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Cover image: The mudskipper *Periophthalmus argentilineatus* on the mangrove of Ulo Beach, Cabo Delgado, North Mozambique. © José Paula, 2006

First evaluation of coral recruitment in Madagascar

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Abstract

The distribution of larvae and recruitment of scleractinians in the southwest region of Madagascar were evaluated for the first time between October 2013 and September 2014 at 3 sites. The presence of coral larvae (planulae) was monitored through weekly sampling using a plankton net and the recruitment rate evaluated by monthly sampling of the newly settled corals (<1 year stage) on recruitment tiles and by a monitoring of the recruitment of juveniles (1< Juveniles < 2 years) using the quadrat method. Planulae were present in the plankton for 9 months during the survey. The recorded mean annual density of planula varied from 0.43 ± 0.41 larvae m^{-3} to 3.23 ± 5.72 larvae m^{-3} depending on site, with a peak in larval density towards the end of November and the beginning of December. The variability in the occurrence of planula is very high and implied that the density observed in the year does not present a significant difference between the sites (p_{KW}=0.33). The average density of total recruits was 620.13 ± 621.30 recruits m^{-2}, 40.28 ± 50.97 recruits m^{-2} and 36.34 ± 33.82 recruits m^{-2}, respectively at the sites of Nosy Tafara, Grande Vasque and Rose Garden. Seasonal distribution of coral recruitment was different between the sites. The mean annual density of newly settled recruits (< 1 month stage) was significantly higher at Nosy Tafara with 94.91±101.08 recruits m^{-2} compared to Grande Vasque and Rose Garden with 18.75±34.32 recruits m^{-2} and 11.57±18.47 recruits m^{-2} (p_{KW}<0.001), respectively. The highest density of newly settled recruits was observed between October to December. Higher density of recruits was also observed in March at Nosy Tafara and in May at all three sites. Results of juvenile monitoring showed high rates (> 10 juveniles m^{-2}) compared to other regions and the threshold, but it revealed high mortality among recruits. Coral recruitment in the southwest region of Madagascar was found to be high and could result in increased resilience of the coral reef assemblages.

Keywords: recruitment, planula, recruits, juveniles, scleractinians, Madagascar

Introduction

Madagascar is part of the tropical Indo-Pacific Region where coral reefs constitute the typical coastal marine ecosystem (Pichon, 1978). The eastern part of the island, exposed to the Indian Ocean, is much less rich in coral reefs than the west, near the Mozambique Channel. In the west, coral reefs are mostly developed from Androka (in the south) bounded by the Linta River, to Antsiranana in the north. In the east, the coral reefs are distributed from Amber Cape (Antsiranana) to Toamasina. In total, coral reefs extend over approximately 1,400 km of coastline, in addition to coral banks and offshore shoals. Together, they cover an estimated area of 2,400 km^2 (Cook *et al.*, 2000).

The southwest (SW) region of the island (between the Manombo river in the north - latitude 22 ° 58 ‘S - and the Onilahy river - latitude 23 ° 34’ S - in the south) is characterized by the presence of several types of coral reefs, which are divided into three zones from north to south: (1) Ranobe Bay which groups together barrier reefs and coral banks; (2) the area between the village of Ifaty and the Fiherenana river which is characterized by a long fringing reef; and (3) the Tulear Bay which is distinguished by the presence of the largest coral reef in the Indian Ocean, the Grand Récif de Tulear (GRT) behind which are several coral banks and the fringing reef of Sarodrano (Clausade *et al.,* 1971). In total, the region contains more than

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20 coral reefs; more than 10 in the Bay of Ranobe, one between Ifaty and the Fiherenana river, and 10 in the Bay of Tulear (Clausade *et al.,* 1971).

Coral reefs provide goods and services that are essential for the economy (tourism, fishing), society, ecology (protects coasts from damage caused by storms) and aesthetics (Woodhead *et al.*, 2019). This is important for coastal populations in the tropical Indian Ocean region (Moberg and Folke, 1999), including the coastal communities in SW Madagascar, who are particularly dependant to the reef resources (Mahafina, 2011). However, coral mortality has increased in recent decades (Prada *et al*., 2017). The long-term survival of reef ecosystems is threatened by various anthropogenic stressors and global climate change (Hoegh-Guldberg, 1999). Over 50 % of the structure of coral reefs is directly threatened by human pressure (Wilkinson, 1999; Nyström *et al.*, 2000). Anthropogenic activities in coastal areas include overfishing, pollution of the sea and land runoff (Hughes *et al.*, 2003; Wilkinson, 2008), which greatly affects the reefs and causes change in the coral communities in Ranobe Bay and in Toliara Bay in SW Madagascar (Belle *et al.*, 2009, Todinanahary *et al.*, 2018). In addition to these pressures, climate change and associated warming also increases the vulnerability of the reefs (Hughes *et al.*, 2003; Hoegh-Guldberg *et al.*, 2007). In particular, the rise in seawater temperature is the main cause of coral bleaching events which lead to the degrading of the structure of the coral community (Hoegh-Guldberg, 1999).

Moreover, bleaching also reduces the productive capacity of coral populations (Szmant, 1991). Ward et al., (2000) mentioned that even corals that have recovered from bleaching no longer contained gametes and did not reproduce during the normal season. It should also be noted that juveniles are more sensitive to environmental disturbances than adults (Ward and Harrison, 1997). It is therefore particularly important to protect and restore this ecosystem and improve management before degrading effects cause its loss (Woodhead *et al.*, 2019). The resilience of the coral reefs is attributed to their ability to continue producing larvae (Richmond, 1997). Thus, understanding the ecological processes that influence this resilience is particularly essential and has become a high priority (Hughes and Tanner, 2000). Information on recruitment processes is important to understand the dynamics and resilience of coral reefs (Adjeroud *et al.*, 2016).

Scleractinian coral spawning is well documented in several regions of the world and is known to occur a few days after the full moons of the warm season. Mass spawnings were observed between October and November (spring) on the Great Barrier Reef and between March to April (autumn) on the Western Australian coast facing the Eastern Indian Ocean (Rosser and Baird, 2008). In the Western Indian Ocean (WIO), the first spawning studies were performed more recently. In South Africa and in La Réunion *Acropora austera* and *Platygyra daedalea* spawnings were observed in February (Massé, 2014). Monthly assessment of their sexual reproduction suggested an extended spawning period between September and March, with a recruitment period that covers the summer and winter seasons (Massé, 2014). In Madagascar, only the spawning of *Acropora* species were recorded from the coral reefs of Andavadoaka, in the SW region (Gress *et al*., 2015).

Notable differences in spatial distribution of coral recruitment have been recorded at a regional scale, notably between Indo-Pacific and Atlantic reefs (Ritson-Williams *et al*., 2010), and at a local scale within reefs or between sites of the same region. In the Pacific, the recruitment rate is much lower (e.g., ~40 recruits m^{-2} $year^{-1}$ at Mo'orea in French Polynesia (Adjeroud, 2007; Pénin, 2007) than in the Western Pacific reefs where ~200 to 700 recruits m^{-2} $year^{-1}$ and up to 4,590 recruits m^{-2} $year^{-1}$ were recorded (Hughes *et al.,* 1999). The recorded recruitment rates in the WIO are comparable to the higher rates, but have been proven to be higher in subtropical latitudes (548 recruits m^{-2} $year^{-1}$ in South African reefs) than in tropical latitudes (305 recruits m^{-2} $year^{-1}$, La Réunion Island) (Massé, 2014).

