Special issue "Proceedings of the 2nd International Invasive Sea Squirt Conference"
(October 2-4, 2007, Prince Edward Island, Canada)
Andrea Locke and Mary Carman (Guest Editors)

Research article

Invasive tunicates fouling mussel lines: evidence of their impact on native tunicates and other epifaunal invertebrates

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Abstract

Blue mussel *Mytilus edulis* aquaculture lines and associated gear provide habitat for sessile and mobile epifaunal fouling organisms. Due to food limitations and substrate space, these species are likely to interact among themselves and with mussels. In some areas of Prince Edward Island and elsewhere in Atlantic Canada, invasive sea squirts such as the vase tunicate, *Ciona intestinalis*, colonize mussel socks and rapidly become the dominant species in terms of abundance and biomass. A relevant question for these systems is which native epifauna are most affected by the growth of these invasive tunicates. Our study documents local variations in the abundance of vase tunicates and relates this information to the abundance patterns of three groups of native epifauna with distinctive levels of mobility: sessile tunicates of the genus *Molgula*, sedentary polychaetes and errant polychaetes. Following recruitment, large abundances of vase tunicates created a significant among-site variation pattern that was consistent over time irrespective of the season when the mussel socks were deployed. In contrast, native tunicates of the genus *Molgula* colonized the mussel socks in lower numbers and in a spatial pattern opposite to that of invasive tunicates. With the exception of one sampling period, sedentary polychaete colonization also displayed a negative relationship with invasive tunicates. Errant polychaetes displayed erratic patterns that were apparently unrelated to the other species studied. Overall, these results suggest that invasive tunicates have negative effects on many epifaunal species, particularly those that are sessile or have limited mobility.

Key words: invasions, aquaculture, *Ciona*, *Molgula*, polychaetes

Introduction

The deployment and growth of blue mussels in suspended line systems provides a hard, three-dimensional substrate that is quickly colonized by a variety of fouling and epifaunal organisms (Lutz et al. 1991; Ellis et al. 2002; Khalaman 2001). This artificial habitat is of particular importance in estuarine areas where there is little natural hard substrate available (Tyrrell and Byers 2007). In aquaculture, epifaunal organisms are usually considered harmful or beneficial depending on their effects on mussel growth (cf. Drapeau et al. 2006; Ellis et al. 2002). However, from a community ecology perspective, it is more meaningful to classify epifaunal organisms by characteristics of their life history. For instance, based on their post-colonization mobility, epifaunal communi-

ties are composed of sessile, sedentary and mobile organisms (e.g., Fauchald and Jumars 1979; Rosenberg 2001). This classification becomes particularly relevant while addressing the effects of strong epifaunal competitors on community structure (Khalaman 2001), as the intensity of their effects will likely differ depending on the relative mobility of other members of the community.

Mussel growth, death, fall-off, and movement within the socks represent usual sources of disturbance to which the resident epifauna respond (Freeman 1996; Drapeau et al. 2006). However, the arrival and establishment of new competitor species may cause more severe changes in species composition and diversity (Khalaman 2001). Invasive tunicates represent prime examples of strong competitors, although their direct effects on co-occurring epifaunal

communities are still not thoroughly understood (Grosholz 2002; Locke et al. 2007; McKindsey et al. 2007). Several mechanisms explain the success of invasive tunicates in colonizing and establishing large populations on natural and artificial substrates, such as mussel socks: early onset of reproduction, high reproductive rates, fast colonization and growth rates aid invasive tunicate establishment (Stachowicz et al. 2002; Bourque et al. 2007; Howes et al. 2007; McKindsey et al. 2007). Once established on the mussel socks, invasive tunicates have the potential to reduce water flow (LeBlanc et al. 2003; Lodeiros and Himmelman 1996), and the availability of food and oxygen, thereby harming mussels and sessile filter-feeding epifauna (LeBlanc et al. 2003; Taylor et al. 1997). Effects of invasive tunicates on mobile epifauna should be considerably less, given their ability to move away from competitors. In some cases, mobile epifauna may prevail over the invasive tunicates by preying on the newly metamorphosed tunicate juveniles (e.g., Osman and Whitlach 2004).

