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Negative sea level anomalies with extreme low tides in the South-West Indian Ocean shape Reunion Island's fringing coral reef flats

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A R T I C L E I N F O

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A B S T R A C T

Among induced mass-mortality events on coral reef, extreme low tides may ultimately lead to considerable reef community deaths on intertidal reef flats due to unusually long and significant aerial exposure. Here, we report an extensive coral mortality event induced by a negative sea level anomaly (nSLA) that occurred across Reunion Island during the austral winter season between June and October 2015 preceding the 2015–2016 El Niño Southern Oscillation (ENSO) event. The nSLA was strong and long in duration with a rapid drop of 35 cm in the mean sea level over a one-month period. Surveys conducted over seven reef flat sites before and after the nSLA revealed that mean coral cover drastically decreased from 54.5 ± 12.7% in early 2015, to 27.4 ± 6.9% in November 2015, which is an equivalent cover loss of 50% following the 2015 nSLA event. The shallowest sites showed a greater decrease in coral cover while the deepest parts of the reef flat remained unaffected. We found a significant correlation between the bathymetry and the relative coral cover variation. Using this relationship between depth and coral cover changes, high-resolution hyperspectral imagery and Lidar bathymetric airborne data, we mapped the impacts of this event at the scale of the whole reef. Overall the modeled loss reached 13.0 ha, which represents a decrease of 45.5% of all live coral cover in this area during the 2015 nSLA event. The impact of a nSLA on emersion times is much greater than the regular variation in tide amplitude between neap and spring tides, reaching new bathymetric ranges that are usually stable in terms of water submersion. Temporal variation of coral cover on Reunion Island reef flat revealed regular decreases to be compared with mean low-water-level events among other sea and climatic related disturbances and stressors.

1. Introduction

Extreme low tides that expose benthic reef organisms to air can be detrimental for coral reefs. Few recent studies have focused on the effects of extreme low tides induced by negative sea level anomalies (thereafter nSLA) as a natural disturbance on coral reefs (Ampou et al., 2017; Raymundo et al., 2017; Buckee et al., 2019). In meso- and macrotidal coasts of the world the aerial exposure of corals during extreme low tides is a common phenomenon (Eakin and Glynn, 1996; Rosser and Veron, 2011; Glynn et al., 2017; Mejía-Rentería et al., 2020). Most studies have directed their attention towards reef coral mortality associated with extreme spring low tide events (e.g., Anthony and Kerswell,

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2007), which are predictable natural disturbances occurring twice annually (Allen, 1997). However, such extreme tidal events corresponding to a long and/or acute drop in the sea level under the current mean level also have the potential to arise as a result of an anomalous lowering in the region's mean sea level. Such events are less predictable in microtidal coasts of the world and can potentially cover a broad spatial and time scale.

Impacts of desiccation with air exposure (emersion) on benthic reef organisms depend on species that have developed mechanisms to resist dehydration and UVs. For instance, corals cover themselves with a mucus produced by the polyps that help retain water in their tissue (Huettel et al., 2006). Mass mortality of reef organisms may occur when the duration of the low tides becomes unusual (Yamaguchi, 1975; Loya, 1976; Pearson, 1981) and can be amplified due to particular conditions such as elevated air and sea temperatures (Glynn, 1968; Loya, 1972; Raymundo et al., 2017), periods of high solar radiation (Dunne and Brown, 2001; Brown et al., 2002; Anthony and Kerswell, 2007; Buckee et al., 2022), high sun altitude (Glynn, 1968; Fishelson, 1973; Glynn, 1976; Brown et al., 1994), or midday exposures (Loya, 1972; Eakin and Glynn, 1996; Brown et al., 2002; Mejía-Rentería et al., 2020). Changes in underwater light regime (Dune and Brown, 2001), or oxygen rates and water temperatures (Fadlallah et al., 1995; Hoegh-Guldberg et al., 2005) driven by unusual low tides constitute significant stressors for reef flat corals. These extreme environmental conditions may reach the physiological limits of coral tolerance, leading to mass bleaching and mortalities at a broad spatial scale.

The synchronic combination of these physical stressors with astronomical low tides is scarce and nSLAs are rare reef disturbance events. Yet they are likely to play a critical role in reef flat coral cover and diversity (Brown et al., 2002). Previous reports of nSLAs in the literature are often associated with oceanographic climate-related events. In western Thailand (Ko Phuket), a drop of ~ 30 cm in sea level in 1997–1998 combined with warm temperature from the Indian Ocean Dipole (Webster et al., 1999) resulted in major changes in coral cover and diversity across shallow reef flats (Brown et al., 2002). Coral mass bleaching and extensive mortalities were also reported in the Java Sea due to a drop in sea level of 10 to 15 cm during the 1982–1983 El Niño Southern Oscillation (ENSO) thermal event (Tomascik et al., 1997). Recent studies have documented the detrimental effects of extreme low tides on shallow reef flat corals that coincided with the first phases of the 2014–2015 ENSO event in Guam, Micronesia in the Western Pacific, which resulted in an estimated 53% decline in staghorn *Acropora* cover as the sea level dropped (Raymundo et al., 2017). Coral mortality was estimated to reach up to 85% on Bunaken reef in Indonesia due to a rapid fall in sea level during the 2015–2016 El Niño years (Ampou et al., 2017). Recently, Buckee et al. (2019) documented that live *Acropora* cover decreased from 24% to 11.1% and total cover from 35% to 21.7% following extended and repeated daytime low sea levels during the austral spring in the Houtman Abrolhos Islands. The authors underlined the universality of interannual variability in mean sea level related to ENSO driving changes in coral cover on intertidal reef flats.

In the South-West Indian Ocean (SWIO), sea level variability is dominated by westward-propagating anomalies accounting for four to five events per year (Schouten et al., 2002; Palastanga et al., 2007; Pous et al., 2015). Although the formation process of these anomalies is still unclear, it has been suggested they are associated to Rossby waves crossing the Indian Ocean and originating from eddies propagating off the west coast of Australia. Pous et al. (2015) found a westward propagation speed of 8 cm.s^{-1} in a Eulerian perspective, at a spatial scale of 400 km and with a predominant time scale of 60 days in the vicinity of the Mascarene islands (i.e., Reunion Island, Mauritius and Rodrigues). Extreme low tides due to prolonged and acute nSLAs have been succinctly reported in Reunion Island. Two extreme low tides occurred concomitantly with ENSO events in 1982–83 and 1998–99, resulting in mass mortalities of reef corals and changes in the structure of benthic communities (Guillaume et al., 1983; Naim, 1993). Live coral cover decreased from 31% in 1998 to 22% in 1999 in the Saint-Gilles reef flat, with this drop attributed to exceptional low tides affecting the upper parts of corals exposed to the air (Tessier et al., 2008). In spite of the coincidence with the strong ENSO events, there is a low predictability of such extreme low tides inducing mass die-off of reef organisms in a complex coupled ocean–atmosphere dynamic of the Indian Ocean basin (Webster et al., 1999).

Although it has been suggested that these events are responsible for mass die-off of shallow reef flat corals in Reunion Island (Guillaume et al., 1983; Tessier et al., 2008; Tourrand et al., 2013), this is the first study to quantify change in coral cover associated with mean low-water-level events. Here, we provide quantitative field observations of benthic mortalities, in particular corals, associated with long daytime emersion events that occurred between May and August 2015 in Reunion Island's coral reef flats. During these events, reef flat communities in the intertidal zone, which are subject to daily tidal fluctuations, were exposed to significant emersion times specifically during low tides following a drop in the mean sea level. We provide support for the view that changes in coral reef flat covers are related to bathymetry and we modeled and mapped these changes in coral cover associated with the 2015 emersion event at the scale of the entirety of the island's reef flats. We hypothesized that the increased emersion times as a result of the 2015 nSLA event have significant effects on sessile benthic organisms and are much stronger than during spring and neap tides. A better understanding of these effects is necessary for apprehending temporal variability in coral cover and for the prediction of future impacts of disturbances. We then examine historical coral cover changes in the light of past major coral reef disturbances in order to find out the role of water-level variability in shaping shallow fringing coral reef flats in Reunion Island.

2. Materials and methods

2.1. Reef sites

The dry western coast of Reunion Island is bordered by a discontinuous narrow fringing reef that is approximately 25 km long and 500 m wide at the most. These reefs are made up of four main reef complexes: Saint-Gilles/La Saline, Saint-Leu, Etang-Salé and Saint-Pierre (Fig. 1). They are structured from the coast seawards by i) the back-reef compartment composed of sand, rubble, seagrass beds and patchy corals, ii) a reef flat forming the shallow inner reef (0.5–1.2 m) surrounded by iii) a gentle slope formed of spurs and grooves in the outer reef. The tidal regime is mixed semidiurnal with a northward propagation. Neap and spring tides range respectively from 0.1 m to 0.9 m, the mean spring tide range is 0.4–0.6 m and the mean neap tide range is 0.1–0.3 m (Farrow and Brander, 1971; Soler, 1997; Cordier et al., 2013) consistent with a microtidal environment where tides have little effect on relative sea level fluctuations. The variations in sea level (SL) inside the reef flats are influenced by both the tides and water circulation with the open ocean (Cordier et al., 2013).

2.2. Benthic mortality and coral cover changes

We conducted benthic biodiversity surveys using skin diving on Reunion Island coral reef flats during the 2015 austral winter. Coral emersion was observed with some pale, bleached and recently dead coral colonies with recent colonization of turf algae. Fourteen surveys carried out on a weekly basis were specifically conducted to assess benthic mortalities during and after the emersion events between June and November 2015. During these surveys, we reported bleached and recent dead corals (either partial or total) in randomly selected patches of reef flat communities each covering a 100 m^2 area at different sites. Partial mortalities on corals were characterized by a strong horizontal delineation between the colorful live tissue and recently dead parts, which were either white or already colonized by turf algae. Mortality of benthic organisms exposed to air increased substantially over the time

