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The short-term impacts of a cyclone on seagrass communities in Southwest Madagascar

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ABSTRACT

Cyclones are large-scale disturbances with highly destructive potential in coastal ecosystems. On February 22, 2013, a powerful tropical cyclone made landfall on the southwest coast of Madagascar, a region which is infrequently hit by such extreme weather events coming from the Mozambique Channel. Seagrass ecosystems, which provide valuable ecosystems services to local communities, are especially vulnerable because they thrive in shallow waters. The impact of Cyclone Haruna on seagrass diversity, height and coverage and associated fish diversity, abundance and biomass was assessed in 3 sites near Andavadoaka (22°07′S, 43°23′E) before and after the event using fish underwater visual census, video-transects, and seagrass quadrats. The cyclone caused a significant loss in seagrass cover at all 3 sites. *Thalassia hemprichii* and *Syringodium isoetifolium* were the most affected species. Andavadoaka beach, the most exposed site, which was also subject to human use and was most fragmented, suffered the largest negative effects of the cyclone. Cyclone Haruna was not found to significantly affect fish assemblages, which are highly mobile organisms able to use a diversity of niches and adjacent habitats after seagrass fragmentation. Extensive sampling and longer time-scale studies would be needed to fully evaluate the cyclone impact on communities of seagrass and fish, and track potential recovery in seagrass coverage. The intensity and destructive potential of cyclones is expected to increase with global warming, which is of concern for developing countries that encompass most of the world's seagrass beds. This study provided a unique and key opportunity to monitor immediate impacts of an extreme disturbance in a region where cyclones rarely hit coastal ecosystems and where local populations remain highly dependent on seagrass meadows.

1. Introduction

Madagascar is extremely vulnerable to cyclones, tropical storms and floods. While cyclones are particularly common on the northeast and east coasts, the southwest coast is much less affected, as the deviation or formation of cyclones in the Mozambique channel is relatively rare, with 94 tropical cyclones recorded from 1948 to 2010 (Matyas, 2015). Intense storms and cyclones hitting this region cause large increases in expected rainfall, as well as other major damage caused by exceptionally strong winds. Besides destruction and tragic loss of human life, these remarkable weather events can also dramatically impact coastal systems, especially seagrass meadows. As coastal ecosystems are of prime importance for Malagasy subsistence fishing communities, strong cyclones are likely to both negatively effect the marine environment, and impact food security.

Tropical Cyclone Haruna made landfall on the southwest coast of Madagascar on February 22, 2013 and was the first full strength cyclone to hit the southwest region since Cyclones Fanele in 2009 and Angele in 1978. Other cyclones made landfall occasionally in the region, such as Boloetse in 2006, but none were as powerful and destructive. Before hitting the coast, Haruna stayed 7 days in the Mozambique Channel before forming a tropical cyclone category 3 (Australian scale) that hit the coast as a powerful category 2 cyclone, with its center near Manombo (NASA, 2013), 50 km north of the regional capital of Toliara. On February 21, when Haruna approached the coast but was still in the Mozambique channel, maximum sustained winds were of 186 km h^{-1} with gusts of 210 km h^{-1}, generating waves of 7.6 m and a maximum storm surge of 0.8 m (GDACS, 2013; NASA, 2013). As a result of its interaction with land on February 22, the maximum winds dropped to 130 km h^{-1} as the cyclone moved southeast slowly at 12 km h^{-1} (NASA, 2013).

Coastal ecosystems such as seagrass meadows can be damaged by

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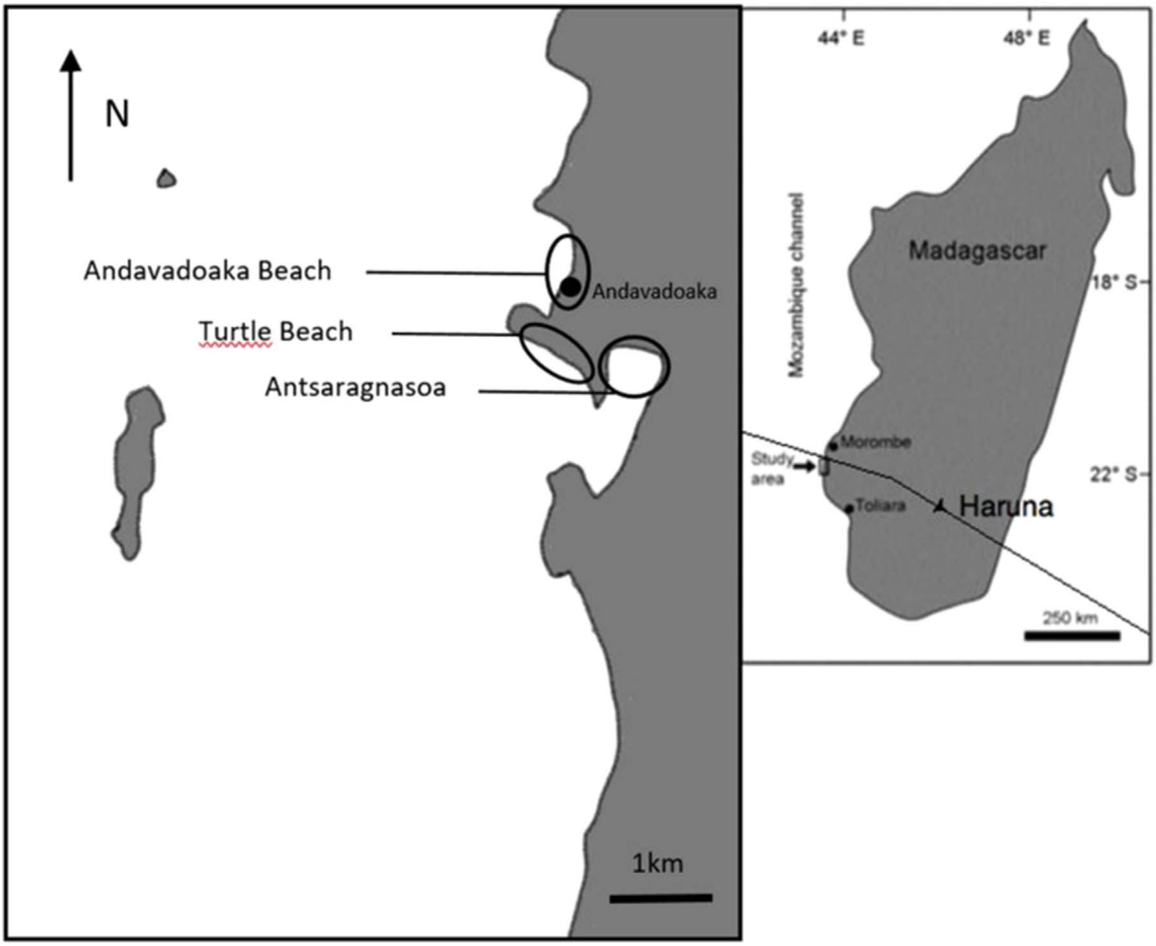

Fig. 1. Location of the 3 survey sites near the village of Andavadoaka, Southwest Madagascar (adapted from Nadon et al., 2005).

violent winds creating exceptional swell and waves that break on the coastline. The consequences of cyclones on seagrass communities are extremely difficult to monitor due to the unexpected nature and unpredictable occurrence of such events. Nevertheless, some authors have reported serious impacts of cyclones, typhoons or hurricanes on seagrass meadows (Preen et al., 1995; Heck et al., 1996), while others found small impacts (Tilmant et al., 1994; Fourqurean and Rutten, 2004; Byron and Heck, 2006) and recorded rapid recovery of seagrasses following cyclones (Birch and Birch, 1984). For example, Cyclone Sandy in the Gulf of Carpinteria, Australia, uprooted 70% of the seagrass bed with 12 m waves generated by 220 km h^{-1} winds (Poiner et al., 1989). However, extreme weather events do not always have negative impacts, such as category 4 Hurricane Andrew that passed over South Florida in 1992, with negligible impacts on seagrasses despite its intensity (Tilmant et al., 1994).

Disturbances of seagrass beds may decrease canopy height and density by damaging plants, as well as uprooting seagrass in some parts of the bed, resulting in fragmentation of the meadow into smaller patches (Nakamura, 2010). After an intense storm or a cyclone, it is typical to find dead seagrasses piled up in extensive wrack lines along the shore (Eleuterius and Miller, 1976; Hemminga and Nieuwenhuize, 1990). Seagrass loss also results from smothering by sediments and light limitation due to increased turbidity from suspended sediments (Preen et al., 1995; Moncreiff et al., 1999; Wanless et al., 1988). If the disturbances are too intense or prolonged, seagrass fragments may keep decreasing into smaller units until they disappear completely (Horinouchi et al., 2009). This would be increasingly probable if a cyclone was passing over an already highly fragmented bed. However, the extent of the impact is itself highly variable even in a single region, and may cause substantial damage in several scattered beds whilst leaving others almost intact (Anton et al., 2009). Fragmentation and loss of seagrass beds may also negatively affect fishes and invertebrates (Pihl et al., 2006; Horinouchi et al., 2009; Nakamura, 2010). Any reduction in seagrass cover and the resulting increase in open bare sand habitats is generally believed to decrease overall marine species diversity and abundance, although it is suggested that fragmentation could possibly increase the number of micro-habitats, and thus increase diversity and abundance of some species (Horinouchi et al., 2009).

