NOTE

Competitive interactions between corals and *Trididemnum solidum* on Mexican Caribbean reefs

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Abstract The ascidian *Trididemnum solidum* competes for space on Caribbean reefs and is capable of overgrowing live scleractinian corals. From 2006 to 2009, we monitored over 30,000 coral colonies and quantified competitive interactions with this ascidian at four reef sites along the Mexican Caribbean. The total number of competitive interactions increased in time, but the mean percentage of coral colonies involved in interactions remained lower than 1% in all reefs. Bottom cover by *T. solidum* was also low (mean < 0.5%) in all reef sites in all sampling years. We conclude that during the temporal scope of our study, the overall potential effect of *T. solidum* on the dynamics of Mexican Caribbean coral populations was minimal.

Keywords Coral · Ascidian · Competitive interactions · *Trididemnum*

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Introduction

Competition for space is among the most important processes that influence the composition and structure of benthic communities like coral reefs (Lang and Chornesky 1990). Studies on the competition between reef-building corals and other major benthic components of reefs, such as algae, sponges, and soft corals, are plentiful (Lang and Chornesky 1990; Hughes 1994; McCook et al. 2001). Competitive interactions between corals and ascidians, on the other hand, have been scarcely studied, even though these tunicates have biological and chemical properties that make them strong space competitors with the potential to cause significant changes in the structure of benthic communities (Bak et al. 1981, 1996; Lambert 2001; Shenkar et al. 2008). In healthy reefs, native ascidians usually have high diversity and low biomass (Lambert 2002). Nevertheless, global reef degradation associated with coral bleaching, overfishing, and eutrophication might give colonial ascidians a competitive advantage over corals, as invasive colonial ascidians possess rapid growth rates, reach sexual maturity in a few weeks, produce large numbers of larvae with a short planktonic phase, and have few predators (Bak et al. 1981; Lambert 2001, 2002). Rapid spread of some ascidian species on coral reefs over the past several years has been attributed to the following: increasing coastal development and subsequent eutrophication (Shenkar et al. 2008), increased densities of suspended bacteria in the water (Bak et al. 1996), storms and hurricanes, which create open spaces (Vargas-Ángel et al. 2009), and global disturbances, such as El Niño events, that alter environmental conditions, reduce diversity, and favor the dominance of a few ascidian species (Kelmo et al. 2006).

In the Caribbean, the native colonial ascidian *Trididemnum solidum* has the capacity to overgrow living corals (Lambert 2002), and anecdotal evidence (www.coral.noaa.

gov2008) suggests that the abundance of this species has increased greatly in some Caribbean reefs. However, only Bak et al. (1996) quantified a 900% increase in its abundance in Curaçao, between 1978 and 1993, and speculated that this was the result of localized disturbance. Recently, Sommer et al. (2010) found large colonies of *T. solidum* overgrowing scleractinian corals and increasing *T. solidum* cover with depth, in relatively undisturbed reefs of Bonaire.

Given the striking coastal development and resulting pollution (Baker et al. 2010; Metcalfe et al. 2010), the relatively high prevalence of coral diseases (Harvell et al. 2007), and the recent impact of major hurricanes (i.e., Wilma in 2005 and Dean in 2007) on Mexican Caribbean reefs, the goal of this study was to test the hypotheses that the abundance of *T. solidum* has increased over time and that this increase has lead to more interactions with live scleractinian colonies. To test these hypotheses, we monitored the number of coral colonies involved in a competitive interaction with *T. solidum* and percent bottom cover of *T. solidum* on four reefs sites along the Mexican Caribbean. This study represents the largest survey to date of coral-ascidian competitive interactions on Caribbean coral reefs.

