local species richness. Stand offs combined with opportunistic growth over bare substrata along free borders may allow exploitation of disturbed habitats where bare substratum is provided by physical or biological disturbance (Karlson 1980, Schmidt & Warner 1986). This ability in *Didemnum perlucidum* confers on this species a potential to become invasive, as suggested by Rocha & Kremer (2005).

Several studies have examined how competition for space affects the reproduction of clonal organisms, both sexually and asexually (López-Legentil et al. 2005, Stocker & Underwood 1991), and contradictory theories have been proposed, most of which suggest a 3-way trade-off. The Williams (1975) Strawberry–Coral model predicts that in situations where open space is available, asexual reproduction will predominate. On the other hand, in crowded habitats where space is the limiting resource, sexual reproduction will be favored because genetically diverse propagules will increase the chances of survival and colonize unoccupied space elsewhere. The iteroparous morph of the ascidian, *Botryllus schlosseri*, grows indeterminately and reproduces sexually when extrinsic factors such as substratum limitation intervene, corroborating the Strawberry–Coral model (Harvell & Grosberg 1988). *Didemnum perlucidum* had a smaller percentage of zooids with ovaries when competing, but no difference in production of testes. As expected by the Strawberry–Coral model, these colonies produced ovulae early when limited by competitors, suggesting, as for

B. schlosseri, a modification in the ratio of investment between sexual and asexual reproduction. The consequences of this potential early production of gametes by the colony must be assessed, since the asynchronous spawning of gametes would reduce larvae production. A more suitable hypothesis is that colonies of *D. perlucidum* competing for space had their gonad production affected by the depletion of food by surrounding filter feeders. Thus, in this extreme situation of reduction in nutrient availability and alimentary stress, the classic asexual–sexual trade-off may not be valid for *D. perlucidum*. Data similar to our findings were obtained by Stocker & Underwood (1991) for *D. moseleyi* in contact with sponges. Competing colonies had a ratio of the number of larvae per colony to the number of fission events per colony (sexual:asexual reproduction) of nearly half that observed in colonies without competitors. The authors argued that chemicals produced by the sponge might be involved, but this hypothesis was not tested. Competition for food and allelopathy have also been suggested by Marshall et al. (2006) to explain the reduced growth rate of colonies of *Botrylloides violaceus* when in contact with pre-established colonies.

Our observation that the production of testes was not affected by competition is similar to past studies showing that male reproductive traits, such as pollen number and size and sperm number, are less sensitive than are female traits to environmental variation (Young et al. 1994, Havens et al. 1995, Vogler et al. 1999, Newlon et al. 2003). Additionally, in hermaphroditic organisms, an emphasis on male reproduction frequently occurs in high-density and nutrient-depleted situations (Newlon et al. 2003). Thus, *Didemnum perlucidum*, under conditions of stress caused by competitors, reduced female reproduction, but maintained sperm production unaltered. The production of female gametes requires more nutrient investment, and for didemnid ascidians, also requires investment in larval incubation.

Our results demonstrate that *Didemnum perlucidum* is affected strongly by surrounding organisms, and the identity of its competitors influences the success of the colony in acquiring and holding space. We suggest that food depletion by surrounding competitors restricts ovary production and, thus, that competition reduces both the sexual and asexual capacities of *D. perlucidum*. Future studies should test how shading, depletion of food, and chemicals produced by competitors affect the reproduction of colonial organisms, and which of these competitive mechanisms lead to reductions in colony fitness.

Acknowledgements. This manuscript was greatly improved by comments from 4 anonymous reviewers. The authors thank the Centro de Biologia Marinha da USP (CEBIMar-

USP) for field support, J. W. Reid for English revision, P. R. Guimarães for help in the statistical analyses and revision of the manuscript, and F. S. MacCord, P. F. MacCord and E. G. Martins for revision of the manuscript. G.M.D. also thanks Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for providing a graduate (PhD degree) scholarship. This work was supported by FAEPEX/UNICAMP.

