



Original Article

Destructive outbreaks of the corallivorous starfish *Acanthaster cf. solaris* spare coral assemblages in the shallowest reef flat areas in New Caledonia

Pascal Dumas ^{1,2,*}, Christophe Peignon¹, Mahé Dumas¹, Bertrand Bourgeois³, Hugues Gossuin⁴, and Sylvie Fiat¹

¹IRD, UMR 9220 ENTROPIE, BP A5, Nouméa, New Caledonia

²Laboratoire d'Excellence "Corail," 58 avenue Paul Alduy, 66860 Perpignan, France

³IRD, US IMAGO, BP A5, Nouméa, New Caledonia

⁴Aquarium des Lagons de Nouméa, 61 promenade Roger Laroque, 98800 Nouméa, New Caledonia

*Corresponding author. Email: pascal-paul.dumas@ird.fr

Dumas, P., Peignon, C., Dumas, M., Bourgeois, B., Gossuin, H., and Fiat, S. Destructive outbreaks of the corallivorous starfish *Acanthaster cf. solaris* spare coral assemblages in the shallowest reef flat areas in New Caledonia. – ICES Journal of Marine Science, 79: 350–361.

Received 1 September 2021; revised 14 December 2021; accepted 17 December 2021; advance access publication 20 January 2022.

Outbreaks of the corallivorous starfish *Acanthaster cf. solaris* (COTS) are not fully understood, especially in the shallowest areas behind the reef crests where limited COTS impacts are often reported. Here, we investigated the outbreak occurrence and compared post-outbreak habitat impacts in reef flats vs. upper fore reefs at 13 sites in New Caledonia. In this Pacific territory so far considered marginally affected by COTS, we documented wide occurrences of aggregations, combining massive population increases (maximum 605 COTS per swim, abundances > 100 COTS recorded in 46% of the sites) with limited spatiotemporal boundaries. Abundance levels met the highest values in the literature, but were restricted to relatively small, isolated mid-shelf reefs. Typical residence time was short (< two years), with at least one site where COTS seemingly disappeared within seven months. The spread of COTS population and subsequent impacts appeared self-contained, and never affected the reef flats (0.5–1.5 m). The transition to severely affected fore reefs was abrupt, with live coral cover divided by nine and morphological diversity halved within a very few meters (3–5 m). We suggest that these differential impacts likely result from harsh environmental conditions making shallow, coral-rich areas less suitable for COTS, thereby pushing predation pressure further downwards.

Keywords: *Acanthaster* outbreaks, coral reef management, habitat degradation, pest species.

Introduction

The large, voracious crown-of-thorns starfish *Acanthaster* spp. (COTS) is a specialized coral predator characterized by unpredictable, massive population fluctuations eventually reaching unsustainably high densities in tropical and subtropical reefs (Edean and Chesher, 1973; Moran, 1986; Zann *et al.*, 1990). Studies suggest an increasing prevalence of these outbreaks in the very recent decades, most likely driven by a combination of natural and anthropogenic disturbances (Baird *et al.*, 2013; Pratchett *et al.*, 2017a; Haywood *et al.*, 2019). Managing the consequences of severe coral

mortalities (e.g. >95%, Tkachenko *et al.*, 2020) with cascading effects across all ecosystem compartments adds considerable pressure on decision-makers, leading to unprecedented conservation concerns and management effort in Pacific island countries (Dumas *et al.*, 2020; Plagányi *et al.*, 2020).

Sustained research efforts during the recent decades have emphasized the need to develop proactive, effective management approaches that are able to address the intrinsic variability of the COTS phenomenon (Hoey *et al.*, 2016; Pratchett and Cumming, 2019). Outbreaks differ greatly in severity, duration and size across COTS distribution range: from recurrent, almost chronic events

eventually spreading across entire, connected reefs systems to punctual disturbances affecting single sites or isolated reefs (review in Pratchett *et al.*, 2014). They typically start along the reef slope at various depths before opportunistically extending upwards, under the combined influence of ontogenic changes in the feeding behaviour of starfish and an increasing competition for food within adult populations (Moran, 1986; Keesing, 1990; Johnson *et al.*, 1991). Greater impacts on coral assemblages are generally expected on the fore reef for highest population densities (hundreds to thousands COTS.ha⁻¹) and longer outbreak persistence, e.g. 3–5 years or more (Osborne *et al.*, 2011; De'ath *et al.*, 2012; Pratchett *et al.*, 2014; Pratchett *et al.*, 2017b). However, the effects of outbreaks will strongly vary depending upon site characteristics (including composition/structure of local coral assemblages, reef geomorphology and hydrodynamics, frequency/intensity of other disturbances), the structure and dynamics of local COTS populations, and the management framework eventually in place (Pratchett *et al.*, 2009; Vanhatalo *et al.*, 2017; Westcott *et al.*, 2020). Marked food preferences for certain genera and coral growth forms (such as fast-growing, branching *Acropora* and *Montipora* spp.) are in particular exhibited by COTS, which entails spatially heterogeneous mortality—especially at low/intermediate predation levels whereas species-specific, sequential depletion of corals is often observed across the fore reef and deeper areas (Birkeland and Lucas, 1990; De'ath and Moran, 1998a; Kayal *et al.*, 2012). Impact patterns are less clear in the upper reef areas behind the reef crest, where lower COTS predation is often reported despite an abundance of prey, suggesting that other behavioral and environmental clues also influence their fine scale distribution (De'ath and Moran, 1998b; Saponari *et al.*, 2018). However, few studies have focused on the prevalence and fine scale patterns of predation in these shallowest coral areas, where reduced COTS occurrence and marked logistical constraints (hydrodynamics, water depth, COTS residence time) make sampling uneasy.

Here, we investigated outbreak occurrence in the shallow coral assemblages (reef flats vs. upper fore reefs <5m depth) in New Caledonia, a Pacific territory whose highly diversified coral reef formations were until recently considered preserved from widespread COTS damage. While no dedicated management framework is in place, citizen monitoring reported highly localized, ephemeral increases in COTS population affecting a number of coastal and barrier reefs since 2015 (Adjeroud *et al.*, 2018; Dumas *et al.*, 2020). We surveyed the trajectory of COTS abundances to assess their typical residence time in 13 very shallow, coastal fringing and mid-shelf reef sites affected by outbreaks. We also assessed the post-outbreak structure of coral habitats in reef flats vs. fore reefs to investigate if massive, yet potentially ephemeral COTS population outbreaks may eventually entail differential impacts across these areas.

Material and methods

The study area was located in the Southwestern lagoon of New Caledonia, a large area of approximately 5500 km² with an average depth of 15–20 m, harboring a highly diversified reef complex including coastal fringing reefs, mid shelf reefs, inner-shelf barrier reefs and outer reef slopes (Richer de Forges, 1991). We surveyed COTS and shallow coral assemblages in 13 reefs where a recent citizen science programme emphasized the increasing occurrence of outbreak populations (the OREANET initiative, <http://oreanet.ird.nc/>)

(Figure 1). Sites were repeatedly surveyed for COTS between 2016 and 2020, following the first report of unusually high starfish abundances by participants of the OREANET monitoring programme. The number of surveys varied between two and five per site, mostly depending upon logistical constraints including the site distance from the capital city Noumea, the depth range and accessibility of the upper reef areas, the exposure to the dominant trade winds, and the overall meteorological conditions (Table 1).