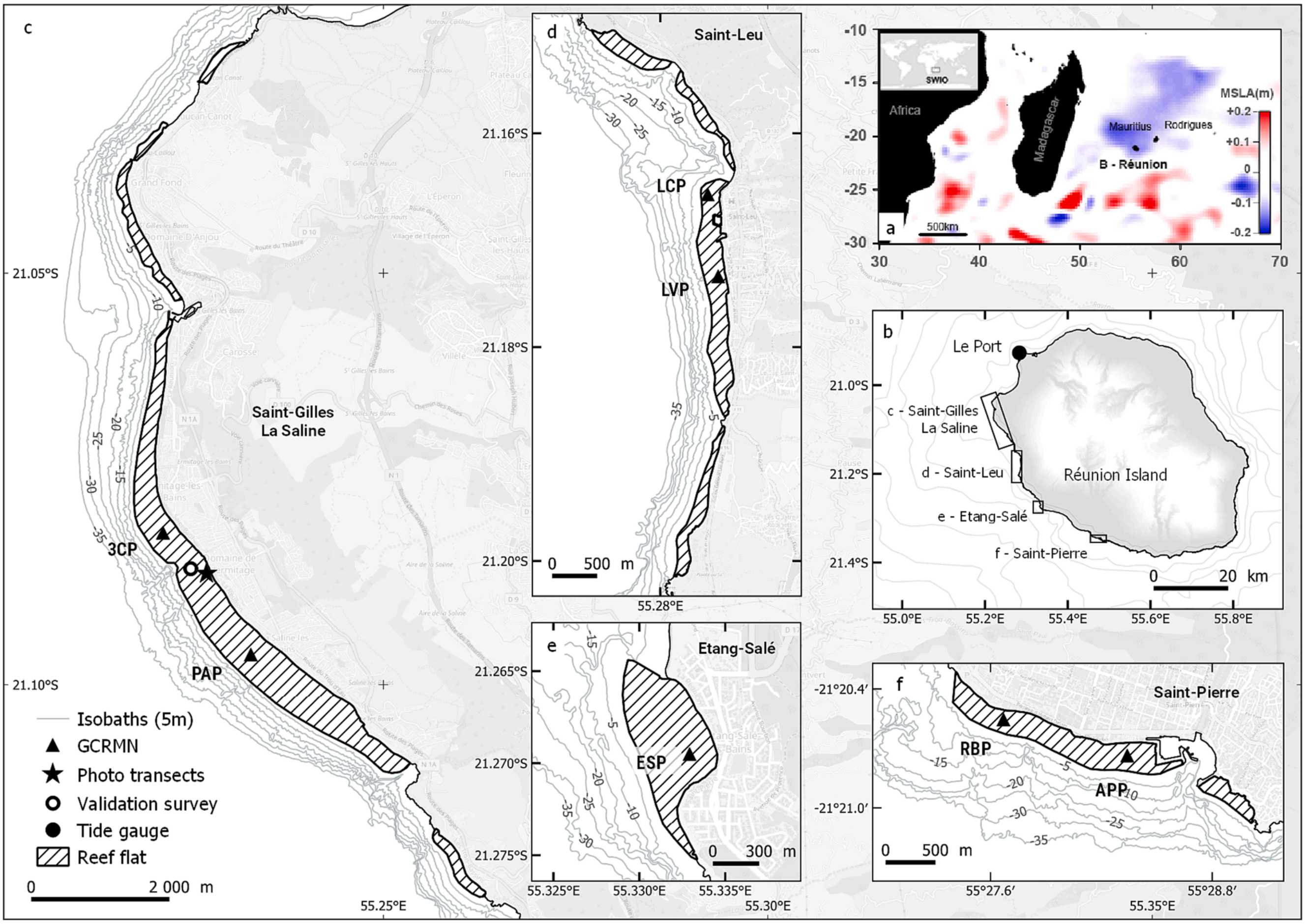

Fig. 1. Location map of the study sites. **a**. Mean sea level anomalies (MSLA) in the South-West Indian Ocean aggregated from 25 May to 17 August 2015 (Source: AVISO satellite imagery). **b-f**. Location of the shallow reef flat sites in Reunion Island: Trois Chameaux Platier (3CP), Planche Alizés Platier (PAP), La Corne Platier (LCP), La Varangue Platier (LVP), Etang-Salé Platier (ESP), Ravine Blanche Platier (RBP) and Alizé Plage Platier (APP), and the location of the tide gauge in Le Port.

period. By the end of July 2015, recent dead corals were observed at all sites.

We used long-term data series of benthic cover from the annual Global Coral Reef Monitoring Network (GCRMN, Hill and Wilkinson, 2004) surveys carried out by the Marine Reserve of Reunion Island (RNMR) over seven reef-flat sites (Fig. 1**c-f**) between February and April from 1998 to 2000 to 2016. The Line Intercept Transect method (LIT) (English et al. (1997) was used to estimate benthic cover along three 20-meter-long permanently marked transects oriented parallel to the reef front. Live hard and soft corals were identified to genus level and other benthic components were assigned to crustose coralline algae (CCA), algae (turf and macroalgae), other benthic organisms (e.g., sponges) and sand/rubble. A supplementary survey using the same LIT method was carried out at all GCRMN reef flat sites on 17–20 November 2015 (after the nSLA).

Live coral cover variation on shallow reef flat during the nSLA was additionally surveyed using photo-quadrats at the inner reef flat site of La Saline/Ermitage on 15 June and 25 September 2015 (Fig. 1**c**). Mortality of corals and benthic cover were estimated from 10 photo-quadrats along three 50 m transects using high-resolution underwater images. The transects were laid on inner-reef margin sites homogenous with respect to coral cover (over 40% before the event) and bathymetry (between −1 m and 0 m). The camera is held vertically from the sub-surface by a scuba diver, automatically acquiring sea bottom photographs every 10 s, covering a bottom area of 1 m^2, depending on bathymetry. Corresponding pre- and post-event images are then paired together using their position recorded by a Global Positioning System (GPS) receiver held above the surface by the diver. Positioning uncertainties linked to the accuracy of the GPS, the angle of sight and the field of view, are taken into account by considering only the photographs closer than 3 m to each other in the pairing process (Supplementary Figure 1). Each image was imported into a custom-developed user interface for visual estimation of covers by a trained operator. Benthic covers were reported using ten percentage categories with 10% intervals (adapted from Dahl, 1973) falling into the above-mentioned GCRMN benthic categories: live hard and soft corals, crustose coralline algae (CCA), algae (turf and macroalgae), other sessile benthic organisms (e.g., sponges) and sand/rubble. Coral cover variations were computed by diachronic analysis of each image couple and averaged by transect (Supplementary Table S1).

Changes in coral cover (CC) following the extreme low tides were expressed as the Relative Coral Cover Variation (RCCV), as the ratio between Absolute Coral Cover Variation (ACCV) and the coral cover before the 2015 emersion:

$$RCCV = \frac{ACCV}{CC_{before}} = \frac{CC_{after} - CC_{before}}{CC_{before}}$$

The position of each photo and GCRMN transect, localized on the reef flats' margins, was used to extract their fine-scale bathymetry (Mean ± SD) from high-resolution bathymetric maps (see in Mouquet et al., 2016a; Bajjouk et al., 2019). These data were used to characterize the correlation between RCCV and bathymetry on the impacted reef flats. The remote sensing hyperspectral methodology used to retrieve water depth was developed for white coral reef sand areas, but in Etang-

Salé at the ESP site, the sandy bottoms are mainly of black volcanic origin. As water-depth overestimation could therefore occur for this kind of material (see in Bajjouk et al., 2019), the ESP site was excluded from further analysis.

To assess for historic temporal changes in coral cover at each GCRMN site (20-m transects are treated as statistical replicates), the mean derivative of hard coral cover (CC_d) was estimated over time as:

$$CC_d = \frac{\Delta CC}{\Delta t} = \frac{CC_{t+1} - CC_t}{(t+1) - t}$$

where *ΔCC* corresponds to the coral cover variation between two successive benthic surveys at dates $t + 1$ and t, with this time interval Δt expressed in weeks. All sites were pooled together in order to assess for variations at the scale of the whole reef, computing corresponding CC and CCd means and standard deviations.

The map of potential impacts of coral emersions was elaborated with data from hyperspectral and Lidar remote sensing projects (Petit et al., 2017; Bajjouk et al., 2019). This analysis was performed on the southern part of the Saint-Gilles reef flats at the south of Passe de l'Ermitage, exploiting two base data layers: the *fine-scale hyperspectral bathymetry* of the reef flats (Mouquet et al., 2016a) and the *coral entities* (CE) layer used as an estimation of the live coral colonies (Mouquet et al., 2016b). Both data layers of high spatial resolution (i.e., 40 cm) were computed from airborne hyperspectral imagery acquired on 21 and 23 May 2015 just before the nSLA event and represent the state of the reef at that time. We used the previously-established relation between bathymetry and RCCV (linear regression) to model impacts based on this assumed relationship between depth and coral death. The CE layer was used as a mask to focus the analysis on live coral colonies and estimate impact levels based on bathymetry. The reef flat was then spatially clustered to aggregate data and highlight the impact of the 2015 emersion at the scale of the entire reef by dividing it into 20-meter-wide rectangular polygons oriented perpendicular to the coastline extending from the shore to the reef crest front (see Bajjouk et al., 2019). In addition, *linear coral cover aggregations* (Mouquet et al., 2016c) were plotted along the shoreline to highlight areas with the highest coral cover.

The map of the estimated impacts was validated using 48 ground truth points acquired during biodiversity surveys in the reef flats of the La Saline/Ermitage site on 29 July and 10 August 2015, at the end of the most intense phase of the nSLA. Each location was randomly surveyed in 10 m x10 m areas to assess the cover of biotic organisms and live coral. For each point, the presence/absence of bleached coral and recent mortality (either partial or total) were reported as Recently Dead Corals (RDC/NO RDC respectively).

2.3. Water levels

In situ data of mean sea level (tide gauge data at Le Port, Fig. 1**b**) were confronted to data from the AVISO satellite imagery (Fig. 1**a**). Sea level anomaly (SLA) delayed time (DT) data were obtained from the SSALTO/Duacs system (distributed by CMEMS, Copernicus Marine Environment Monitoring Service) along ¼° grid spatial resolutions to quantify changes in mean sea level. They were processed in order to consider the mean sea level rise in the region, which was estimated at 3.21 mm.y^{-1} for the 1993–2018 period in the Indian Ocean (AVISO, 2018): Aviso SLA-DT data are computed with respect to a 20-year mean of sea level (1993–2012), which may lead to an over- or underestimation of actual nSLA. To correct for this bias, we computed and subtracted the MSL of the previous five years from the SLA-DT value (see Aviso recommendations for daily Sea Level Anomalies over the 1993–2015 period, AVISO, 2018). Time series of SLA were extracted from the four pixels encompassing the station at La Rivière des Galets, Le Port (55.285115° E and 20.934891° S) (~20 km from the reef sites) for comparison with *in situ* tidal gauge. Daily minimum, mean, and maximum SLs for 2015 were computed from the high-frequency sea level (HFSL) at a time-step of one minute (REFMAR, 2018). Daily and cumulative emersion times were computed from HFSL for bathymetric steps within the range [-0.6 m; 0.6 m] by increments of 0.01 m and 0.05 m. Different temporal periods were selected: 13–28 July for negative SLA, 16–30 November for positive SLA. The typical MSL profile was obtained using the whole 2015 HFSL dataset from which dMSLs were subtracted; neap tide days when tidal range is below 0.35 m, average tide days when tidal range is between 0.35 m and 0.65 m, and spring tide days when tidal range is above 0.65 m. See Supplementary Table S2 for details about sea levels and tides for each situation.