Invasive tunicates that have colonized coastal habitats in Prince Edward Island (PEI), Atlantic Canada, and elsewhere are well known for their harmful effects on aquaculture (Lambert and Lambert 1998; Thompson and MacNair 2004; MacNair 2005; Locke et al. 2007). As adults, invasive tunicates attach to mussels, socks and associated gear, weigh down the longlines and increase drop off and loss of mussels. This makes mussel harvesting difficult and increases the labor and maintenance costs for mussel farmers (Thompson and MacNair 2004; Drapeau et al. 2006). The clubbed tunicate (*Styela clava*) and, more recently, the vase tunicate (*Ciona intestinalis)* have become nuisance species and a detriment to the aquaculture industry of PEI. To date, research has focused on the economic implications of invasive tunicates on the mussels rather than their effects on epifaunal communities. Our study takes advantage of local scale variations in the abundance of the vase tunicate (c.f., Ramsay et al. 2008a) and examine its potential effect on three native epifaunal groups with contrasting levels of mobility: sessile tunicates of the genus *Molgula,* polychaetes with primarily sedentary habits, and errant (highly mobile) polychaetes (c.f., Fauchald and Jumars 1979). We hypothesize that the influence of invasive species is greater on species of no or low mobility, and is least relevant on highly mobile species. In order to test the consequences of this hypothesis, we investigated the epifauna of mussel longlines deployed at two different seasons (winter and spring), and sampled in summer and fall when the invasive tunicates had established as the dominant species on the mussel socks.

Methods

Study site

Our study was conducted in the Montague-Brudenell estuarine system of eastern PEI (Figure 1). This estuarine system sustains large mussel aquaculture facilities and, since 2001, has become heavily colonized by two of the four invasive tunicate species known to the region (*Styela clava, Ciona intestinalis*), while the other two *(Botryllus schlosseri, Botrylloides violaceus*) have also been reported in this area (Ramsay et al. 2008a). Georgetown Harbor is situated in close proximity to this system and is thought to be one of the major entrance points for invasive species to PEI (Locke et al. 2007). Since preliminary sampling and identification of epifaunal organisms associated with mussel socks has already been done in the Montague-Brudenell area (Ellis et al. 2002), this area constitutes the ideal location for the study of interactions between invasive tunicates and co-occurring native epifaunal species.
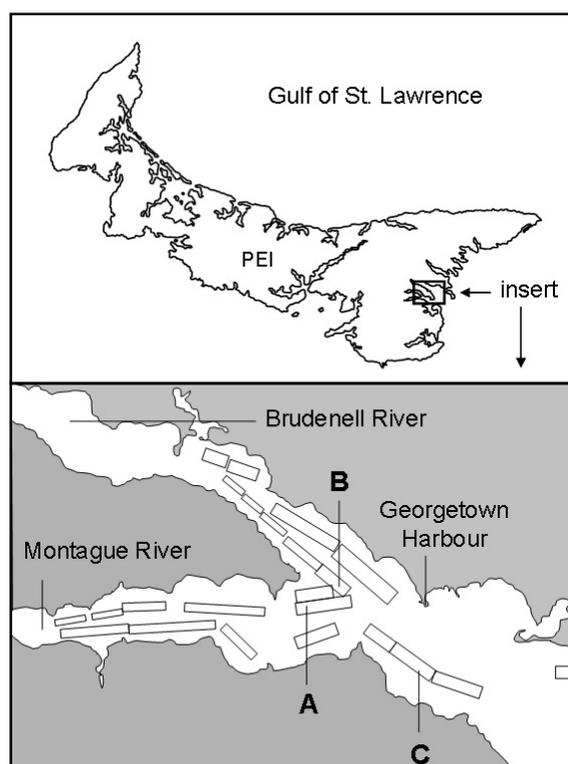

Figure 1. Prince Edward Island (PEI), showing its location in the southern Gulf of St. Lawrence, and a view of the study area (insert) in the Montague-Brudenell estuarine system. The mussel socks used for this study were deployed at sites A, B and C.