Methods

Annual surveys were carried out along the ∼350 km Mexican Caribbean reef tract between 2006 and 2009. Four reef sites, separated by 50–100 km, were targeted: Puerto Morelos (PM), Yalku (Ya), Punta Allen (PA), and Mahahual (Mh) (Fig. 1). All reef sites are relatively close to the shoreline (1–8 km). Surveys were carried out in the fore-reef spur and groove area.
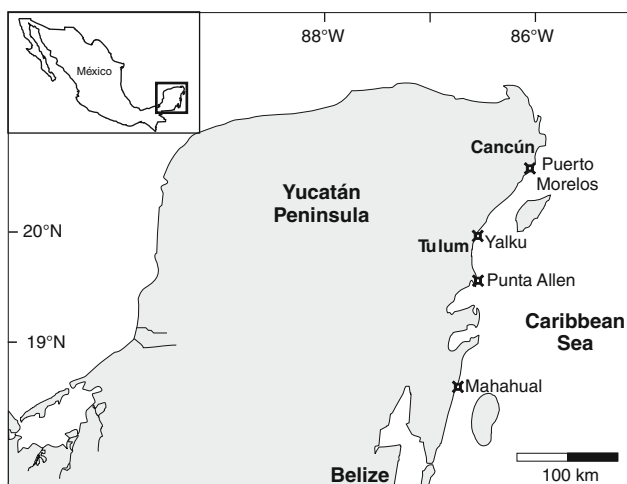
Fig. 1 Location of the four coral reefs sampled in the Mexican Caribbean: Puerto Morelos, Yalku, Punta Allen, and Mahahual

On each reef site, 24 permanent belt transects (25 m long by 2 m wide, haphazardly separated from each other by 3–35 m) were deployed on the top of spurs at a depth of 10–15 m. At PM, only 12 transects could be deployed in the fore-reef, as spur and groove features are spatially limited (6 m). The remaining transects were deployed on the well-developed back-reef zone (4 m). All corals with colony center within the transect were recorded and identified to species level. Whenever a colony of *T. solidum* was touching or overgrowing a coral colony, a competitive interaction was recorded (CTIs hereafter). Percent cover by corals and *T. solidum* was estimated using the line intercept technique on each transect (Loya 1972). Surveys were conducted during the summer coinciding with peak growth of several ascidian species (Carballo 2000; Shenkar et al. 2008).

Partial mortality of coral colonies, manifested as tissue lesions that had not been closed by the surrounding tissue (Meesters et al. 1997), was recorded in 2009. The extent of dead area was visually estimated and recorded as follows: 1–25, 26–50, 51–75, and 76–99%. Dead corals overgrown by *T. solidum* were not counted. In 2006, only six transects were sampled in Ya, and in 2008, PM and Ya reefs were not sampled.

To test the hypothesis that CTIs have increased over time, we estimated the percentage of coral colonies involved in competitive interactions with *T. solidum* per transect on each reef from 2006 to 2009. The relative contribution of CTIs per coral species to the total number of CTIs recorded across the four reefs was calculated as a percentage of the total number of CTIs in all coral species per sampling year. Changes in bottom coverage by *T. solidum* and corals through time were tested with nonparametric pair-wise Friedman's ANOVAs. Sample size estimations and generalized linear modeling were carried out in R (R Development Core Team 2010).

Study area development and characteristics

The coastal zone of the Mexican Caribbean was largely undeveloped until the mid-1970 s. At present, there is a high degree and rate of urban (over 1,000,000 inhabitants) and tourist (over 60,000 hotel rooms) development along the northern coast, from Cancún to Tulum on the mainland (PM and Ya reef sites; Fig. 1), and a low development at the southern coast, from Tulum to the border with Belize (PA and Mh reef sites, Fig. 1), where populations near sampled reefs are less than 1,000 inhabitants and have less than 500 hotel rooms (INEGI 2010). All reefs have a similar coral community structure, with *Montastraea*, *Agaricia*, and *Porites* being the dominant genera (E. Jordán-Dahlgren pers. obs.) and mean coral cover between 9 and 10% (in 2009). Climatic conditions along the reef tract are relatively

homogeneous, with trade winds in summer and mild cold fronts in the winter. The main oceanographic influence is the Yucatan current. There are no surface rivers in the karstified Yucatan Peninsula, but rain water percolates into the water table and exits through underwater springs, fissures, and seepage through beaches (Jordán-Dahlgren and Rodríguez-Martínez 2003).

Results and discussion

Competitive interactions between corals and *T. solidum* were present in all reef sites. Overall, the percentage of coral colonies involved in a competitive interaction with *T. solidum* was low during the 4-year observation period, with yearly mean values of less than 0.7% of the sampled coral colonies per reef site (Fig. 2). The highest number of CTIs across the four reef sites ($n = 114$) was recorded in 2009 and involved only 0.4% of the recorded coral colonies ($n = 31,840$) (Table 1). The sample size attained was

adequate to estimate such low percentages ($n = 16,005$, 95% CI, $\alpha = 0.05$, $\beta = 0.8$). Surveys were conducted during the summer, when seawater temperatures were around 28–30°C (dive computer temperature). Therefore, CTI values were most likely recorded near the peak of *T. solidum* growth, when colonies tend to be the largest, most capable of rapid growth and have highest production of free-swimming larvae (Bak et al. 1981).