Traditionally, the reference sea level used by the French Navy Hydrographic and Oceanographic Service (SHOM) is that of the lowest astronomical sea level, while that of the French National Geographic Institute (IGN) is the average sea level. In Reunion, the chart datum, to which tide gauge is referenced, is therefore 0.554 m under the IGN1989 height reference system in use, to which bathymetric Lidar/hyperspectral data are referenced (SHOM, 2020). Data related to sea levels (tide gauge) were then shifted to the reference IGN datum for analysis of bathymetry and live coral covers.

2.4. Contextual climatic and oceanographic data

Tropical and intense tropical cyclones (i.e., scales 5/5, 4/5, and 3/5) that passed near the western coast of Reunion Island within a 300-km radius between 1998 and 2015 were identified. Strong southwest austral winter swells with significant wave height (H_s) ≥ 5 m, a period (P) ≥ 20 s and a duration (T) ≥ 6 h were also considered as significant hydrodynamical disturbances on coral reefs.

Anthropogenic stressors along with chronic disturbances such as submarine groundwater discharges, eutrophication and mudflow were not taken into consideration as their quantification is difficult, and beyond the objectives of this study.

To determine the heat stress of corals on the Reunion Island reef flats in 2015, Sea Surface Temperature (SST) and Bleaching Degree Heating weeks (DHW) time series data (2000–2016) were extracted from NOAA Coral Reef Watch (2000) (https://coralreefwatch.noaa.gov/satellite/hdf/index.php), Satellite Virtual Station Time Series in Reunion Island (i.e., 0.5° resolution). The DHW is a measure of thermal stress severity where 1 DHW corresponds to a + 1 °C anomaly above the maximum monthly mean (MMM) sea surface temperature for a given region lasting for one week over a 12-week rolling period (Liu et al., 2013). The coral bleaching threshold SST for Reunion Island reef was assumed to be MMM + 1 °C (i.e., 28.6 °C).

Two main phenomena affecting the climate of a large part of the tropical and subtropical Indo-Pacific regions are ENSO and the Indian Ocean Dipole (IOD). The intensity of ENSO was plotted using the Multivariate ENSO Index (MEI). Time series data of the MEI were extracted from the NOAA Earth System Research Laboratory (https://www.esrl.noaa.gov/psd/enso/mei/). The intensity of the Indian Ocean Dipole (IOD) is represented by a temperature gradient named the Dipole Mode Index (DMI). Time series data of the DMI were extracted from JAMSTEC (http://www.jamstec.go.jp/aplinfo/sintexf/iod/dipole_mode_index.html).

All statistical analyses were performed using R.3.5.0 (R Core Team 2016). To statistically estimate the differences in mean covers of coral and algae from the GCRMN before and after the nSLA, we perform a *t* test after checking for the normality of the data using a Shapiro-Wilk's normality test. We conducted Wilcoxon signed-rank test to test for differences in RCCV between groups with RDC and no RDC as the data were not normally distributed. Correlations between time-series data (CC, CCd, SLA, MEI, IOD and DHW) were determined on a trimestral basis using Pearson's correlation tests.

3. Results

3.1. Benthic mortality and coral cover changes

In Reunion Island, bleaching and mass mortalities were reported in corals, calcareous algae and seagrasses at each reef flat site surveyed in mid-2015. The mass mortality event affected diverse sessile benthic taxa including hydrocorals (*Millepora* spp.), scleractinian reef-building corals (*Acropora* spp., *Porites* spp.), soft corals (*Sinularia* sp., *Lobophytum* sp.), crustose and foliaceous coralline algae *Mesophyllum* sp. and mono-specific beds of the seagrass *Syringodium isoetifolium* (Fig. 2). The mortality rate of benthic species increased rapidly between June and October 2015. During the first eight weeks of the event, the observed mortality rate of sessile benthic organisms was low and localized, but subsequently increased rapidly in July to reach the maxima, occurring at each site surveyed by the end of that month. Subsequent field observations from September/November 2015 to March 2016 revealed significant turf algae colonization on these recently dead corals (Fig. 2, Fig. 3).

Results showed a clear decrease in live coral cover between just before and just after the event for all reef flat sites, from −5.4% at the deepest GCRMN reef flat site (i.e., site LCP) to a maximum loss of −51.3% at the shallowest site RBP. Considering all sites pooled together, mean coral cover abruptly and significantly declined by 27.1% after the nSLA from 54.5 ± 12.7% in early 2015, to 27.4 ± 6.9% in November 2015 (*t* test, $p = 0.0028$), while turf algae increased from 33.8 ± 11.2% to 57.5 ± 9.9% (*t* test, $p = 0.0035$; Fig. 3**b**).

Photo-quadrat transects on the specific reef site of La Saline/Ermitage also showed an overall decrease in coral cover, but with a clear difference in response depending on the bathymetry. The shallowest transects Tr1 (-0.27 m ± 0.10) and Tr3 (-0.28 m ± 0.07) displayed strong decline in coral cover between June and September (-62.9 ± 21.3% and −95.0 ± 10.0% in RCCV respectively), while coral cover at the deeper transect Tr2 (-0.73 ± 0.18 m) remained heterogeneous (–3.4 ± 54.5%) (Fig. 4, Supplementary Table S1).

After the 2015 nSLA, coral cover variation estimated from both quadrats and LIT-GCRMN methods, displayed substantial differences depending on their depth distribution. The three deepest sites Tr2, LVP and LCP with a mean bathymetry of below −0.60 m were only slightly affected (variations < 30%), whereas shallower reef sites (i.e., Tr1, Tr3, PAP, 3CP, RBP and APP) with an overall bathymetry of above −0.40 m displayed a higher relative coral cover variation (>50%, reaching 72% for RBP and 95% for Tr3) (Supplementary Table S1).

There is a significant positive correlation between changes in coral cover and the mean bathymetry of reef flat sites ($y = -98.95x - 86.17$; $R^2 = 0.67$; $p = 0.0075$), with an x-intercept of −0.87 m below which there is no impact, and a maximum bathymetric value of + 0.14 m above which the RCCV reaches 100%. Impacts are strong above the bathymetric threshold of –0.40 m, with the coral cover halved. HFSL distributions show that the highest impacts are reached for corals around the normal MSL (0 m), decreasing with depth. They are still very sensitive (-25%) at the recorded minimum sea level during this event (-0.59 m), and even beyond within a range of 0.30 m where coral cover decrease is still perceptible even without direct air exposure (Fig. 4).

Using the layer of coral entities, the bathymetric data and the above-determined relationship, we modeled and mapped the impacts of this nSLA at the scale of the overall reef flat of Saint-Gilles (Fig. 5). The central zone, with locally high coral cover consisting of sparse coral colonies flourishing in the deep back reef (Fig. 5**c**), was less affected than the zones further north, where corals grow on shallower substrates (Fig. 5**d**). In the northern zone, the bathymetry is heterogeneous, which results in some deeper corals close to the back-reef margins being less affected than those on the shallower reef flats (Fig. 5**e**).

Similarly, the summary map shows that coral patches in the central reef zone were less affected (RCCV: −20% to −30%) than those located northward (RCCV: −50% to −70%) (Fig. 5**b**). Applying our estimates

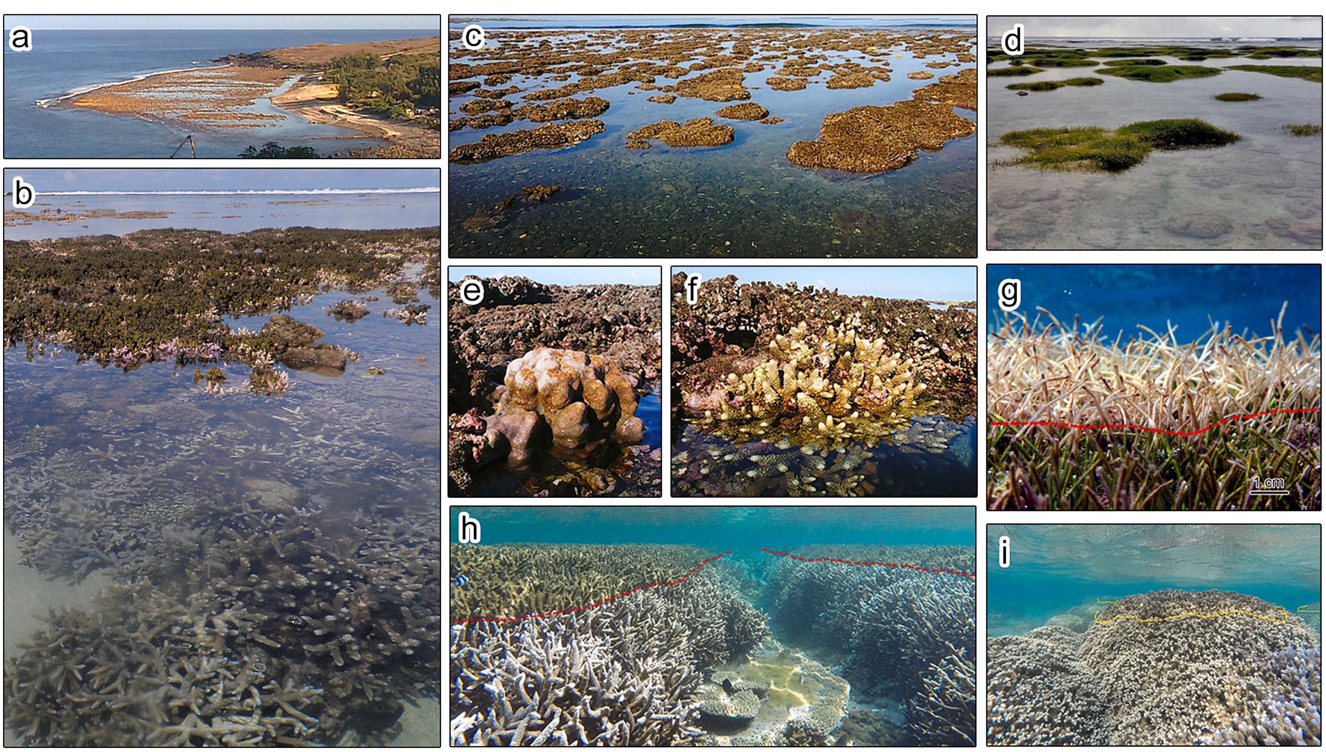

Fig. 2. Aerial and underwater view of coral reef flats of Reunion Island between May and September 2015. **a**. The reef flat of Saint-Leu totally exposed to air in June 2015. **b**, **c**. and **d**. Closer views of the reef flat with emersion of hard coral colonies and seagrass beds *Syringodium isoetifolium* at Saint-Gilles and Saint-Leu. Visible impacts (partial bleaching and mortality) of the 2015-nSLA on **e**. *Leptoria phrygia*, **f**. *Acropora* sp. **g**. *S. isoetifolium*. **h**. *A. muricata* and **i**. *Porites sinarea rus*. The red and yellow lines delineate the bleached and dead parts colonized with turf algae in September 2015 from live tissues in *S. isoetifolium, A. muricata* and *P. sinarea rus* respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