It is very important to monitor seagrass beds regularly to measure their present status, short and long-term trends and possible effects of disturbance on these ecosystems. Seagrasses fulfill crucial roles in coastal ecosystems, from essential habitat and nurseries for juvenile fish to nutrient cycling (Duarte, 2002; Short et al., 2011). They also indirectly and directly support artisanal fisheries and the subsistence livelihoods of millions of people living along the coast, mostly in tropical regions (Björk et al., 2008; Unsworth and Cullen, 2010). Local populations use seagrass meadows for harvesting invertebrates and fish for food, particularly when fishing further out at sea is impossible due to bad weather. The value of these ecosystem services has been estimated to be $1.9 billion per year (Waycott et al., 2009), greater than any terrestrial or other marine habitat (Short et al., 2011). However, their specific features confine them to coastal environments, where they are at risk from anthropogenic and natural disturbances. Globally, seagrasses are highly threatened, with an annual rate of decline of 7% since 1990 (Waycott et al., 2009).

Seagrass meadows in southwest Madagascar are believed to be relatively well protected, in part due to the Velondriake locally managed marine area (LMMA) of 823 km^2 that was created in 2006. Even though small-scale traditional fishing gears are still used, the combination of migration to the coast due to low agricultural productivity inland, high population birth rates and the introduction of seafood commercialization have increased pressures on local ecosystems (Harris, 2007). In addition, the tropical Indo-Pacific region is severely lacking in research targeted at seagrass (Short el al, 2011), even though they can show measurable and timely responses to impacts (Orth et al., 2006).

In this respect, very few studies have specifically assessed the short-term effects of cyclones on both seagrasses themselves and the associated fauna (i.e. seagrass communities) directly before and after extreme events. The main goal of this study was thus to investigate the short-term impacts of Cyclone Haruna on seagrass communities in this relatively well protected area of southwest Madagascar. It was hypothesized that a tropical cyclone such as Haruna would strongly affect seagrass (species diversity, canopy height, total and species-specific coverage), as well as seagrass-associated fishes (family and species diversity, abundance, biomass, size-class distribution, trophic category and location of fish in the seagrass patches).

2. Material and methods

2.1. Study area

The study area was located near the village of Andavadoaka (22°07′S, 43°23′E) on the southwest coast of Madagascar (Fig. 1). Andavadoaka is a remote fishing village in the Mozambique channel, lying 185 km north of the regional capital of Toliara and 50 km south of Morombe. The region supports extensive belts of tropical seagrass meadows (Hantanirina and Benbow, 2013) that are widely used by the local population living in close vicinity to the meadows. The village of Andavadoaka is the administrative center of the Velondriake LMMA, which is one of the largest community-based marine protected areas in the western Indian Ocean (Harris, 2007).

Three seagrass patches were identified around the village of Andavadoaka (Fig. 1). Andavadoaka Beach site was located directly in front of the village of Andavadoaka and was more exposed than the other two sites. This site was already fragmented and many coral patches were present. Turtle Beach was more sheltered and was the only site not facing a village. Antsaragnasoa is a protected semi-enclosed bay facing the small village of Antserananangy and adjacent to mangrove habitats to the south. This site was characterized by high turbidity and muddy sediments.

2.2. Experimental design and sampling procedure

The 3 sites (Fig. 1) were surveyed immediately before and after the landfall of Cyclone Haruna on February 22. The seagrass and fish surveys before Cyclone Haruna were performed from February 8 to February 13, ending 8 days before the cyclone hit the coast. The post-cyclone surveys were completed between February 28 and March 1st for the seagrasses (3 days after the cyclone passed), and from March 8–10 for the fish (12 days after the cyclone). Seagrass and fish surveys after the cyclone were spaced owing to the poor visibility, not allowing any fish visual census for more than 10 days after the cyclone. Seagrass surveys do not require particularly good visibility, and sites were re-surveyed as soon as possible after the cyclone to monitor the direct impacts of the storm on the plants.

Standard underwater visual census (UVC) and video-transects were used to monitor fish while snorkelling, and quadrats placed along the transects were used to record seagrass data. UVC is a standard method often used in studies to monitor fish abundance and density (Pelletier et al., 2011; Watson, 2005; Wartenberg, 2012). At each site, the size of the seagrass patch was first estimated visually from the beach. The surveyor then snorkelled to the beginning of the meadow at a random point perpendicular from the beach and counted 50 fin kicks parallel to the beach to ensure the starting position was not too close to the seagrass patch edge. Fin kicks were previously tested and found to average 1 m per frog fin kick. At this point, the surveyor stopped to record several parameters, including: time of day, compass heading direction, horizontal visibility (in meters), cloud cover (1–8), wind intensity (Beaufort scale 1–12), tidal state (always ebb), current and wave surge (classification: none, weak, strong), general sediment type (seagrass, sand patches, mud, etc.) and depth using a measuring tape (0–1 m, >1 m). The depths encountered during this survey never exceeded 2–3 m. After the completion of each individual transect, the snorkeler swam 50 m back to the end of the surveyed transect, and then another 50 m parallel to the beach to start the next transect. When 3 transects parallel to the beach were completed, the snorkeler swam 50 m perpendicularly to the next depth interval to carry out another set of 3 transects parallel to the beach, equidistantly spaced 50 m from each other. The depth intervals were approximately the same at each site, varying usually between 0.5 m (low tide) to a maximum 3 m (end of survey, rising tide). This sampling procedure was chosen to make sure that there was no overlap between transects. Five quadrats were monitored for each transect, for a total of 45 quadrats per site. In total 135 quadrats were surveyed before the cyclone, and the same number was observed after the cyclone.

A total of 54 fish transects of 100 m^2 were conducted, and a total of 270 seagrass quadrats were sampled over the 12 sampling days. Sampling usually occurred in the morning (between 7:00 and 13:00) to avoid high winds during the afternoon that could reduce visibility and the surveyor's ability to move around in the water. Sampling was always conducted at spring low tide to remove the possible effect of tide on the recorded parameters, and because it was easier to survey fish and seagrass at shallower depths given the average visibility conditions. The maximum tidal range during the surveys was 6.3 m and the minimum tidal range 4.2 m. The tidal table of Morombe (tides4-fishing.com) was used to estimate the ideal survey hours at low tide.

2.2.1. Seagrass surveys

The seagrass transects were surveyed directly after the fish transects (2.2.2) due to the mobile nature of fish. The snorkeler rolled the fish transect back and stopped every 10 m to record seagrass data. A 0.5 m×0.5 m (0.25 m^2) quadrat was placed with the lower left corner laid on the mark on the right side of the transect. All seagrass species present in the quadrat were noted, as well as the total percent cover and the percent cover of each species present. The total seagrass coverage was the sum of individual species percent covers (Short et al., 2002). The seagrass canopy height was also assessed using a measuring tape by randomly sampling a clump of the dominant seagrass (ignoring the tallest 20% leaves) in the quadrat and measuring them from the substrate to the leaf tip (Short et al., 2002). A photograph covering the 4 corners of the quadrat was also taken from at least one meter above the canopy.

2.2.2. Fish surveys

Nine transects were deployed at each site for a total of 27 fish transects pre-cyclone. Nine different transects were conducted in the same area, but at different locations, at each of the 3 sites after the cyclone had passed.

Following the recording of the physical parameters, the snorkeler waited 2–3 min to minimise fish disturbance. A 50 m transect, fixed at the start point with 2 dive weights and attached to the snorkeler's belt to deploy by itself, was then unrolled slowly as the snorkeler was swimming and surveying at a constant speed of approximately 0.2 m s^{-1} parallel to the beach. An underwater compass was used to keep the direction constant. While swimming, the surveyor filmed fishes using an underwater video Canon G12 set on high definition (HD) and underwater function.