Our data show an increase in the total number of CTIs over time in PM and Mh (Table 1). Because of the limited number of CTIs overall, it was not possible to test this apparent trend by applying a factorial repeated measures model. Instead, we compared the net change in total number of CTIs at the initial (2006, $n = 33,644$, CTI's $= 79$) and final (2009, $n = 31,840$, CTIs $= 114$) surveys across the four reef sites (Table 1). The obtained sample size was adequate for both years ($\alpha = 0.05$, $\beta = 0.8$, for dependent data). A simple generalized linear model for count data was applied where the total number of CTIs was modeled as a function of survey year using a
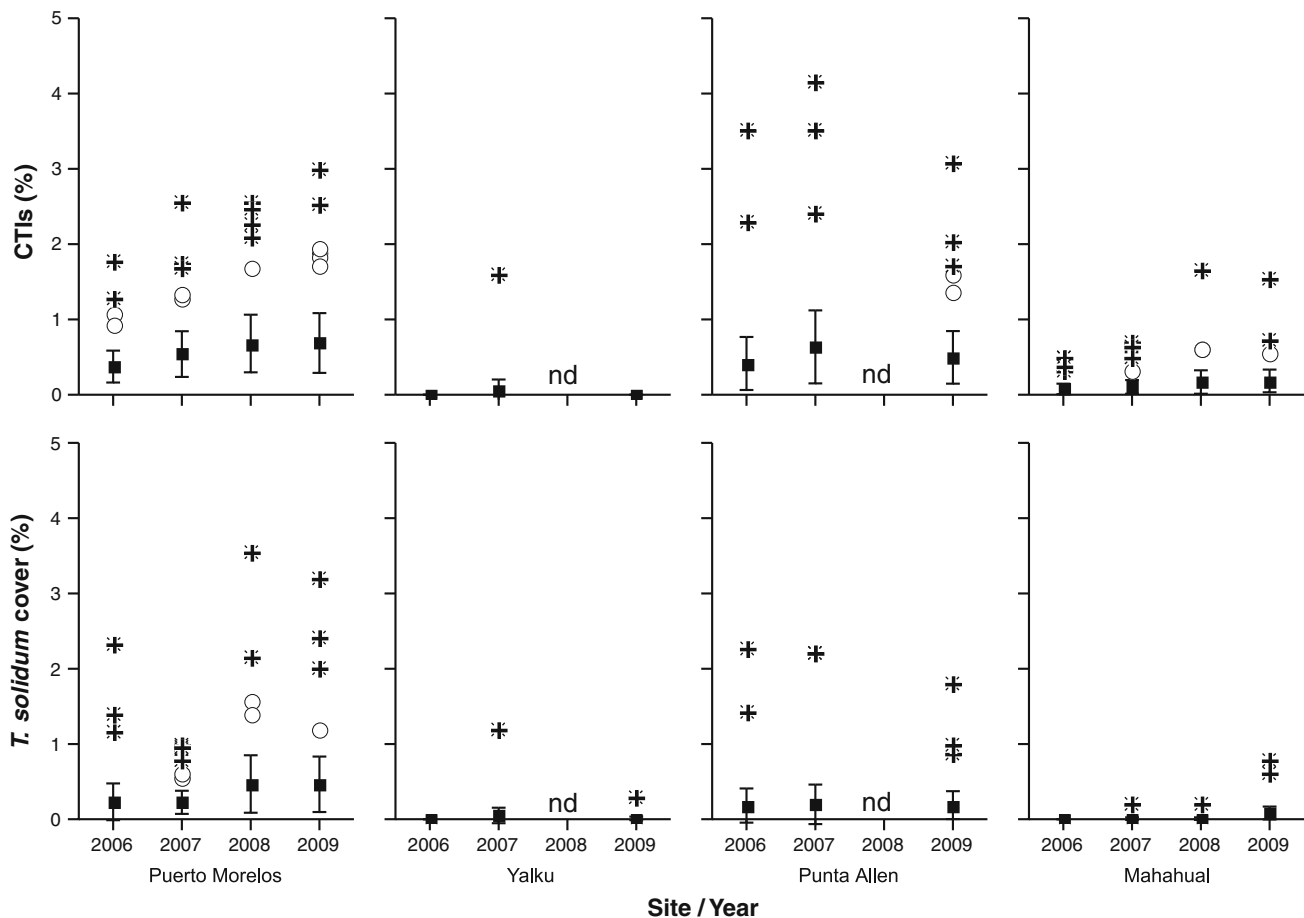
Fig. 2 Mean plot (±95% CI) detailing the percentage of coral colonies involved in a competitive interaction with *T. solidum* (CTIs) and bottom coverage by *T. solidum* over time in four Mexican Caribbean reefs ($n = 24$ 50-m² transects per reef per sampling year, except for Yalku 2006 where $n = 12$), *nd* no data. Annotations *above the plots*: o = outliers, *asterisk* = extreme data points