LITERATURE CITED

- Aerts LAM (2000) Dynamics behind standoff interactions in three reef sponge species and the coral *Montastraea cavernosa*. PSZN I: Mar Ecol 21:191–204
- Ayre DJ, Davis AR, Billingham M, Llorens T, Styan C (1997) Genetic evidence for contrasting patterns of dispersal in solitary and colonial ascidians. Mar Biol 130:51–61
- Barnes DKA (2006) Temporal–spatial stability of competition in marine boulder fields. Mar Ecol Prog Ser 314:15–23
- Barnes DKA, Rothery P (1996) Competition in encrusting Antarctic bryozoan assemblages: outcomes, influences and implications. J Exp Mar Biol Ecol 196:267–284
- Bell JJ, Barnes DKA (2003) The importance of the competitor identity, morphology and ranking methodology to outcome in interference competition between sponges. Mar Biol 143:415–426
- Bruno JF, Witman JD (1996) Defense mechanisms of scleractinian cup corals against overgrowth by colonial invertebrates. J Exp Mar Biol Ecol 207:229–241
- Buss LW (1979) Habitat selection, directional growth and spatial refuges: why colonial animals have more hiding places. In: Larwood G, Rosen BR (eds) Biology and systematics of colonial organisms. Academic Press, London, p 459–497
- Buss LW (1990) Competition within and between encrusting clonal invertebrates. Trends Ecol Evol 5:352–356
- Connell JH (1961) Influence of interspecific competition and other factors on distribution of the barnacle *Chthamalus stellatus*. Ecology 42:710–723
- Engel S, Pawlik JR (2000) Allelopathic activities of sponge extracts. Mar Ecol Prog Ser 207:273–281
- Greene CH, Schoener A, Corets E (1983) Succession on marine hard substrata: the adaptive significance of solitary and colonial strategies in temperate fouling communities. Mar Ecol Prog Ser 13:121–129
- Harvell CD, Grosberg RK (1988) The timing of sexual maturity in clonal animals. Ecology 69:1855–1864
- Havens K, Preston KA, Richardson C, Delph LF (1995) Nutrients affect allocation to male and female function in *Abutilon theophrasti* (Malvaceae). Am J Bot 82:726–733
- Hughes TP, Jackson JBC (1985) Population dynamics and life histories of foliaceous corals. Ecol Monogr 55:141–166
- Jackson JBC (1977) Competition on marine hard substrata: the adaptive significance of solitary and colonial strategies. Am Nat 111:743–767
- Karlson RH (1980) Alternative competitive strategies in a periodically disturbed habitat. Bull Mar Sci 30:894–900
- Karlson RH, Jackson JBC (1981) Competitive networks and community structure: a simulation study. Ecology 62:670–678
- Karlson RH, Hughes TP, Karlson SR (1996) Density-dependent dynamics of soft coral aggregations: the significance of clonal growth and form. Ecology 77:1592–1599
- Kay AM, Butler AJ (1983) 'Stability' of the fouling communities on the pilings of two piers in South Australia. Oecologia 56:70–78
- Kay AM, Keough MJ (1981) Occupation of patches in the epifaunal communities on pier pilings and the bivalve *Pinna bicolor* at Edithburgh, South Australia. Oecologia 48:123–130
- Keough MJ (1984) Effects of patch size on the abundance of sessile marine invertebrates. Ecology 65:423–437
- Konar B, Iken K (2005) Competitive dominance among sessile marine organisms in a high Arctic boulder community. Polar Biol 29:61–64
- López-Gappa JJ (1989) Overgrowth competition in an assemblage of encrusting bryozoans settled on artificial substrata. Mar Ecol Prog Ser 51:121–130