To date, few papers have reported on the distribution patterns of coral juveniles, despite the relatively developed observation methods (Baird *et al*., 2006). For instance, Zahir *et al*. (2002) reported a juvenile (< 10 cm size) recruitment rate of 30 – 49 m^{-2} in the Maldives Islands. In Mayotte and the Glorieuses Islands, the observed juvenile recruitment rate was < 30 juveniles m^{-2} (< 5 cm size).

Limited resolution in the identification of recruits is one of the main constraints in coral recruitment monitoring. The methods used generally depend on the survey level. At the level of newly settled recruits, unglazed terracotta and ceramic tiles are the most widely used, while for the juveniles that are observable *in situ* (mostly < 5 cm size), the method of *in situ* quadrat is usual (Hill and Wilkinson, 2004). Based on morphological characteristics, recruits are only observable to the level of the 3 families Acroporidae, Pocilloporidae and Poritidae (Babcock *et al.,* 2003).

The present paper is the first to record scleractinians recruitment in Madagascar. It aims at characterizing the spatial and temporal distribution of coral larvae, recruits and juveniles off the coral reefs of the SW region, using the most recent survey methods and recruit identification techniques.

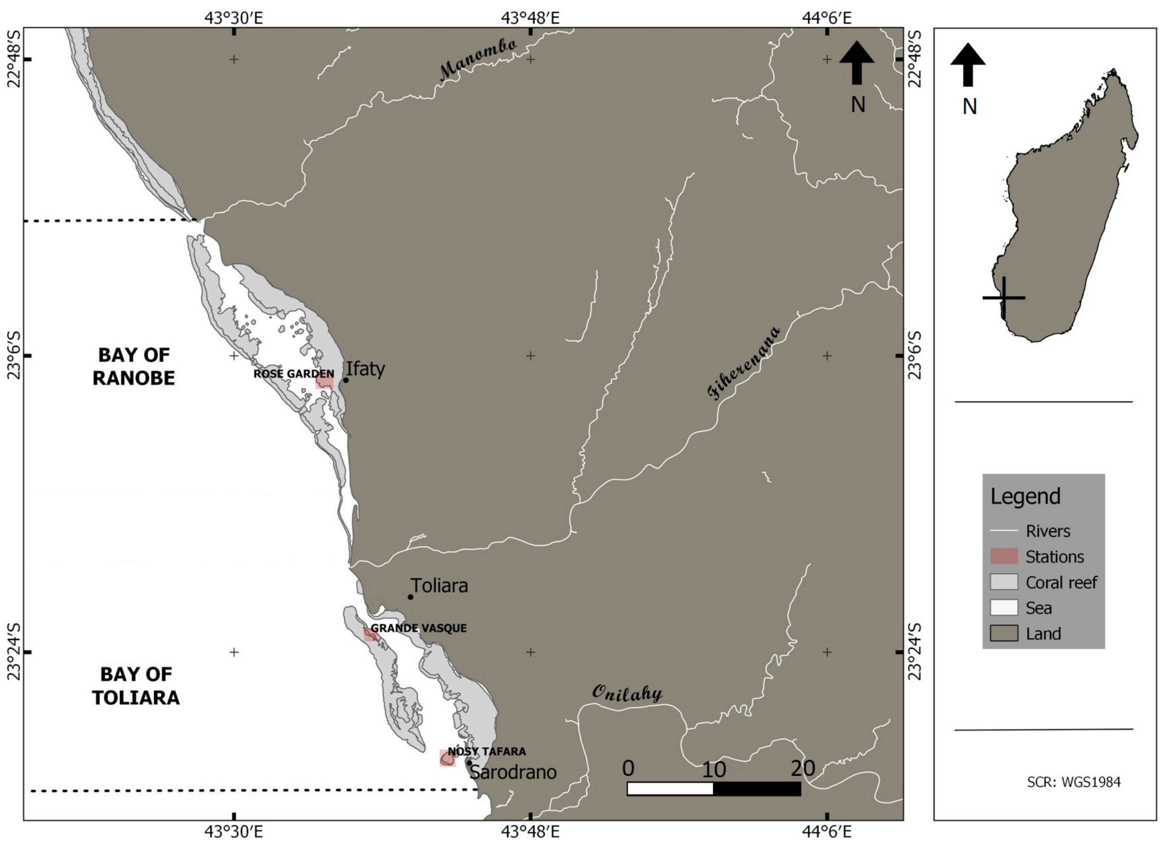

Figure 1. Location of the studied sites.

Materials and methods

Study area

The present study was performed on the coral reefs of SW Madagascar, between the latitude 22°58'S in the north and the latitude 23°34'S in the south (Fig. 1). Three distinct sites were chosen. The first site was located on the coral reef of Nosy Tafara (latitude 23°30'S), which is a complex of patch reefs located between the southern tip of the GRT and the sandy coast of Sarodrano village. The second site was located in the "Grande Vasque" (latitude 23°22' S), a basin of 1 km diameter situated in the flat of the GRT. These two reefs are located in the Bay of Toliara. The third site was located at the Rose Garden reef, in the Bay of Ranobe (latitude 23° 8' S), which is a reef patch dominated by *Montipora* species and is a locally managed protected area.

Monitoring of physicochemical parameters of the water

At each site, temperature of the bottom water, at the same depth that the recruitment tiles were situated (see *Recruitment monitoring* below) was measured every hour with a HOBO pendant temperature logger (©ONSET) from which data were downloaded and calculated using the ONSET HOBOware Pro version 3.7.0 (Onset Computer Corporation, 2002-2014). Salinity and water visibility were measured weekly using a refractometer and Secchi disc respectively.

Planula records

Weekly sampling of zooplankton was performed to record the planula larvae for one year from October 2013 to September 2014 at the 3 sites. Sampling was performed every week at the surface (< 1 m depth),

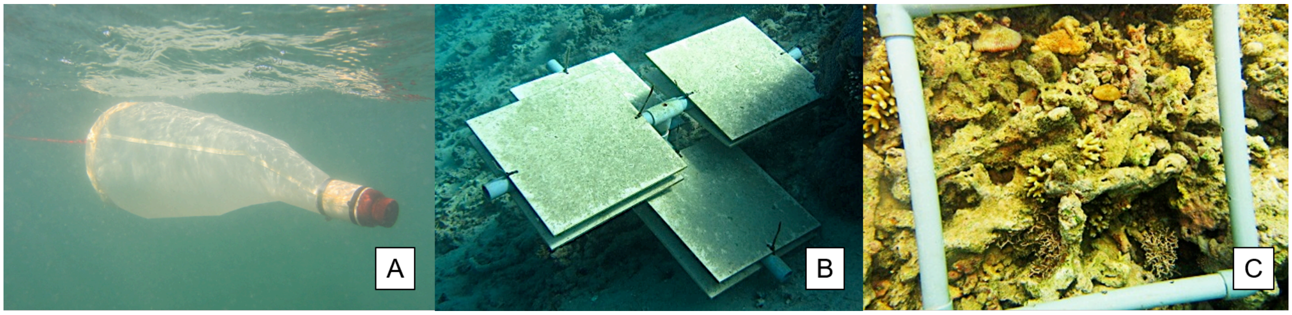

Figure 2. Equipment used for planula, recruit and juvenile sampling: A. 63 µm mesh plankton net with a 25 cm diameter mouth; B. Recruitment tiles setup on PVC cross-system, each tile measuring 30 cm x 30 cm; C. Recruitment quadrat of 25 cm x 25 cm.

between 6 am and 8 am, successively for the 3 sites. A 63 µm mesh plankton net was used with a 25 cm diameter mouth that was dragged by a small boat (7 m long) for 15 minutes, covering a distance of approximately 900 m. For each sample, the volume of filtered seawater was 44 m^3. Samples were filtered to separate the plankton of different sizes using sieves (63 µm, 80 µm, 100 µm and 250 µm). The filtration aimed at facilitating observation and counting of larvae within the sampled zooplankton. Eight replicates of 50 µl for each sieve size and each site were observed and coral larvae were identified and counted using an Euromex Oxion photonic microscope.