The area observed over the 50 m transect was 2 m wide (1 m each

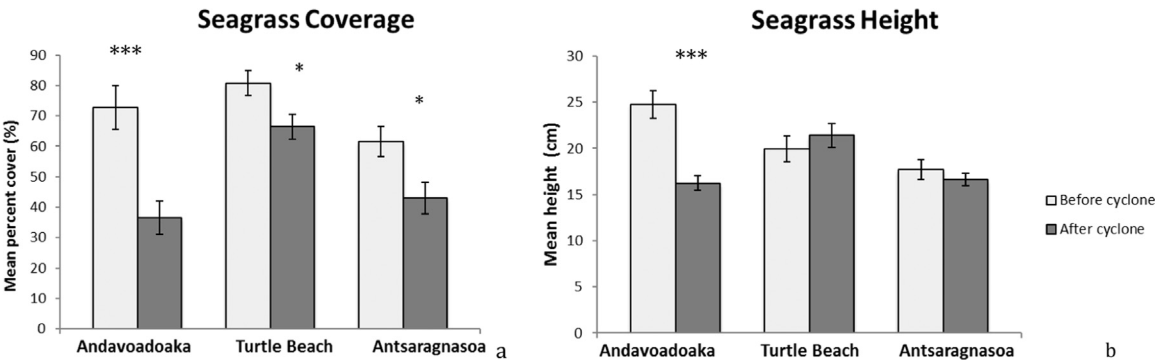

Fig. 2. Mean total seagrass percent cover (a) and mean canopy height per transect at each site before and after Cyclone Haruna (b). Standard errors are shown for each. Legend: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, (*) $p < 0.1$.

side of the transect and 1 m above). The 2 m width was selected due to visibility constraints and because only one snorkeler was able to survey the transects, increasing the accuracy and precision in such conditions. The survey was non-instantaneous, meaning that any individuals that entered the transect whilst the survey was conducted were also included in the census (Jind, 2012). The larger active and mobile fishes were counted first because of their tendency to leave the area quickly (Samoilys and Carlos, 2000; Bozec et al., 2011), while cryptic benthic species were recorded posteriorly by manually agitating the canopy. The snorkeler remained close to the bottom at all times. When the visibility was poor and fish abundance relatively low, standard Underwater Visual Census (UVC) was used as an alternative to videos to record fish species on an underwater notebook.

2.3. Data analysis

Fish videos were analyzed thoroughly for species identification, size estimation (< 5 cm, 5–10 cm, 10–15 cm, 15–20 cm, 20–25 cm, and > 25 cm) and location of the fish in the patch (over seagrass, sand or corals). Fish biomass was estimated using length-weight relationships found in Fishbase (Froese and Pauly, 2013):

$W=a * L^b$

where W=weight of fish (g), L=length of fish (cm), and a and b are length-weight relationship constants.

Medians of fish size-class categories were used as fish length (L) and biomass was expressed as grams of fresh weight per m^2. Where a species-specific length-weight relationship was not available in Fishbase, the constants were taken from the closest species in the genus or family relative to fish length of the observed fish.

Trophic categories were also assigned to fish using Fishbase (Froese and Pauly, 2013). The following categories were used:

Omnivores – Feeding on benthic invertebrates, fish, plankton and/or seagrass, epiphytes, algae, etc.

Benthivores – Consuming benthic invertebrates.

Herbivores – Feeding on seagrass, epiphytes, algae, etc.

Piscivores – Feeding on fishes.

The seagrass quadrats photographed in the field were re-evaluated using the seagrass percent cover photo guide by Short et al. (2002), in order to corroborate or modify the field estimates.

The software RStudio was used to perform statistical analyses. Data was tested for normality using a Shapiro-Wilk test and equality of variance using a Levene test. Non-normal and non-homogenous data were transformed using $\log_{10}(x+1)$. If the data met the assumptions for normality and homoscedacity, one-way analysis of variance (ANOVA) was used, while if the assumptions were not met even after transformation, a non-parametric Mann-Whitney U test was performed. These tests were used to evaluate if there were any significant differences between the means of the different parameters measured (species diversity, fish diversity, seagrass coverage, etc.) between sites before and after the cyclone, and before and after the cyclone at each site.

3. Results

3.1. Abiotic variables

Environmental variables were measured before the start of each site survey. The visibility was variable but usually not very good, particularly after the cyclone. The mean visibility was higher before the cyclone (3.6 ± 0.6 m) than after the cyclone (1.8 ± 0.8 m). The surveying width of the transects was adapted to these particular visibility conditions and was kept to 2 m.

3.2. Seagrass

Thirteen of the world's seagrass species are found in the Western Indian Ocean (Gullström et al., 2002), with 8 of these reported on the southwest coast of Madagascar (Hantanirina and Benbow, 2013). In this study area, a total of 6 seagrass species were sampled, with all species found at all sites (*Thalassia emprichii, Syringodium isoetifolium, Thalassodendron ciliatum, Halodule uninervis, Halophila ovalis, Cymodoceae rotundata*), except *H. ovalis,* which was not found at Andavadoaka Beach (Fig. 3f). At Andavadoaka Beach, *S. isoetifolium* and *H. uninervis* were the dominant species, while at Turtle Beach and Antsaragnasoa, *T. ciliatum* and *T. emprichii* were predominant, respectively.

Cyclone Haruna had a significant effect on total seagrass coverage at each of the 3 sites (Fig. 2b). Mean seagrass percent cover per transect decreased significantly from 72.8 ± 7.2% to 36.5 ± 5.4% in Andavadoaka (ANOVA, $p < 0.001$), from 80.8 ± 3.9% to 65.5 ± 3.8% in Turtle Beach (ANOVA, $p < 0.05$) and from 61.6 ± 4.8% to 43.0 ± 5.3% in Antsaragnasoa (ANOVA, $p < 0.05$). This represents an average decrease in total seagrass cover per transect of 36.3% at Andavadoaka Beach, 15.3% at Turtle Beach and 18.6% at Antsaragnasoa. Prior to the cyclone, the seagrass coverage was already different between Turtle Beach and Antsaragnasoa (ANOVA, $p < 0.01$), while after the cyclone, the decrease in seagrass coverage at Andavadoaka Beach induced a significant difference with the 2 other sites (ANOVA, $p < 0.01$).

Seagrass height was different between Andavadoaka Beach and the 2 other sites before the cyclone (ANOVA, $p < 0.05$ for Turtle Beach, and ANOVA, $p=0.001$ for Antsaragnasoa). Seagrass canopy height was significantly reduced after the cyclone at Andavadoaka Beach (Fig. 2a; ANOVA, $p < 0.001$), but no significant reduction was observed at either Turtle Beach or Antsaragnasoa (Fig. 2a; ANOVA, $p > 0.05$). At Andavadoaka Beach, the mean canopy height per transect decreased from 24.8 ± 1.4 cm (± SE) before the cyclone to 16.3 ± 0.7 cm after the cyclone, representing a mean height decrease of 8.5 cm. The mean seagrass height after the cyclone at Andavadoaka Beach was not significantly different from the one at Antsaragnasoa (ANOVA, $p > 0.05$), but there was a significant difference in height between Turtle Beach and the 2 other sites (ANOVA, $p < 0.01$).