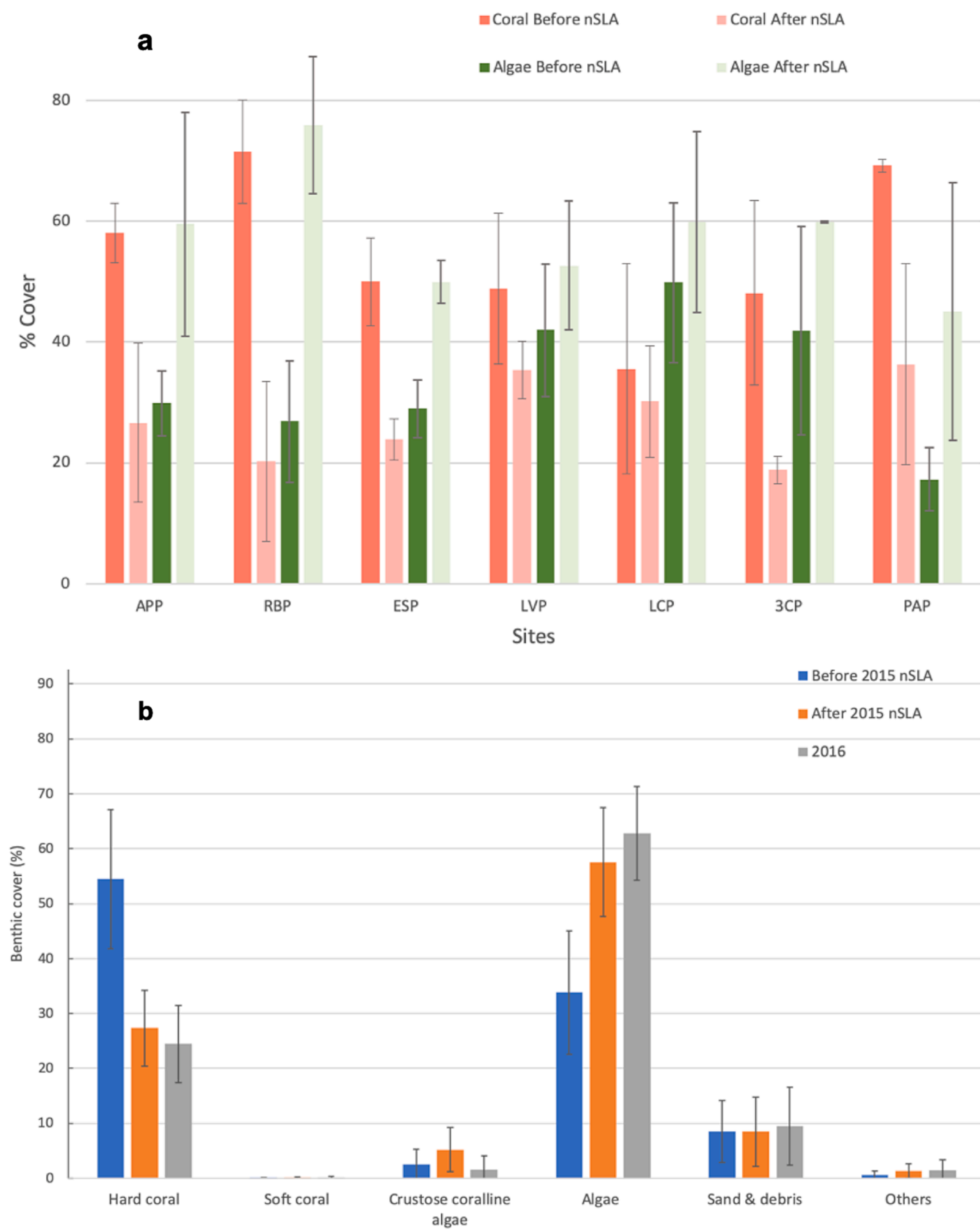

Fig. 3. Average benthic cover at Reunion Island GCRMN shallow reef sites recorded before (February 2015), after low-water-level events in November 2015 and in March 2016. **a**. Average coral and algae cover per site and **b**. across all transects before and after the low water events at sites Trois Chameaux Platier (3CP), Planche Alizés Platier (PAP), La Corne Platier (LCP), La Varangue Platier (LVP), Etang-Salé Platier (ESP), Ravine Blanche Platier (RBP) and Alizé Plage Platier (APP). Error bars correspond to ± SD Standard Deviation.

based on bathymetry, we calculated that the cover of the corals affected was 28.6 ha, as 96.5% of corals live in shallow waters, above the computed −0.87 m depth threshold. This means a total coral cover loss of −13.0 ha (RCCV: −45.5%) during the 2015 nSLA event.

Validation ground truth points show a good agreement between observed RDC and modeled RCCV: no dead coral was observed in the deeper parts while all points with recent dead corals were localized on the shallower areas of the reef, as predicted by the impact map (Fig. 5e). Although estimated RCCV was not estimated from the validation points because of the lack of pre-event cover information from the field, the ground truth data show that the predicted RCCV for the observed RDC group (51.9 ± 14.9%) was significantly higher than for the NO RDC group (3.4 ± 7.0%) (Wilcoxon signed rank test, $W = 263.5$, $p = 0.000$; Supplementary Figure 2).

3.2. Water levels

The analysis of the daily MSL (dMSL) in the South-West Indian Ocean region in 2015 showed an unusual nSLA event, delimited in time, starting on 25 May and ending on 17 August 2015 (duration ∼ 3 months). This nSLA extends over > 900 km wide, covering both Reunion Island and Mauritius (Fig. 1a). During this period the dMSL in Reunion Island was ∼ 0.2 m lower than the MSL of the previous five years. This event was the most significant nSLA recorded over the last decade in

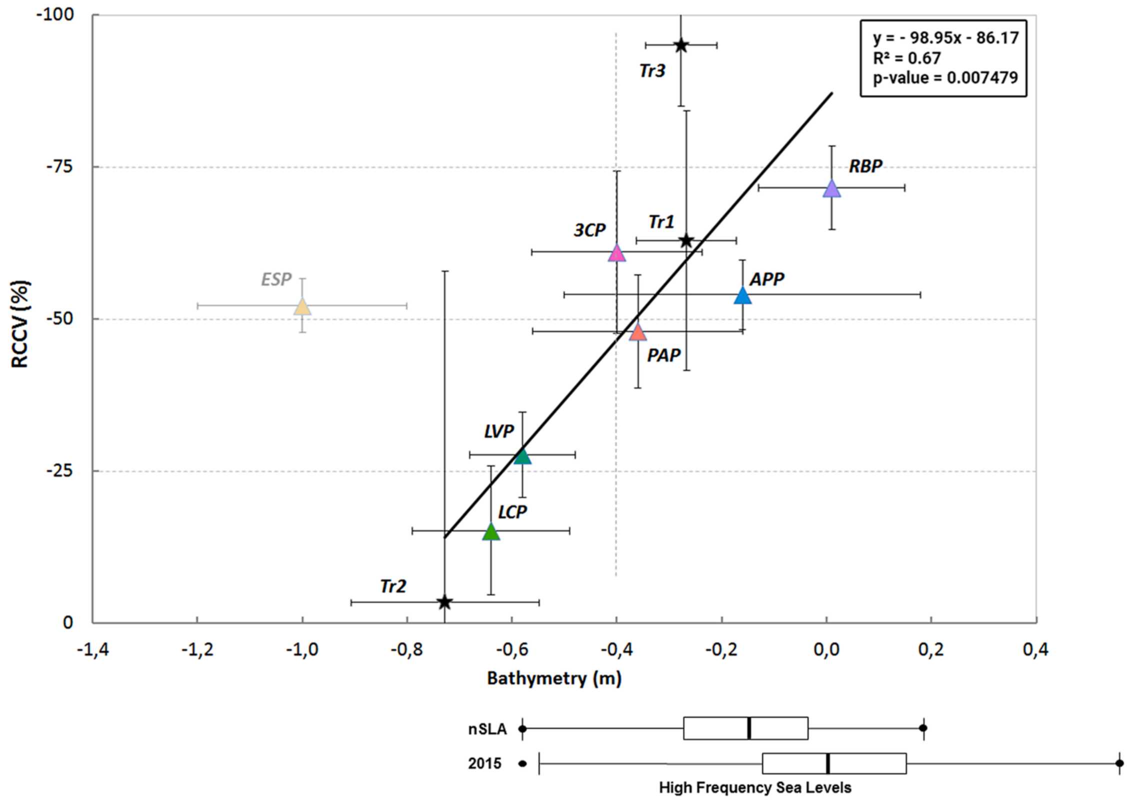

Fig. 4. Relative coral cover variation (RCCV in % ± SD) as a function of bathymetry (Mean in m ± SD) along the three photo transects surveyed during the nSLA (black stars) and those from GCRMN long-term monitoring (colored triangles). Bathymetric data obtained from the processing of the hyperspectral imagery acquired between 21 and 23 May 2015. Due to depth uncertainty ESP data was excluded from the regression (see text). The vertical dashed line indicates the emersion threshold (-0.4 m) above which>50% of coral cover is lost during the event; Bathymetric data are referenced to the reference altimetric system for Reunion Island (IGN1989), 0.554 m above zero hydrographic and equivalent to the historical MSL. The boxplots below the graph refer to the distribution of high frequency sea levels during nSLA and for the entire year 2015. Study sites: Trois Chameaux Platier (3CP), Planche Alizés Platier (PAP), La Corne Platier (LCP), La Varangue Platier (LVP), Etang-Salé Platier (ESP), Ravine Blanche Platier (RBP) and Alizé Plage Platier (APP).

terms of amplitude. However, the duration of this event was not the longest recorded. In 2011–2012, an nSLA lasted approximately one year, although it was lower in intensity (Fig. 6**a**). Time-series from tidal gauge and satellite were similar in terms of profiles, trends, magnitudes and breaking-points, specifically in 2015 (Spearman's rank correlation Rho $= 0.68$, $p < 0.0001$). The MSL estimated for the previous five years (2011–2015) from these two datasets is 0.55 m (thereafter 5yMSL). Both datasets show a rapid drop in the mean dMSL in May 2015. Tide gauge shows a daily sea level height of 0.75 m in early May 2015, dropping to a minimum of 0.31 m in July. The dMSL remained low and below normal (under 0.55 m) over more than five months between May and November, except for a few days in August (Fig. 6**b**). No bleaching stress related to sea surface temperatures was reported during this winter period. Sea surface temperatures remained relatively low, even though they were slightly above the maximum monthly mean climatology in early May (Fig. 6**c**).