Recruitment survey

A total of 144 ceramic tiles measuring 30 cm x 30 cm (48 per site) were immersed to estimate the distribution of newly settled recruits. The tiles were installed in July 2013 over a total surface area of 4.32 m^2 at each site. About 3 months of conditioning are needed to allow the substratum to become suitable for settlement (Erwin *et al.,* 2008; Massé, 2014). Therefore, the one-year experiment started in October 2013 until September 2014. Four conditioned tiles were collected per site per month. The tiles were fixed horizontally, unglazed face down on a Polyvinyl chloride (PVC) cross-system (Fig. 2) after pre-research experiments that revealed the resistance of the system against waves and other conditions at the sites. Each system was fixed to the substrate with an iron rod treated with antirust, which was planted into the substrate.

In addition, *in situ* observation was performed to estimate coral juveniles at two of the three sites (Nosy Tafara and Grande Vasque). The survey was performed in September and October 2013 at Nosy Tafara, while at Grande Vasque it was performed in January 2014. Juveniles were not recorded at Rose Garden as it was considered a monospecific site with a dominance of *Montipora* species. Juveniles observable *in situ* are colonies of <5cm size, which are typically aged at least 1 year (Adjeroud *et al.*, 2016). The method described below provided a reliable estimation of future coral species assemblages and allowed estimation of the post-settlement rates of mortality that are often very high during the first weeks following the settlement, mainly due to predation, competition, sedimentation and stress (Adjeroud *et al.*, 2016). The recruitment quadrat method of Atlantic and Gulf Rapid Reef Assessment (AGRRA) (Hill and Wilkinson, 2004) was used and adapted for the characteristics of the studied sites. The length of the 50 x 2 meters transect was swum, and the 25 cm x 25 cm quadrats were placed on the substratum in areas lacking large (> 25 cm diameter) sessile invertebrates. Eighty quadrats per site were observed. All small scleractinians were counted (two classes: early juveniles with < 2 cm diameter and older juveniles with 2 cm < diameter < 5 cm) within the quadrats separated into four groups (Acroporidae, Pocilloporidae, Fungidae and "others"), grouping the families that were not reliably distinguishable during *in situ* observations.

Identification method

Once in the laboratory, each newly settled recruit was photographed directly on the tiles using a trinocular stereoscopic Novex microscope (Euromex microscopes). Based on the morphology of the first skeleton, recruits were identified to the level of the 3 distinguishable families of Acroporidae, Pocilloporidae and Poritidae using the scleractinian recruit identification key proposed by Babcock *et al.* (2003) and summarised in Table 1, and the unidentified recruits grouped as "others". In addition, recruits were classified by age: less than a month and more than a month, on the basis of the same criteria developed by Babcock *et al*. (2003). This allowed the recruitment rate per month to be assessed, which is difficult to perform with most of the recruitment counting methods considering the conditioning period of tiles (Erwin *et al.*, 2008; Massé, 2014). The morphological

Table 1. Summary of the morphological description of early stage recruits for 3 distinguishable families (after Babcock *et al*., 2003).

	Acroporidae	*Pocilloporidae*	*Poritidae*
0-1 month	Basal plate,	Basal plate,	Basal plate,
	12 basal ridges in a single cycle,	Corallite wall formed through the growth and fusion of lateral outgrowths of the basal ridges,	Epitheca,
	Corallum grown by extension of the basal plate,	After 1 week: solid coenosteum,	6 primary septa thickened,
	Lateral processes evident on the inner end of basal ridges,		Prominent vertical toot
	Prominent laminar septa in 2 cycles,		
	A porous coenusteum,		
	Absence of columella,		
	Secondary corallites appeared within 3 weeks		
>1 month	Secondary corallites developed	Solid coenosteum	Corallite beyond the epitheca,
	Mound and small juvenile had yet to develop adult colony morphology	Prominent septa	Primary septa grown
		Prominent columella, Secondary corallites developed	2nd cycle of septa originated at the perimeter of the basal plate,
			Fusion of the secondary and the primary septa to form 4 pairs of laterals and a triplet leaving the directive independent
			Epitheca still visible within corallite,
			Presence of 2 corallites,
			Epitheca no longer visible,
			10 to 12 corallites.

characteristics of the observed early stages of corals are presented in the supplementary material.

Statistical analysis

All the statistical analyses were performed using the R software (R Core Team, 2017). Descriptive statistics were calculated first. For physicochemical parameters, the annual mean, the mean per season and mean per site, as well as the minimum and maximum values were calculated. For planula, recruits and juvenile records, annual and/or monthly mean density were calculated per site. Normality of the data was determined using a Shapiro-Wallis test and homogeneity of the variance was calculated using Levene's test. The significance (or not) of the difference in means was determined using ANOVA, the t-test or the Kruskal-Wallis test (KW), and the Nemenyi test, at a level of 5 %.

Results

Physicochemical parameters of the water

The water temperature varied from 17.8 °C during the dry-cold season to 32.4 °C during the wet-warm season. The highest temperature was recorded in January and February while the lowest occurred in July and