Design, deployment, sampling, and processing

Thirty 2.5-m long mussel socks were stocked at each of three representative densities (90, 250, and 500 mussels per 0.3 m sock), and deployed along the longline at each of the three sampling sites (hereafter called sites A, B, and C; Figure 1). Half of these mussel socks were deployed in the winter (N=15 per site, December 2005) and the remainder were deployed the following spring (N=15, April 2006). Five socks per stocking density were randomly distributed along an individual longline at each of the three sites. Mussel socks were sampled in June, August and October 2006 (although due to the absence of tunicates in June, only August and October are reported here). A boat equipped with a hydraulic boom was used to lift the mussel socks from the water for sample collection. For each sample collection, the contents of the bottom 0.3 m section of the stock were removed and discarded, and the 0.3 m section immediately above the bottom section was collected. Samples were transported to the laboratory for processing, sorting, identification, and quantification. Mussels, large tunicates, and all other epifauna were separated and rinsed under a gentle stream of water and collected using an 870 μm sieve. All the organisms were preserved in 70% ethanol and identified to species, in most cases, under a dissecting microscope. The majority of molgulid tunicates collected contained tadpole larvae within their body cavities and this indicated that they were either *Molgula citrina* or *M. complanata*, the two viviparous species found in this area. However, because most specimens were very small in size (<5mm), and had not been fixed prior to preservation in 70% ethanol, they had lost structural integrity, and so it was impossible to distinguish between these two species. Therefore, although there are non-indigenous *Molgula* spp. found in this region, we are referring to species that are generally accepted as native to the area. Our study also reports on the most abundant invasive tunicate (the vase tunicate, *Ciona intestinalis),* and the most abundant and diversi-fied epifaunal group, the polychaetes (Lutz-Collins 2007). Polychaetes were categorized according to their relative mobility as sedentary or errant species following Fauchald and Jumars (1979).

Data analyses

Analyses of variance of tunicate and epifaunal polychaete abundances were used to compare the effects of stocking densities, but the differences were all not significant (P>0.05) (Lutz-Collins 2007, Ramsay et al. 2008a). Thus, in all subsequent

analyses, data from the three stocking densities were pooled together. Due to the existence of significant interactions among the other main factors under study (season of deployment and sampling date), one-way ANOVA analyses reported here focus primarily on the comparison among sites for each sampling date and season of deployment (see Figures 2-4). ANOVA assumptions (Sokal and Rohlf 1994) were checked for each comparison, and data transformations (Square root or Log (n+1)) were applied in those cases where those assumptions were not met. Subsequent post-hoc comparisons (Scheffé test) were used to identify sites that were significantly different. All the analyses were conducted using MINITAB 15 (Minitab Inc., Austin, TX).

Results

Invasive and native tunicates

Overall, average abundances of vase tunicates varied between 98.4 and 828.6 tunicates / 0.3 m mussel sock (Figure 2). Tunicate abundance in both the winter and spring deployments increased from August to October. In some cases, tunicate abundances doubled in just two months. Average abundances were consistently and significantly higher at site C than at sites A and B (P<0.001; Table 1, Figure 2). Spatial differences in average numbers of native tunicates (*Molgula* spp.) among sites were striking and directly opposite to the pattern for the average numbers of invasive tunicates (plotted as the background bars in Figure 2): site C consistently showed the lowest average abundance of *Molgula* spp. (5.3 tunicates / 0.3 m mussel sock in August), whereas site A showed the highest average (110.9 tunicates / 0.3 m mussel sock, also in the August sampling). Among-site differences were significant in statistical comparisons (P=0.000-0.048; Table 1, Figure 2).