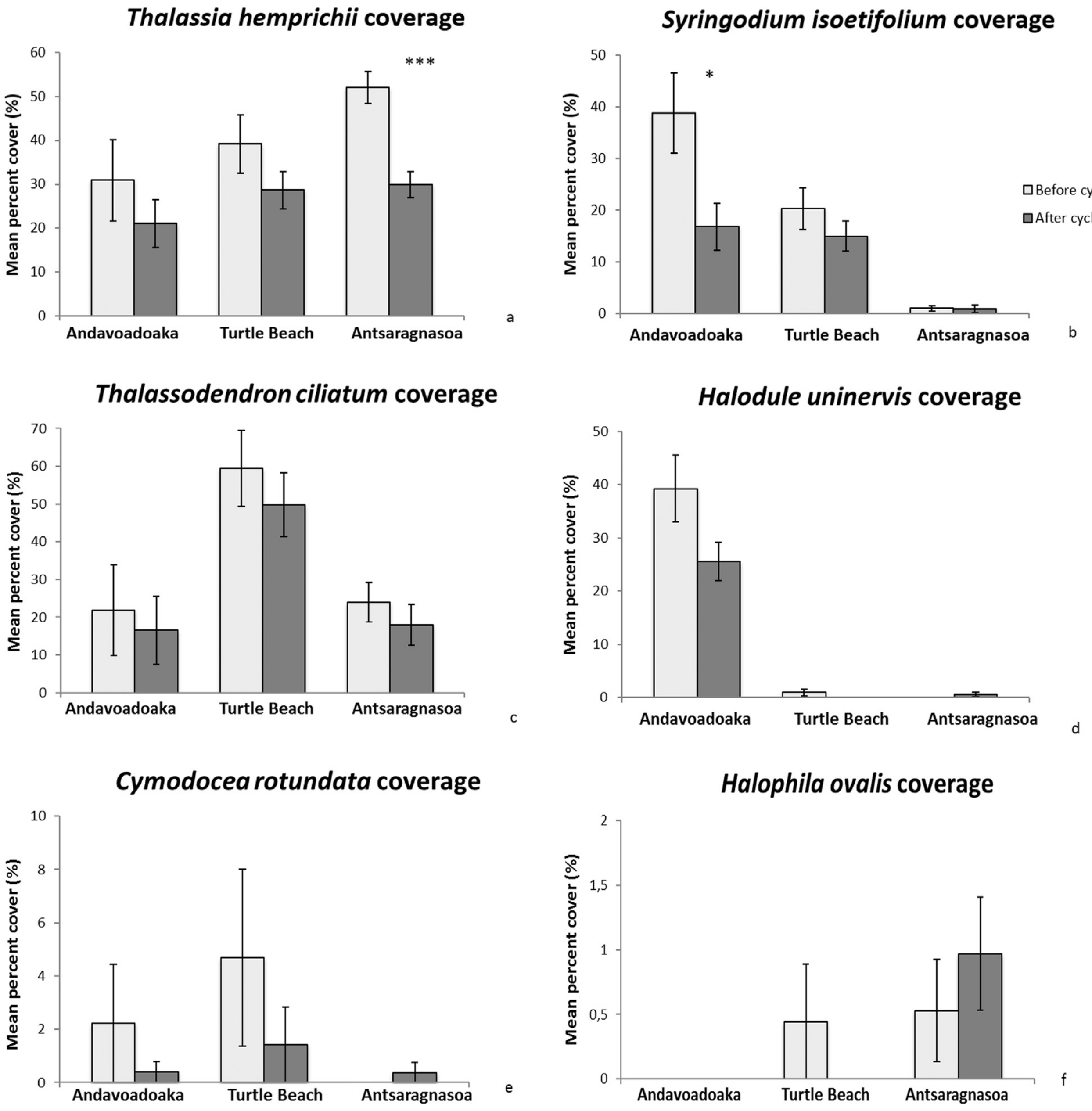

Fig. 3. Mean species-specific seagrass percent cover per transect at each site before and after Haruna cyclone for *T. hemprichii* (a), *S. isoetifolium* (b), *T. ciliatum* (c), *H uninervis* (d), *C. rotundata* (e) and *H. ovalis* (f). Standard error bars are shown for each. Legend: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, (*) $p < 0.1$.

The effect of the cyclone differed according to the species of seagrass. *T. hemprichii* coverage was significantly different after the cyclone only in Antsaragnasoa (Fig. 3a; ANOVA, $p < 0.001$). *T. hemprichii* was the dominant species at this site, and decreased 22% in coverage. The only other significant decrease in canopy cover was for *S. isoetifolium* in Andavadoaka (Fig. 3b.; ANOVA, $p < 0.05$), where the cover also declined by 22% post-cyclone. This species was the dominant species at this site along with *H. uninervis*. The p-value for *H. uninervis* was close to the $\alpha=0.05$ level (Fig. 3d; ANOVA, $p=0.075$), with a mean decrease of 13.7%. All the other seagrass species showed no significant impact of the cyclone on their coverage at any site (Fig. 3.; $p > 0.05$), although we can see trends in decreasing coverage for most species, but with large standard errors. The cyclone did not change the species coverage site differences. *H. uninervis* coverage was very different between Andavadoaka Beach and the 2 other sites both before and after the cyclone (Mann-Whitney, $p < 0.001$). *S. isoetifolium* coverage was much lower in Antsaragnasoa compared to Andavadoaka Beach and Turtle Beach (Mann-Whitney, $p < 0.01$). *T. ciliatum* coverage was significantly different between Turtle Beach and the 2 other sites (Mann-Whitney, $p < 0.05$), both before and after the cyclone.

3.3. Fish

In general, most fish species at Andavadoaka Beach were single individuals associated with coral reefs, while at Turtle Beach fish species were often found in large, highly mobile mono or multispecific schools over the seagrass bed. At Antsaragnasoa, most fish species were solitary, and fishes were less abundant at this site. The effect of the cyclone on fish species was assessed and no significant differences were found between transects surveyed before and after the cyclone (Fig. 4a; ANOVA, $p > 0.05$). Variability in the number of fish species per transect was however high. The species diversity was not found to be significantly different between the sites before or after the cyclone (ANOVA, $p > 0.05$).

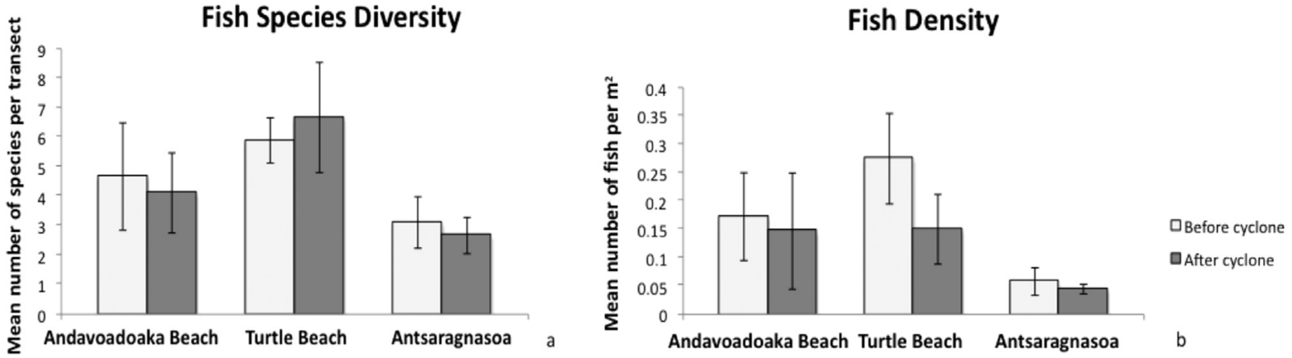

Fig. 4. Fish species diversity (a) and density(b) per transect at each site before and after Haruna cyclone. Standard errors are shown for each. Legend: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, (*) $p < 0.1$.

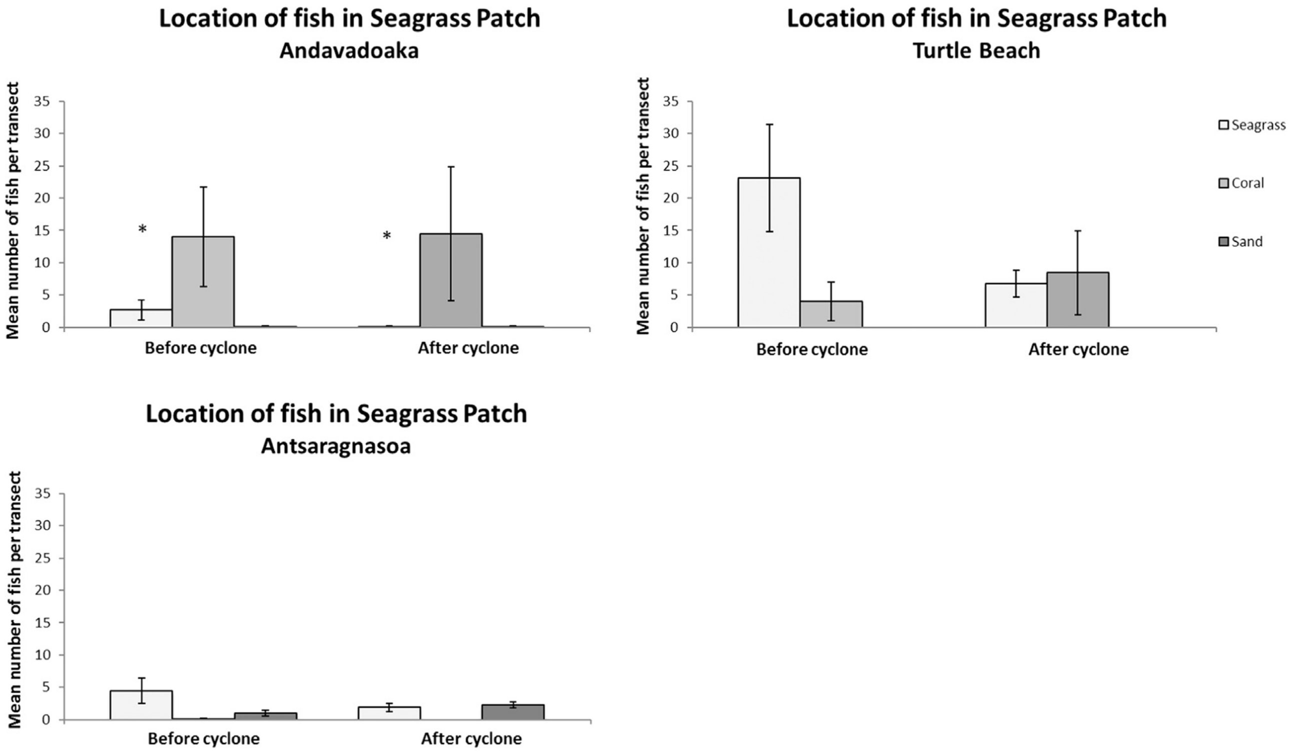

Fig. 5. Location of fish in the seagrass patch at each site before and after Haruna cyclone. Standard errors are shown for each. Legend: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, (*) $p < 0.1$.