COTS census

At each site, COTS abundances were recorded during the day using standardized 10-minute swims, conducted by a team of two to five experienced snorkelers swimming parallel to the reef edge. All surveys focused on the shallow portion of the reef (0.5–5 m depth). Observers progressed at a constant speed and carefully searched COTS in the reef flat vs. upper fore reef areas, with 5–10 m between observers to avoid overlap. The position of the timed swims was recorded by a handheld Garmin GPSMAP 64 GPS placed in an underwater housing. We then used an empirical conversion ratio based upon the average reef surface covered during a typical 10-minute swim to derive estimates of COTS density, expressed in number of COTS per hectare. The area surveyed was calculated by using the linear distance travelled along the reef edge, multiplied by an estimate of the corridor width where observers actually looked for COTS (2 m). We used the three-levels abundance/density thresholds recently developed in New Caledonia to classify the COTS populations by Dumas *et al.* (2020), where values above five starfish. 10 min⁻¹ (100 COTS.ha⁻¹) were indicative of an outbreak. The potential duration of an outbreak event was estimated as the duration between the initial survey with outbreak densities and the first consecutive survey where densities were back under the threshold.

Habitat description

On the last visit (2020), benthic substratum surveys were performed simultaneously with COTS census along a series of transects, to investigate the spatial distribution of COTS impacts in shallow coral habitats. At each of the 13 reef sites, a total of 20 random, 20 m-transects were surveyed in two regions of the upper reef area, each side of the reef crest: 10 transects along the reef flat (mean depth 1.0 ± 0.5 m) vs. 10 transects along the upper fore reef (mean 4.0 ± 1.0 m). The transects were materialized by a color-marked survey tape attached to the substratum. The surface cover of corals and other benthic categories was estimated using a quantitative photographic approach. A total of 21 m² photo quadrats per transect (one every meter) were recorded with a digital camera equipped with a wide-angle lens and subsequently imported into a dedicated image analysis program (CPCe software, Kohler and Gill, 2006). Eighteen local habitat variables related to coral growth forms (10 categories), rocky substrates (4 categories), fine sediments (2 categories) and cyanobacteria/algae and macrophytes cover (2 categories) were considered (Table 2). For coral assemblages, the number of unique coral categories recorded per transect was used as a proxy of morphological richness. Surface estimates expressed in percentage covers were derived from random stratified point count techniques using a 9 points.m⁻² ratio (Dumas *et al.*, 2009). Percentage covers were then aggregated at the transect level.

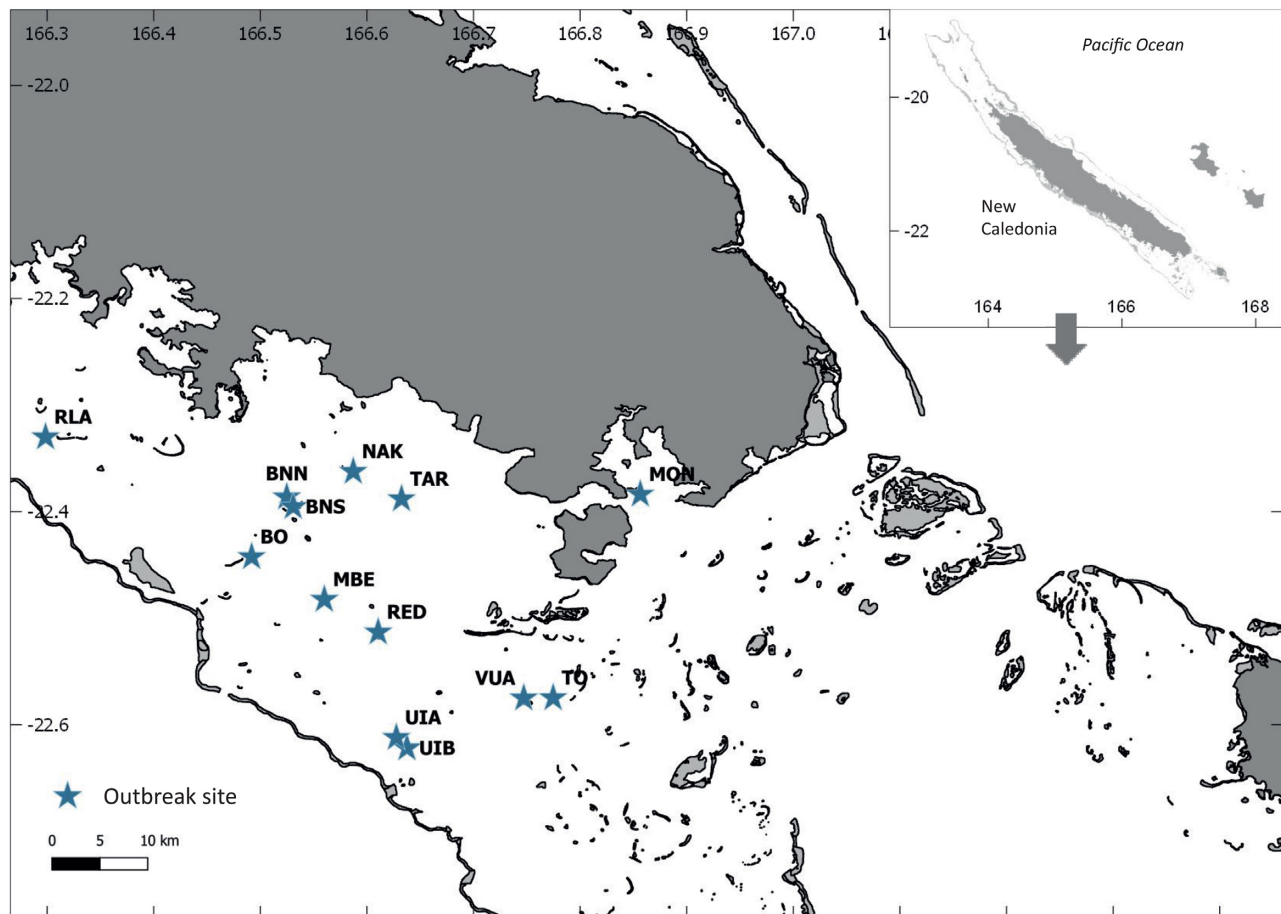


Figure 1. Location of COTS survey stations in the southwestern lagoon of New Caledonia (South Pacific). See Table 1 for site details and abbreviations.

Table 1. Characteristics of the study sites in the southwestern lagoon of New Caledonia (South Pacific). Distance from the capital city Noumea (km); reef type and exposure to the dominant trade winds for the 13 survey sites. Total number of surveys with total number of COTS recorded per site and COTS abundance (mean, SE, maximum) expressed in number of COTS per swim during outbreaks. Density equivalents in COTS per hectare.

Site	Distance (km)	Reef type	Wind exposure	Nb surveys	COTS total	Mean COTS/swim	Max COTS/swim	Mean COTS/ha ⁻¹	Max COTS/ha ⁻¹
BNN	14.64	mid-shelf	Leeward	2	97	16.2 (2.9)	26	402 (73)	646
RLA	16.4	mid-shelf	Windward	3	279	16.3 (4.3)	101	404 (107)	2 500
NAK	16.41	mid-shelf	Leeward	3	331	18.4 (5.5)	82	457 (137)	2 037
TAR	21.88	mid-shelf	Leeward	3	183	22.9 (1.3)	30	568 (32)	745
BO	17.81	mid-shelf	Windward	2	357	29.8 (7.1)	90	739 (175)	2 236
UIB	41.86	mid-shelf	Windward	2	205	34.2 (16.6)	122	849 (413)	3 031
TO	46.21	mid-shelf	Leeward	2	288	48.0 (10.7)	80	1 193 (257)	1 987
BNN	13.47	mid-shelf	Leeward	2	506	50.6 (7.6)	95	1 257 (190)	2 360
RED	30.04	mid-shelf	Leeward	4	2162	56.9 (20.7)	605	1 413 (515)	15 030
UIA	40.42	mid-shelf	Windward	2	1074	59.7 (15.2)	214	1 482 (379)	5 316
VUA	44.22	mid-shelf	Leeward	5	1520	17.1 (4.0)	210	424 (100)	5 217
MON	43.19	coastal fringing	Windward	4	4731	68.6 (8.3)	280	1 703 (206)	6 956
MBE	24.48	mid-shelf	Leeward	2	1398	116.5 (33.6)	350	2 894 (834)	8 695

Data analysis

We tested the influence of site and exposure (leeward vs. windward areas) on COTS abundances using 2-way permutational multivariate analysis of variance (PERMANOVA), with subsequent pair-wise

tests by permutation using 9999 permutations. The structure of shallow reef habitats was investigated using a combination of univariate and multivariate approaches. First, a multidimensional similarity matrix based upon the calculation of Euclidian distances

Table 2. Benthic categories used for habitat characterization in the sampling sites, southwestern lagoon of New Caledonia (South Pacific).