Table 1 Comparison of the total number of coral colonies and the total number of coral-*T. solidum* competitive interactions over time across replicate transects in four Mexican Caribbean reef sites

Reef (depth)	Year	Coral colonies (N)	Coral-*T. solidum* competitive interactions (N)
Puerto Morelos (4–6 m)	2006	6,575	30
	2007	6,401	40
	2008	6,546	52
	2009	6,935	52
Yalku (10–15 m)	2006[a]	2,994	0
	2007	6,045	3
	2008	nd	nd
	2009	5,799	0
Punta Allen (10–15 m)	2006	9,384	38
	2007	9,121	58
	2008	nd	nd
	2009	8,915	45
Mahahual (10–15 m)	2006	14,691	11
	2007	15,122	14
	2008	9,750	14
	2009	10,191	17
Total	2006	33,644	79
	2007	36,689	115
	2008[b]	16,296	66
	2009	31,840	114

Total numbers of coral colonies and of competitive interactions across reef sites per year are shown. $n = 24$ 50-m^2 transects per reef per sampling year

nd No data

[a] Data for Yalku 2006 are for 12 transects only

[b] Yalku and Punta Allen reefs were not sampled in 2008

Table 2 Results of a generalized linear model for count data applied to the total number of coral-*T. solidum* interactions in 2006 and 2009 across four Mexican Caribbean reef sites as a function of year

	Estimate	SE	z	P
Intercept	−6.054	0.113	−53.81	0.000***
Year	0.421	0.146	2.88	0.004**

** $P \leq 0.01$, *** $P \leq 0.005$

Poisson error distribution. The fit of the applied model had no over-dispersion (residual deviance = 2241; $df = 65,482$), and the difference between the total number of CTIs in 2006 and 2009 was significant ($P = 0.004$, Table 2).

Bottom cover by *T. solidum* was also low in all surveyed reef sites, with mean values ranging from 0.0 to 0.5% in all sampling years (Fig. 2), and remained without significant changes throughout the study period (Friedman ANOVA, $P < 0.05$). This lack of increase in *T. solidum* cover was observed regardless of the significant reduction in coral cover in three of the reef sites (by 17% in PA, by 37% in Mh, and by 38% in Ya; Table 3), due to hurricane damage in southern reef sites and to coral diseases in all reef sites (Jordán-Dahlgren unpublished data). Mean percent cover by *T. solidum* in Mexican Caribbean reefs was similar to that reported by Sommer et al. (2010) for shallow (5 m) reefs in Bonaire, where the ascidian occupied $0.2 \pm 0.1\%$ (mean $\pm$ SE) of available substrata (sensu Bak et al. 1996), but lower than the cover recorded by these authors on deeper reefs across six locations ($3.2\% \pm 0.6$ at 10 m and $6.3 \pm 0.8\%$ at 20 m).

Throughout the study period, CTIs were recorded in 18 of the 40 scleractinian coral species registered across the four reef sites. Table 4 compares the total number of coral colonies and the percentage of coral colonies involved in a competitive interaction with *T. solidum* per species across reefs in 2006 and 2009. During this period, the percentage of CTIs increased in 11 species, decreased in six, and remained without change in 23 (Table 4). In 2006, the highest percentages of CTIs occurred in *Colpophyllia natans* (1.7% of 119 colonies) and *Agaricia tenuifolia* (1.2% of 953 colonies), and in 2009 in *A. tenuifolia* (3.1% of 641 colonies) and *Madracis aurentenra* (2.6% of 116 colonies) (Table 4). The number of CTIs was positively correlated with the number of coral colonies per species in both years (Spearman's rho = 0.70 in 2006 and 0.75 in 2009, $P < 0.05$). In 2009, four coral species had 77% of the total number of CTIs across reef sites: *Agaricia agaricites* (32%), *Porites astreoides* (18%), *A. tenuifolia* (18%), and *Montastraea faveolata* (9%) (Table 4). *A. agaricites* and