Total fish density varied substantially from one site to the other, with Turtle Beach, a very pristine site, having the highest densities and Antsaragnasoa, a daily used site, having much lower densities. No significant differences in fish density (number of fishes per m^2) before and after the storm event were found (Fig. 4; ANOVA, $p > 0.05$). Even though results were not statistically significant, we observed a decreasing trend in density, particularly in Turtle Beach (Fig. 5). Large variability between replicates was again important, with very few fish in some transects, and schools of fish or group of individuals in other transects. The fish density was only different between Turtle Beach and Antsaragnasoa prior to the cyclone (ANOVA, $p < 0.05$).

The effects of Cyclone Haruna on fish biomass, size class distribution, location of the fish in relation to the seagrass patch (over seagrass, sand or corals), trophic group, and benthopelagic (mobile) and benthic (cryptic) fish distribution were also tested and in most cases no significant difference was found. Fish biomass per transect at each site did not differ significantly (ANOVA, $p > 0.05$), although there was high variability of the estimates and trends of decreasing biomasses at all sites were observed after the cyclone.

Most fish encountered at all sites were juveniles, characterized by very small sizes, mostly of less than 10 cm, with correspondingly very small biomasses. There were no significant differences in size class distributions at each site after Haruna (Mann-Whitney, $p > 0.05$), with fishes of the 0–5 cm class and of the 5–10 cm size class dominating before and after the cyclone at Andavadoaka Beach and Turtle Beach, respectively. However, in Antsaragnasoa, trends showed a slight dominance of the 5–10 cm class before the cyclone, whereas the less than 5 cm sizes tended to be more dominant after the cyclone.

The location of each fish individual in the seagrass bed during the survey was assessed in order to determine if the fishes were more dominant on seagrass, coral or sand before and after Cyclone Haruna. A significant result was found for Andavadoaka Beach (Fig. 5; Mann-Whitney, $p=0.04997$), with a decrease in fish over seagrass after the cyclone, but no increase over the other habitats. The number of fish over corals at Andavadoaka Beach remained the same (Mann-Whitney, $p > 0.05$) and in general fishes were much more abundant on corals than on seagrass at that site. Turtle Beach showed a decrease in fish over seagrass after Haruna, however, the decrease was not significantly different at the $\alpha=0.05$ level (ANOVA, $p=0.0767$). A slight increasing tendency was observed for the fish surveyed over coral after the cyclone at Turtle Beach. In Antsaragnasoa, a minor increase in the number of fish over sand (Mann-Whitney, $p=0.076$) compared to seagrass was

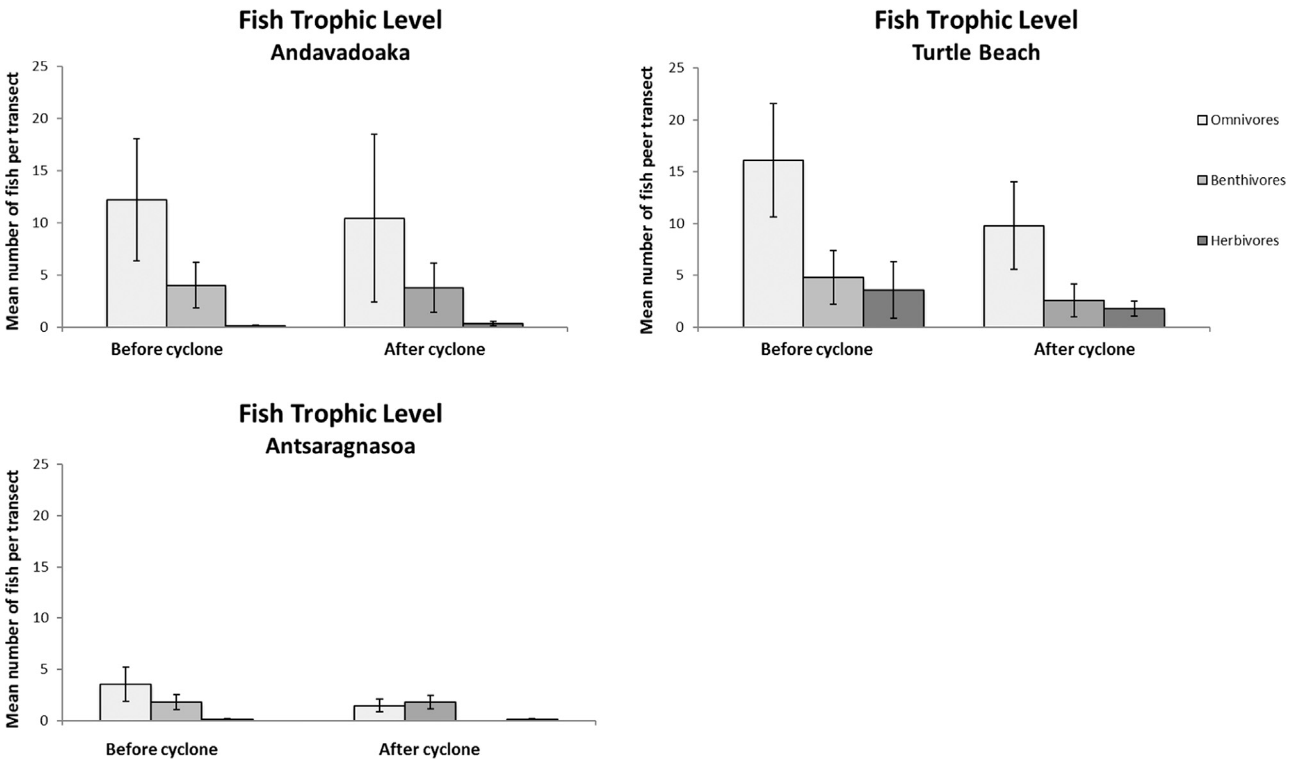

Fig. 6. Mean number of fish per transect for each trophic category at each site before and after Haruna cyclone. Standard errors are shown for each. Legend: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, (*) $p < 0.1$.

found after Haruna, although again the difference was not statistically significant. There was a significant site difference for the number of fish surveyed over seagrass between Andavadoaka Beach and Turtle Beach (ANOVA, $p < 0.01$) pre-cyclone and post-cyclone, and after the cyclone in Antsaragnasoa compared to Turtle Beach (Mann-Whitney $p < 0.05$). More fish were recorded over seagrass in Turtle Beach. A site difference was also observed between Antsaragnasoa and the 2 other sites for fish over sand post-cyclone (Mann-Whitney, $p < 0.001$), as a small increase of fish over this habitat was detected at Antsaragnasoa. Andavadoaka Beach and Antsaragnasoa were also different in terms of fish over coral after the cyclone (Mann-Whitney, $p < 0.01$).

The effect of Cyclone Haruna on fish feeding guilds was also assessed. In all sites (except in Antsaragnasoa after the cyclone), most fishes surveyed were omnivorous, feeding on a combination of plankton, invertebrates, seagrass, epiphytes and small fishes (Fig. 6). No differences were found in feeding guilds ($p > 0.05$) at each site, with more fish being omnivores, then benthivores and herbivores, respectively. However, in Antsaragnasoa, the trend was for a switch from omnivores to benthivores after Cyclone Haruna, and omnivores were much more important in Turtle Beach compared to Antsaragnasoa both before and after the cyclone (Mann-Whitney, $p < 0.05$).

Finally, the difference in number of benthopelagic (more mobile) and benthic (more cryptic, less mobile) fishes was tested to see if the cyclone could have affected the benthic cryptic fishes that may depend more on seagrass canopy. No significant differences were found ($p > 0.05$) except in Antsaragnasoa, where more benthic cryptic fishes were surveyed after the cyclone (Mann-Whitney; $p=0.03$). The trend shows a very large proportion of mobile fish over the seagrass canopy (benthopelagic), and much fewer benthic cryptic fish surveyed.

4. Discussion

Recovery of seagrass habitats from natural perturbations has been poorly investigated in the past (Waycott et al., 2004), mainly because of the long time-scale monitoring required to understand such large-scale disturbances and the unpredictability of extreme events, even though such studies are crucial for conservation and management of damaged seagrass ecosystems (Fourqurean and Rutten, 2004). This research found that Cyclone Haruna had a short-term impact on the coverage of the seagrass canopy, but not on the seagrass-associated fish assemblages. In contrast to most research done in this field, this study offered a unique opportunity to monitor seagrass ecosystems just before and after the event at the same sites, reducing the possible biases due to spatial (inter-sites) and temporal (chronic human disturbances, natural cycles) variability.