Corals	Sediment	Other
Branching (BR)	Mud (MUD)	Seagrass (SEAG)
Digitate (DIG)	Sand (SA)	Algae, cyanobacteria (ALG)
Tabular (TAB)	Coral rubble (RUB)	
Massive (MASS)	Boulders (<100 cm) (BOUL)	
Submassive (SUBMASS)	Dead Corals (DEAD)	
Foliose (FOL)	Bedrock (RO)	
Encrusting (ENC)		
Soft (Alcyonarians) (SO)		
Fire (FI)		
Bleached (BLEA)		

between all transects was built using all 18 substratum variables. The transects were then ordinated using Principal Coordinates analysis (PCO) to establish a multivariate typology of habitats. Habitat differences between depth zones (reefflat vs. upper fore reef) and sites were tested using 2-way PERMANOVAs and subsequent pair-wise tests by permutation. The potential influence of contrasted depth difference between pairs of transects (reefflat vs. upper fore reef) on habitat variables was tested using Pearson's correlation moment. The influence of zone and exposure on the live coral cover and the morphological richness was further investigated using 2-way PERMANOVAs and subsequent pair-wise tests by permutation. All calculations (arithmetic means \pm SE) and subsequent analyses were performed using PAST3 and Primer v.6 with PERMANOVA add-on packages.

Results

COTS trajectory

Elevated abundances of starfish were confirmed in all the survey sites, with initial values systematically well above the threshold considered for outbreak populations (threshold five COTS per swim). The mean abundance per site ranged from 16.2 ± 2.9 to 116.5 ± 33.6 COTS per swim, with a maximum record of 605 COTS per swim. About half of the sites (46%) exhibited values > 100 COTS per swim on a least one occasion. While the sites were characterized by contrasted COTS abundance levels, reefs with different exposure (leeward vs. windward) did not exhibit significant differences (PERMANOVA, pseudo-F = 1.34, $p < 0.001$ /pseudo-F = 0.006, $p = 0.89$, N.S. for site and exposure, respectively).

COTS population trajectory exhibited very similar patterns in the surveyed reefs. Following the initial report of abnormal abundances, values progressively dropped to reach non-outbreak levels during the course of the study in all but one (RLA) sites (Figure 2). In the latter, COTS densities were still above the threshold during the final survey (400 ± 155 COTS.ha⁻¹, 8.1 months after the initial report). A slightly different pattern was observed in VUA, where COTS population continued to grow after the initial report of outbreak densities (307 ± 114 COTS.ha⁻¹) to reach extreme values (1843 ± 567 COTS.ha⁻¹ after seven months); densities then decreased and eventually returned below the threshold. The estimated duration of outbreak events ranged from 7.1 months (TAR) to >45 months (VUA), with a median value of 21.7 months. COTS were not recorded anymore in nine sites during the last survey, and were barely observable in two (BNN/VUA:1 or 2 COTS observed). The last two sites still exhibited well-developed COTS populations,

with densities slightly below (MON; 94 ± 32 COTS.ha⁻¹) or clearly above (RLA; 400 ± 155 COTS.ha⁻¹) the threshold.

Coral habitat

In the 13 reef sites, the depth difference between upper (reef flat) vs. lower (upper forereef) stations was very limited (mean 3.0 ± 0.9 m, range 1.3–4.6 m). However, the multivariate analysis of the 18 benthic variables highlighted contrasted benthic habitats (PERMANOVA, pseudo-F = 12.383, $p = 0.002$ for upper vs. lower stations). PCO ordination highlighted a marked coral/rubble gradient, discriminating the upperstations characterized by more developed coral assemblages with a variety of ecomorphs, from the lower stations with reduced live corals and increased bedrock/rubble cover (Figure 3). Significant differences were recorded for the overall live coral cover (mean 46.2% vs. 5.1% for upper vs. lower stations, respectively; pseudo-F = 42.23, $p = 0.001$), including dominant branching corals (30.5% vs. 2.6%; pseudo-F = 17.92, $p = 0.004$), tabular corals (5.7% vs. 0.1%; pseudo-F = 11.06, $p = 0.007$) and digitate corals (2.3% vs. 0%; pseudo-F = 7.49, $p = 0.013$). In contrast, lower stations (fore reef) had significantly more bare rock substratum (21.3% vs. 13.7% for lower vs. upper stations; pseudo-F = 41.015, $p = 0.001$) and much higher coral rubble cover (40.7% vs. 12.2% for lower vs. upper stations; pseudo-F = 30.98, $p = 0.002$) (Figure 4).

For most habitat variables, the magnitude of the observed changes was not related to the depth difference between the upper and lower stations (Pearson's correlation, r^2 with depth difference < 0.2 for live corals, rubble, rocky substratum, algae; N.S.). This was particularly evident for live coral, which generally exhibited marked reductions across very limited depth range. This was for example observed in BO where live coral cover dropped from 82.4% at 1 m to 6.7% at 3 m, i.e. a -75% difference within 2 m depth. A very similar pattern was observed in a number of sites: RLA, -68.9% coral drop within 2.5 m; UIA, -49.8% drop within 3.0 m; RED, -61.2% drop within 3.3 m; MON, -60.1% drop within 3.7 m.

The exception was for dead corals, where larger differences in cover were generally found in reef sites with greater depth range ($r^2 = 0.36$, $p < 0.05$); however, no significant pattern could be discerned when comparing upper vs. lower stations (PERMANOVA, Pseudo-F = 0.10, N.S.).

Coral assemblages also exhibited a much higher morphological richness in the shallowest zones (Figure 5). Transects in the reef flats harbored a maximum of nine different coral categories (i.e. branching, digitate, tabular, massive, sub-massive, foliose, encrusting, soft, firecorals) with an average of 4.7 ± 0.2 categories per transect;

