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Research Article

# Distribution of the invasive orange cup coral *Tubastraea coccinea* Lesson, 1829 in an upwelling area in the South Atlantic Ocean fifteen years after its first record

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## Abstract

A survey of the distribution and abundance of the invasive orange cup coral *Tubastraea coccinea* Lesson, 1829 was conducted using photoquadrats during 2014/2015, fifteen years after its first documented introduction in a Cabo Frio upwelling area in the western South Atlantic (42º00′W–22º44′S). These data were related to local currents and to a dispersion model of particles and with sea surface temperatures (SST). The objective was to investigate how variations in environmental conditions (local currents and temperatures) influence the dispersion and survival of *T. coccinea*. Complementary laboratory experiments were performed to investigate the effects of low temperatures on the survival of this species. *T. coccinea* has expanded its distribution and larval dispersion seems to be driven by the local currents. Furthermore, higher densities of colonies and recruits were observed within areas with higher water temperatures (>20 °C), while no coral was found in the area of direct upwelling influence, suggesting that cold waters limited the distribution of *T. coccinea*. These findings were corroborated by laboratory experiments that showed a negative effect of cold water (≤ 12.5 °C) on colony survival. The present data contribute to our understanding of the worldwide geographical expansion of *T. coccinea* and could be particularly important for management decisions to prevent new invasions.

**Key words:** bioinvasion, orange cup coral, temperature, western South Atlantic, Brazil

## Introduction

The globalization of maritime trade plays a key role in the spread of marine species beyond their native ranges since many of them are dispersed as fouling on vessels and in ballast water (Seebens et al. 2013; Williams et al. 2013; Katsanevakis et al. 2014). Non-indigenous marine species (NIMS) generally exhibit fast growth, high recruitment rates, and elevated competition potential (Lodge 1993), being recognized as one the major drivers of biodiversity changes worldwide (Montefalcone et al. 2015). These attributes facilitate their establishment in new environments and may cause a range of negative effects on the health of native ecosystems (Gallardo et al. 2015), such as alterations in species interactions and nutrient cycles, disturbance in natural communities integrity, and sometimes the extinction of native species (Carlton and Geller 1993; Lodge 1993; Grosholz and Ruiz 1996; Lafferty and Kuris 1996; Crooks 1998; Blackburn et al. 2014).

The orange cup coral *Tubastraea coccinea* Lesson, 1829 is native to the Indo-Pacific province—from the Red Sea and Madagascar to the tropical Americas, occurring mostly in shallow waters (Fofonoff et al. 2003). This azooxanthellate coral successfully invaded the Western Atlantic Ocean in the 1930s through shipping activities in the eastern Caribbean Sea (Cairns 2000). Thereafter, *T. coccinea* expanded its geographical distribution worldwide, especially in tropical zones (Fenner 2001; Fenner and Banks 2004), but also to higher latitudes (Cairns and Zibrowius 1997; Paz-Garcia et al. 2007). *T. coccinea* was recorded in Southwestern Atlantic on artificial substrates off southeastern Brazilian in the late 1990s (Castro and Pires 2001). Subsequently, *T. coccinea* was observed on natural substrates in two coastal areas located in Rio de Janeiro state (23ºS–43ºW) and about 300 kilometers apart: Ilha Grande Bay (de Paula and Creed 2004) and Arraial do Cabo Bay (Ferreira 2003). While Ilha Grande Bay is located in a typical tropical area, Arraial do Cabo is within the central zone of the Cabo Frio upwelling system (Coelho-Souza et al. 2012), and it is recognized as an unusual region where tropical and subtropical species co-occur (Guimaraens and Coutinho 1996; Ferreira 2003; Granthom-Costa et al. 2016). Both localities have port areas with vessel traffic related to commercial, recreational, offshore, and fisheries activities.

After the initial records of *T. coccinea*, the situation in the two invaded areas is very distinct. At Ilha Grande Bay, *T. coccinea* and its congener *Tubastraea tagusensis* Wells, 1982 are nowadays considered pest corals and occur in high abundances (>700 colonies $m^{-2}$) on several rocky shores at varying depths, spreading over a substantial distance (25 km) in less than five years (De Paula and Creed 2005; Mantellato et al. 2011; Silva et al. 2014). In contrast, the spread of *T. coccinea* has been slower at Arraial do Cabo than in Ilha Grande Bay. One year after the detection of six colonies 3 to 5cm in diameter, Ferreira (2003) observed that coral colonies had tripled in number and size in Arraial do Cabo. After ten years, Mizrahi (2008) reported the presence of small colonies on seven rocky shores, only on the underside of boulders. In addition, *T. tagusensis* has recently colonized natural substrates in Arraial do Cabo but, until now, its abundance was not comparable to that of *T. coccinea*. It is also important to note that secondary dispersals of both species has recently occurred to four localities along the Brazilian coast, northward (12ºS; 20ºS) and southward (23.5ºS; 26ºS) in Rio de Janeiro State (Mantellato et al. 2011; Sampaio et al. 2012; Miranda et al. 2012; Capel 2012; Costa et al. 2014; Miranda et al. 2016).