4.1. Seagrass

Cyclone Haruna hit the coast during spring low tide when seagrass beds were very exposed to winds and waves, thus increasing their susceptibility to acute damage. Many seagrasses where uprooted, broken off, or smothered due to burial and reduced light penetration from sediment re-suspension. Even though seagrasses are fast-growing plants with different life histories that are adapted to cyclic disturbances (Waycott et al., 2005), a change in seagrass species assemblages may only be detectable weeks to months after the cyclone, which was beyond the scope of this study.

In general, canopy height and coverage were strongly affected in Andavadoaka Beach, while in Turtle Beach and Antsaragnasoa, seagrass coverage was also significantly affected, but to a lesser extent. In Andavadoaka Beach, the species that decreased the most in coverage were the dominant ones, namely *S. isoetifolium* and *H. uninervis*, which are often found together (Aleem, 1984). The dominance of these two species, coupled with their location in a highly exposed bay during spring low tide, probably reduced their densities. The exposure of Andavadoaka Beach to high wind at low tide may also have contributed to decreasing substantially canopy height at that site due to suspended sediment causing burial and light limitation. Seagrass height and coverage might have been more affected in Andavadoaka Beach due to the exposure of this site to high winds and waves. Moreover, this site was already fragmented before the cyclone and became even more fragmented post-cyclone. Fonseca and Bell (1998) showed that highly exposed sites typically had more discontinuous beds, whereas more sheltered sites (such as Turtle Beach or Antsaragnasoa) had more continuous beds. Andavadoaka Beach was also the site that was the most impacted by human activities, since it was directly in front of a large village where fishing, collecting and gleaning were daily activities. Eckrich and Holmquist (2000) found that human trampling was a major cause of seagrass decline, increasing proportionally with intensity and duration of foot traffic.

Cyclone Haruna had differing impacts on species-specific coverages across the three survey sites. For example, the strong decline of *T. hemprichii* only in Antsaragnasoa might, in part, be explained by the observed high turbidity present at that site. Lower seagrass coverage and root networks probably allowed greater sediment re-suspension in these sparse beds, decreasing light availability for photosynthesis. Minimal light requirements for seagrass are much higher than for other plants, hence, light availability is often the first and most crucial requirement for seagrass growth (Wetzel and Penhale, 1983; Dennison and Alberte, 1985). The greater decline in seagrass coverage at that site might also be attributable to the sediment substrate itself, consisting of fine mud (pers. obs.). Chansang and Poovachiranon (1994) and Terrados et al. (1998) found that a silt and clay content exceeding 15% negatively affected seagrass leaf biomass, diversity and productivity. Furthermore, it was found that sites with softer substrates contributed to a greater sensitivity and susceptibility of seagrasses to trampling (Eckrich and Holmquist, 2000). Continued trampling, even at generally low intensity, can result in increased seagrass loss, leading to sparse or bare sand beds (Eckrich and Holmquist, 2000). The population of the small village in front of Antsaragnasoa site used the meadow daily for subsistence activities. The combination of less light and a soft substrate, plus trampling and direct storm damage to seagrass could be responsible for the dramatic decline in *T. hemprichii* at that particular site.

All the species present at the 3 different sites showed a tendency to decrease, except for 3 species at Antsaragnasoa (*C. rotundata, H. ovalis* and *H. uninervis*) that increased slightly after the cyclone. *C. rotundata* and *T. ciliatum* have a high resilience and tolerance. For example, *C. rotundata* tolerates an intermediate level of disturbance (Carruthers et al., 2002), and *T. ciliatum* is also able to tolerate considerable wave action (Waycott et al., 2004) and thrives in exposed habitats (Hantanirina and Benbow, 2013). *T. hemprichii* and *S. isoetifolium* were also not significantly impacted in the more sheltered bays (Turtle Beach) or in the sites where they were not dominant (Andavadoaka Beach).

Seagrass response to sedimentation is also species-specific. A stimulation of seagrass vertical growth induced by seagrass deposition was observed in species such as *T. hemprichii*, *S. isoetifolium*, *C. rotundata, H. ovalis* and *H. uninervis* (Duarte et al., 1997). The gaps created by sediment burial are usually replaced by small fast growing pioneer species such as *H. ovalis* and *H. uninervis*, or species from the genus *Syringodium* (Duarte et al., 1997). The recovery of seagrasses also depends on the magnitude of burial, with extensive sediment deposition (> 50 cm) causing important long-term seagrass losses (Fourqurean and Rutten, 2004). Deeply anchored rhizomes and roots, shoot flexibility and strength, and resilience to mobile sediments are also factors that influence species-specific responses to burial (Cruz-Palacios and Tussenbroek, 2005; Fourqurean and Rutten, 2004).

4.2. Fish

In this study, the reduction in seagrass cover that provides food, shelter and protection for fishes did not appear to significantly affect fish assemblages in the short term, although some declining trends were observed.

Fish diversity was not significantly impacted by the cyclone at any of the sites. Since fishes are highly mobile, they can hide or swim away, and may come back or be replaced by other fish after extreme perturbations, resulting in no perceptible changes in diversity. Furthermore, fish species that use other niches inside seagrass beds, such as coral or sand patches, might not be affected by a loss in seagrass cover.

Seagrass loss in the three sites did not appear to significantly influence fish density. A high seagrass reduction and an increased fragmentation of the different microhabitats in Andavadoaka Beach might not have affected fish parameters since the fishes at this site were associated to (or preferred) coral habitats, or alternatively that fish may have moved from corals or seagrass to adjacent areas. Horinouchi et al. (2009) affirmed that a mosaic of different microhabitats would give rise to some niches that were not necessarily available in continuous beds, which could be used as new habitats. The level of seagrass loss and fragmentation necessary to cause a decrease in fish populations is very difficult to evaluate (Mönkkönen and Reunanen, 1999): for example, mobile organisms can use a highly fragmented area of small patches as one single niche if the distance between patches is short enough (Bell et al., 2001). Highly skewed fish distributions are typical of biological communities, and may be explained by the fact that seagrass habitats were highly heterogenous (mosaic of niches with different structural complexities that concentrate fishes due to their different sheltering and foraging properties) and by the fact that many fish have schooling behaviours.

Fishes sampled before and after the cyclone consisted mostly of juveniles of very small sizes. Juveniles are highly abundant in seagrass meadows because the dense canopy cover provides a refuge from predators (Heck and Crowder, 1991; Orth et al., 1984). The absence of changes in size class distributions post-cyclone suggests that juveniles likely still used the less dense seagrass meadow as an important protection and foraging site.

Fish surveyed over seagrass decreased at all sites after Haruna, indicating that fish likely remained or switched to more protected niches in the site, or moved to safer adjacent habitats, such as in Andavadoaka Beach. Even though fish are mobile organisms, they can have preference for some niches that provide different benefits. For example, the fishes at Andavadoaka Beach may have remained on corals because these structures offered more protection and food for juveniles. In Antsaragnasoa, the nearby mangroves offered an appropriate shelter for escaping fishes, and the sand-associated fishes may have stayed because this available niche increased in size.

Most fishes observed during both rounds of surveys were omnivorous. Unsworth et al. (2009) also found that omnivores were more abundant in seagrass beds. Strict herbivores are usually less prevalent because of the difficulty to feed on seagrass high carbon fibers and cellulose content (Cebrian and Duarte, 1998). Since omnivores feed on a variety of food sources, they may be less affected by a loss in seagrass density. Moreover, these types of disturbances may not affect fish preys, in particular mobile plankton or invertebrates. For example, Anton et al. (2009) found no difference in epifaunal invertebrates and benthic microalgae in seagrass beds in Sandy Bay, after the passage of Hurricane Katrina in 2005. In Antsaragnasoa, the decreasing trend of omnivores may be related to the increase in the number of sand-associated fishes that could be more specialized on benthic food resources.

Cryptic fishes would have been expected to decline after the cyclone, because of their higher dependency on seagrass substrate. However, most fishes surveyed pre and post-Haruna were mobile benthopelagic species, that can swim over and between seagrass beds to exploit varied food sources, as well as being able to swim rapidly to adjacent areas or inside seagrass refuges when at risk (Vega Fernández et al., 2005). Nevertheless, the surveys might have underestimated benthic fishes due to poor visibility or to the difficulty in observing them hidden or camouflaged under the canopy. In Antsaragnasoa, the considerable decrease in seagrass cover in an already sparse bed made the observations of benthic species easier, especially gobies, which were also probably favoured due to an increase in niche availability.