- López-Legentil S, Ruchty M, Domenech A, Turon X (2005) Life cycles and growth rates of two morphotypes of *Cystodytes* (Ascidacea) in the western Mediterranean. Mar Ecol Prog Ser 296:219–228
- Lotufo TMC (1997) Ecologia das ascídias da Baía de Santos: período reprodutivo, crescimento e aspectos sucessionais. MS dissertation, Universidade de São Paulo
- Marshall DJ, Cook CN, Emler RB (2006) Offspring size effects mediate competitive interactions in a colonial marine invertebrate. Ecology 87:214–225
- Monniot C, Monniot F, Laboute P (1991) Coral reef ascidians of New Caledonia. Coléction faune tropicale no. 30, Orstom Editions, Paris
- Muko S, Sakai K, Iwasa Y (2001) Dynamics of marine sessile organisms with space-limited growth and recruitment: application to corals. J Theor Biol 210:67–80
- Newlon AW, Yund PO, Stewart-Savage J (2003) Phenotypic plasticity of reproductive effort in a colonial ascidian, *Botryllus schlosseri*. J Exp Zool 297A:180–188
- Pemberton AJ, Sommerfeldt AD, Wood CA, Flint HC, Noble LR, Clarke KR, Bishop JDD (2004) Plant-like mating in an animal: sexual compatibility and allocation trade-offs in a simultaneous hermaphrodite with remote transfer of sperm. J Evol Biol 17:506–518
- Raymundo LJ (2001) Mediation of growth by conspecific neighbors and the effect of site in transplanted fragments of the coral *Porites attenuate* Nemenzo in the central Philippines. Coral Reefs 20:263–272
- Rocha RM, Kremer LP (2005) Introduced ascidians in Paranaguá Bay, Paraná, southern Brazil. Rev Bras Zool 22:1170–1184
- Rocha RM, Monniot F (1995) Taxonomic and ecological notes on some *Didemnum* species (Ascidacea, Didemnidae) from São Sebastião Channel, South-eastern Brazil. Rev Bras Biol 55:639–649
- Santelices B (2004) A comparison of ecological responses among asexual (unitary), clonal and coalescing macroalgae. J Exp Mar Biol Ecol 300:31–64
- Schmidt GH, Warner GF (1986) Spatial competition between colonial ascidians: the importance of stand-off. Mar Ecol Prog Ser 31:101–104
- Sebens KP (1982) Competition for space: growth-rate, reproductive output, and scape in size. Am Nat 120:189–197
- Stocker LJ, Underwood AJ (1991) The relationship between the presence of neighbours and rates of sexual and asexual reproduction in a colonial invertebrate. J Exp Mar Biol Ecol 149:191–205
- Tarjuelo I, Turon X (2004) Resource allocation in ascidians: reproductive investment vs. other life-story traits. Invertebr Biol 123:168–180
- Vogler DW, Peretz S, Stephenson AG (1999) Floral plasticity in an iteroparous plant: the interactive effects of genotype, environment, and ontogeny in *Campanula rapunculoides* (Campanulaceae). Am J Bot 86:482–494
- Williams GC (1975) Sex and evolution. Princeton University Press, Princeton, NJ

Young HJ, Stanton ML, Ellstrand NC, Clegg JM (1994) Temporal and spatial variation in heritability and genetic correlations among floral traits in *Raphanus sativus*, wild radish. *Heredity* 73:298–308

Yund PO, Marcum Y, Stewart-Savage J (1997) Life-history

variation in a colonial ascidian: broad-sense heritabilities and tradeoffs in allocation to asexual growth and male and female reproduction. *Biol Bull (Woods Hole)* 192:290–292

Zar JH (1999) *Biostatistical analysis*, 4th edn. Prentice Hall, Upper Saddle River, NJ

*Editorial responsibility: Matthias Seaman,
Oldendorf/Luhe, Germany*

*Submitted: September 13, 2007; Accepted: February 13, 2008
Proofs received from author(s): June 18, 2008*