Here we tested the hypothesis that the distribution of *T. coccinea* in Arraial do Cabo region (22º57′ to 23º00′S, 41º59′ to 42º01′W) is controlled by low seawater upwelling temperatures. We described the distribution and abundance of *T. coccinea* at Arraial do Cabo Bay fifteen years after its first record, and these data were related to local currents, to a dispersion model of particles, and to sea surface temperatures (SST). In addition, laboratory experiments were performed to confirm the effects of low temperature on the survival of this species and compared to the field observations.

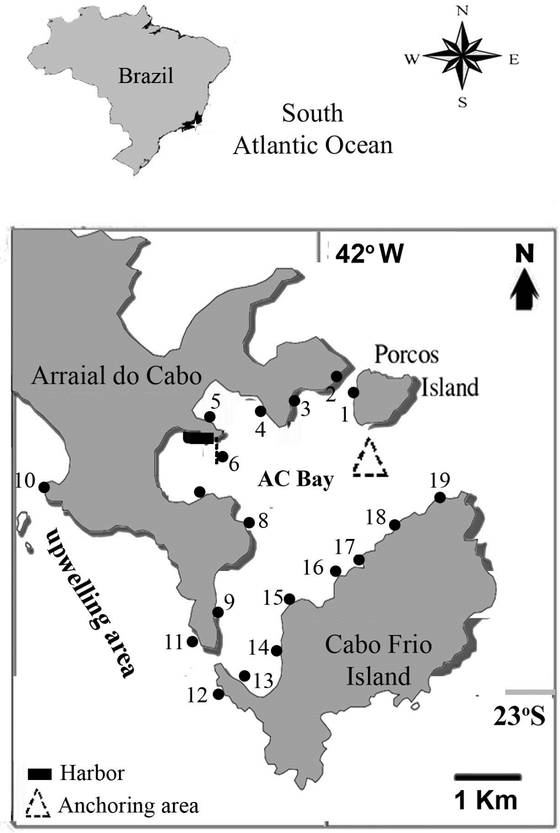


**Figure 1.** Map of the study area and the sites examined around Arraial do Cabo Bay (AC Bay; sites 1, 2, 3, 4, 5, 6, 7, 8, 9, 13, 14, 15, 16, 17, 18 and 19) and outside of Cabo Frio Island (sites 10, 11 and 12). The site 6 corresponds to breakwater.

## Material and methods

### *Study area*

Arraial do Cabo is located 160 km east of Rio de Janeiro City, southeastern Brazil (42º00′W–22º44′S) (Figure 1). This region experiences the strong influence of coastal upwelling of the South Atlantic Central Water (SACW) due to the local wind regimes and coastal geomorphology (Valentin 1994; Cirano et al. 2006).

Two general weather conditions dominate the area. Under good weather conditions, the atmospheric circulation is driven by South Atlantic anticyclone with northeastern winds. In opposition, poor weather situations are related to the passage of cyclonic low pressure systems and winds from southwest/south direction. Generally, NE wind events are longer in duration than SW/S wind events (Coelho-Souza et al. 2012). The coastal water mass typically has a temperature range from 20 to 23 °C. In contrast, SACW temperature varies from 6 to 18 °C (Candella 1999). Based on temperatures recorded from Arraial do Cabo Bay, the coldest daily temperature was 9.8 °C (8 August 1998) and the warmest was 28.7 °C (28 March 1975) (Calil 2009). Northeastern winds are prevalent in the region and are essential to upwelling occurrence, although they are not the only condition. In general, upwelling season starts in September and extends to March, but with great interannual variability (Calil 2009).

Arraial do Cabo has two distinct features concerning morphological and bathymetric characteristics (Figure 1). The outside southern portion of Cabo Frio Island is deep (> 20 m) with rocky shores exposed periodically to cold water (< 18 °C), especially during the upwelling season, and exhibit subtropical fauna and flora (Ferreira 2003). The inner portion, Arraial do Cabo Bay, consists in a sheltered, shallow (15 m maximum depth), bottle-shaped bay that is bounded by the mainland, Cabo Frio Island and Porcos Island (Candella 2009). Coastal water is predominant inside Arraial do Cabo Bay with water temperatures predominantly > 20 °C (Guimaraens and Coutinho 1996) and rocky shores are characterized by tropical reef communities (Ferreira 2003). Hence, Arraial do Cabo region represents a unique site with co-occurrence of tropical and subtropical species in close proximity (Laborel 1970; Valentin 1984; Castro et al. 1995; Ferreira 2003; Villaça et al. 2008; Lanari and Coutinho 2014).