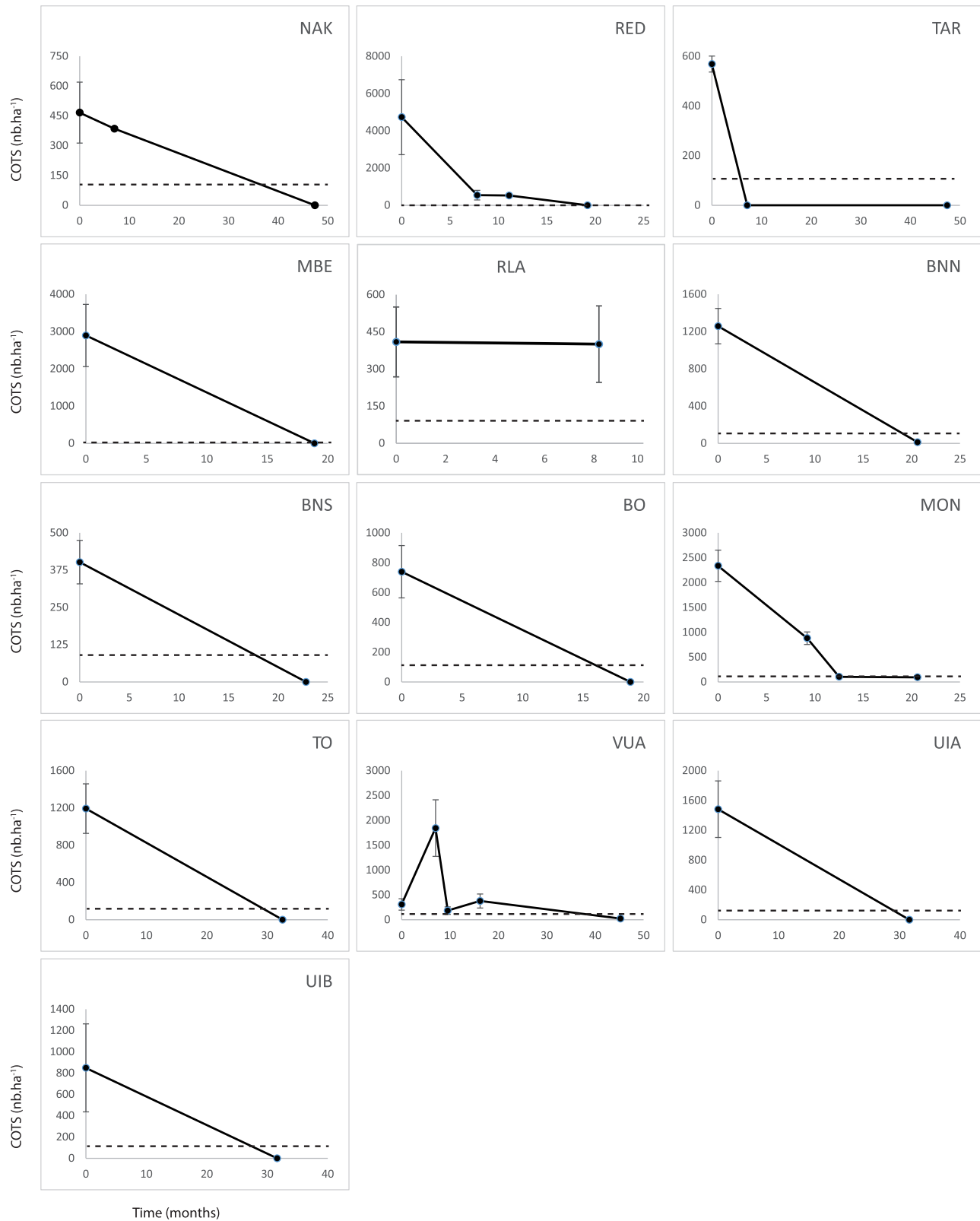


Figure 2. Temporal patterns of COTS abundances in outbreak sites in the SW lagoon, New Caledonia. Means \pm SE for number of COTS per ha. Dashed line: outbreak threshold in New Caledonia from Dumas et al., 2020. See Table 1 for site abbreviations.

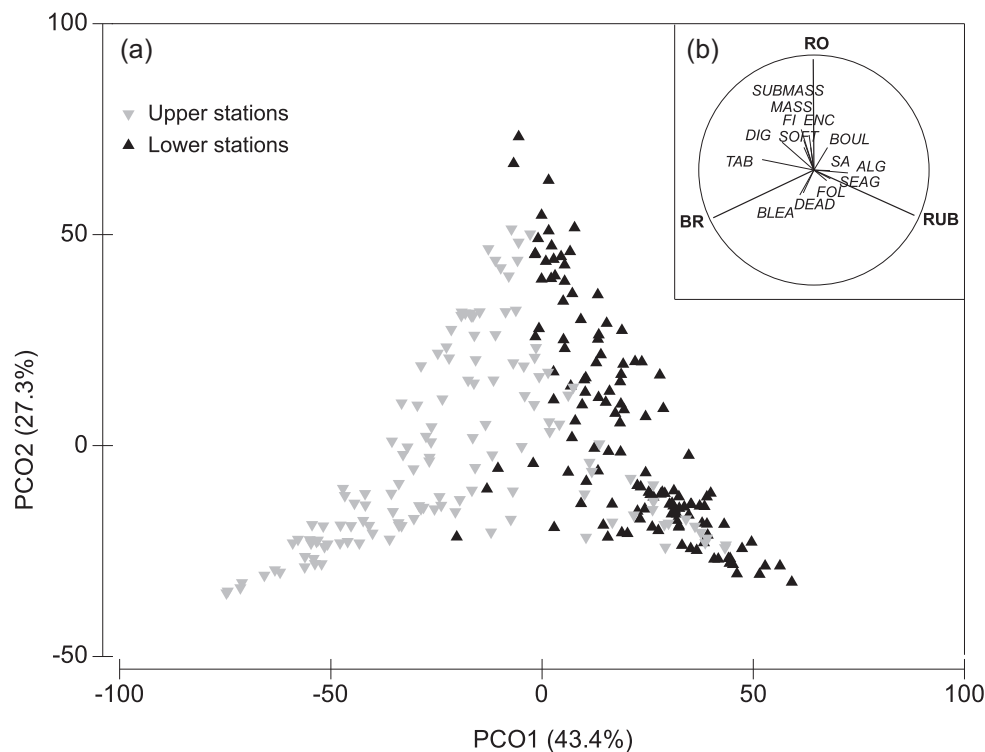


Figure 3. Multivariate typology of shallow coral habitats in outbreak sites in the SW lagoon, New Caledonia. Ordination diagrams from PCO for A. upper (reef flat) vs. lower (fore reef) stations B. habitat variables. See Table 2 for abbreviations.

values were significantly lower in the lower (fore reef) stations (maximum six different coral categories observed per transect; mean 2.6 ± 0.2 per transect, PERMANOVA, Pseudo-F = 90.54, $p = 0.001$). Cover and morphological richness were similarly affected by reef exposure. Windward stations always had more diversified assemblages, with slightly higher morphological richness compared to leeward stations (mean 4.3 ± 0.2 vs. 3.3 ± 0.2 coral categories per transect for windward vs. leeward stations; PERMANOVA, Pseudo-F = 20.71, $p = 0.001$). They were also characterized by significantly higher live coral cover (35.2% in windward vs. 20.0% in leeward stations; PERMANOVA, Pseudo-F = 60.93, $p = 0.001$), with much greater differences recorded between depths than in the leeward stations (Figure 6).

Discussion

In this work, we investigated the occurrence of COTS outbreaks and their impacts in the upper areas (reef flat and fore reef in 0–5 m depth) of fragmented coral reefs in New Caledonia, South Pacific. In addition to establishing the first COTS baseline in a country whose extensive coral formations were until recently considered less affected than most surrounding territories (Moritz *et al.*, 2018; Dumas *et al.*, 2020), our results provide an original and complementary perspective on the differential consequences of COTS outbreaks in the shallowest, generally under-researched coral habitats.