Between June and August 2015, the SLA was equivalent to the mean tidal range during neap tide (~30 cm), resulting in high tide sea levels equal to or even lower than the expected low tide levels for those days, while low tides were similar to regular/strong spring low tides. Spring low tides in Reunion Island usually occur in early morning or late evening (8 am/pm), whereas the neap low tides occur at midday, preserving the immersed reef flat from the daily maximum solar radiation (Fig. 7). A drop in dMSL, while maintaining the tide characteristics (tidal range), has three instant consequences: an increase in the emersion time at fixed bathymetry, an intermittent emersion of deeper areas previously permanently underwater, and a permanent emersion of higher areas previously submersed a least once a day. Variation in tide intensity (weekly succession of neap and spring tides) while maintaining a constant dMSL has different consequences compared to SLA, with variations of daily emersion times that are lower and centered on the dMSL (Fig. 8**a**). Daily emersion time differences show that variation of tide amplitude is responsible for an increase in the emersion time below dMSL and a decrease above, with maximum values reached midway, with + 6 h for –0.4 m and −6h for + 0.15 m respectively. Importantly, the emersion time variation is null around the dMSL. For a −0.2 m nSLA, the difference in emersion time is always positive and much higher for the whole bathymetric range, with maximum values reached around the dMSL (+11 h30). This pattern is different from the regular variation in tide amplitude between neap and spring tides, affecting bathymetric ranges around MSL that are usually very stable in terms of water submersion/emersion alternation (Fig. 8**b**).

Starting from mid-May, the reef flat sea bottoms around the 5yMSL started to emerge much more than the expected 12 h per day, reaching 20 h per day early June, and were continuously exposed to air during several days in late July, and deeper bathymetric zones at between −0.6 m and −0.3 m (Supplementary Figure 3**a**). During this three-month nSLA period, the Cumulative Emersion Time (CET) increased drastically for all bathymetric levels. Our results show a cumulative duration of one hour for the deeper level of −0.55 m to over a week for the level of −0.35 m (Supplementary Figure 3**b**). We found that a week of cumulative exposure time at −0.40 m over a 3-month time period caused the death of 50% of the live coral cover.

3.3. *Coral cover time series, sea-related disturbances and climatic anomalies*

GCRMN data show regular cycles of increase and decrease in live

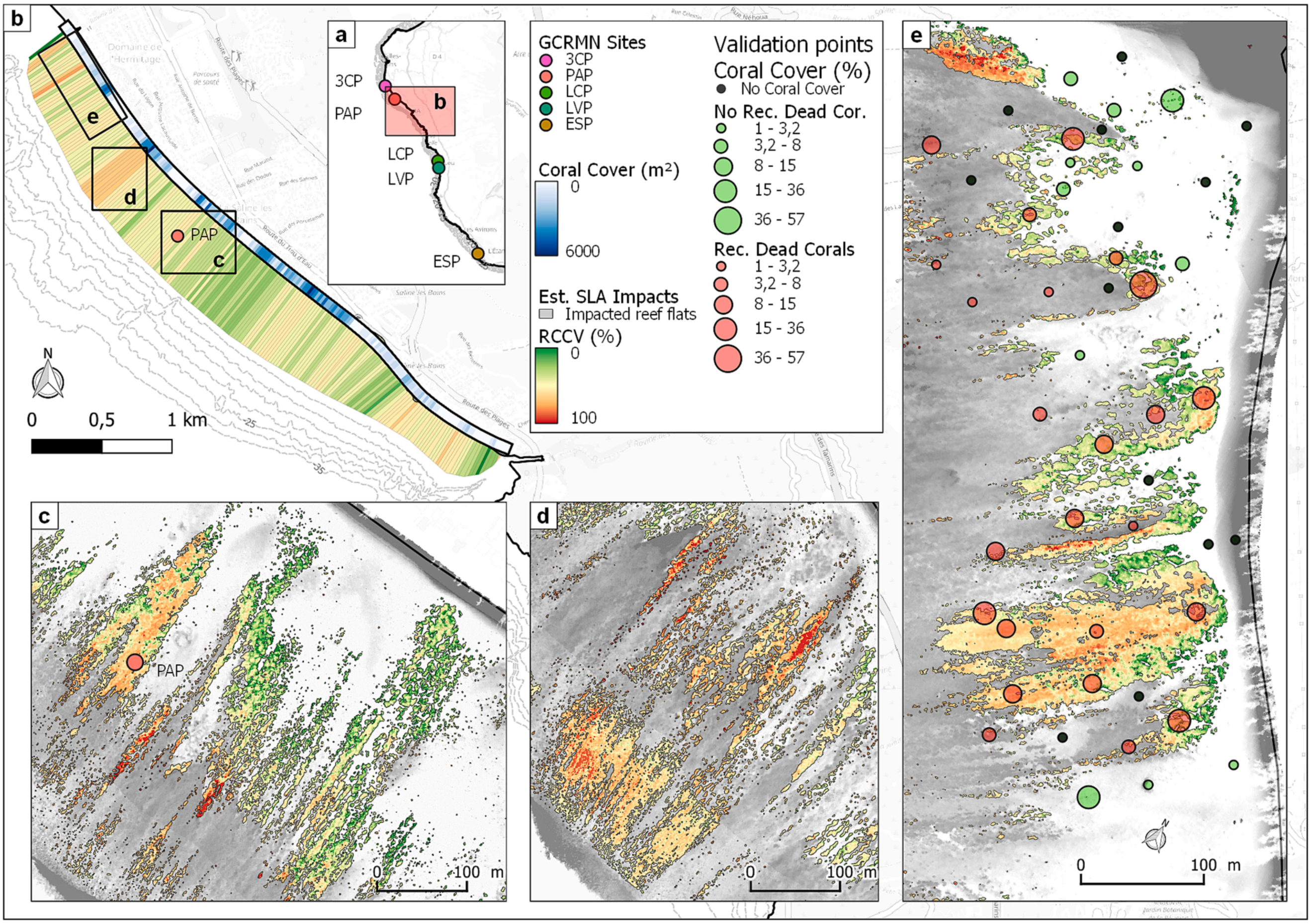

Fig. 5. Live coral cover loss estimated over the entire Saint-Gilles reef flat after the 2015 nSLA event from high resolution hyperspectral and Lidar remote sensing data. **a.** The southern part of the Saint-Gilles/La Saline reef flat in **b.** is the most developed reef complex (4 km long by 450 m wide) along Reunion Island's western coasts. The impact of nSLA is heterogeneous from north to south as shown by the differences in relative coral cover variations (RCCV) between area **c** and **d**. In **e**. validation points with presence (red) or absence (green) of Recent Dead Corals. Coral cover increases with symbol size, and points without coral are in black. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

coral cover over time, but with different amplitudes and timing for each reef flat site (Fig. 9). Our results highlight four major declines in coral cover on Reunion Island reef flat identified since 2000 (2003–2004, 2008–2009, 2011 and 2015–2016) (Fig. 10**a-b**). In 2015 the mean coral cover across reef sites declined by −49.7% at the high rate of CCd = -0.6% per week between the January and November surveys (Fig. 10**c**).

Over the past decades, five major cyclonic events with associated high hydrodynamic and meteorological conditions have been recorded in the close vicinity of Reunion Island (<300 km) (Fig. 10**d**). These include intense tropical cyclones Dina in January 2002 and Gael in February 2009, and tropical cyclones Gamède in February 2007, Dumile in January 2013 and Bejisa in January 2014. Likewise, during the austral winter, five strong austral swells have been recorded (i.e., 2003, 2006, 2007, 2011, and 2014) (see Cuvillier et al., 2017).

The multivariate ENSO and IOD indexes display some important variations with extreme values across the considered time period (Fig. 10**e-f**). The long-lasting but moderate decline in coral cover in 2003–2004 may be the result of Dina-induced bleaching in 2002 and severe bleaching events in 2003 and 2004 (Fig. 10**g**).

We found some correlations across trimestral time series coral data. CC and CCd are positively correlated to SLA (respectively r = 0.35, p = 0.01 and r = 0.34, p = 0.029). CC is negatively correlated to MEI (r = -0.43, p = 0.036). CCd and SLA are negatively correlated to IOD (respectively r = -0.30, p = 0.04 and r = -0.32, p = 0.019) (Supplementary Figure 4).

4. Discussion

The effects of temporal variability in sea level on benthic communities have rarely been studied. Yet, extreme low tides associated with increased emersion times of intertidal reef flats are significant drivers of benthic cover dynamic. At the global scale, these tidal events are primarily related to seasonal and interannual variability in mean sea level (Menéndez and Woodworth, 2010). The impacts of emersion are variable across geographical regions but depend on its duration and time of day, both of which are related to the tidal cycle (form, amplitude/range and timing) and mean sea level (Buckee et al., 2022). Moreover, benthic communities exposed to local harsh environmental conditions (e.g. high solar radiation, high or low sea and air temperatures, low salinity, wind stress) during these emersion events are at important risk of massive mortality (Loya, 1976; Hoegh-Guldberg et al., 2005; Leggat et al., 2006; Anthony and Kerswell, 2007; Mejía-Rentería et al., 2020). During the austral winter season from June to August 2015 in Reunion Island (South-West Indian Ocean), the emersion of the shallow reef flat, particularly at low tides, caused benthic communities to die. A negative sea level anomaly led to a drop in mean sea level over several months, resulting in a drastic decline in live benthic organisms on reef flats.

4.1. Negative sea level anomalies

Although there is a high degree of variability of ocean circulation around the Mascarene islands, mean sea levels along Reunion Island's