The eastern part of the bay near Cabo Frio Island is relatively undisturbed while the northern region is influenced by anthropogenic activities, including domestic sewage discharges and a port for commercial and fishery use (Port of Forno). A breakwater was constructed to reduce wave-impact in the docking area. The port currently supports domestic and low-amounts of commercial traffic, but occasionally receives supply ships, tug boats, and other vessels from commercial and offshore trades. Outside the breakwater, there is an anchoring area where vessels wait for permission to enter the port. The anchoring area (mostly between Porcos and Cabo Frio islands) was used to perform repairs to platforms and ships until 2006, but environmental authorities have since prohibited this activity (Ferreira et al. 2006).

*Sea surface temperature patterns*

Sea Surface temperatures (SST) were obtained using temperature data loggers (iButtons, Dallas Semiconductor, USA) installed at five rocky shores within the Arraial do Cabo Bay (sites 1, 3, 6, 12, 16 and 18) and two located outside the bay (sites 10 and 11) (Figure 1). Data were measured every hour for a period of three years at a depth of 4 meters; totaling 25,920 temperature records per site. In addition, the frequency of occurrence of low temperatures (<12.5 °C) persisting for 48 hours was calculated.

*Local circulation and dispersion*

The local circulation patterns were estimated with the Princeton Ocean Model—POM (Blumberg and Mellor 1983). We used its 2-d configuration forced by external currents at each open border, local winds, and tides. Conditions were maintained constant until the kinetic energy of the domain reached stability. A simple Lagrangian model was used to evaluate particle dispersion, whose position in space and time is given by:

$$P_{n+1} = P_n + \Delta t \frac{dP_n}{dt} + \frac{\Delta t^2}{2!} \frac{d^2 P_n}{dt^2}$$

where $P_n$ is the position at time n. The model can account for advective and diffusive transport. The initial point of particle dispersion was between Porcos and Cabo Frio Island (the NE area of the bay); this position corresponded to the anchoring area.

*Distribution and abundance survey*

The field study was carried out between April 2014 and September 2015. Surveys were conducted in nineteen sites around Arraial do Cabo Bay, including three located outside the Bay (Figure 1). Fifty-meter transects were placed parallel to the shoreline at two depths (3 and 6 meters). Along the transects, all colonies and recruits were photographed using 0.12 $m^2$ quadrats coupled to a digital camera (Canon Powershot G-15; Japan) up to a distance of 1.5 meters on each side of the transect (150 $m^2$).

Images were analyzed using Image J Pro software (National Institutes of Health, USA) to quantify the number of *T. coccinea* colonies and to measure each colony's area. The total number of colonies was divided by the total area covered at each site to estimate the total density expressed in colonies or recruits per 15 $m^2$. The areas of the colonies themselves (in $cm^2$) were classified into three groups: (1) < 5 $cm^2$; (2) 5–30 $cm^2$; and (3) > 30 $cm^2$. The relative frequency (%) of the colony sizes was ascertained for each site.

*Laboratory experiment*

Complementary laboratory experiments were carried out to investigate the effect of low temperature on the survival of *T. coccinea*. Colonies (5 to 7 cm diameter) were collected by scuba diving off the rocky shores

**Table 1.** Minimum-maximum Sea Surface Temperature (°C) and cold water frequency, i.e. ≤ 15°C (times/ 3 years) in different sites distributed around Arraial do Cabo Bay.

| | Sites | Minimum (°C) | Maximum (°C) | Frequency of ≤ 15°C |
|---|---|---|---|---|
| Arraial do Cabo bay | 1 | 16.5 | 26.5 | 0 |
| | 3 | 14.0 | 26.5 | 5 |
| | 6 | 16.5 | 29.0 | 0 |
| | 13 | 12.5 | 27.5 | 126 |
| | 17 | 13.5 | 28.5 | 69 |
| | 19 | 15.0 | 26.0 | 31 |
| Upwelling area | 10 | 12.0 | 29.0 | 217 |
| | 11 | 11.0 | 27.5 | 893 |

of Porcos Island (22º57′57″S; 41º59′36″W). Just after collection, colonies were individually placed into plastic bags with natural seawater and immediately transported to the laboratory. In the laboratory, all the epibionts associated with the *T. coccinea* colonies were removed. Before starting the experiments, the colonies were acclimated at a temperature of 22 °C and a salinity of 35 (the most common condition at the collection site) in 250-liter tanks for 48 hours.