Sedentary and errant polychaetes

The average abundance of sedentary polychaetes varied significantly among sites (P<0.05 in all comparisons; Table 1, Figure 3). However, the pattern of variation was not the same in every sampling. For the winter deployments, average sedentary polychaete abundances in August were higher at site C (up to an average of 47.7 tunicates / 0.3 m mussel sock). In contrast, during the October sampling, when the overall epifaunal abundances were higher, site C had a lower abundance of sedentary polychaetes (average of 21.71 polychaetes / 0.3 m mussel sock). The latter pattern, higher average numbers at site A, which was
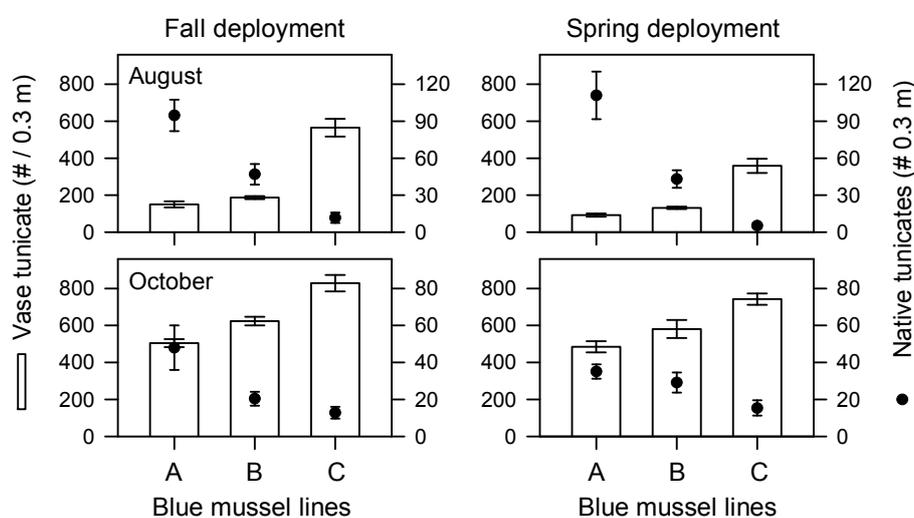
Figure 2. Average (+/- SE) abundances of tunicates *Molgula* spp. (filled circles linked by lines) estimated on mussel socks at sites A, B, and C, deployed either in winter 2005 or spring 2006, and subsequently sampled in August and October 2006. Background abundances of the vase tunicate estimated from the same samples are also presented (open bars).

Table 1. One-way ANOVA comparing epifaunal abundances in August and October among three sites (main factor) where mussel socks were deployed in winter and spring. F-values are accompanied by P-values (between parentheses). Total N values are also presented for each sampling date and season of deployment. (*): For native tunicates in October (winter deployment), N=28.

Epifaunal group	Winter deployment				Spring deployment			
	August (N=45)		October (N=43)*		August (N=45)		October (N=43)	
Vase tunicates	59.33	(0.000)	25.38	(0.000)	72.63	(0.000)	11.73	(0.000)
Native tunicates	20.91	(0.000)	3.79	(0.036)	20.23	(0.000)	3.35	(0.048)
Sedentary polychaetes	2.77	(0.044)	14.42	(0.000)	9.94	(0.000)	19.22	(0.000)
Errant polychaetes	8.72	(0.001)	5.35	(0.009)	0.35	(0.708)	0.58	(0.566)

opposite to the pattern exhibited by the invasive tunicates (background bars) was also observed during the August and October samplings of the mussel socks deployed during spring (highest averages in site A: 15.9 and 96.0 polychaetes in August and October, respectively; Figure 3). Spatial variation in the average number of errant polychaetes was significant only in the samples collected from mussel socks deployed in the winter (P= 0.000-0.009; Table 1, Figure 4). On both sampling dates, errant polychaete abundance was higher at site C (up to 302.6 polychaetes / 0.3 mussel sock in August). Minimal spatial differences were detected on socks deployed in spring (averages between 65.3 in August and 132.9 errant polychaetes / 0.3 m mussel sock in October), and these differences were not significant (P=0.566-0.708; Table 1; Figure 4).