Prevalence of COTS outbreaks

Dedicated monitoring highlighted for the first time the widespread distribution of massive COTS aggregations across the Southwest-

ern lagoon of New Caledonia, with severe but differential impacts on the coral assemblages. Beyond the frequent observation of regular, low-density populations, we documented an unexpected high occurrence of outbreak events characterized by massive population increases, but limited spatial and temporal boundaries. Abundance levels of several hundreds of COTS per 10 minutes-swim, i.e. several thousand COTS per hectare (maximum 15 000 COTS.ha⁻¹) were repeatedly recorded in a number of reefs, meeting or exceeding the highest values in the literature. This was unexpected since New Caledonia has been the subject of a number of monitoring programs during the recent decades, which apparently failed to gauge the scale of the phenomenon (but see Dumas *et al.*, 2020). The first notices of isolated specimens date back to the late 1940s (Catala, 1950); however, no systematic observations were made before the seminal work of Conand (1983), who reported the regular occurrence of *A. planci* in the 1980s. Opportunistic field surveys highlighted low to moderate population density (< 50 COTS.ha⁻¹) in most stations, except in a single, mid-shelf reef (IlotMaitre) where outbreak densities were repeatedly documented since then (Conand, 1983). Specific observations of COTS aggregations, including the mainland northern and eastern coasts and the less populated Loyalty islands, progressively increased since 1997, when regular monitoring started as part of the GCRMN using modified Reef Check methods (Wantiez, 2008; CRISP, 2009; Chin *et al.*, 2011). Evidence of punctual, apparently disconnected COTS population burst progressively arose from the yearly monitoring reports of the RORC (Coral Reef Observation Network of New Caledonia); however, the averaged densities reported were generally low and the authors never explicitly referred to “outbreaks” (e.g. 2013–2020: 22 to 78 stations surveyed; average density from 6.8 to 26.4 COTS.ha⁻¹;

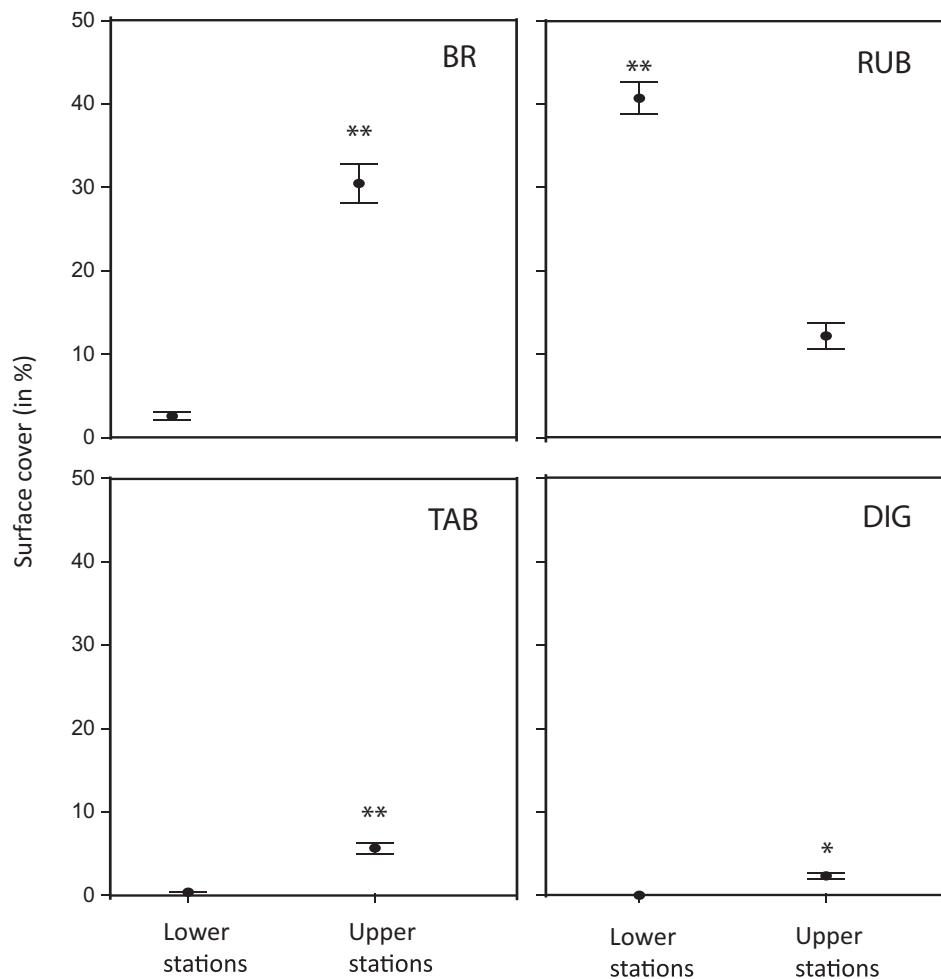


Figure 4. Differences in shallow benthic habitats in outbreak sites in the SW lagoon, New Caledonia. Means \pm SE in upper (reef flat) vs. lower (fore reef) stations for Branching corals (BR), Tabular corals (TAB), Digitate corals (DIG) and coral rubble (RUB) with results from PERMANOVAs (* $p < 0.05$; ** $p < 0.01$).

RORC, 2014, 2016, 2018, 2019). It was not until 2012 that multiple sightings of abnormal COTS abundances gained research attention, and ephemeral outbreaks were eventually suspected across New Caledonia (Buttin, 2018; Adjeroud *et al.*, 2018). This led to a dedicated, citizen-based regional COTS monitoring program, which demonstrated that the spread of COTS was substantially wider than expected (Dumas *et al.*, 2020). Despite the accumulation of scientific evidence, the idea that COTS may constitute a threat in New Caledonia is still the issue of heated debate; no consensus has yet been reached at decision levels, and no management framework is currently applied (Oremus *et al.*, 2021).

Implication of spatiotemporal scales for COTS monitoring and management

This apparent discrepancy may partly result from methodological issues. In New Caledonia such as in surrounding territories (e.g. Vanuatu and Fiji), most coral reef expert monitoring initiatives rely upon traditional underwater transect-based surveys. This is the case of the country-scale GCRMN-RORC program, which

was built historically around a network of 20–80 fixed, 400m² benthic stations. While maintaining a long-term, country-scale monitoring is a challenge in itself, spatial coverage and representativeness are clearly insufficient when confronted to the ~4500 km² New Caledonia coral reef formations. This approach is even less suitable for the detection of rapidly moving, spatially heterogeneous COTS populations with fast locomotion rates and active prey-searching roaming behavior (e.g. 50 cm.min⁻¹, up to approximately 20 m day⁻¹, Moran, 1990; Mueller *et al.*, 2011; Ling *et al.*, 2020). More flexible, adaptive methods providing better coverage such as random search and/or timed surveys (Hill and Wilkinson, 2004) are required here, especially during the initiation phase where fixed, transect-derived methods are not well suited to detect COTS densities rapidly evolving across a variety of habitats and depths. This pleads in favor of dedicated, long-term COTS survey programs, such as on the GBR where COTS are integrated inside a national, strategic management framework, and monitoring built on decades of COTS research combines a variety of approaches (including expert-based manta-tow, snorkel- and SCUBA surveys; drone observation; citizen science etc.) (GBRMPA, 2020).

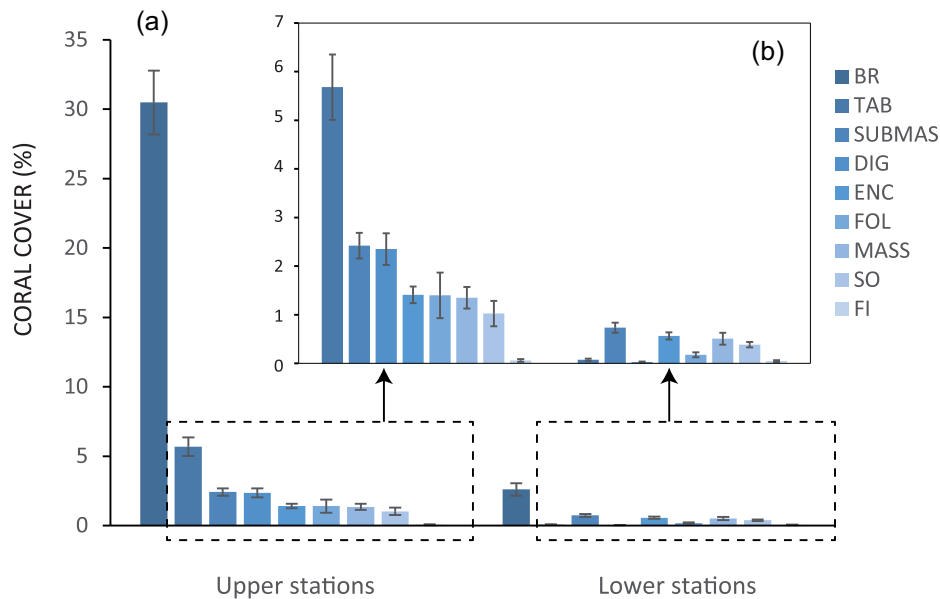


Figure 5. Composition of shallow coral communities in outbreak sites in the SW lagoon, New Caledonia. Means \pm SE in upper (reef flat) vs. lower (fore reef) stations for (a) all coral categories; (b) less represented categories. BR: branching; TAB: tabular; SUBMAS: submassive; DIG: digitate; ENC: encrusting; FOL: foliose; MASS: massive; SO: soft; FI: fire corals.