After the acclimation period, colonies (N = 15 per treatment) were transferred to aquaria with seawater at temperatures 5, 10, 12.5, and 15 °C. Each temperature was replicated five times and each aquarium received three colonies. After 24, 48 and 96 hours, five colonies in each treatment (one colony from each aquarium) were transferred to aquaria containing seawater at 22 °C. Colonies in the control condition were kept at 22 °C during the entire experiment. To evaluate whether the “transfer” procedure influenced the results, control colonies that were kept at 22 °C were also transferred to new aquaria with seawater at the same temperature. Fifteen aquaria were prepared to receive the colonies. Each aquarium received the five colonies removed from each temperature (5, 10, 12.5, 15, and 22 °C) in each period (24, 48, and 96 hours). At all stages of the experiment, colonies were maintained with constant aeration. The colonies that returned to the temperature of 22 °C were monitored for up 168 hours to assess mortality. Colonies that did not respond to tactile stimulation with a Pasteur pipette and exhibited tissue degradation were considered dead.

To verify whether colony mortality differed significantly among treatment and immersion time, a Factorial ANOVA was applied to the log (x + 1)-transformed data and the Bonferroni post-hoc test was used to identify differences between treatment means. Normality and homogeneity of variances were verified by the Kolmogorov-Smirnov and Levene’s tests, respectively. The level of significance was set at $\alpha < 0.05$. Statistical tests were performed using Statistic 8 software (SAS Institute Inc., USA).

## Results

### *Sea surface temperature*

During the three years of measurements inside the bay, maximum temperatures ranged from 26 to 29.5 °C among sites and temperatures of the upwelling cold waters (< 18 °C) were observed during summer and spring, but never below 12.5 ºC (Table 1; Figure 2). Frequency of temperatures ≤15 °C varied from zero (site 1 and site 6) to 126 times at site 13 inside Arraial do Cabo Bay (Table 1). In contrast, sea surface temperature of the outer area of the bay (sites 10 and 11) were influenced several times by upwelling phenomenon throughout the spring and summer (Figure 2), reaching a minimum of 11 °C. In this area, temperatures ≤ 15°C occurred 217 times at site 10 and 893 times at site 11 (Table 1). Moreover, temperatures ≤ 12.5ºC during 24 to 48 hours were detected 22 times at sites 10 and 12 times at site 11. The maximum temperatures registered were 29 °C at site 10 and 27.5 °C at site 11 (Table 1; Figure 2).

### *Local circulation and dispersion*

The most frequent circulation (Northeast Wind) under strong external currents from the NE border indicates that water from inside the enclosed area tends to flow outwards (Figure 3A). There is a “main channel” between the Northeast and Southwest openings, with minor mixing in the small sub-bays inside the domain. Furthermore, the currents effectively isolate the island from the mainland. In the opposite conditions (Southwest Cold Fronts) the SW wind and currents and the circulation inside the bay allow water from outside the bay to enter (Figure 3B).

In relation to the dispersion model results (Figure 4A–D), particles outside the central axis of the current will be driven out of the domain by recirculating cells. It is clear that the probability of being transported to certain points is much reduced, such as the port inner bay and its proximities. Under

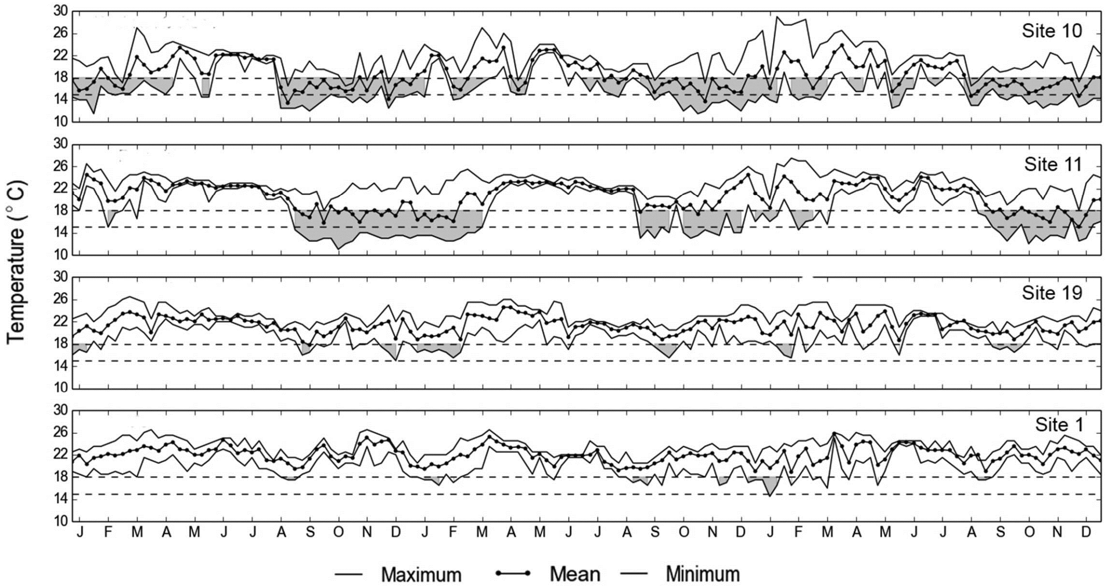


**Figure 2.** Minimum, maximum and median of sea surface temperature (°C) registered during three years of collected data. These sites represent the general pattern found at Arraial do Cabo Bay (sites 1 and 19) and at out of Cabo Frio Island (sites 10 and 11). Gray part corresponds to the occurrence of temperatures below 18°C.