Discussion

Mussel socks function as a living substrate, providing refuge from physical stress and predation while converting plankton into nutrients that certain epifaunal species may then utilize (LeBlanc et al. 2003; Hartstein and Rowden 2004). Natural mussel beds (Tsuchiya and Nishihira 1986) and seeded bottom beds (Quijón et al. 1996) also provide these ecosystem services, however, these habitats also contain older or denser patches of mussels which are richer in debris and organic matter and sustain higher epifaunal or infaunal species diversities than suspended mussel socks. In suspended mussel socks, the amount of detritus and shell fragments is typically low because the socks do not remain in the water column long enough to
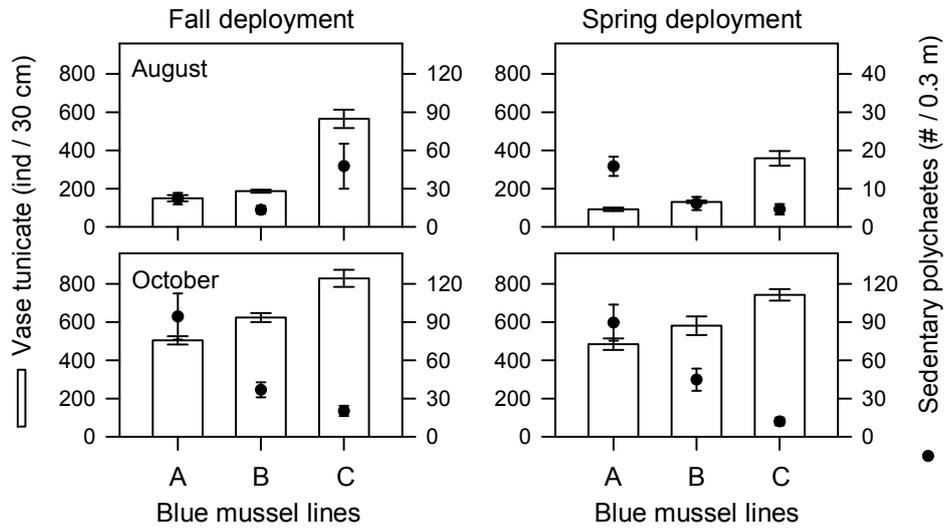
Figure 3. Average (+/- SE) abundances of sedentary polychaetes (filled circles linked by lines) estimated on mussel socks at sites A, B, and C, deployed either in winter or spring, and subsequently sampled in August and October 2006. Background abundances of the vase tunicate estimated from the same samples are also presented (open bars).
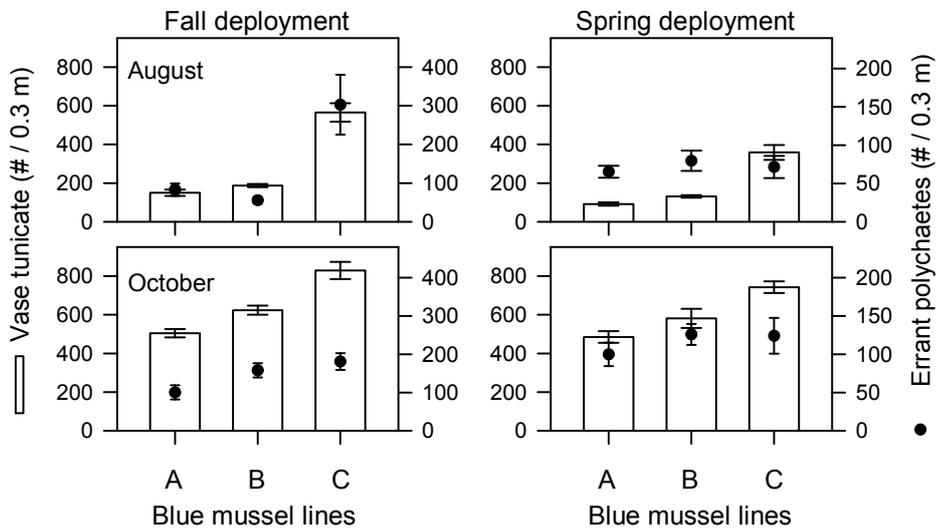

Figure 4. Average (+/- SE) abundances of errant polychaetes (filled circles linked by lines) estimated on mussel socks at sites A, B, and C, deployed either in winter or spring, and subsequently sampled in August and October 2006. Background abundances of the vase tunicate estimated from the same samples are also presented (open bars).

accumulate these materials, and much of the debris and waste material that does accumulate falls to the bottom (Freeman 1996). Despite that, spatial differences in the amount of detritus on the socks were readily visible in the three sites under study.

Due to its position within the Montague-Brudenell estuarine system, site C was exposed to higher sediment and organic input from re-suspended nutrients (c.f., Chester et al. 1983), a difference that became evident from the amount of detritus and sediments accumulated on the mussel socks when the samples were collected. Increased loads of detritus likely provided enhanced food for numerous deposit feeders and filter feeders that were present on these socks (Lutz-Collins 2007). Secondarily, these organisms may have attracted a large number of predatory poly-chaetes (c.f., Commito and Ambrose 1985), such as those of the genus *Harmothoë* and may explain the higher abundance of these polychaetes recorded in that area (Lutz-Collins 2007).