Table 3 Mean cover and standard deviation of live corals for four Mexican Caribbean reef sites from 2006 to 2009

Reef	Mean coral cover (SD)				Friedman's ANOVA	Conclusion
	2006	2007	2008	2009		
PM	11.4 (6.1)	10.7 (5.3)	10.2 (5.7)	10.0 (5.8)	$N = 24$, $df = 3$, $\chi^2 = 5.87$, $P = 0.1179$	n.s.
Ya	13.8 (4.3)	9.6 (4.9)	nd	9.3 (4.8)	$N = 12$, $df = 2$, $\chi^2 = 11.17$, $P = 0.0038$**	2006 > (2007 = 2009)
PA	11.5 (5.0)	11.1 (5.5)	nd	9.6 (4.9)	$N = 24$, $df = 2$, $\chi^2 = 7.00$, $P = 0.0302$*	(2006 = 2007) > 2009
Mh	15.0 (4.7)	14.3 (3.8)	10.5 (4.1)	9.6 (4.8)	$N = 23$, $df = 3$, $\chi^2 = 33.05$, $P = 0.0000$***	(2006 = 2007) > (2008 = 2009)

PM Puerto Morelos, *Ya* Yalku, *PA* Punta Allen, *Mh* Mahahual

n.s.: not significant ($P > 0.05$), * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.005$. Post hoc sign tests were used when differences are significant

Table 4 Comparison of the total number of coral colonies and the percentage of coral colonies involved in a competitive interaction with *T. solidum* (CTIs) per coral species across four Mexican Caribbean reef sites in 2006 and 2009

Coral species	Number of coral colonies		Percentage of coral colonies involved in a CTIs		Relative contribution to the total number of CTIs (%)		Coral colony partial mortality
	2006	2009	2006	2009	2006	2009	2009
Acropora cervicornis	236	136	0	0	0	0	5.2 (0.9)
Acropora palmata	113	130	0.9	0.8	1.3	0.9	5.1 (1.5)
Agaricia agaricites	12,537	14,035	0.1	0.3	20.3	31.6	5.7 (0.1)
Agaricia fragilis	170	154	0	0.6	0	0.9	4.0 (1.0)
Agaricia humilis	82	46	0	0	0	0	0
Agaricia lamarcki	18	5	0	0	0	0	5.0 (2.6)
Agaricia tenuifolia	953	641	1.2	3.1	13.9	17.5	10.8 (0.7)
Colpophyllia natans	119	72	1.7	0	2.5	0	31.5 (2.8)
Dendrogyra cilindrus	1	3	0	0	0	0	8.3 (14.4)
Dichocoenia stokesi	363	303	0	0	0	0	7.8 (1.0)
Diploria clivosa	26	21	0	0	0	0	20.5 (5.7)
Diploria labyrinthiformis	157	118	0	0	0	0	38.2 (2.6)
Diploria strigosa	918	844	0.2	0.5	2.5	3.5	16.7 (0.8)
Eusmilia fastigiata	72	56	0	0	0	0	8.8 (2.4)
Favia fragum	2	1	0	0	0	0	0
Isophyllastrea rigida	165	123	0	0	0	0	5.4 (1.2)
Isophyllia sinuosa	12	12	0	0	0	0	8.3 (6.4)
Leptoseris cucullata	481	378	0.4	0	2.5	0	3.4 (0.6)
Madracis auretenra	203	116	0.5	2.6	1.3	2.6	5.9 (1.2)
Madracis decactis	429	351	0.7	1.1	3.8	3.5	8.0 (1.0)
Manicina areolata	9	30	0	0	0	0	1.8 (3.0)
Manicina mayori	16	29	0	0	0	0	0
Meandrina meandrites	292	225	0	0.4	0	0.9	9.8 (1.3)
Montastraea annularis	1,232	828	0.3	0.2	5.1	1.8	51.2 (1.0)
Montastraea cavernosa	1,551	1,358	0.1	0.4	2.5	4.4	15.3 (0.6)
Montastraea faveolata	1,677	1,191	0.1	0.8	2.5	8.8	42.1 (0.8)
Montastraea franksi	262	182	0	0.5	0	0.9	26.8 (1.8)
Mussa angulosa	2	1	0	0	0	0	0
Mycetophyllia aliciae	13	5	0	0	0	0	24.0 (11.4)
Mycetophyllia danaana	71	69	0	0	0	0	1.2 (0.6)
Mycetophyllia ferox	1		0		0		
Mycetophyllia lamarckiana	217	239	0	0	0	0	3.9 (0.9)
Porites astreoides	4,580	4,345	0.5	0.5	30.4	17.5	6.6 (0.2)
Porites divaricata	42	30	0	0	0	0	5.0 (2.6)
Porites furcata	97	21	0	0	0	0	4.8 (1.3)
Porties porites	2,396	1,546	0.3	0.2	10.1	2.6	6.5 (0.4)
Scolymia sp	12	9	0	0	0	0	0
Siderastrea radians	262	323	0	0	0	0	5.4 (0.9)
Siderastrea siderea	3,510	3,583	0	0.1	0	2.6	10.7 (0.3)
Stephanocoenia intercepta	345	281	0.3	0	1.3	0	9.5 (1.0)
Total	33,644	31,840	0.2	0.4			