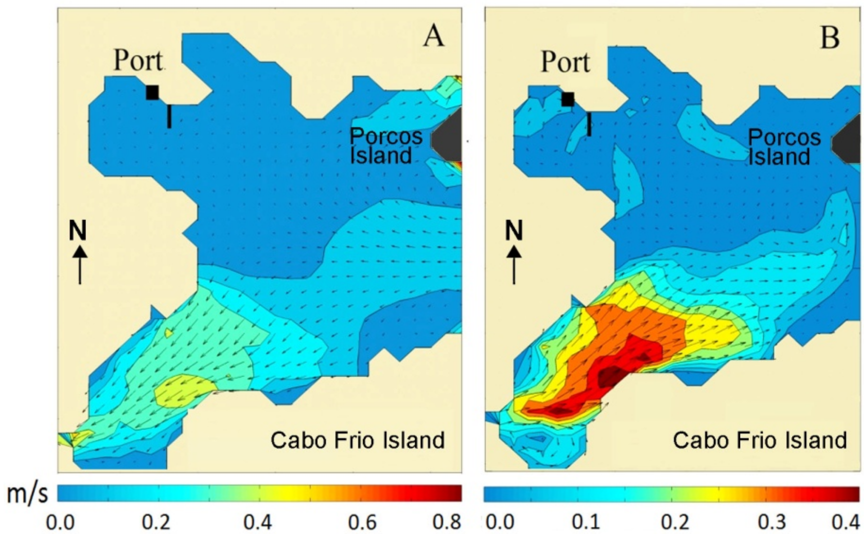


**Figure 3.** Mean circulation inside Arraial do Cabo Bay under the most frequent condition, with wind and external currents coming from the northeast to the southwest (A) and; under conditions of wind and currents coming from the southwest (B). Northeastern winds are essential to upwelling occurrence, although they are not the only condition.

weaker external currents, the lateral recirculation cells do not occur, but the main characteristics of the currents and consequently, of the dispersion, are the same. However, considering the larvae source in the anchoring area, it is possible that most of the particles are driven to the region of Porcos Island and towards the south opening (Figure 4A–D). Water circulation induced by SW wind should carry those larvae outside Arraial do Cabo Bay (data not shown).

*Distribution and abundance survey*

*Tubastraea coccinea* colonies are generally distributed in patches on the rocky shores and the higher densities were observed in the northern portion of the inner bay (Figure 5A). Porcos Island (site 1) showed the highest total density of colonies (98 col. 15 $m^{-2}$), followed by site 18 (64 col. 15 $m^{-2}$) and site 19 (54 col. 15 $m^{-2}$) at Cabo Frio Island. In contrast, low colony densities (< 5 col. 15 $m^{-2}$) were observed off south-