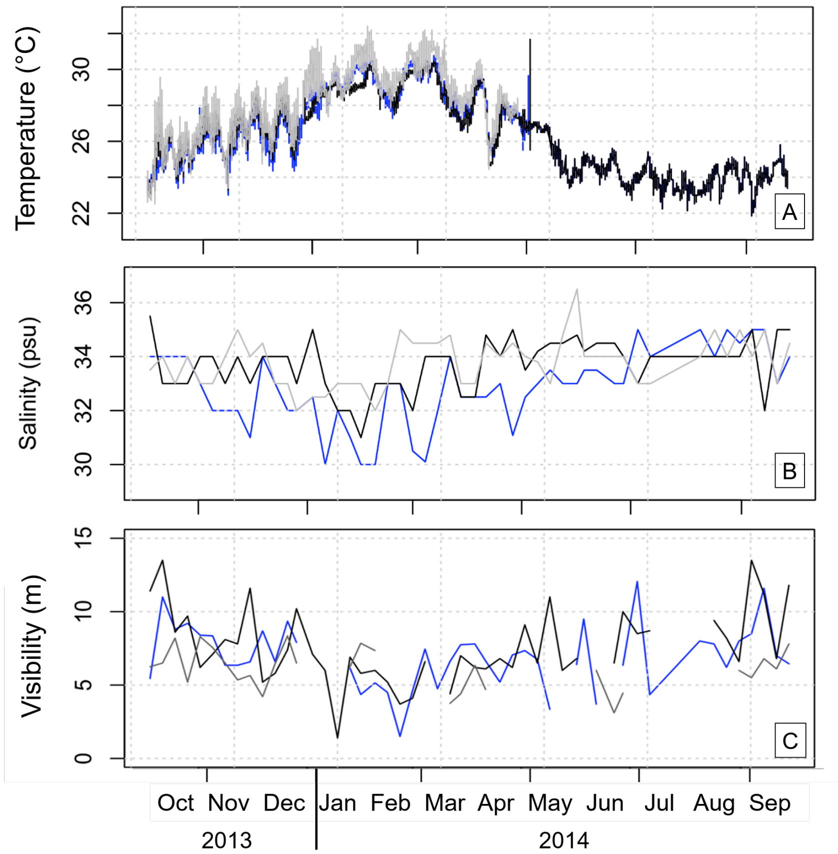

Figure 3. Variation of temperature, salinity and visibility (Secchi depth, in meter) in the water at the studied sites. A. Temperature at the bottom; B. Salinity; C. Weekly variation in visibility. Blue line: Nosy Tafara; Black line: Grande Vasque; Grey line: Rose Garden.

August (Fig. 3A). The mean annual temperature was 25.5 ± 2.3 °C. The mean temperature was significantly lower during the dry-cold season at 24.7 ± 1.3 °C compared to wet-warm season at 27.9 ± 1.6 °C (ANOVA, $p<0.001$). No significant difference in temperature was observed between the 3 sites (ANOVA, $p=0.793$).

The salinity varied from 30 psu to 36.5 psu with an average of 33 ± 1.3 psu in the wet-warm season and 34±0.8 psu in the dry-cold season. The salinity was significantly higher during the dry-cold season (ANOVA, $p<0.001$). The mean annual salinity was 33.4 ± 1.2 psu. The mean annual salinity was significantly lower at Nosy Tafara compared to the other sites (ANOVA, $p<0.001$) with 32.8 ± 1.4 psu at Nosy Tafara, and 33.7 ± 1 psu and 33.8 ± 0.9 psu respectively at Grande Vasque and Rose Garden. The lowest salinity occurred in the wet-warm season (Fig. 3B).

The water visibility varied from 1.4 m (lowest during wet-warm season) to 13.5 m (highest during dry-cold season). Results showed that the visibility was significantly lower

Table 2. Annual occurrence and density of planula (larvae m-3). Dark grey shading corresponds to occurrence but where the number could not be counted due to very low density. Cases filled with the light grey shading correspond to weeks where sampling could not occur due to bad weather or where samples were not usable.

	October 2013	November 2013	December 2013	January 2014	February 2014	March 2014	April 2014	May 2014	June 2014	July 2014	August 2014	September 2014
Nosy Tafara		13.4			0.37		0.26	0.34				1.80
Grande Vasque		0.43			0.24		0.02	0.34				1.10
Rose Garden		1.30										

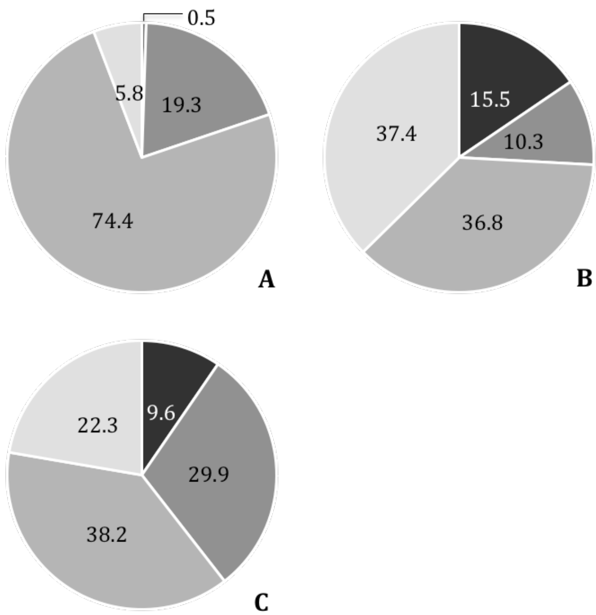

Figure 4. Dominance (%) of recruit families (all ages combined). A. Nosy Tafara, B. Grande Vasque, C. Rose Garden. Colours represent families. Black: Acroporidae; Dark Grey: Pocilloporidae; Grey: Poritidae; Light Grey: Others.

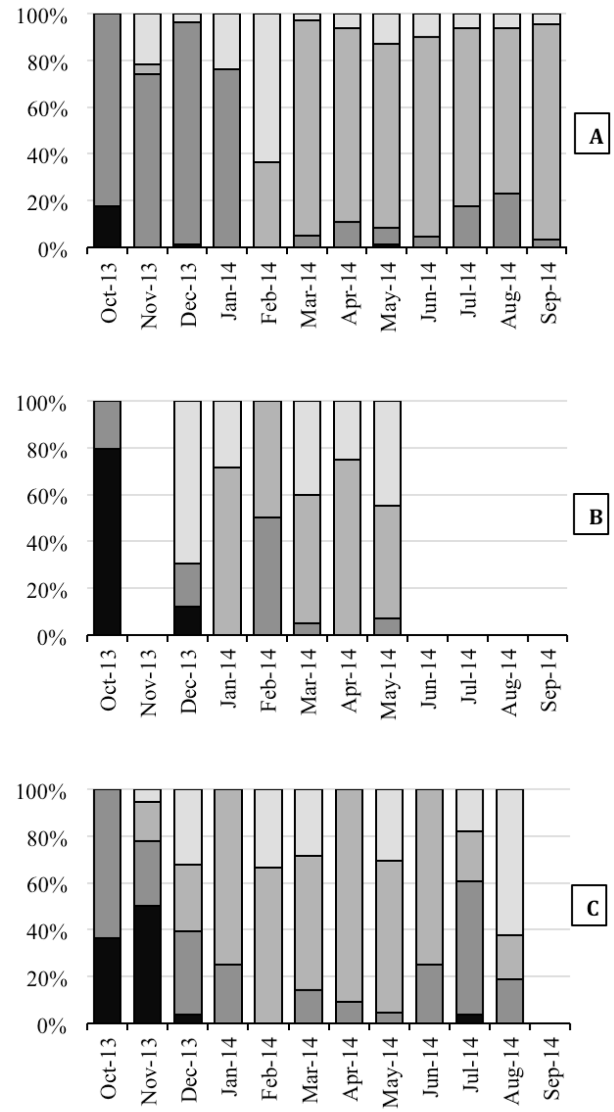

Figure 5. Dominance (%) of recruit families per month (all ages combined). A. Nosy Tafara, B. Grande Vasque, C. Rose Garden. Colours represent families. Black: Acroporidae; Dark Grey: Pocilloporidae; Grey: Poritidae; Light Grey: Others

during the wet-warm season (6.3 ± 1.6 m) compared to the dry-cold season (7.6 ± 2.2 m) (ANOVA, $p<0.001$). The highest values of water visibility were observed from September to December, during which it reached > 8 m (Fig. 3C). The highest mean annual visibility was observed at Grande Vasque (7.6 ± 2.5 m) and the lowest at Rose Garden (6.3 ± 1.2 m) with a significant difference observed between sites (Tukey, $p=0.002$). The visibility observed on Nosy Tafara was not significantly different from the 2 other sites (Tukey, $p>0.1$).