With increasing temperatures, many species reproduce and recruit onto the mussel socks causing a substantial increase in epifaunal size and biomass (LeBlanc et al. 2003; Howes et al. 2007). Spatial differences become obvious only after June (not reported here) when the different conditions for recruitment have played a role and the post-settlement interactions have begun to take place. Recruitment/colonization and community development may occur in alternative ways depending on the arrival time of each constituent species (Sutherland 1974), which may differ depending on environmental factors and spatial scale (Harms and Anger 1983). For example, the conclusions of the latter authors were gathered from the comparison of three coastal sites located at rather small distances from each other (less than 1 km apart). The significant differences reported here and elsewhere in relation to even smaller scales (e.g., kelp holdfasts, Goodsell and Connell 2002) likely reflect local-scale variation. The sharp increase in tunicate and total epifaunal abundances detected in the three sites during August suggests that recruitment and colonization occurred between June and August. In August, site C was the most distinctive in terms of introduced tunicate abundances and epifaunal community composition (Lutz-Collins 2007). Once epifaunal colonization of the mussel socks has taken place, the distance between longlines may become an obstacle for subsequent dispersal, making the differences among sites persistent, particularly for those species that only hatch larvae early in the season. This applies to sessile species (e.g., tunicates) and non-sessile species with restricted levels of dispersal (e.g., sedentary polychaetes; Hunt and Scheibling 1998; Giangrande et al. 1994). In addition, colonization and recruitment of other epifaunal species later in the growing season is likely limited once *Ciona* has heavily infested the mussel socks.

Despite the apparently better conditions for colonization and growth at site C (as inferred from spatial differences in abundances), native tunicates and sedentary polychaetes displayed a spatial pattern that is likely the result of negative interactions between these organisms and the more abundant vase tunicate (c.f., Osman and Whitlatch 2004; Blum et al. 2007). Before tunicate invasions were first detected in PEI, *Molgula* spp. were dominant fouling organisms during the mid summer months (LeBlanc et al. 2003). However, with the arrival of the clubbed and vase tunicates (Ramsay et al. 2008b) the abundance of *Molgula* spp. appears to have decreased. It is not clear which mechanisms explain the success of *Ciona* over *Molgula* spp., however, the high particle clearance rates exhibited by *Ciona* (Lesser et al. 1992) are likely to outcompete other species. Another mechanism to explain the success of *C. intestinalis* is the timing of reproduction. Larvae of *C. intestinalis* colonize the mussel socks early, out-competing other species, including *Molgula* spp., for space. One other alternative explanation for the success of *Ciona* is that it may not be as vulnerable to disturbance as many other species (Altman and Whitlach 2007).

The effects of the vase tunicate are not restricted to aquaculture farms but also occur in more uniform habitats such as settlement plates (Blum et al. 2007). The vase tunicate has been shown to monopolize space by creating "monospecific stands" (Lambert and Lambert 1998) and to change local scale species composition and overall species richness (Blum et al. 2007). The negative relationship between *C. intestinalis* and *Molgula* spp. is evident from both sampling dates. Irrespective of location, *Ciona* increased in numbers between August and October, whereas *Molgula* spp. numbers decreased. Sedentary polychaetes responded negatively to the large abundances of the vase tunicate essentially in the same way as *Molgula*. In studies documenting the effects of *Ciona intestinalis* on an array of epibenthic species, Blum et al. (2007) determined that exclusion of *Ciona* increased the abundance of four species of polychaetes, all of which belonged to families of sessile worms (e.g., Serpulidae, Terebellidae; Fauchald and Jumars 1979). The negative interaction between *Ciona intestinalis* and sedentary polychaetes, including sessile forms, may be at least partially

explained by the unsuitability of the substrate for secondary settlement of other organisms after *Ciona* has colonized it. Although some evidence suggests that solitary tunicates like *C. intestinalis* constitute secondary substrates, most literature suggests otherwise (c.f., Gulliksen 1980). Errant polychaetes exhibited a more erratic pattern in the presence of high abundances of vase tunicate. This is not surprising considering that errant polychaetes have the ability to migrate on mussel socks or any other substrate (Osman 1977) if conditions become somehow unfavorable. Although many of these polychaete species may not be attracted to areas of high debris accumulation like those at site C, the initial arrival of sedentary species may facilitate their subsequent arrival, along with other predatory species such as decapods and some species of gastropods (eg. *Mitrella lunata;* Osman and Whitlach 2004; Thompson and MacNair 2004). Some predatory species (eg. scale worms of the genus *Harmothoë*) have attracted the interest of the aquaculture industry as potential biological controls of vase tunicate recruits. However, experimental evidence needs to be provided in order to establish their actual utility as biological controls.

Acknowledgements

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