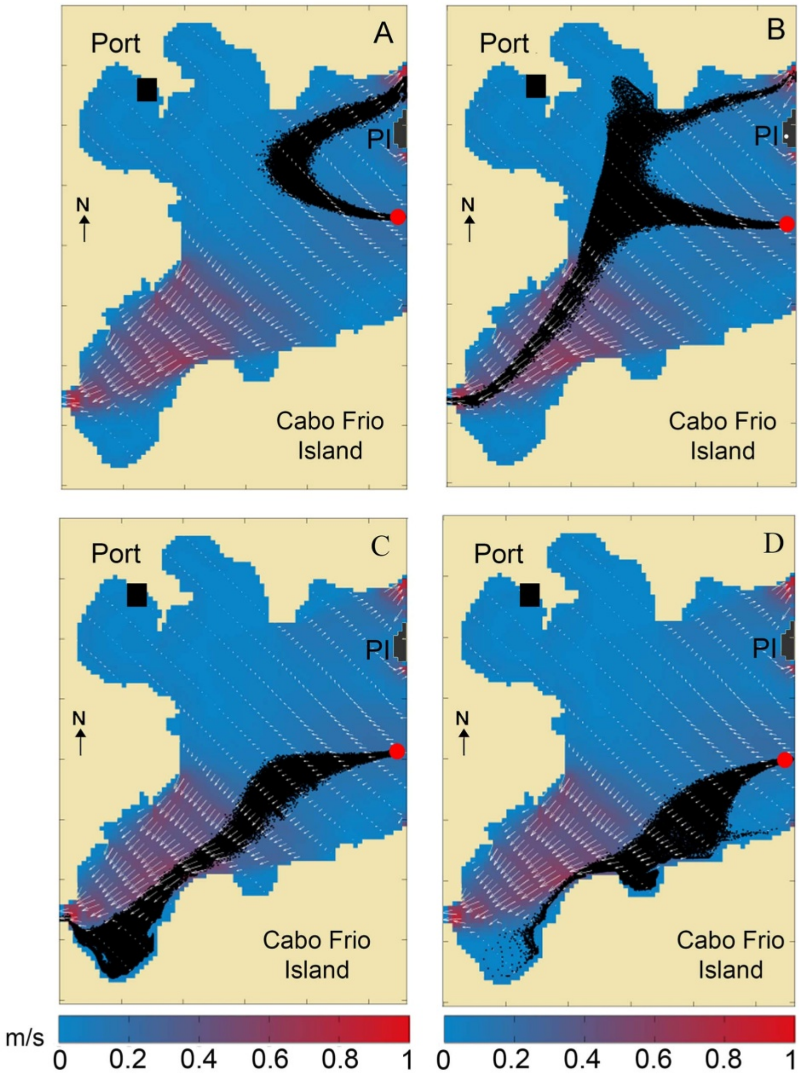


**Figure 4.** (A-C) Dispersion of particles from different points of the northeast opening under the most frequent condition of the NE wind. The particles are represented in black. The white arrows represent the direction and intensity of the currents. Most of the particles tend to leave the bay by the southwest opening or stay in the vicinity of Porcos Island (PI). Red circle represent the initial point of particles dispersion.

eastern Cabo Frio Island (site 13) and at other sites around the bay, including site 6 located at the port. No colonies were found in most of the western side of the bay (sites 5, 7, 8 and 9) and away from Cabo Frio Island.

The density of recruits around the bay followed the same pattern observed for adult colonies (Figure 5B). The highest density of recruits (44 rec. 15 $m^{-2}$) was observed at site 1 located at Porcos Island. Intermediate recruit densities were observed at sites 18 and 19 at Cabo Frio Island (21 rec. 15 $m^{-2}$ and 15 rec. 15 $m^{-2}$, respectively). Similarly, no recruits were found at sites 5, 7, 8 and 9, in addition to the areas located outside Cabo Frio Island (sites 10, 11 and 12).

In general, colony size varied such that the highest frequency of large (> 30 $cm^2$) colonies was observed at sites 1, 3 and 6, constituting up to 50% of the total population (Figure 6). More than 70% of the population at site 6 (Port breakwater) is composed of large colonies (> 30 $cm^2$). In contrast, at the southeastern sites (13 and 15), small colonies (< 5 $cm^2$) make up to 50% of the total population, while large ones constitute less than 2% (Figure 6). Similarly, small colonies (< 5 $cm^2$) represent 80% of the total population found at site 16.

*Laboratory experiment*

Temperatures of 5 °C, 10 °C and 12.5 °C caused the death of all *T. coccinea* colonies (Figure 7). Colonies kept at 5 °C died within the first 24 hours of immersion, while the colonies submitted to 10 and 12.5 °C

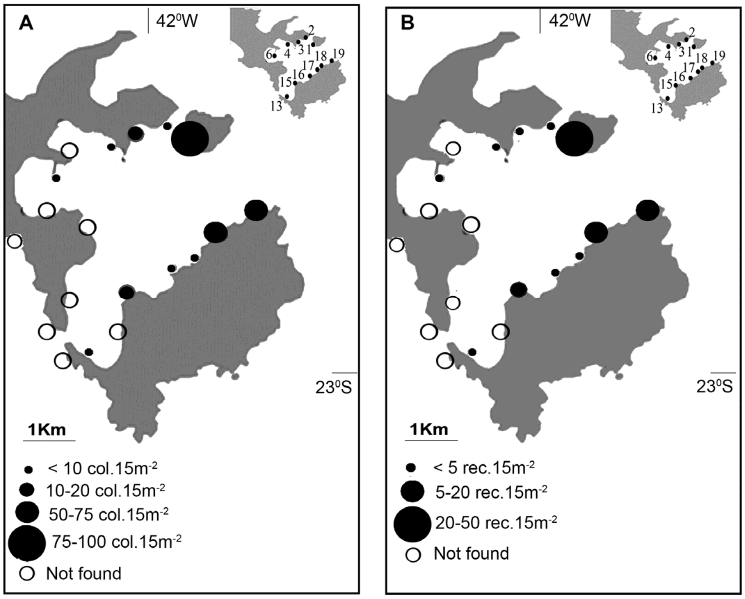


**Figure 5.** Density of (A) adult colonies (col.15 $m^{-2}$) and (B) recruits (rec.15 $m^{-2}$) of *T. coccinea* on the rocky shores of Arraial do Cabo 15 years after their introduction.