Planula records

The variability in the occurrence of planula is very high and implied that the density observed in the year does not present a significant difference between the sites (Kruskal-Wallis, $p=0.33$). The maximum occurrence of planula was during 9 months of the year, from August to December and from February to May. Planula occurred most often at Nosy Tafara (9 months) compared to Grande Vasque and Rose Garden where planula were observed in 8 and 3 months of the year, respectively. During 7 weeks between December and February, samples were not useable due to the high levels of non-biological material in suspension, or because sampling was interrupted due to bad weather (Table 2). For the rest of the year, samples from successive weeks with the occurrence of planula were mixed to maximize the efficiency of larval observation. The highest density of planula was observed in the last week of November and the first week of December (Table 2). Nosy Tafara presented a relative higher mean annual density of planula (3.23 ± 5.72 larvae m^{-3}) compared to the other sites, with 0.43 ± 0.41 larvae m^{-3} and 0.65 ± 0.92 larvae m^{-3} for Grande Vasque and Rose Garden, respectively.

Recruit records

Total recruitment

The first recruits were observed in October 2013. Observation from 20 tiles out of 144 were not taken into account due to *in situ* breakages, lowering the reliability of the obtained results. A total of 3010 recruits were observed from all the sites: 2679, 174 and 157 recruits were identified respectively on 48 tiles from

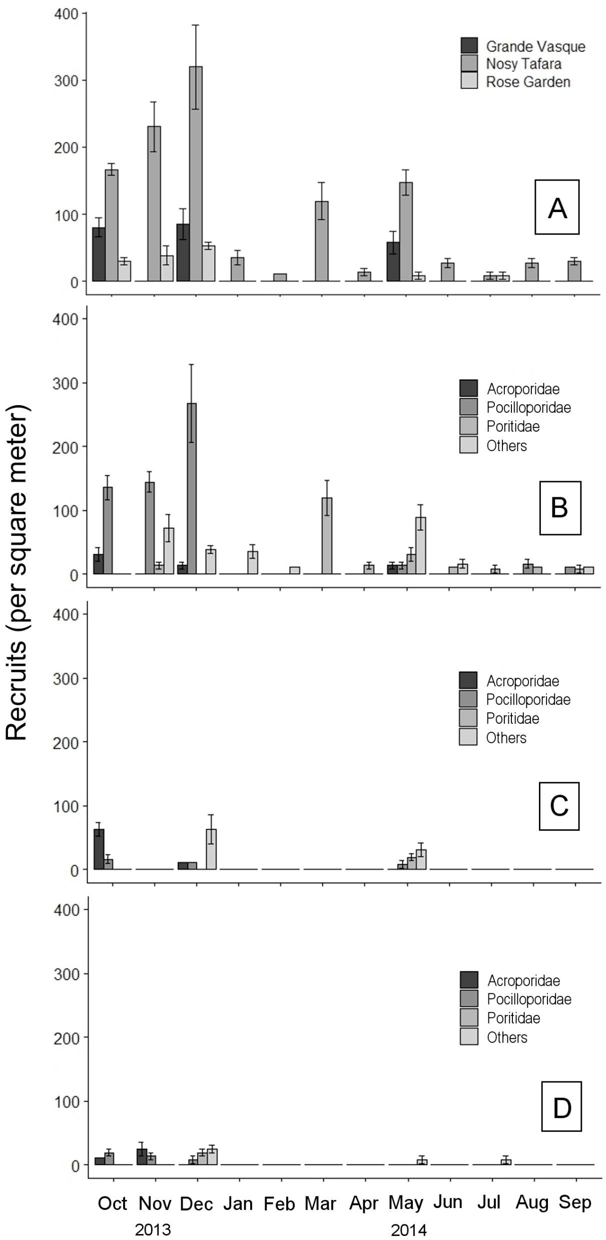

Figure 6. Average density of recruits per site per month (A), and monthly distribution of recruit families. (B) Nosy Tafara; (C) Grande Vasque; (D) Rose Garden. The bars represent standard deviation.

Nosy Tafara, on 32 tiles from Grande Vasque and 44 tiles from Rose Garden. The number of recruits per tile varied from 0 (Grande Vasque in November 2013) to 218 (Nosy Tafara in August 2014). The mean density of total coral recruits was significantly higher at Nosy Tafara compared to Grande Vasque and Rose Garden, with 620.13 ± 621.30 recruits m^{-2}, 40.28 ± 50.97 recruits m^{-2} and 36.34 ± 33.82 recruits m^{-2} (KW, $p<0.001$), respectively. The Post hoc Nemenyi test confirmed a significant difference between Nosy Tafara and Grande Vasque ($p<0.001$) and between Nosy Tafara and Rose Garden ($p<0.001$), and no difference between Grande Vasque and Rose Garden ($p=0.88$).

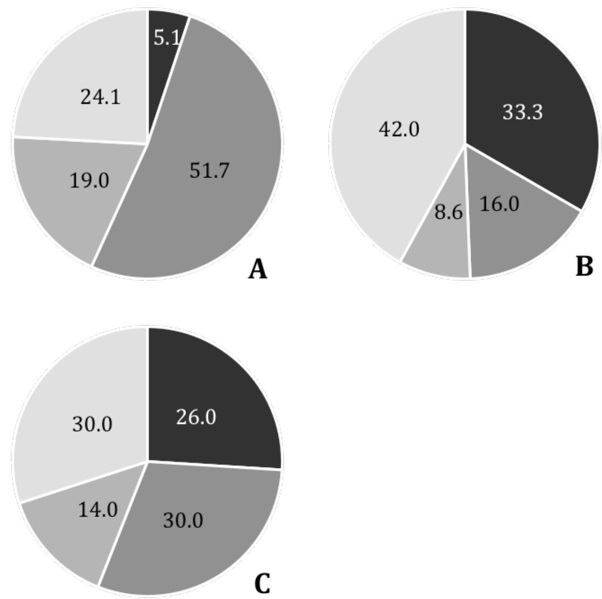

Figure 7. Dominance (%) of recruit families (age < 1 month). A. Nosy Tafara, B. Grande Vasque, C. Rose Garden. Colours represent families. Black: Acroporidae; Dark Grey: Pocilloporidae; Grey: Poritidae; Light Grey: Others.

During the year, the overall recruitment rate (all ages included) was significantly dominated by Poritidae species that represented 49.8 % of the total recruits from all the sites. The site at Nosy Tafara presented the most important dominance of Poritidae with 74.4 % of the total recruits observed on the tiles (Fig. 4A), followed by Pocilloporidae with 19.3% of the total recruits. Acroporidae species are poorly represented at this site (0.5 %, Fig. 4A). At Grande Vasque and Rose Garden, Poritidae represented 36.8 % and 38.2 %, Pocilloporidae 10.3 % and 29.9 %, and Acroporidae 15.5 % and 9.6 %, respectively (Fig. 4). Monthly observation showed that at Nosy Tafara, the Pocilloporidae species represented more than 75 % of the composition of the recruits from October 2013 to January 2014 (Fig. 5A). Four months after immersion of the tiles, from February, recruitment is dominated by Poritidae species. At the site Grande Vasque and Rose Garden, no obvious dominance of any family was observed from October to December, but Poritidae also represented more than 50 % of the composition of the recruits from January at both sites (Fig. 5B and 5C).