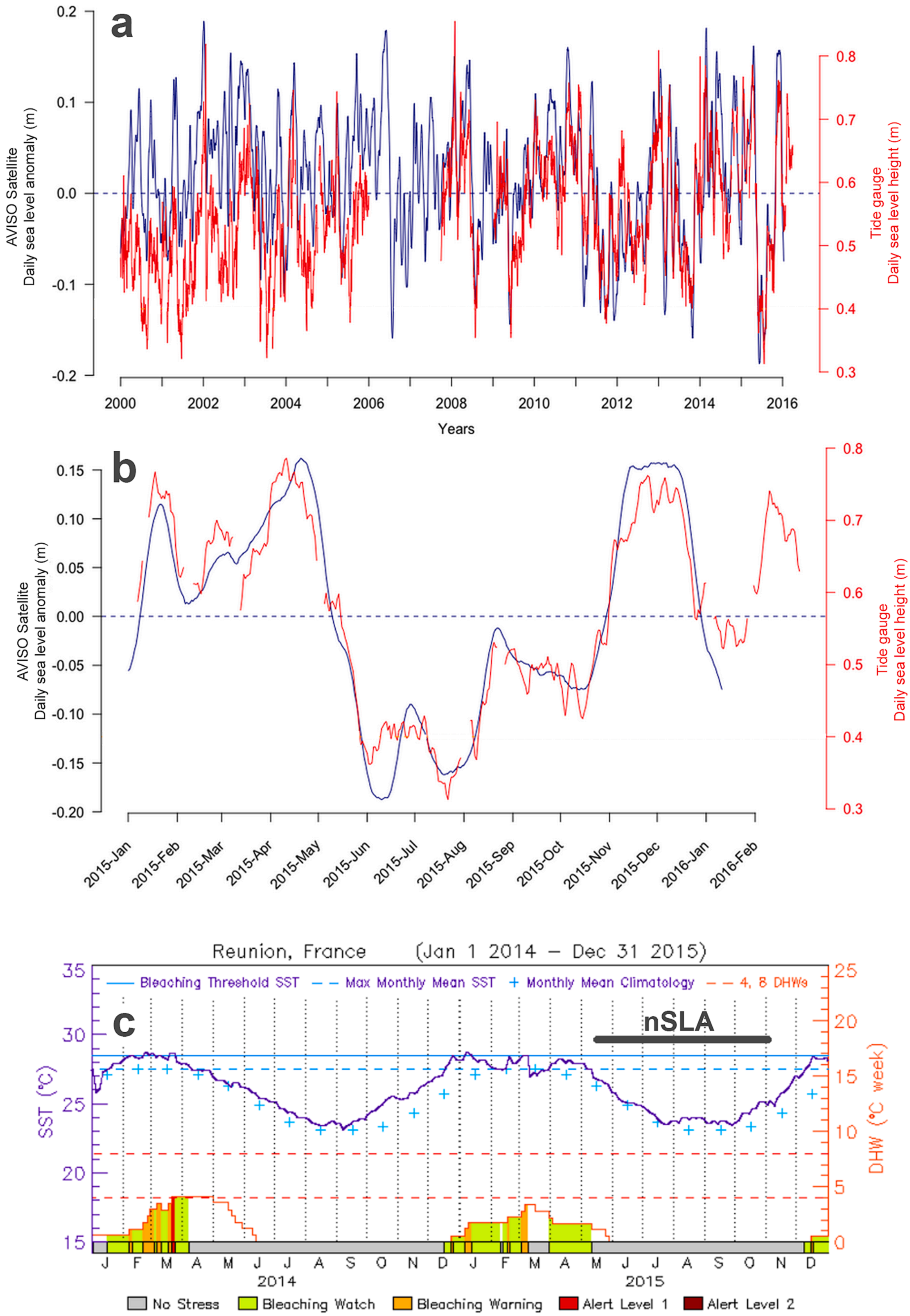

Fig. 6. **a.** Time series of daily mean SLA extracted from satellite altimeter data (blue line) referenced to a five-year period mean and *in-situ* tide gauge at Le Port (red line) from 2000 to 2016 and **b.** zoom in 2015. The blue dotted line in **a.** and **b.** indicates the mean daily sea level for the 2011–2015 period. Time series of sea surface temperature (°C) and During Heating Weeks (°C week) from NOAA data sea surface temperatures for 2014 and 2015 in **c**. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

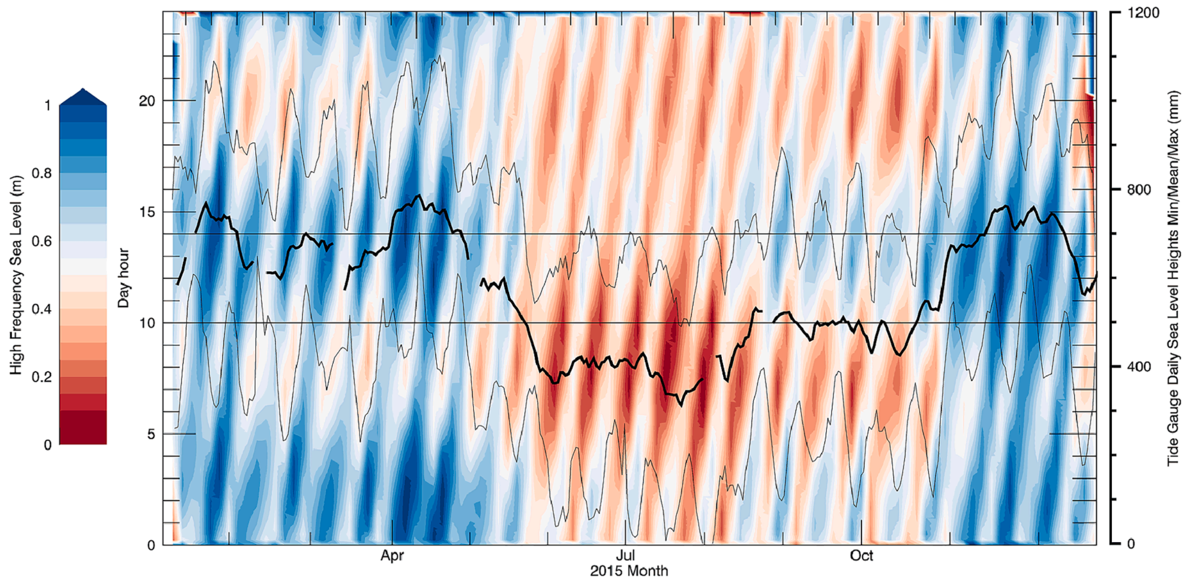

Fig. 7. High frequency sea level matrix according to the day of the year and time of day for 2015, highlighting much lower sea levels at low and high tides (light dark curves) during the May-August negative daily sea level (black curve) anomaly (nSLA). The horizontal lines at 10 h and 14 h indicate times of the day when the sun elevation is at its maximum, during which sea levels were lower between mid-May and mid-August than during usual spring low-tide levels.

coasts are strongly bound to SLA positive or negative cells crossing the Indian Ocean from east to west (Pous et al., 2015). The extreme low tides observed in Reunion Island in 2015 were a result of a drop in the daily mean sea level, which was directly related to these westward propagating mesoscale features, with a wide negative cell that "hit" the Mascarene islands between late May and late October 2015.

While the maximum tidal amplitude at Reunion Island is approximately one meter, the daily mean sea level dropped by 0.44 m in early June 2015 and reached its lowest value since 1999 on 22 July 2015 (i.e., 0.313 m based on daily mean sea level tidal gauge data). This drop in sea level has considerably lengthened the emersion time of the intertidal zone, especially on the bathymetry around the mean tide level (Fig. 8). Large portions of the reef flats and their benthic communities were thus directly exposed to air and high irradiance stresses, notably at midday, over approximately a three-month period. The magnitude and duration of this 2015 event make it quite unique over the last decade (Fig. 10; Supplementary Figure 5). The strong intensity and wide spatial extent of the 2015 nSLA had impacts on coral reefs at a spatial scale exceeding the limits of Reunion Island. Satellite maps of sea surface altimetry computed over a few weeks earlier display this wide depression pattern centered around Rodrigues Islands and then Mauritius, highlighting a regional phenomenon likely affecting most of the South-West Indian Ocean's fringing intertidal coral reefs (Fig. 1).

4.2. Temporal and spatial variability of benthic mortalities

The temporal mortality dynamic of reef flat benthos during the 2015 nSLA can be split into three successive phases: i) the preliminary phase: low or no apparent sign of bleaching or benthic mortality was observed during the first five weeks after the occurrence of the nSLA, until late June 2015; ii) the short-term impact phase: a drastic and rapid increase in coral/crustose coralline algae/seagrasses bleaching and mortalities was observed 5–6 weeks after the beginning of the nSLA (from 7 July 2015). At this stage, nearly 50% of corals were observed bleached or dead; and iii) an extended impact phase occurring 10 weeks after the beginning of the nSLA, when the estimated mortality rates of benthic communities reached up to 90% in places. Bleaching and mortality were very rapid following the nSLA, occurring consistently after 4–6 weeks; this is also in line with thermal-stress-associated coral bleaching temporal dynamics (Baird and Marshall, 2002).

Although low tides in 2015 affected the upper parts of hard corals, numerous other benthic organisms were also affected. For example, soft corals, seagrass beds, and foliaceous crustose coralline algae also died following this event. Thermally-induced bleaching and coral mortality vary greatly across coral species, genera, locations and water depth (Penin et al., 2007) at local, regional (Connell et al., 1997; Goreau et al., 2000; McClanahan et al., 2005) and global scales (Eakin et al., 2019). Our results also highlight considerable variability of the nSLA's impact, depending on the reef flat complexes. These impacts were directly related to water depth, since coral cover declines were the weakest at the deepest reef sites. Benthic organisms of around 5yMSL, whose emersion times are usually little affected by regular variations in tidal range, are those who are the more impacted by an nSLA, which is tallies with the observed RCCV that is much more considerable for those corals at high bathymetric levels. A decrease in coral cover was restricted to 15% of the total cover in Saint-Leu (LCP) where the mean depth (±SD) is −0.64 m (±0.15). In contrast, a decrease of 72% in total coral cover was observed at the shallowest site in Saint-Pierre (RBP), where the mean depth is + 0.01 m (±0.14). The hyperspectral imagery for 2015, acquired only a few days before the nSLA, coupled with very detailed bathymetry, revealed that changes in coral cover reached −45.5% in the southern part of La Saline/Saint-Gilles' inner reef flats, where>95% of all corals are found above the depth of −0.9 m (this corresponds to a loss of 13.0 ha of live coral cover). There was indeed a heterogeneous distribution mortality pattern on this reef area despite the transects being geographically close (i.e., 50 m between transects) and exposed to the same environmental conditions (e.g., water drop, currents, sunlight, temperature, etc.), which may be explained by depth location of reef benthic organisms.

The new remote-sensing methods based on hyperspectral data and Lidar were especially useful in helping to understand and predict the potential impacts of such events. Their high spatial resolutions accurately position the various benthic components in the three-dimensional space, and coupled with impact models make it possible to map and accurately estimate the impacts of such events. Despite the high quality of these data, uncertainties persist, and improvements still need to be made such as in estimating the bathymetry in difficult or specific areas like the surf zone or black sand beaches. Precise spatial information (with location and bathymetric range on the reef) about functional traits and life-history strategies of corals would have been of great interest for