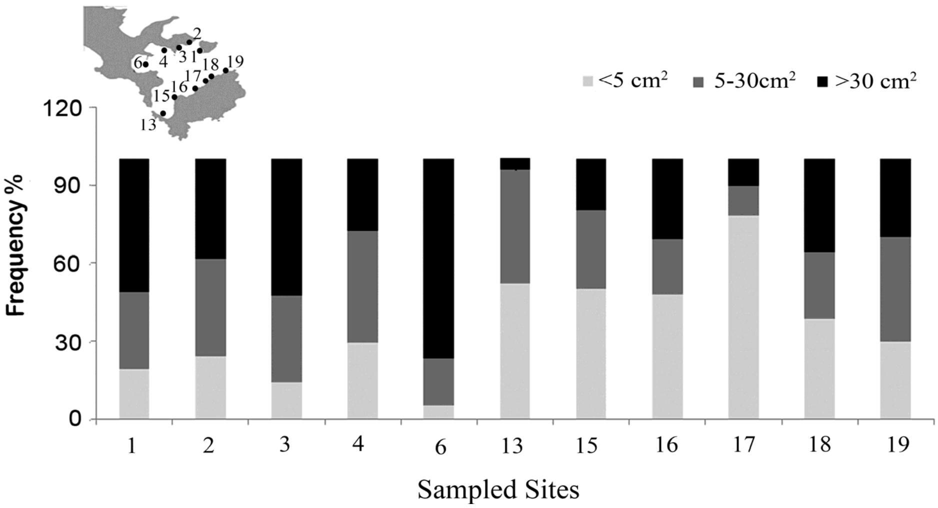


**Figure 6.** Relative frequency of colony size (%) recorded at 11 sites sampled where *T. coccinea* was found in Arraial do Cabo Bay.

died after 48 hours. No mortality occurred at 15 °C and 22 °C (the control condition). Moreover, colony manipulation had no detectable effect on *T. coccinea*, as all colonies in the control treatment remained healthy until the end of the experiment.

The interaction between the temperature and immersion time significantly influenced the mortality of *T. coccinea* colonies (ANOVA, $F_{8,60}$ = 226.1, $P < 0.001$). After 24 hours, the mortality at 5°C was significantly higher than that registered for other temperatures. Mortality did not differ at 5 °C, 10 °C and 12.5 °C after 48 and 96 hours, but was significantly higher at these temperatures than at 15 °C and 22 °C.

## Discussion

The orange cup coral, *T. coccinea*, has expanded rapidly in the tropical and sub-tropical Western Atlantic, as already reported for the Caribbean Sea (Cairns 2000), Gulf of Mexico (Fenner and Banks 2004), and Western South Atlantic (Silva et al. 2011). The present survey showed that the orange cup coral also expanded its distribution during the last fifteen years in Arraial do Cabo Bay (23ºS; SE Brazil). Currently, *T. coccinea* is detected at 11 sites around Arraial do Cabo and on some rocky shores, patches up to 11,600 m² can be found (unpublished data).

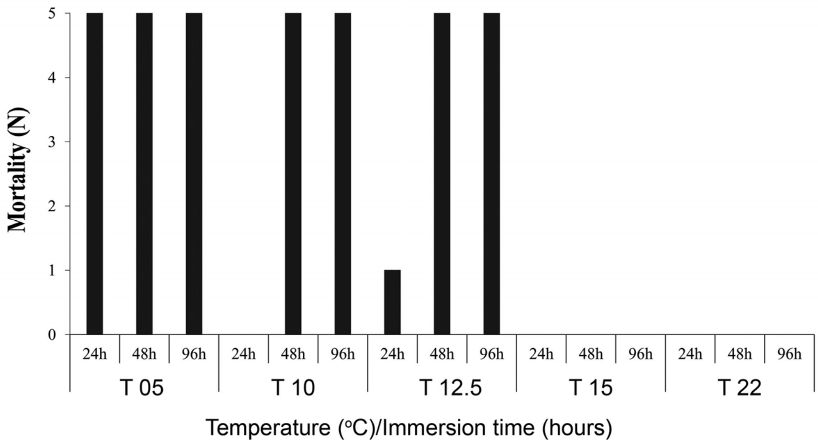


**Figure 7.** Mortality of *Tubastraea coccinea* colonies at five temperatures (5, 10, 12.5, 15, and 22 °C) after 24, 48, and 96 hours.

However, it is important to note that the expansion of *T. coccinea* in Arraial do Cabo is clearly driven by different processes compared to those previously described for Ilha Grande Bay (23ºS; SE Brazil) (Ferreira 2003; Mizrahi 2008). In Ilha Grande Bay, the orange cup coral spread so quickly that in just a few years it had showed very high densities on natural substrates (700 colonies $m^{-2}$) (De Paula and Creed 2005), approximately 100-times greater than we found in our study 15 years post-colonization of Arraial do Cabo Bay.