4.3. Overview: Haruna impact

This study revealed that Cyclone Haruna had an immediate impact on seagrass cover, but that this seagrass loss was insufficient to trigger clear changes in fish assemblages in the short-term. The magnitude of the damage to seagrass appeared to be considerable in a region that does not typically experience cyclones. However, seagrasses are generally able to cope with cyclical patterns of change in their abundance, leading to an eventual equilibrium of the seagrass bed. Mechanical storm damage in the long-term could positively influence seagrass meadows as moderate disturbances help in maintaining high diversity in ecosystems in general (Connell and Slatyer, 1977; Paine and Levin, 1981). Intermediate disturbances would remove the late-successional species that are superior competitors, allowing the colonization of early-successional and fast-growing species through dispersal, thereby increasing overall diversity (Connell and Slatyer, 1977; Tilmant et al., 1994).

Fish assemblage responses to large-scale disturbances are much less clear than the response of seagrass meadows, due to the mobile nature of these organisms. Generally, most studies agree on the fact that as seagrass complexity decreases, fish diversity and abundance will eventually decline correspondingly (Hughes et al., 2002). However, some studies suggest that fragmentation increases the co-occurrence of a mosaic of habitats that would augment the number of generalist feeders (Vega Fernández et al., 2005). Nonetheless, if the bed is highly impacted, the minimum habitat requirements will not be met and communities will eventually become similar to the ones of bare sand patches (Horinouchi et al., 2009).

The three sites differed in seagrass total coverage and canopy height prior to the cyclone. Turtle Beach is a very protected bay with low human impact, whereas Andavadoaka Beach suffered from more human activities and was very exposed to wind and surge, causing the dramatic decrease in the parameters surveyed after the cyclone. Most of the seagrass species coverage showed no difference between the sites, except for the dominant species at Andavadoaka Beach and Turtle Beach. The dominant species in the daily used and exposed site (Andavadoaka Beach) decreased more importantly than the dominant species in the unexposed and untouched site (Turtle Beach). Due to high fish mobility, no difference was generally detected between sites for fish diversity and density, except for the fact that the pristine Turtle Beach site showed greater density than Antsaragnasoa. Finally, the 3 sites were also different in terms of fish preferred microhabitats (seagrass, coral, or sand), as the number of fish surveyed over each habitat was significantly different between each site. Turtle Beach, a healthier site, also had more fish of each trophic category, in particular omnivores.

4.4. Conclusion

Developing tropical countries are experiencing the greatest present and future rate of environmental degradation (Duarte, 2002), with largely unknown seagrass population trends (Short et al., 2011). Even though the Velondriake LMMA has implemented various sustainable management practices, as in other tropical countries worldwide, the coastal population is expected to increase significantly in the near future (Hantanirina and Benbow, 2013), increasing the pressure and dependency of coastal communities on marine ecosystems.

In this study, it was clear that the impact of the cyclone was strongly influenced by both human and physical exposure, with the more patchy seagrass meadows located directly in front of the fishing villages more impacted by the cyclone than the ones without a village in the near vicinity. As expected, the more exposed seagrass beds were also more affected by the cyclone.

Studies by Emanuel (2005), Trenberth (2007) and Webster et al. (2005) suggest that future global warming would increase the intensity and lifetime duration of extreme disturbances. The exponential explosion of human populations is presently escalating to unprecedented levels, and this, coupled with greater future destructive potential from extreme storms, could soon lead to major consequences in the poorest countries. This study provided a very unique opportunity to monitor the impacts of an extreme storm directly before and after the event, in a region where cyclones rarely hit coastal ecosystems and where the local population is highly dependent on seagrass meadows. Global long-term monitoring programs are needed to better understand the long-term consequences of large-scale disturbances on seagrass meadows.

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References

Aleem, A.A., 1984. Distribution and ecology of seagrass communities in the Western Indian Ocean. Deep Sea Res. Part A Oceanogr. Res. Pap. 31 (6), 919–933.

Anton, A., Cebrian, J., Duarte, C.M., Heck, J., Kenneth, L., Goff, J., 2009. Low impact of Hurricane Katrina on seagrass community structure and functioning in the Northern Gulf of Mexico. Bull. Mar. Sci. Univ. Miami-Rosenstiel Sch. Mar. Atmos. Sci. 85 (1), 45–59.

Bell, S.S., Brooks, R.A., Robbins, B.D., Fonseca, M.S., Hall, M.O., 2001. Faunal response to fragmentation in seagrass habitats: implications for seagrass conservation. Biol. Conserv. 100 (1), 115–123.

Birch, W. and Birch, M., 1984. Succession and pattern of tropical intertidal seagrasses in Cockle Bay, Queensland, Australia: a decade of observations. Aquatic Botany, Elsevier, 19(3), pp. 343–367.

Björk, M., Short, F.T., McLeod, E., Beer, S., 2008. Managing Seagrasses for Resilience to Climate Change. IUCN, Gland, Switzerland.

Bozec, Y.M., Kulbicki, M., Laloë, F., Mou-Tham, G., Gascuel, D., 2011. Factors affecting the detection distances of reef fish: implications for visual counts. Mar. Biol. 158 (5), 969–981.

Byron, D., Heck, K.L., 2006. Hurricane Effects on Seagrasses along Alabama's Gulf CoastEstuaries and Coasts 29. Springer, 939–942.

Carruthers, T.J.B., Dennison, W.C., Longstaff, B.J., Waycott, M., Abal, E.G., McKenzie, L.J., Long, W.J., 2002. Seagrass habitats of northeast Australia: models of key processes and controls. Bull. Mar. Sci. 71 (3), 1153–1169.

Cebrian, J., Duarte, C.M., 1998. Patterns in leaf herbivory on seagrasses. Aquat. Bot. 60 (1), 67–82.

Chansang, H., Poovachiranon, S., 1994. The distribution and species composition of seagrass beds along the Andaman Sea coast of Thailand. Phuket Mar. Biol. Cent. Res. Bull. 59, 43–52.

Connell, J.H., Slatyer, R.O., 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Am. Nat. JSTOR, 1119–1144.

Cruz-Palacios, V., Van Tussenbroek, B.I., 2005. Simulation of hurricane-like disturbances on a Caribbean seagrass bed. J. Exp. Mar. Biol. Ecol. 324 (1), 44–60.

Dennison, W.C., Alberte, R.S., 1985. Role of daily light period in the depth distribution of Zostera marina (eelgrass). Mar. Ecol. Prog. Ser. 25 (1), 51–61.

Duarte, C.M., Terrados, J., Agawin, N.S., Fortes, M.D., Bach, S., Kenworthy, W.J., 1997. Response of a mixed Philippine seagrass meadow to experimental burial. Mar. Ecol. Prog. Ser. 147, 285–294.

Duarte, C.M., 2002. The future of seagrass meadows. Environ. Conserv. 29 (2), 192–206.

Eckrich, C.E., Holmquist, J.G., 2000. Trampling in a seagrass assemblage: direct effects, response of associated fauna, and the role of substrate characteristics. Mar. Ecol. Prog. Ser. 201, 199–209.

Eleuterius, L.N., Miller, G.J., 1976. Observations on seagrasses and seaweed in Mississippi Sound since Hurricane Camille. J. Miss. Acad. Sci. 21, 58–63.

Emanuel, K., 2005. Increasing destructiveness of tropical cyclones over the past 30 years. Nature 436 (7051), 686–688.

Fonseca, M.S., Bell, S.S., 1998. Influence of physical setting on seagrass landscapes near Beaufort, North Carolina, USA. Mar. Ecol. -Prog. Ser. 171, 109.

Fourqurean, J.W., Rutten, L.M., 2004. The impact of Hurricane Georges on soft-bottom, back reef communities: site- and species-specific effects in south Florida seagrass beds. Bull. Mar. Sci. 75 (2), 239–257.

Gullström, M., de la Torre Castro, M., Bandeira, S.O., Björk, M., Dahlberg, M., Kautsky, N., Rönnbäck, P., Öhman, M.C., 2002. Seagrass ecosystems in the western Indian Ocean. AMBIO: J. Hum. Environ. BioOne 31 (7), 588–596.

Hantanirina, J.M.O., Benbow, S., 2013. Diversity and coverage of seagrass ecosystems in south-west Madagascar. Afr. J. Mar. Sci. 35 (2), 291–297.

Harris, A., 2007. “To live with the Sea” development of the velondriake community-managed protected area network, Southwest Madagascar. Madag. Conserv. Dev. 2 (1), 43–49.

Heck Jr., K.L., Crowder, L.B., 1991. Habitat structure and predator-prey interactions in vegetated aquatic systems. Habitat Structure, Springer, vol. 8, pp. 281–299.

Heck, J.R., Sullivan, K.L. Zande, M.J. J.M., Moncreiff C.A., 1996. An ecological analysis of seagrass meadows of the Gulf Islands National Seashore. Final Report to the National Park Service, Gulf Islands National Seashore, Gulf Breeze, Florida.