Under detection or under reporting may be further exacerbated by the restricted spatiotemporal scales of COTS events, which clearly emerge from this study. In contrast with persistent, massive outbreaks which can affect continuous reef systems such as the GBR for years or even decades (e.g. Chesher, 1969; De'ath *et al.*, 2012; Kayal *et al.*, 2012; Nakamura *et al.*, 2014; Li *et al.*, 2019, among others), almost all events were restricted to relatively small, isolated mid-shelf reefs and faded away during the course of the study. The typical residence time was less than two years per reef, with at least one site where COTS seemingly “disappeared” after a few months. The absolute values must be considered with care, because of the varying delays between two consecutive surveys in certain sites and the limited course of this study (four years). Outbreak duration may actually be shorter in the eight sites where monitoring gap was highest, and where COTS populations may have returned earlier to the baseline levels. Conversely, the return to baseline densities may not necessarily imply the end of an outbreak, which could persist undetected elsewhere if COTS switched area. The latter hypothesis, however, is unlikely given the limited extension and the physical isolation of mid-shelf reefs, which (i) facilitate the detection of dense COTS populations by observers, and (ii) would require COTS crossing extensive lagoon areas at about 20 m depth to reach other reefs (but see Goreau *et al.*, 1972). These results are consistent with COTS population trajectories punctually observed by Adjeroud *et al.* (2018). They emphasize that COTS events can be highly ephemeral in nature, with a narrow window of opportunity for detection and potential management responses. Once the wave of starfish has passed, traces of their presence quickly fade away: in the clear, warm waters of New Caledonia, feeding scars remain visible for only a couple of weeks before algae and a variety of sessile organisms colonize the coral skeletons. Beyond monitoring, these results also have very practical implication, as they very likely contribute to underestimating the actual impacts of COTS. In New Caledonia, significant coral decline has been subsequently attributed to unreported outbreaks in the recent decade, without

being able to provide quantified evidence for it (CRISP, 2009; Guillemot *et al.*, 2016; Sulu *et al.*, 2002; Wantiez, 2008). This argument is often used by decision-makers to justify the current policy of non-intervention, in particular the prohibition of methods to control COTS population densities.

This also raises the question of the future of COTS populations once these brief, self-contained events are over. It seems unlikely that natural, massive post-outbreak COTS mortality can be expected among the populations within such a narrow temporal frame, as these biological processes usually take longer to operate (Moran, 1986; Pratchett, 2005; Pratchett *et al.*, 2014). Mass movement to adjacent reefs across the lagoon is conceivable, as it is now widely recognized that adult COTS can effectively travel across deep, open sandy areas under certain conditions (e.g. Mueller *et al.*, 2011; Clements and Hay, 2017; Pratchett *et al.*, 2017b). With an extensive reef and lagoon area of 40 000 km² including a 1500 km long continuous barrier reef, the ability to model adult migrations and predict the potential spread of outbreaks is crucial to develop operational management at country scale. There is rising evidence that successive population bursts may recurrently affect the same reefs with a few years interval (P. Dumas, pers. obs.); unfortunately, we are currently hampered by the limited technical ability to track individuals and populations over long periods, and by the lack of historical, quantitative data to address potentially cumulative impacts.

Differential impacts of COTS outbreaks on the benthic habitats

On initial examination, the short residence times observed may point to a rapid shortage of food supply, following massive COTS population bursts in the affected areas. Outbreak may end naturally once depleted live coral stocks cannot sustain the resident COTS populations, leaving them with the option to migrate to more favorable areas, or to die of starvation (Suzuki *et al.*, 2012)—the latter process likely exacerbated in small, fragmented mid-shelf reefs

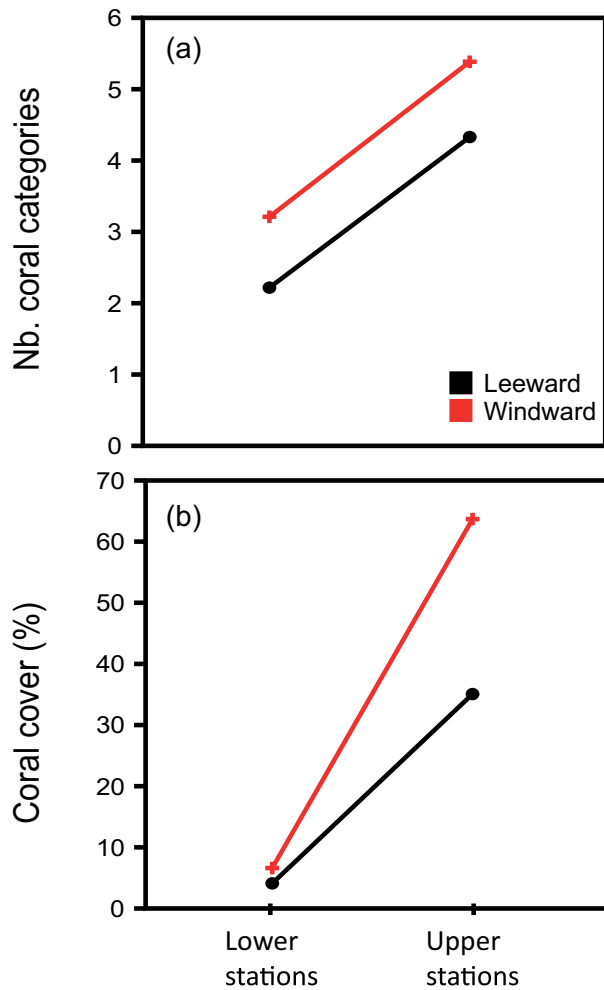


Figure 6. Influence of depth and exposure on the shallow coral assemblages in outbreak sites in the SW lagoon, New Caledonia. Interaction plots from 2-way PERMANOVAs for live coral cover (a) and morphological richness (b) in upper (reef flat) vs. lower (fore reef) stations with different wind exposure.

isolated by extensive areas of deep waters. This hypothesis is highly unlikely because our results document, for the first time in the area, the persistence of abundant and diversified coral assemblages in each of our 13 reefs immediately after the declines in COTS densities. Impact patterns, however, drastically changed within a very narrow depth range (0–5 m). Following outbreaks, we observed a clear delineation between seemingly unaffected, shallowest reef flat areas (0.5–1.5 m) with flourishing corals, and almost devastated areas located a few meters deeper (3–5 m) along the same continuum. Our results confirmed that reef flat areas located in less than 2 m depth harbored pristine benthic habitats still dominated by well-developed, morphologically diversified coral assemblages. Very high coral covers were eventually reported (maximum 98.2% per transect; half of the site had average live coral cover per transect > 60%), along with a variety of growth forms typically observed in the surrounding, unaffected reefs from the same complex (Adjeroud *et al.*, 2019). The transition to the 3–5 m depth areas where COTS were observed during the study was abrupt: live coral cover was divided by nine to an average 5% within a few meters, along with a marked reduced morphological richness. This

eventually materialized in the field as a clear visual demarcation line along the reef, below which corals were degraded and dense populations of COTS were repeatedly seen during the surveys, whereas they were never observed in the upper, unimpacted areas. In the absence of before-and-after data, it is not possible to formally attribute this decline to COTS alone. However, this hypothesis is supported by the abrupt differences in coral assemblages within the very narrow depth range observed. Such delineation is highly unusual along this natural benthic continuum where coral assemblages are naturally the most developed, both quantitatively and qualitatively, in the Southwestern lagoon of New Caledonia in the absence of COTS (Chevalier, 1973; Faure *et al.*, 1981; Lasne, 2007).