As expected from the dispersion models, *T. coccinea* has expanded its distribution towards the northern part of the bay indicating that anchoring and surrounding areas were the most likely primary source of larvae. Ferreira et al. (2006) detected 22 exotic species, including *T. coccinea*, on two hulls ships' and platforms anchored inside Arraial do Cabo Bay and suggested that these probable vectors were the source of the introduction to this area. Ports and adjacent areas are widely recognized as "entrance" areas for exotic species as they receive numerous dispersion vectors and indeed facilitate the establishment of exotic species (Ojaveer et al. 2014). It is important to observe that currently, ten years after that environmental authority have prohibited repairs activity in ships and platforms in anchoring area at Arraial do Cabo Bay, *T. coccinea* has continued to expand its distribution, perhaps because of secondary introductions by other vectors or from larval pools from the originally established populations. Furthermore, the probability of larvae being transported from the port inner bay out past the breakwater is much reduced. We believe that the areas in the northern bay are the current source of larvae in this region.

*T. coccinea* exhibits its highest densities on the rocky shores of Porcos Island and the northeastern part of Cabo Frio Island. These sites are protected from the prevailing NE winds and higher seawater temperatures are observed even with the upwelling influence (Carriére et al. 2009), corroborating the present SST analyses that showed only a few records of cold waters (<15 °C) and no records of temperatures below 12.5 °C. These sites are also dominated by the large colonies and probably comprise the oldest orange cup corals populations. Indeed, the SST surrounding the northern and northeastern areas of the bay, as also verified in other studies, shows temperatures ranging between 25 and 27 °C, ideal for the maximum calcification rates of azooxanthellate and zooxanthellate corals (Coles and Jokiel 1978; Kajiwara et al. 1995; Marshall and Clode 2004). Furthermore, a previous experimental study demonstrated that an increase in temperature is reflected in fast growth of *T. coccinea* colonies at Arraial do Cabo Bay (Mizrahi 2008).

It is important to note that the local circulation (under predominant NE conditions) does not facilitate larval dispersion in the small bays and it tends to flow toward the open area, outside of the bay. As a result, larvae might be carried by the dominant currents toward the southeastern area of the bay, which has natural substrates suitable for colonization. Nevertheless, only a few colonies of *T. coccinea* were recorded on these rocky shores. In this area, sea surface temperature is influenced by cold water upwelling from outside Cabo Frio Island, and the low temperature is probably constraining the expansion of *T. coccinea* into this area. In our laboratory experiments, colonies exposed to 15 °C remained healthy while those exposed to temperatures below 12.5 °C died within 48 hours. In agreement with these findings, no colonies or recruits were found at rocky shores directly influenced by temperatures lower than 12.5 °C that sometimes occurred for periods of 24 to 48 hours. Moreover, preliminary experiments recently conducted with *T. coccinea* planulae showed that a temperature ≤12.5 °C was lethal to the larvae (L. Altvater, person comm). In addition, those populations inside the bay but under the influence of cold water (<15 °C) were dominated by smaller colonies, suggesting that low temperature also has a negative effect on *T. coccinea* growth as is observed for others corals (Zerebecki and Sorte 2011; Coles and Riegl 2013) and corroborated the results of Mizrahi (2008). Another possible explanation is that colonies inside the bay recruited recently in this area. Regardless of whether the environmental conditions outside Cabo Frio Island allow the establishment of some tropical and subtropical species (Yoneshigue 1985; Guimaraens and Coutinho 1996; Lanari and Coutinho 2014), they certainly are unsuitable for the growth and survival of *T. coccinea.*

In the Western South Atlantic, *T. coccinea* has spread through warmer areas during the last ten years—along with temperatures above 23 °C (Creed et al. 2008; Silva et al. 2011; Sampaio et al. 2012; Costa et al. 2014; Silva et al. 2014). As can be seen in Arraial do Cabo Bay, *T. coccinea* colonized a transitional area between the tropical and subtropical zones (Ferreira et al. 2008), with approximate average annual temperatures of 20 °C (Guimaraens and Coutinho 1996). The present study also detected the expansion of *T. coccinea* into the warmest areas of the bay but, for the first time, this species was recorded on rocky shores exposed to seawater temperatures characteristic of temperate zones (approximately 15 °C). Furthermore, if the theory of ocean "tropicalization" is confirmed (Toledo et al. 2008; Sorte et al. 2013), the expansion of *T. coccinea* toward these south-eastern coastal areas of the Western South Atlantic will be facilitated.

In conclusion, the present results confirmed our hypothesis and showed that the lower seawater temperature, due to the upwelling phenomena, probably controls the fast expansion of *T. coccinea* in Arraial do Cabo Bay. The species is naturally restricted inside the bay, probably because of the influence of upwelling that acts as a natural, cold-water, oceanographic barrier. Our findings provide useful information to better understand the spread of *T. coccinea* worldwide and to predict its expansion. This could be particularly important for management decisions to prevent new invasions.

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