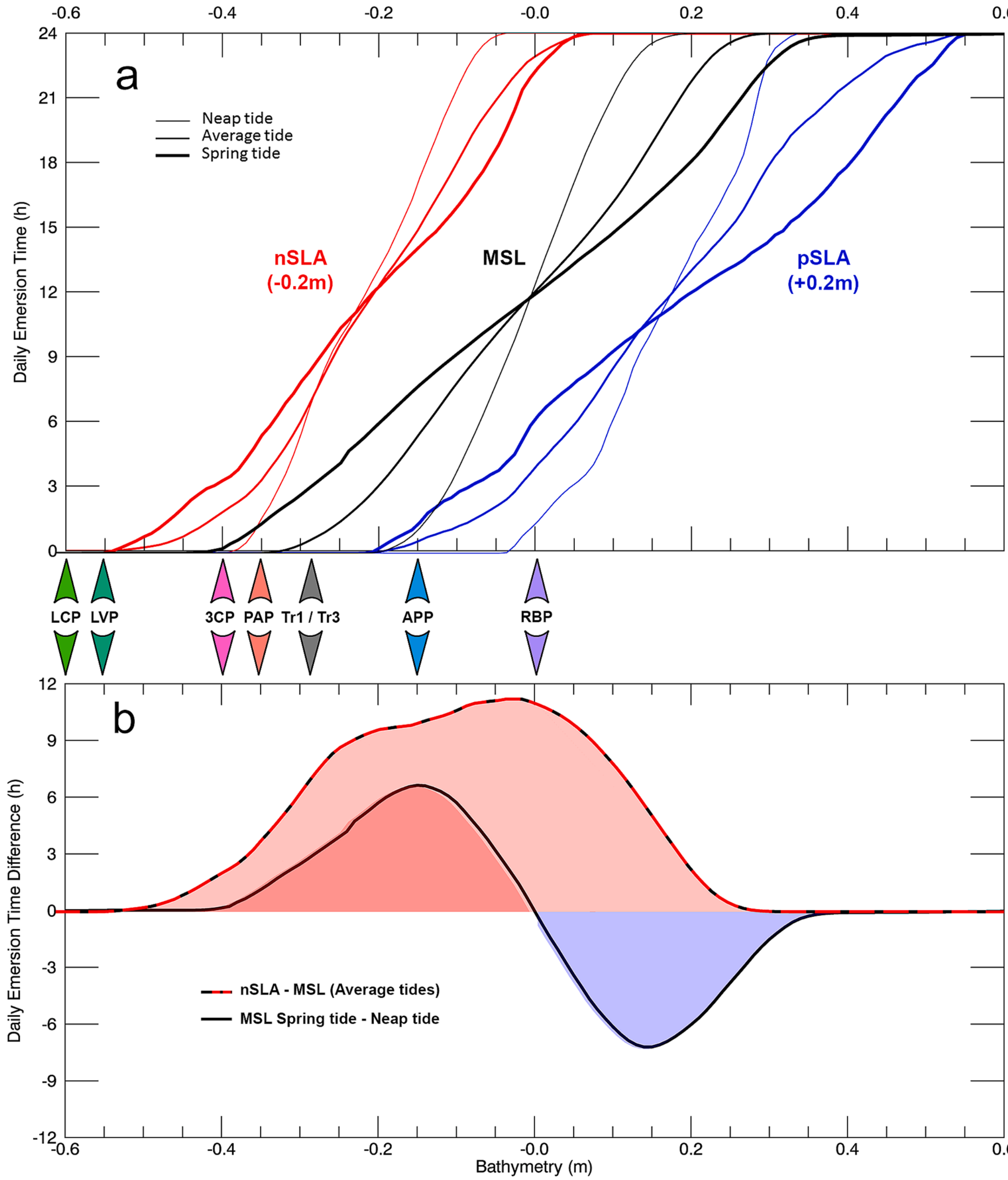

Fig. 8. **a.** Daily emersion time as a function of bathymetry, for three configurations of daily Mean Sea Levels (dMSL): during negative, neutral and positive sea level anomalies (nSLA in red, MSL in black and pSLA in blue respectively), and for three configurations of tides: neap tides (NT, thin lines), average tide (AT, intermediate lines), and spring tides (ST, thick lines). **b.** Difference in emersion times between nSLA and MSL, and ST and NT for MLS. Colored arrows for mean bathymetric positions of surveyed reef sites: Trois Chameaux Platier (3CP), Planche Alizés Platier (PAP), La Corne Platier (LCP), La Varangue Platier (LVP), Etang-Salé Platier (ESP), Ravine Blanche Platier (RBP) and Alizé Plage Platier (APP). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

investigating their potential sensitivity to nSLA disturbances, as coral species show contrasted responses to environmental disturbances (Carpenter et al., 2008; Darling et al., 2012; Hughes et al., 2018). For instance, massive corals are likely more resistant to long emersion than branching and digitate corals (Fishelson, 1973) which may be related to more efficient mechanisms to resist dehydration and UVs in massive coral forms (Krupp, 1984; Brown et al., 1994) through for example mucus secretion (Brown and Bythell, 2005).

The emersion of coral reefs depends on multifactorial parameters which are mainly linked to the characteristics of the bathymetry, tide and mean sea level. Variations in the dMSL as well as variations in tide intensity have significant effects on the emersion time of deeper reef flat areas that are usually continuously immersed, but also on the emersion time of the central intertidal zones with depth approximating the MSL, which can result in prolonged exposure of benthic communities to air for many hours. These prolonged emersion times are to be put into perspective with the conjunction of other aggravating factors such as cold/warm air temperature or high solar radiation (e.g., Fadlallah et al.,

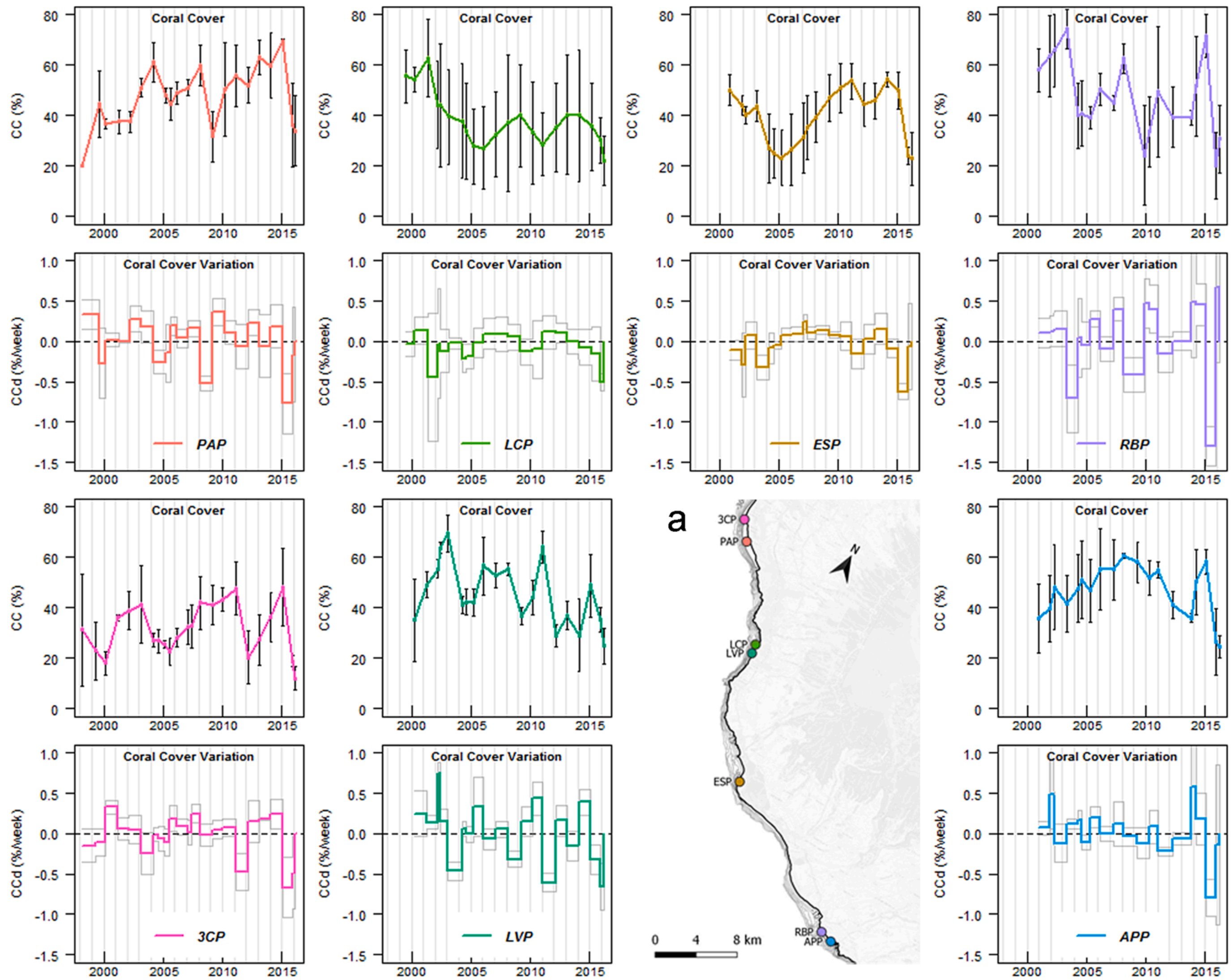

Fig. 9. Dynamics of Reunion Island's live coral cover across the 7 GCRMN reef flat sites at Trois Chameaux Platier (3CP), Planche Alizés Platier (PAP), La Corne Platier (LCP), La Varangue Platier (LVP), Etang-Salé Platier (ESP), Ravine Blanche Platier (RBP) and Alizé Plage Platier (APP) **a.** between 1998–2000 and 2016. Coral covers (CC) are expressed in percent, and the derivative (CCd) is the variation of these covers in percent per week. Error bars and grey lines correspond to ± SD Standard Deviation.

1995; Anthony and Kerswell, 2007). In 2015, between June and August, emersions of benthic communities occurred daily whatever the tidal range, frequently at noon (i.e., between 10 h and 14 h) while temperatures and solar radiations were at their highest. Higher coral survival rates during extreme low tides are likely to be related to greater water circulation favored along deeper substrates (Raymundo et al., 2017). Meteorological forcing (wind, breaking waves on the reef crest) induces an increase in water exchanges between the open ocean and the reef, causing water influx over the reef flats and an elevation in sea level (Cordier et al., 2013). In addition, the wave breaking induces mist and moistening and is likely to play a critical role in preventing coral mortality (Raymundo et al., 2017). Further studies would be required to precisely assess the specific factors, conditions and application rules of these multiple beneficial or deleterious factors, and their impacts on water levels along the reef flats.

4.3. Major disturbances on reef flats

Previous extreme low-tide events resulting in significant mortality of reef flat corals were reported in Reunion in the austral summers of 1982–1983 (Guillaume et al., 1983; Naim, 1993), in 1998–1999 (Tessier et al., 2008) and in 2011 and 2013 (source tide-gauge; undescribed event in the literature). The 2015 nSLA was long in duration (>3 months) and also the strongest in amplitude over the past decade (minimum daily mean sea level of –0.24 m compared to −0.16 m in 2011). During the summer of 1982–83, shifts in benthic communities were observed following a series of extreme low tides (Guillaume et al., 1983), which resulted in substantial mortality of reef corals (Naim, 1993) at the La Saline/Ermitage site. A 9% decline in coral cover at 3CP attributed to extreme low tides was also reported in 1998–1999. In our study, a decrease of 29.3% in coral cover was estimated at this site following the 2015 nSLA. Overall reef flat coral cover decreased significantly from 54.5 ± 12.7% in early 2015, to 27.4 ± 6.9% in November 2015. This is equivalent to a relative coral cover loss of 49.7% following the 2015 nSLA event, which is the largest decline of corals recorded in Reunion Island over nearly two decades of surveys. The reduction in live coral cover due to this environmental disturbance was accompanied with increases in dominance by turf algae, which may lead to phase-shifts of reef-building coral to algal dominance (Hughes, 1994; McCook, 1999; Diaz-Pulido and McCook, 2002; McClanahan and Muthiga, 2002; Rogers and Miller, 2006; Hughes et al., 2007).