The relative contribution of CTIs per coral species to the total number of CTIs recorded across reefs was calculated as a percentage of the total number of CTIs in all coral species. Mean (SE) coral colony partial mortality per species is presented for 2009. Sample sizes were 84 (50 m²) transects in 2006 and 96 (50 m²) transects in 2009

P. astreoides were also the most abundant species (Table 4), comprising 44 and 14% of the total number of coral colonies recorded, respectively. The relative high contribution of both species to the recorded coral colonies might have favored their contact with *T. solidum*. *A. agaricites* also was reported by Bak et al. (1981) as one

of the three most common neighbors to *T. solidum* in Curaçao. However, other abundant coral species, such as *Siderastrea siderea*, which comprised 11% of the sampled coral colonies in 2009, had only 2.6% of the total number of CTIs, while *A. tenuifolia* and *M. faveolata*, which had a relatively low colony abundances (<5% of sampled colonies) throughout the study period, were ranked high in their relative contribution to the CTIs recorded (Table 4). These results suggest that coral colony abundance is not the only factor in determining the abundance of CTIs.

A significant positive correlation was also recorded between the number of CTIs and mean partial mortality of coral colonies in 2009 (Spearman's rho = 0.400, $P <$ 0.05), suggesting that *T. solidum* larvae prefer to settle on dead coral surfaces as reported by Bak et al. (1996). The high partial mortality in *M. faveolata* colonies (42.1 ± 0.8% in 2009), mostly due to diseases, and in *A. tenuifolia* (10.8 ± 0.7%), could have favored the establishment of *T. solidum* larvae in these coral species. Some coral species, however, also had relatively high partial mortality (>20%), but none of those colonies were found to be involved in CTIs (i.e., *Diploria clivosa*, *D. labyrinthiformis*, and *Mycetophyllia aliciae*, Table 4). These species are relatively rare in the study sites (Table 4), and therefore, the probability of being colonized by *T. solidum* larvae is low, even when partial mortality is relatively high.

In 2009, 46% of all recorded CTIs were found at the PM reef site, in the highly developed coastal zone sector of the Mexican Caribbean, where waste water and sewage inputs are largely untreated (Murray 2007; Baker et al. 2010). This suggests that local factors, such as eutrophication, may favor ascidians. However, this was not the case for the Ya reef site, which is also in the northern, highly developed sector. Only three CTIs were registered during the whole study period, all of which were reported in 2007. Furthermore, in reefs within the low developed southern sector, a high percentage of CTIs was recorded at the PA site (39% of all CTIs in 2009; Table 1). PA represents a remote reef that is relatively protected from anthropogenic influence as it is located within the Sian Ka'an Biosphere Reserve. The scarce presence of CTIs in Ya, and the relatively higher abundance of interactions in PA, suggests that proximity to coastal pollution sources may not be the driving factor in the increase of the abundance of this ascidian on Mexican Caribbean reefs. The persistent low number of CTIs and *T. solidum* cover throughout the observation period in all reef sites lead us to conclude that the overall effect of *T. solidum* on the dynamics of scleractinian coral populations in the Mexican Caribbean appears to be minimal.

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