

Effects of temperature on growth rates of colonial ascidians: A comparison of *Didemnum* sp. to *Botryllus schlosseri* and *Botrylloides violaceus*

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An invasive colonial ascidian, *Didemnum* sp. [described as *Didemnum lahillei* by Lambert (2004) and *Didemnum vestum* by Kott (2004) and ecologically similar to *Didemnum vexillum* (Kott, 2002)], has occupied unusually large areas of seafloor and spread rapidly throughout the New England region (Valentine et al., 2007-this issue; Bullard et al., 2007-this issue). Its extreme abundance at depths > 30 m suggests that *Didemnum* sp. may be more successful in cooler, deeper waters than other recent ascidian invaders into the New England region. These other invaders are often restricted to shallow warmer-water embayments (e.g., Whitlatch and Osman, 2001) and have greatly increased recruitment in years with warm winter temperatures (Stachowicz et al., 2002). Because the distribution of *Didemnum* sp. suggested that it may be affected by temperature differently than the other invaders, we examined whether small differences in ambient water temperature that occur between different depths or

between warm and cold summers might affect the growth and mortality of *Didemnum* sp. colonies. We also contrasted the responses of these colonies to those of two other colonial ascidians common in shallow embayments, *Botrylloides violaceus* and *Botryllus schlosseri*.

Growth rates were examined by conducting replicated one-week-long laboratory experiments from 12 July 2004 to 13 August 2004. Pieces of ascidian colonies were collected from the field, separated into similar sizes, attached to 10 × 10 cm PVC panels by rubber bands and placed in unfiltered, flowing sea-water. The successful attachment of colony fragments was tested after 2 d and only those panels with well-attached colonies were used in the study. A total of 39 *B. schlosseri* colonies, 16 *B. violaceus* colonies and 85 *Didemnum* sp. colonies were used.

Four plastic containers (~20 L) were used to represent four distinct temperature environments. Each container received a constant flow of unfiltered sea-water at a rate of approximately 0.3 L min⁻¹. Temperature treatments were: Ambient, Cold (3–4 °C below ambient), Warm 1 (2 °C above ambient), and Warm 2 (4–5 °C above ambient). The Ambient

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treatment was unaltered and temperatures varied according to environmental conditions. The Cold treatment was submerged in a chiller bath and kept at temperatures 3–4 °C below ambient. Warm 1 and Warm 2 treatments were heated with heating coils placed near the bottom of each bath to ensure minimal stratification. The temperature of each treatment was monitored and recorded every 2 h using a temperature data logger. Each treatment had 4–7 panels with *Didemnum* sp. and 2–3 panels for the other two ascidians. Each panel was photographed with a digital camera and the surface area of each colony was digitized using image analysis software. The proportional change in colony size for each of these species was the measure used to compare treatment affects. Data were analyzed using nested analysis of variance with panels nested by experiment.

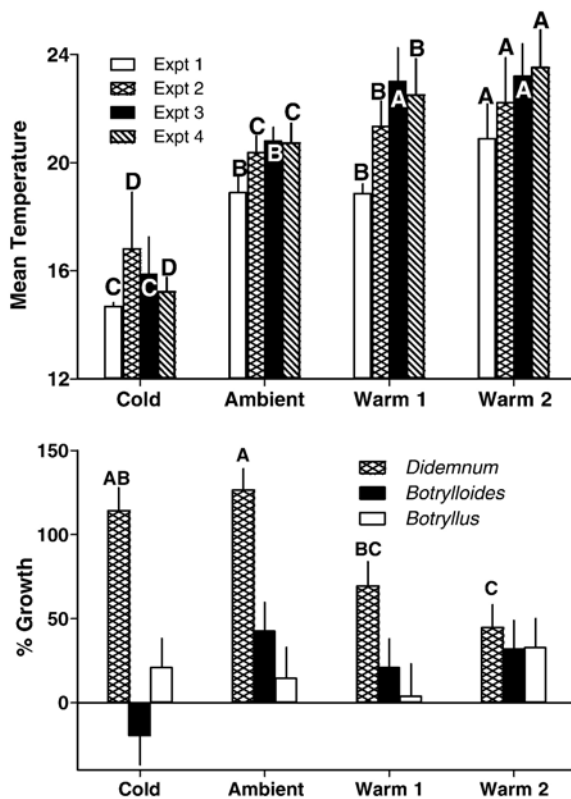


Fig. 1. Top: Mean temperatures for the four treatments during each experimental run. Letters link treatments within each experiment with no significant difference based on a one-way ANOVA and Tukey HSD a posteriori tests (JMP 5.1). Bottom: Overall results for the laboratory temperature experiment. The results of the nested ANOVA are shown for *Didemnum* sp. Letters indicate treatments that were not significantly different from each other. No significant differences were found for *B. schlosseri* and *B. violaceus*.

Ambient seawater temperatures generally increased from July to August (Fig. 1). Although there were differences between the temperatures achieved during the experiments and the target temperatures, the Cold treatment was significantly lower than Ambient and the Warm 2 treatment was significantly higher than Ambient in all four experiments (Fig. 1). The Warm 1 treatment was significantly higher than Ambient in all but Experiment 1 and significantly lower than Warm 2 in all but Experiment 3 (Fig. 1).

Across all four experiments the growth of *Didemnum* sp. differed significantly among the four treatments (Fig. 1). Growth was highest in the Ambient treatment and significantly greater than either of the Warm treatments. The Cold treatment was intermediate and not significantly different from either the Ambient or Warm 1 treatments but *Didemnum* sp. growth was significantly greater than in the Warm 2 treatment. There was a weak but significant negative relationship ($R^2=0.220$) between experimental temperature and *Didemnum* sp. growth. Neither *B. violaceus* nor *B. schlosseri* exhibited any significant differences among the four treatments (Fig. 1). Growth of both species was positively, but not significantly, correlated with temperature.

It appears that the summertime growth rate of the colonial ascidian, *Didemnum* sp., declined as temperature was increased above ambient and that at all temperatures *Didemnum* sp. grew faster than the colonial ascidians, *B. schlosseri* and *B. violaceus*. Although the relationship of growth to temperature was weak, it could be one factor contributing to the distribution of *Didemnum* sp. and its ability to invade different habitats. First, the lack of a significant difference in *Didemnum* sp. growth between Ambient and Cold coupled with significantly lower growth in the two Warm treatments (Fig. 1) suggests that modest warming produced a reduction in growth for this species. Secondly, the lack of any similar effect on either *B. schlosseri* or *B. violaceus* could reduce *Didemnum* sp.'s potential success in competing with these species in shallower, warmer coastal sites. Thirdly, it is possible that warming associated with climate change may not cause increases in *Didemnum* sp. abundances as has been hypothesized for other invading ascidians in this region (Stachowicz et al., 2002). Finally, even if the distribution of *Didemnum* sp. is restricted by temperature, the causes of its dominance in deeper water are still not clear. Its ability to grow faster than competitors in these habitats (Fig. 1) is one potential factor, but given the likely exclusion of other ascidians from these habitats

by predators (Osman and Whitlatch, 2004) it remains unclear the degree to which the absence of competitors affects its distribution.

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