Our findings highlight how changes in coral cover relate to sea level

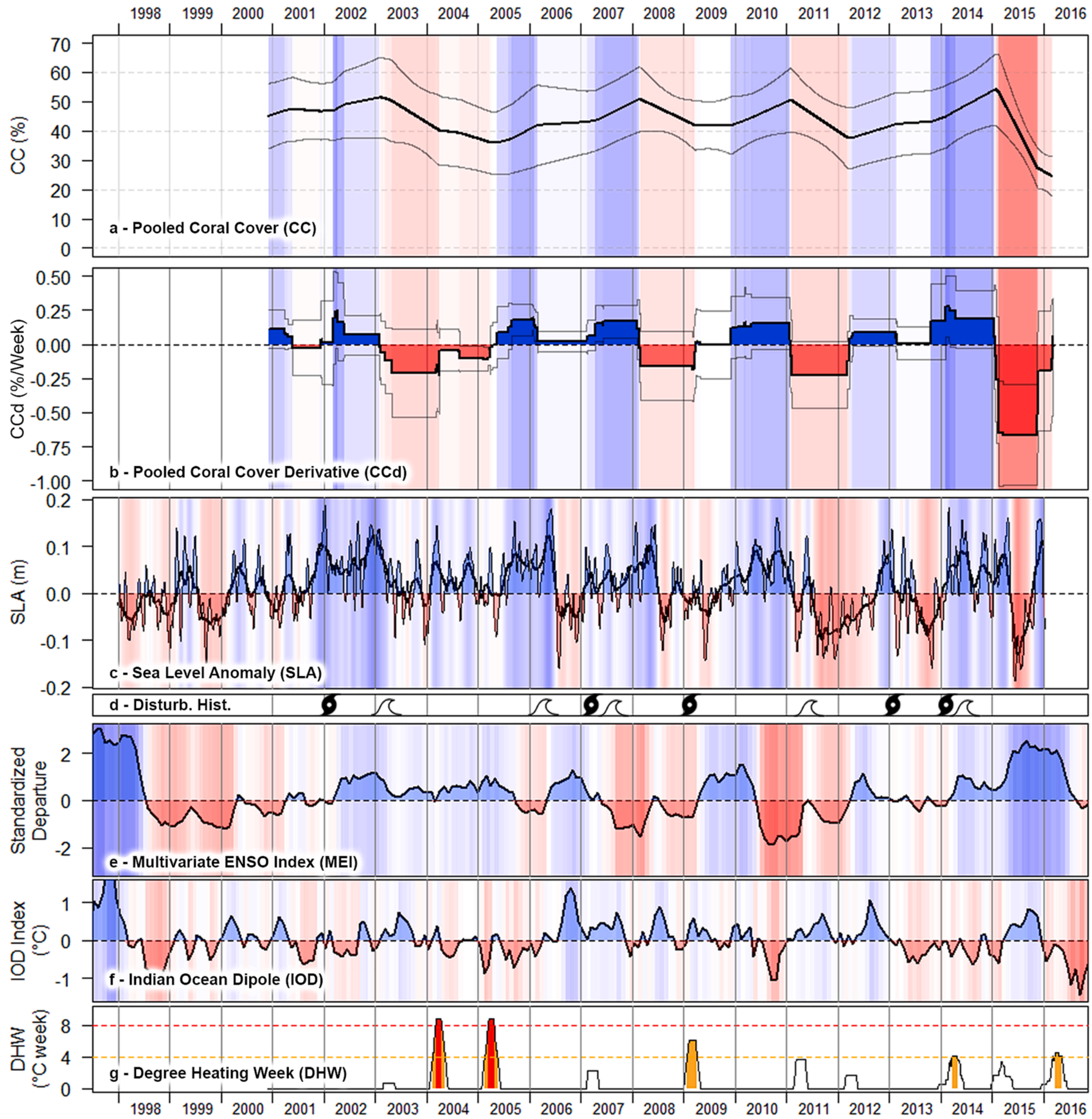

Fig. 10. Time series of **a.** the pooled coral cover and **b.** its derivative over time for the GCRMN data, **c.** the sea level anomaly, **d.** Major hydrodynamic events such as (intense) cyclones (black storm symbol) and austral swells (light wave symbol), **e.** Multivariate ENSO index (MEI), **f.** Indian Ocean Dipole index (IOD), and **g.** Degree Heating Weeks (DHW). Grey lines correspond to ± SD Standard Deviation.

anomalies. Coral cover increases during positive SLA, while a decrease in shallow coral cover is not systematically associated with nSLA values. For instance, significant coral decline was recorded in 2002–2003 when the sea level was relatively stable over the reef flats. In addition, in late 2006 and 2013 nSLAs were not associated with major benthic mortalities but rather were linked to relative stability. The apparent limited impacts of these latter two nSLA events may be explained by i) nSLA being low in duration and magnitude and therefore causing no significant impact on coral cover, ii) the data was collected after the sea level rose to normal and while coral covers were starting to recover. Even if these two nSLA events of 2006 and 2013 cannot be linked to a significant decrease in coral cover, it is noteworthy that no significant variation in coral cover is observed, highlighting a marked slowdown in a three-year period of coral growth (2005–2007 and 2012–2014 respectively).

Nonetheless, since 2000, Reunion Island's reef flat corals have suffered four major declines in coral cover, in 2003–2004, 2008–2009, 2011 and 2015–2016. Except for the period 2003–2004, these declines are associated with the occurrence of nSLAs that lasted over a month. For 2003–2004, temperature anomalies ($DHW > 8$) in summer and a strong austral swell in winter were responsible for this period's decrease in coral cover. In 2009, $DHW < 4$ and intense tropical cyclone Gael weakened already affected reef flat corals, delaying their recovery. Based on our results, the effects of such major hydrodynamic events, including substantial austral swells, on reef flat coral cover are relatively limited in comparison with high nSLAs, although cyclone-induced runoff can be a significant cause of disturbance for coral reef at specific sites (Naim et al., 2000).

The earliest evidences of reef flat exposure mortalities of corals due to unusual low sea levels were documented in the Eastern Pacific in Panama in 1974–75 and in 1988–89. Both extreme reef flat exposure events resulted mass coral bleaching and mortality and occurred during La Niña event (Glynn, 1976; Eakin et al., 1989). Likewise, low tidal exposure events resulted in extensive reef flat mortalities in Costa Rica during La Niña years (Cortés and Jimenez, 2003). Mass coral mortalities due to reef flat exposure events were also documented in the South Pacific during the early phases of El Niño in 1983, in French Polynesia and Tokelau Islands (Glynn, 1984) but were likely broader in the Pacific region as extreme sea level drops were noted in various atolls over the central and northern Pacific region (see Glynn et al., 2017). Our findings show that changes in coral cover in the South-West Indian Ocean region is to some extent correlated with ENSO. Coral cover in the Chagos Archipelago (Central Indian Ocean) dropped by at least 30% at depths of 15 m during the major 2015 ENSO event (Sheppard et al., 2017). Coral mortalities on Reunion Island reef flats coincided with a strong 2015 MEI, while 2008 and 2010 mortalities occurred during a negative MEI. Overall, we found a negative correlation between coral cover and MEI. Although ENSO events can have a global influence on sea levels, there are significant variabilities in space across locations (Menéndez and Woodworth, 2010). Nonetheless, years with MEI > 2 (1998–1999 and 2015–2016) display the two largest drops in mean sea level over the past two decades. Similarly, mass coral bleaching induced by thermal stress coincided with El Niño in the Indian Ocean (Chambers et al., 1999), with anomalous low sea levels around the Mascarene Islands corresponding to a strong El Niño event. Moreover, there is an obvious relationship between changes in coral cover and IOD in Reunion Island reef flats. In particular positive IOD were associated with a decrease in coral cover and negative SLAs. Our results are congruent with previous works (Webster et al., 1999) showing extreme low tides experienced at Ko Phuket, Thailand in 1997–1998 as a result of the Indian Ocean Dipole. As in the Andaman Sea, the fluctuating climate processes of ENSO and IOD, which modulate sea level and temperature, are the primary drivers of coral cover in Reunion Island reefs (Dunne et al., 2021). Nonetheless, further research is needed to clarify such possible correlations. Assessment of coral mortalities during El Niño events must not be restricted only to heating sea temperatures but also to the impacts of drops in sea level (Buckee et al., 2019, 2022; Raymundo et al., 2019).

The mortality event described here supports previous works calling for higher attention to variability in water levels and the importance of considering emersion mortality risks on shallow coral reef platform habitats (Ampou et al., 2017; Buckee et al., 2019, 2022) related to ENSO/IOD impacts (Dunne et al., 2021). These impacts of sea level drop on coral reef were omitted in previous reports on global evaluation of impacts of ENSO on coral ecosystems (Claar et al., 2018; Eakin et al., 2019). In addition, our findings highlight that coral mortality extends across Reunion Island reef. There have been rapid and considerable changes in coral covers due to prolonged and high-amplitude nSLAs, in particular in 2015 during El Niño conditions with the highest overall coral cover decline ever recorded across Reunion Island's reef flat sites. Our findings highlight how nSLA and variability in MSL in combination with depth ranges of substrates are significant drivers of variability in coral cover, which has so far been overlooked in coral reef ecology. Similarly to Buckee et al. (2022), our findings confirm that emersion is a fundamental driver of coral cover on shallow reefs and needs to be taken into consideration when assessing temporal changes in these ecosystems. In addition, in the face of projected global warming, potential reef recovery may be jeopardized by various other reef disturbances, whether they are natural disturbances including cyclones and rainfall-induced freshwater inputs, heat-induced coral bleaching, or anthropogenic disturbances (e.g., water pollution, groundwater discharges, or eutrophication) chronically affecting Reunion Island (Naim, 1993; Naim et al., 2013; Cuet et al., 2011a,b; Tourrand et al., 2013) but also worldwide coral reef ecosystems (Hughes et al., 2003; 2017; 2018; Lesser et al., 2021) and eroding their resilience.

CRediT authorship contribution statement

Ludovic Hoarau: Writing – original draft, Methodology, Validation, Investigation, Conceptualization, Data curation, Formal analysis, Software, Visualization, Writing – review & editing. **Pascal Mouquet:** Writing – original draft, Methodology, Validation, Investigation, Conceptualization, Data curation, Formal analysis, Software, Visualization, Writing – review & editing. **Michel Ropert:** Resources, Supervision, Project administration, Funding acquisition, Writing – review & editing. **Alexis Cuvillier:** Investigation, Conceptualization, Writing – review & editing. **Lola Massé:** Writing – review & editing. **Sylvain Bonhommeau:** Data curation, Formal analysis, Software, Visualization, Writing – review & editing. **Lionel Bigot:** Investigation, Conceptualization, Writing – review & editing. **Bruce Cauvin:** Resources, Writing – review & editing. **Karine Pothin:** Resources, Writing – review & editing. **Touria Bajjouk:** Methodology, Validation, Investigation, Conceptualization, Resources, Supervision, Project administration, Funding acquisition, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2023.110508.

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