Seasonal distribution of newly settled corals

Seasonal distribution of coral recruitment was different between the sites (KW, $p<0.001$). Newly settled corals (<1 month age) were observed at Nosy Tafara every month during the survey, while they were observed

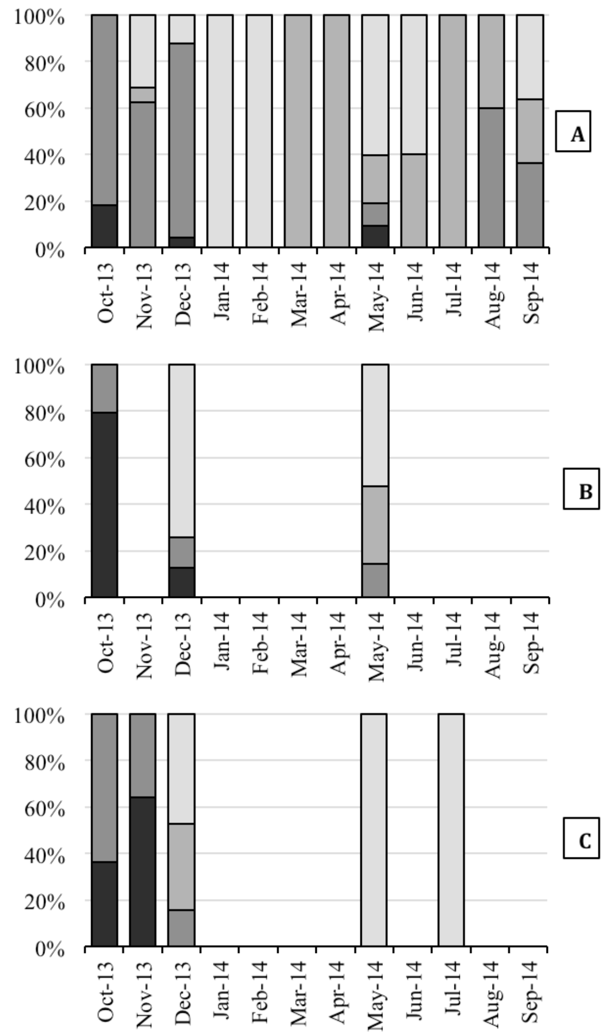

Figure 8. Dominance (%) of recruit families per month (age < 1 month). A. Nosy Tafara, B. Grande Vasque, C. Rose Garden. Colours represent families. Black: Acroporidae; Dark Grey: Pocilloporidae; Grey: Poritidae; Light Grey: Others.

only during 3 months at Grande Vasque and during 5 months at Rose Garden (Fig. 6). The annual mean density of newly settled recruits was significantly higher at Nosy Tafara with 94.91±101.08 recruits m^{-2} compared to Grande Vasque and Rose Garden with 18.75±34.32 recruits m^{-2} and 11.57±18.47 recruits m^{-2}, respectively (Nemenyi test, $p<0.001$). The two last sites presented no significant difference between them (Nemenyi test, $p=0.98$). The highest density of newly settled recruits was observed for all the sites during the period of October to December (Fig. 6A). Higher density of recruits was also observed in March at Nosy Tafara and in May at all three sites.

The newly settled coral recruitment rate at Nosy Tafara is dominated by Pocilloporidae species that represented 51.7 % of the total newly settled recruits (Fig. 7A). A peak of Pocilloporidae recruits was observed in December, but high rates were also recorded in October and November (Fig. 8A). Recruits belonging to the family Poritidae were also abundant at this site with a peak observed in March (Fig. 8B). Recruits of the other families were distributed with approximately the same values. At Grande Vasque, recruits of Acroporidae were the most dominant, representing 33.3 % of the total recruitment rate with a peak recorded in October (Fig. 8C), followed by the Pocilloporidae that represented 16 %. At Rose Garden, a dominance of Pocilloporidae recruits (30 %) compared to Acroporidae (26 %) and Poritidae (14 %) was recorded in December. The newly settled recruits recorded in May and July were all unidentified (Fig. 8C).

Records of coral juveniles

The mean density of early coral juveniles (< 2 cm) at Nosy Tafara was significantly higher with 105 ± 61.7 juveniles m^{-2}, compared to Grande Vasque with 52.8 ± 34.1 juveniles m^{-2} (KW, $p<0.001$). The mean density of older juveniles (2 – 5 cm diameter) was 47 ± 47 juveniles m^{-2} at Nosy Tafara and 32.4 ± 19.1 juveniles m^{-2} at Grande Vasque. No significant difference was observed (KW, $p=0.352$).

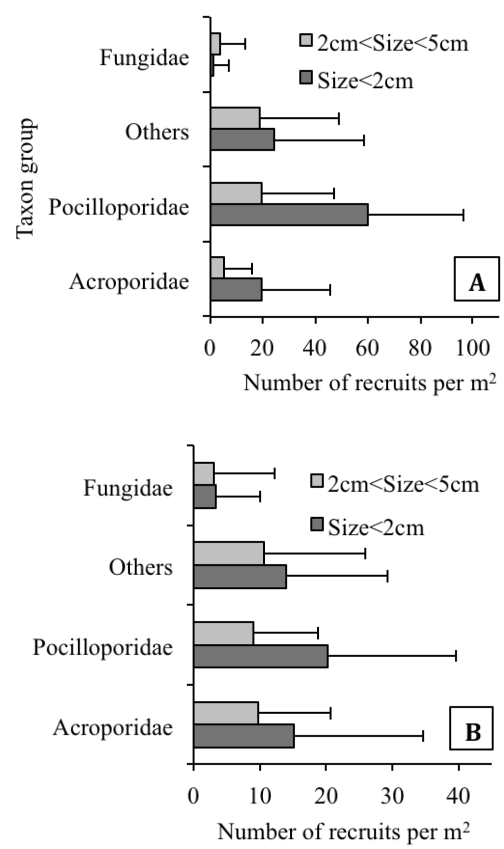

Figure 9. Density of coral juveniles recorded at Nosy Tafara (A) and Grande Vasque (B).

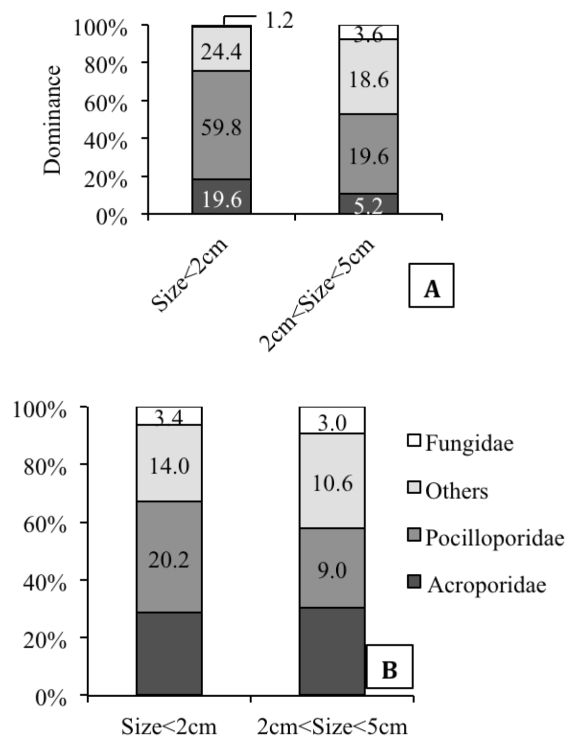

Figure 10. Dominance of juvenile families. A. Nosy Tafara; B. Grande Vasque.