Hemminga, M.A., Nieuwenhuize, J., 1990. Seagrass wrack-induced dune formation on a tropical coast (Banc d'Arquin, Mauritanis). Estuar. Coast. Shelf Sci. 31, 499–502.

Horinouchi, M., Tongnunui, P., Nanjyo, K., Nakamura, Y., Sano, M., Ogawa, H., 2009. Differences in Fish Assemblage Structures between Fragmented and Continuous Seagrass Beds in Trang, Southern ThailandFish. Sci. 75. Springer, 1409–1416.

Hughes, J.E., Deegan, L.A., Wyda, J.C., Weaver, M.J., Wright, A., 2002. The effects of eelgrass habitat loss on estuarine fish communities of southern New England. Estuaries 25 (2), 235–249.

Jind, S., 2012. A Comparison of Two Underwater Visual Sampling Techniques used to Estimate Tropical Reef Fish Communities. Honours Dissertation. Dalhousie University, Canada.

Matyas, C.J., 2015. Tropical cyclone formation and motion in the Mozambique Channel. Int. J. Climatol. 35, 375–390.

Moncreiff, C., Randall, T., Caldwell, J., McCall, R., Blackburn, B., VanderKooy, K., Criss, G., 1999. Short-term effects of Hurricane Georges on seagrass populations in the north Chandeleur Islands: patterns as a function of sampling scale. Gulf Res. Rep. 11, 74–75.

Mönkkönen, M., Reunanen, P., 1999. On critical thresholds in landscape connectivity: a management perspective. Oikos 84 (2), 302–305.

Nadon, M., Griffiths, D., Doherty, E., 2005. The Coral Reefs of Andavadoaka, Southwest Madagascar. Blue Ventur. Conserv..

Nakamura, Y., 2010. Patterns in fish response to seagrass bed loss at the southern Ryukyu Islands, Japan. Marine biology, Springer, 157(11), pp. 2397–2406.

Orth, R.J., Heck, K.L., van Montfrans, J., 1984. Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. Estuaries 7 (4), 339–350.

Orth, R.J., Carruthers, T.J., Dennison, W.C., Duarte, C.M., Fourqurean, J.W., Heck, K.L., Jr, Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., Olyarnik, S., 2006. A global crisis for seagrass ecosystems and others. Biosci. BioOne 56 (12), 987–996.

Paine, R.T., Levin, S.A., 1981. Intertidal landscapes: disturbance and the dynamics of pattern. Ecol. Monogr. Ecol. Soc. Am. 51 (2), 145–178.

Pelletier, D., Leleu, K., Mou-Tham, G., Guillemot, N., Chabanet, P., 2011. Comparison of visual census and high definition video transects for monitoring coral reef fish assemblages. Fish. Res. 107 (1), 84–93.

Pihl, L., Baden, S., Kautsky, N., Rönnbäck, P., Söderqvist, T., Troell, M., Wennhage, H., 2006. Shift in fish assemblage structure due to loss of seagrass *Zostera marina* habitats in Sweden. Estuarine, Coastal and Shelf Science, Elsevier, 67(1), pp. 123–132.

Poiner, I., Walker, D., Coles, R., 1989. Regional studies-seagrasses of tropical Australia. In: Biology of Seagrasses. A Treatise on the Biology of Seagrasses with Special Reference to the Australian Region, Elsevier, New York, pp. 279–303.

Preen, A.R., Long, W.J.L., Coles, R.G., 1995. Flood and cyclone related loss, and partial recovery, of more than 1000 km^2 of seagrass in Hervey-Bay, Queensland, Australia. Aquat. Bot. 52 (1), 3–17.

Samoilys, M.A., Carlos, G., 2000. Determining methods of underwater visual census for estimating the abundance of coral reef fishes. Environ. Biol. Fishes 57 (3), 289–304.

Short, F., McKenzie, L.J., Coles, R.G., Vidler, K.P., 2002. SeagrassNet manual for scientific monitoring of seagrass habitat. QDPI QFS Cairns, 56.

Short, F., Polidoro, B., Livingstone, S. R., Carpenter, K. E., Bandeira, S., Bujang, J. S., Calumpong, H. P., Carruthers, T. J., Coles, R. G., Dennison, W. C., Erftemeijer, P.L. A., Fortes M.D., Freeman A.S., Jagtap T.G., Kamal A.H.M., Kendrick, G.A., Judson Kenworthy, W., La Nafie, Y.A., Nasution, M.I., Orth, R.J., Prathep, A., Sanciangco, J. C., van Tussenbroek, B., Vergara, S.G., Waycott, M. and Zieman, J.C., 2011. Extinction risk assessment of the world’s seagrass species. Biological Conservation, Elsevier, 144(7), pp. 1961–1971.

Terrados, J., Duarte, C.M., Fortes, M.D., Borum, J., Agawin, N.S., Bach, S., Thampanya, U., Kamp-Nielsen, L., Kenworthy, W.J., Geertz-Hansen, O., Vermaat, J., 1998. Changes in community structure and biomass of seagrass communities along gradients of siltation in SE Asia. Estuar. Coast. Shelf Sci. 46 (5), 757–768.

Tilmant, J.T., Curry, R.W., Jones, R., Szmant, A., Zieman, J.C., Flora, M., Robblee, M.B., Smith, D., Snow, R.W., Wanless, H., 1994. Hurricane Andrew's effects on marine resources. Bioscience 44 (4), 230–237.

Trenberth, K.E., 2007. Warmer oceans, stronger hurricanes. Scientific American, Nature Publishing Group, 297(1), pp. 44–51.

Unsworth, R.K., Garrard, S.L., De León, P.S., Cullen, L.C., Smith, D.J., Sloman, K.A., Bell, J.J., 2009. Structuring of Indo-Pacific fish assemblages along the mangrove-seagrass continuum. Aquat. Biol. 5 (1), 85–95.

Unsworth, R.K.F., Cullen, L.C., 2010. Recognizing the necessity for Indo-Pacific seagrass conservation. Conserv. Lett. 3 (2), 63–73.

Vega Fernández, T., Milazzo, M., Badalamenti, F., D'Anna, G., 2005. Comparison of the fish assemblages associated with *Posidonia oceanica* after the partial loss and consequent fragmentation of the meadow. Estuar. Coast. Shelf Sci. 65 (4), 645–653.

Wanless, H.R., Tedesco, L.P., Tyrrell, K.M., 1988. Production of subtidal tubular and surficial tempestites by Hurricane Kate, Caicos Platform, British West Indies. J. Sediment. Petrol. 58 (1), 739–750.

Wartenberg, R., 2012. On the Underwater Visual Census of Western Indian Ocean Coral Reef Fishes (Ph.D. Thesis). Rhodes University, United States, 226.

Watson, D., 2005. A Review of Techniques Used for Assessing Changes in Fish Assemblages. Honours Dissertation. University of Western Australia, Australia, 32.

Waycott, M., Mcmahon, K., Mellors, J., Calladine, A., Kleine, D., 2004. A guide to tropical seagrass of the Indo-West Pacific. James Cook University, Queensland, 72.

Waycott, M., Longstaff, B.J., Mellors, J., 2005. Seagrass population dynamics and water quality in the Great Barrier Reef region: a review and future research directions. Mar. Pollut. Bull. 51 (1), 343–350.

Waycott, M., Duarte, C.M., Carruthers, T.J., Orth, R.J., Dennison, W.C., Olyarnik, S., Calladine, A., Fourqurean, J.W., Heck, K.L., Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., Short, F.T., Williams, S.L., 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proc. Natl. Acad. Sci. 106 (30), 12377–12381.

Webster, P.J., Holland, G.J., Curry, J.A., Chang, H.R., 2005. Changes in tropical cyclone number, duration, and intensity in a warming environment. Science 309 (5742), 1844–1846.

Wetzel, R.L., Penhale, P.A., 1983. Production ecology of seagrass communities in the lower Chesapeake Bay. Mar. Technol. Soc. J. 17 (2), 22–31.

Electronic references

GDACS (Global Disaster Alert and Coordination System), 2013. Green Tropical Cyclone alert for HARUNA-13 from 19 Feb 2013 12:00 UTC to 25 Feb 2013 00:00. [Online]. Available: ⟨http://www.gdacs.org/Cyclones/stormsurge.aspx*eventid=35803 & episodeid=13 & eventtype=TC⟩. [20 January 2017].

Froese, R., Pauly, D., 2013. FishBase. [Online]. Available: ⟨http://www.fishbase.org⟩. [January, 2013].

NASA, 2013. Hurricanes/Tropical Cyclones: Latest Storm Images and Data from NASA. NASA. [Online]. Available: ⟨http://www.nasa.gov/mission_pages/hurricanes/archives/2013/h2013_Haruna.html⟩. [16 April 2013].