These results fit within the general framework of outbreaks initiating at various depths below the reef crest, with subsequent coral mortality gradually spreading upwards as COTS populations ascend the reef slope to reach areas with the highest abundance of coral prey (Endean and Stablum, 1973; Johnson *et al.*, 1991; Johnson, 1992; Wilmes *et al.*, 2020). However, the spread of COTS population and the associated coral depletion appeared spatially self-contained in all sites, as outbreaks never affected the shallowest reef flat areas (0.5–1.5 m depth). In fact, COTS were almost never seen behind the reef crest, with no evidence of feeding scars or significant coral mortality despite careful search. There were only a very few occasions where isolated specimens could be spotted on the reef flat or even on the sand, with their spines barely sticking out of the water at low tide. The occurrence of COTS in the upper sections of coral reefs has been consistently reported across the Western Pacific, from historical reports of waves of adult starfish moving across reef flats in Fiji and Australia during the early 1970s (Endean and Stablum, 1973; Zann *et al.*, 1990), to very shallow aggregations recently affecting Vanuatu's narrow fringing reefs at depths ≤ 1 m (Dumas and Ham, 2015; Dumas *et al.*, 2016). While there are no obstacles or physical boundaries to impede COTS from reaching these coral-rich areas, empirical evidence suggests that this is uncommon, and COTS actually tend to avoid very shallow areas even when their preferred prey are abundant (Chesher, 1969; Moran, 1986; Celliers and Schleyer, 2006; Pratchett, 2005). Under this hypothesis, the rapid declines in once massive COTS densities may not result from a total depletion of prey, but rather to prey resources becoming less accessible (or with more unfavorable risk-benefit balance) in the shallowest reef flat areas, therefore keeping predation pressure downwards. This may be a protective behavior to avoid unsuitable, potentially lethal environmental conditions, including strong hydrodynamism (waves, current), elevated temperatures and periodical emersion (e.g. Endean and Chesher, 1973; Moran *et al.*, 1985). COTS are indeed highly vulnerable to oxygen depletion due to their large size and active metabolism, and death by asphyxiation usually occurs after only a few hours out of the water (P. Dumas, pers. obs.). Moreover, reduced feeding efficiency was reported in exposed locations where currents, turbulence and strong wave action can dislodge adult specimens, hence interrupting feeding activity and potentially damaging the starfish (Goreau *et al.*, 1972; Moran, 1986). This eventually translates into a combined depth and exposure gradient, such as on the GBR where Pratchett (2005) reported highest COT densities deeper on the reef slope at windward locations, while they were more abundant at the reef crest at more sheltered locations. Slightly different post-outbreak distributions were observed in this study, especially in the reef flats where dominant southeasterly trade winds (“Alizees”) generate very active hydrodynamic circulation and swell with variable tidal height and emersion patterns (Ouillon *et al.*, 2010)—hence making these areas particularly

unfavorable for adult starfish. In these areas naturally avoided by COTS, more flourishing coral assemblages were naturally observed in exposed vs. sheltered areas, as generally recorded elsewhere in the Southwestern reef complex of New Caledonia (Lasne, 2007). In contrast, this natural gradient no longer existed a few meters below (3 m and beyond) where predation by COTS was maximum, and the coral stock was severely depleted irrespective of exposure.

Conclusions

As a UNESCO Natural World Heritage and home to the second largest MPA in the world, the preservation of New Caledonia's extensive and diversified reef system is a collective/collaborative responsibility that involves all marine stakeholders, from government agencies and research organizations to NGOs, business operators and private individuals. In a context where an overwhelming proportion of political and public attention is drawn to large-scale, global-change related issues and reef disturbance levels are officially considered "mostly low" (RORC, 2018), is it time to change paradigm? In New Caledonia, COTS outbreaks were so far regarded as very rare and specific events, whose consequences could not jeopardize the balance of coral assemblages. Our results support the view that COTS may now constitute the rule rather than the exception, and frequent small-scale, rapidly evolving and potentially additive outbreaks could result in significant impacts on the longer term. The fact is that shallowest, coral-rich areas are so far seemingly preserved from COTS damage; however, they are also the areas most directly exposed to the adverse effects of climate change. In this context, and if only on the precautionary principle, additional research effort should be urgently dedicated to assess the structure and dynamics of local COTS outbreaks, and better gauge the scale of "the *Acanthaster phenomenon*" (Moran, 1986).

Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

Data availability statement

Data available on request—the data underlying this article will be shared on reasonable request to the corresponding author.

Acknowledgements

The authors express their warmest thanks to the technical staff of the IRD Noumea for technical assistance: M. Clarque, S. Tereua, and P. Naudin. We are also grateful to R. Farman, director of the Aquarium des Lagons and to Olivier Chateau for providing logistical support during the field surveys. This work was conducted within the framework of IRD COTS research programme in New Caledonia, including the OREANET initiative funded by the Government of New Caledonia and the French Fonds Pacifique.

References

Adjeroud, M., Kayal, M., Peignon, C., Juncker, M., Mills, S., Beldade, R., and Dumas, P. 2018. Ephemeral and localized outbreaks of the coral predator *acanthaster cf. solaris* in the southwestern lagoon of new caledonia. *Zool. Stud.* 57. <https://doi.org/10.6620/ZS.2018.57-04>