Records from Nosy Tafara and Grande Vasque showed that Pocilloporidae early juveniles dominated the recorded juveniles with 57 % and 38.3 % of the total abundance, respectively. The density of Pocilloporidae older juveniles was lower with 41.7 % at Nosy Tafara and only 27.8 % at Grande Vasque (Fig. 9). At both sites, juveniles of Pocilloporidae and Acroporidae dominated more than the half of the total rate (Fig. 10).

Estimation of post-settlement mortalities

The results showed that the recruits had higher mortality than early juveniles. The density of early juveniles (< 2 cm) represented 74 % of the density of recruits and the density of older juveniles (2 – 5 cm diameter) represented 53.1 % of the density of early juveniles. The density of older juveniles represented 44 % of the density of recruits, with a lower value for Nosy Tafara (7.6 %) compared to Grande Vasque (80.4 %).

Discussion

The present study reports on the first records and analysis of recruitment and early development of corals in Madagascar. It covers a period of one year and includes larval observation records and cover estimations of coral recruits and juveniles. To date, the only record of coral spawning in Madagascar indicates a spawning event that occurred on the 9th and 24th September 2015 on the coral reefs of Andavadoake located 50 km from the northern coral reefs studied in the present work (Gress *et al.*, 2015). The spawning happened 4 to 6 nights after the new and the full moon and concerned only *Acropora* species. In the present paper, the observation of high planula densities in the last week of November and the first week of December combined with the increasing densities of recruits from October to December suggests the occurrence of massive coral spawning during this period of the year. Also, the extended presence of planula and recruits during February, March, April and August indicates that punctual spawning occurs regularly. This phenomenon is not an isolated case but has been observed in several regions where scleractinian reproduction and spawning occurred over several months of the year with mass spawning following the full moons from September to March (e.g., Guest *et al.,* 2002; Carroll *et al*., 2006; Rosser and Baird, 2008; Massé, 2014). Recently, Terrana and Eeckhaut (2019) observed male and female gametes of the antipatharian species *Cirrhipathes anguina* in Toliara, throughout the year, suggesting a massive spawning event and irregular minor spawning events that may occur during the rest of the year. The phenomenon seems to be common to the Hexacorallia taxon.

The peaks of recruitment recorded from October to December in SW Madagascar correlated with planula observed during the same period. Knowing that planula can survive several weeks before settlement (Baird *et al*., 2012), the observed newly settled recruits may result from spawning that occurred from September. The weak recruitment in January and February suggests the end of massive spawning in December. A difference of recruit and juvenile records between the sites, notably between Nosy Tafara and the two other sites, Grande Vasque and Rose Garden was also observed. Nosy Tafara showed a higher recruitment rate which occurs during each month of the year. At Grande Vasque and Rose Garden, the highest recruitment rate was observed from October to November and was followed by a lower recruitment rate in May (Grande Vasque) to July (Rose Garden). The Nosy Tafara site is more exposed to the open sea compared to Grande Vasque (being a basin in a reef flat) and to Rose Garden (a patch reef in a protected lagoon).

The recruitment rates recorded in Madagascar are comparable to recruitment rates observed in the tropical Pacific reefs (Hughes *et al.,* 1999) and most of the Indo-Pacific countries, including in the WIO such as in La Réunion island and South Africa (Massé, 2014), where the recruitment rates do not exceed 100 recruits m^{-2} $year^{-1}$ (Adjeroud *et al.,* 2007). However, differences between the methods and materials used (tile surface, depth and tile nature) may lead to error in estimating and comparing results of research from different regions. These differences should be analysed by performing recruitment monitoring with all the methods used and comparing the results from the same site and same period. The observed recruitment rates of juveniles at each site were classified as very high compared to the theoretical assessment scale of the scleractinian recruitment rates proposed by Engelhardt (2003). This theoretical scale considers the recruitment rate as very high if the absolute abundance of branching corals (Acroporidae and Pocilloporidae) of 2 – 5 cm size is > 10 juveniles m^{-2}.

The temperature and visibility of the water at the three sites are not significantly different. Salinity in Nosy Tafara is lower than in Grande Vasque and Rose Garden. This might be due to the proximity of the Onilahy River a few kilometres from Nosy Tafara. In Madagascar, the period from September to December corresponds to the transition between the dry-cold season and wet-warm season, during which the water temperature slowly rises to reach the highest values in January and February. During the same period, the light irradiance is at its highest level. Solar light cycles are amongst the main conditions that determine coral spawning (Brady *et al.,* 2009) and the abundance of coral recruitment. The period from January to February 2014 was particularly rainy and strong influences of tropical cyclones were noticed at the sites affecting the salinity and the water visibility. The second period of larval occurrence and recruits recorded (March – May) corresponds to the transition between the wet-warm season and the dry-cold season during which the water temperature was decreasing. Water currents are also known to be one of the main dispersal agents for planula (Adjeroud *et al*., 2016). The high density of larvae and the higher recruitment rate recorded at Nosy Tafara may be explained by the water current regime. The existence of the Southwest Madagascar Coastal Current (SMACC) running along the SW coast of the island may explain the high level of coral recruitment in this area (Ramanantsoa *et al.*, 2018). These authors reported that the SMACC is likely to influence local fisheries and larval transport patterns. Terrana *et al.* (2021) hypothesized after genetical connectivity analysis, that this current influences the settlement the black coral species *Stichopathes cf. maldivensis*, which has a high occurrence in the area compared to other locations in the SW of Madagascar. The high density of coral larvae and high rate of settlement observed at this site may originate from local spawning but also from spawning of corals located to the north of the region.

The post-settlement processes are one of the important keys to characterize the dynamics and resilience of coral reef assemblages. Results presented in the present paper show an important post-settlement mortality, but the abundance of juvenile that survived still represents a higher rate compared to other regions (Wending, 2003; Adjeroud *et al*., 2007). The earlier the coral stage, the higher the mortality, and the major sources of high mortality of early recruits are unsuitable environmental conditions, competition, and predation (Adjeroud *et al*., 2016). Environmental conditions are strongly influenced by the seasons and sedimentation at the studied sites. During the rainy season, upstream factors such as river flow particularly increase and result in erosion of the soils from the watershed of Fiherenana (Payet *et al*., 2011) and of Onilahy (Rakotondralambo, 2008). Sheridan *et al.* (2014a, 2014b) reported that sedimentation induces coral disease and mortality on coral reefs in the SW of Madagascar. In addition, anthropogenic pressures due to destructive fishing techniques (Mahafina, 2011; Bruggemann *et al.,* 2012; Andréfouët *et al.,* 2013) are particularly high on the studied coral reefs where coral trampling is practiced (Salimo, 1997). Competition with algal assemblages is also important, especially on the degraded reef flat (Harris *et al.*, 2010, Bruggemann *et al*., 2012).

In conclusion, the coral recruitment patterns observed in the SW of Madagascar could result in increased resilience of the coral reef assemblages, although several post-settlement factors may induce important mortality of coral recruits and juveniles. Further studies should be performed to identify the main causes of this mortality and the implications for coral recruitment.

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Appendix

Morphological characteristics of the observed early stages of corals.

Most of the early stages of the coral life-cycle have been observed during the present study. Figure 1 presents the stages observed from the 3 stations: (A) a ciliated planula showing endoderm with dense endosymbionts (end), an epidermis that lacks symbionts (ect), the blastopore (blast) and the cilia (cil); (B) newly settled recruit (see description on Fig. 3); (C) early juvenile of *Pocillopora*; and (D) older juveniles of *Acropora* (Acr) and *Stylophora* (Sty).

The morphological characteristics could be differentiated for the newly settled recruits of the families Acroporidae, Pocilloporidae and Poritidae (Fig. 2). Each observed recruit has also been grouped into 2 age categories: <1 month and 1 month to 12 months with the criteria described by Babcock *et al.* (2003) as a reference. The characteristics specific to the Acroporidae family have been noted. The basal plate, septa in 2 cycles, the porous coenosteum and especially the absence of columella are clearly observed on <1 month recruits (Fig. 2A). From 1 month age, secondary corallites are developed (Fig. 2B). For the Pocilloporidae of <1 month recruits, the basal plate and prominent septa are also clearly apparent (Fig. 2C). The solid coenosteum and the prominent columella permit this family to be distinquished. >1 month Pocilloporidae recruits have developed secondary corallites, each with prominent columella (Fig. 2D). The coral family Poritidae presents epitheca and 6 thickened primary septa and prominent vertical toot few days after settlement (Fig. 2E). The main characteristic of the Poritidae recruits after a few weeks is the development of the corallite beyond the epitheca, which remain visible within corallite after the secondary and primary septa fusion (Fig. 2F).

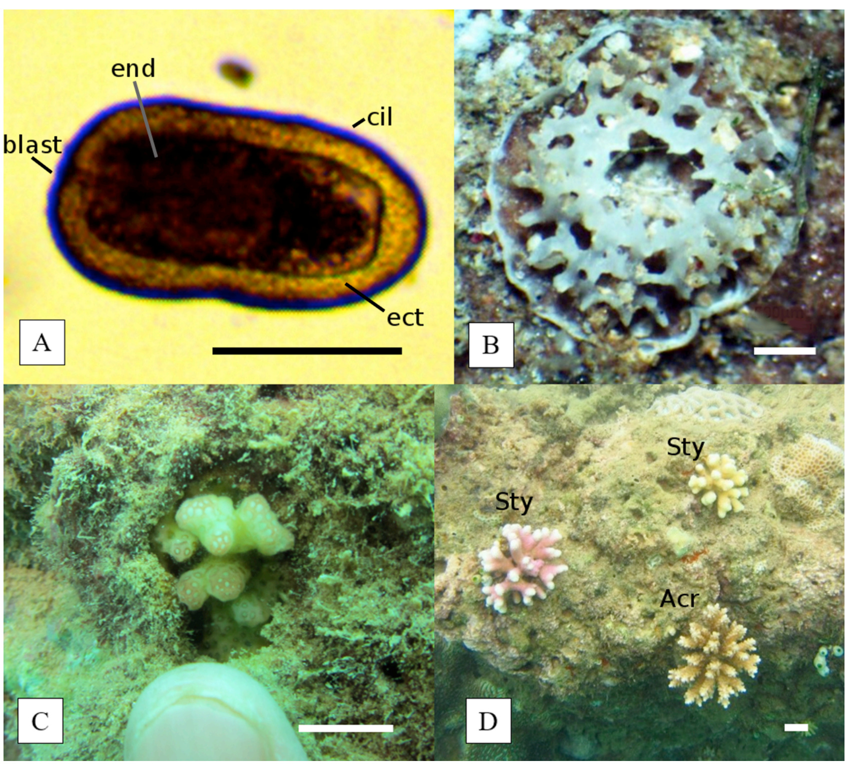

Figure 1. Photographs of scleractinian at the different development stages: A. planula; B. Recruit (Acroporidae); C. Early juvenile of *Pocillopora* (< 2 cm); D. Juveniles of *Acropora* and *Stylophora* (2 – 5 cm). A, B and D were sampled from Nosy Tafara and C from Grande Vasque. Scale bar: A and B = 500 µm; C and D = 1 cm.

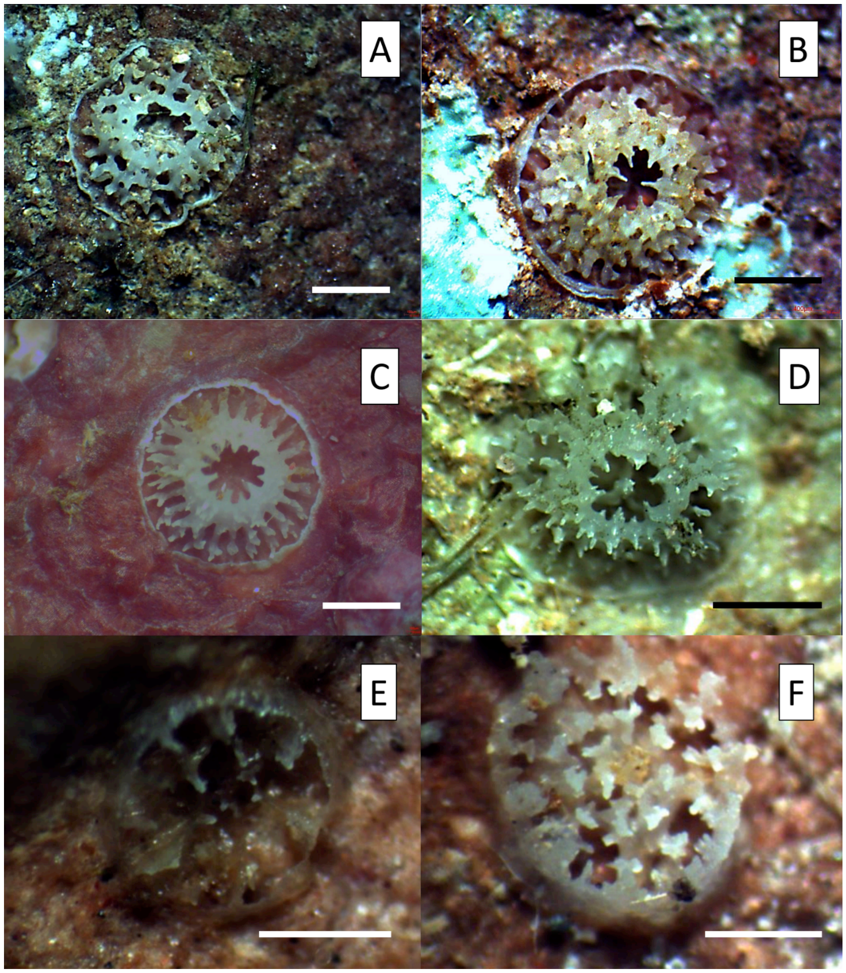

Figure 2. Recruits of the families Acroporidae (A: <1 month, B: >1 month), Pocilloporidae (C: <1 month, D: >1 month) and Poritidae (E: <1 month, F: >1 month). Scale bar: 500 µm.