- Adjeroud, M., Poisson, E., Peignon, C., Penin, L., and Kayal, M. 2019. Spatial patterns and Short-term changes of coral assemblages along a Cross-shelf gradient in the southwestern lagoon of new caledonia. *Diversity* 11: 21.
- Baird, A.H., Pratchett, M.S., Hoey, A.S., Herdiana, Y., and Campbell, S.J. 2013. *Acanthaster planci* is a major cause of coral mortality in indonesia. *Coral Reefs* 32: 803–812.
- Birkeland, C., and Lucas, J.S. 1990. *Acanthaster planci*: Major Management Problem of Coral Reefs. CRC Press, Boca Raton, Florida.
- Buttin, J. 2018. Caractérisation, suivi et impacts écologiques de population d'*Acanthaster cf. solaris* en explosion démographique, au sein du lagon Sud-Ouest de la Nouvelle-Calédonie. IRD, Nouméa, Nouvelle-Calédonie.
- Catala, R. 1950. Contribution à l'étude écologique des îlots coralliens du pacifique sud : premiers éléments d'écologie terrestre et marine des îlots voisins du littoral de la nouvelle-calédonie. *Bulletin Biologique De La France Et De La Belgique* 84: 85.
- Celliers, L., and Schleyer, M. 2006. Observations on the behaviour and the character of an *acanthaster planci* (L.) Aggregation in a high latitude coral community in south africa. *Western Indian Ocean Journal of Marine Science* 5. <https://doi.org/10.4314/wiojms.v5i1.28502>
- Chesher, R.H. 1969. Destruction of pacific corals by the sea star *acanthaster planci*. *Science* 165: 280–283.
- Chevalier, J.-P. 1973. Coral reefs of new caledonia, in: Jones, O.A., and Edean, R. (Eds.), *Biology and Geology of Coral Reef*. Academic Press, New York, pp. 143–167.
- Chin, A., Lison de Loma, T., Reyntar, K., Planes, S., Gerhardt, K., Clua, E., Burke, L. *et al.* 2011. Status of Coral Reefs of the Pacific and Outlook. Global Coral Reef Monitoring Network.
- Clements, C.S., and Hay, M.E. 2017. Size matters: predator outbreaks threaten foundation species in small marine protected areas. *Plos One* 12: e0171569.
- Conand, C. 1983. Abondance, cycle sexuel et relations biométriques de l'étoile de mer *Acanthaster planci* en Nouvelle-Calédonie. Noumea.
- CRISP. 2009. South West Pacific Status of Coral Reefs Report 2007. CRISP, Secretariat of the Pacific Regional Environment Programme, Noumea.
- De'ath, G., Fabricius, K.E., Sweatman, H., and Puotinen, M. 2012. The 27-year decline of coral cover on the great barrier reef and its causes. *Proceedings of the National Academy of Sciences* 109: 17995–17999.
- De'ath, G., and Moran, P.J. 1998. Factors affecting the behaviour of crown-of-thorns starfish (*Acanthaster planci* L.) on the great barrier reef: 2: feeding preferences. *Journal of Experimental Marine Biology and Ecology* 220: 107–126.
- De'ath, G., and Moran, P.J. 1998. Factors affecting the behaviour of crown-of-thorns starfish (*Acanthaster planci* L.) on the great barrier reef: 1: patterns of activity. *Journal of Experimental Marine Biology and Ecology* 220: 83–106.
- Dumas, P., Bertaud, A., Peignon, C., Leopold, M., and Pelletier, D. 2009. A "quick and clean" photographic method for the description of coral reef habitats. *Journal of Experimental Marine Biology and Ecology* 368: 161–168.
- Dumas, P., Fiat, S., Durban, A., Peignon, C., Mou-Tham, G., Ham, J., Gereva, S. *et al.* 2020. Citizen science, a promising tool for detecting and monitoring outbreaks of the crown-of-thorns starfish *acanthaster spp.* *Scientific Reports* 10: 291.
- Dumas, P., and Ham, J. 2015. Macroinvertebrates & habitat survey in crab bay, Malekula (Vanuatu). Fisheries Department of Vanuatu, Port-Vila.
- Dumas, P., Moutardier, G., Ham, J., Kaku, R., Gereva, S., Lefèvre, J., and Adjeroud, M. 2016. Timing within the reproduction cycle modulates the efficiency of village-based crown-of-thorns starfish removal. *Biological Conservation* 204: 237–246.
- Edean, R., and Chesher, R.H. 1973. Temporal and spatial distribution of *acanthaster planci* population explosions in the indo-west pacific region. *Biological Conservation* 5: 87–95.
- Edean, R., and Stablum, W. 1973. A Study of some Aspects of the Crown-of-Thorns Starfish (*Acanthaster Planci*) Infestations of Reefs of Australia's Great Barrier Reef.

- Faure, G., Thomassin, B.A., and Vasseur, P. 1981. Reef coral assemblages on windward slopes in the noumea lagoon (New Caledonia), in: Proceedings of the Fourth International Coral Reef Symposium. Manila.
- GBRMPA. 2020. Crown-of-thorns starfish Strategic Management Framework. Great Barrier Reef Marine Park Authority, Townsville, Australia.
- Goreau, T., Lang, J., Graham, E., and Gareau, P. 1972. Structure and ecology of the saipan reefs in relation to predation by *acanthaster planci* (Linnaeus). *Bulletin of Marine Science* 22: 113–152.
- Guillemot, N., Gaillard, T., and Lagrange, A. 2016. Biodiversité et environnement dans la région de la Côte Oubliée « WoenVùù » : état des connaissances et identification des intérêts écologiques, Rapport d'étude OEIL. Observatoire de l'Environnement en Nouvelle-Calédonie, Nouméa.
- Haywood, M.D.E., Thomson, D.P., Babcock, R.C., Pillans, R.D., Keesing, J.K., Miller, M., Rochester, W.A. *et al.* 2019. Crown-of-thorns starfish impede the recovery potential of coral reefs following bleaching. *Marine Biology* 166: 99.
- Hill, J., and Wilkinson, C. 2004. Methods for ecological monitoring of coral reefs. Australian Institute of Marine Science, Townsville.
- Hoey, J., Campbell, M.L., Hewitt, C.L., Gould, B., and Bird, R. 2016. *Acanthaster planci* invasions: applying biosecurity practices to manage a native boom and bust coral pest in Australia. *Management of Biological Invasions* 7: 213–220.
- Johnson, C.R. 1992. Settlement and recruitment of *acanthaster planci* on the great barrier reef - questions of process and scale. *Marine and Freshwater Research* 43: 611–627.
- Johnson, C.R., Sutton, D.C., Olson, R.R., and Giddins, R. 1991. Settlement of Crown-of-Thorns starfish - Role of bacteria on surfaces of coralline algae and a hypothesis for deep-water recruitment. *Marine Ecology Progress Series* 71: 143–162.
- Kayal, M., Vercelloni, J., Lison de Loma, T., Bosserelle, P., Chancerelle, Y., Geoffroy, S., Stievenart, C. *et al.* 2012. Predator Crown-of-Thorns starfish outbreak, mass mortality of corals, and cascading effects on reef fish and benthic communities. *Plos One* 7: e47363.
- Keesing, J. 1990. Feeding biology of the crown-of-thorns starfish, *Acanthaster planci* (Linnaeus). James Cook University, Queensland.
- Kohler, K.E., and Gill, S.M. 2006. Coral point count with excel extensions (Cpce): a visual basic program for the determination of coral and substrate coverage using random point count methodology. *Computers & Geosciences* 32: 1259–1269.
- Lasne, G. 2007. Les coraux de la nouvelle-calédonie: synthèse bibliographique. CRISP, Nouméa, Nouvelle-Calédonie.
- Li, Y., Wu, Z., Liang, J., Chen, S., and Zhao, J. 2019. Analysis on the outbreak period and cause of *acanthaster planci* in xisha islands in recent 15 years. *Chin. Sci. Bull.-Chin.* 64: 3478–3484.
- Ling, S.D., Cowan, Z.-L., Boada, J., Flukes, E.B., and Pratchett, M.S. 2020. Homing behaviour by destructive crown-of-thorns starfish is triggered by local availability of coral prey. *Proceedings of the Royal Society B: Biological Sciences* 287: 20201341.
- Moran, P., Bradbury, R., and Reichelt, R. 1985. Mesoscale studies of the Crown-of-Thorns/coral interaction: A case history from the Great Barrier Reef. *undefined*.
- Moran, P.J. 1990. *Acanthaster-Planci* (L) - Biographical Data. *Coral Reefs* 9: 95–96.
- Moran, P.J. 1986. The *acanthaster* phenomenon. *Oceanogr. Marine Biology* 24: 379–480.
- Moritz, C., Vii, J., Lee Long, W., Tamelander, J., Thomassin, A., and Planes, S. 2018. Status and Trends of Coral Reefs of the Pacific 2017 - Global Coral Reef Monitoring Network, GCRMN. Global Coral Reef Monitoring Network.
- Mueller, B., Bos, A.R., Graf, G., and Gumanao, G.S. 2011. Size-specific locomotion rate and movement pattern of four common indo-pacific sea stars (Echinodermata; asteroidea). *Aquatic Biology* 12: 157–164.
- Nakamura, M., Okaji, K., Higa, Y., Yamakawa, E., and Mitarai, S. 2014. Spatial and temporal population dynamics of the crown-of-thorns starfish, *acanthaster planci*, over a 24-year period along the central west coast of okinawa island, *Marine Biology* 161: 2521–2530.
- Oremus, M., Dumas, P., and Baritaud, M. 2021. Synthèse de l'atelier de travail sur la problématique de gestion des proliférations d'*acanthasters* en Nouvelle-Calédonie. IRD - WWF, Nouméa, Nouvelle-Calédonie.
- Osborne, K., Dolman, A.M., Burgess, S.C., and Johns, K.A. 2011. Disturbance and the dynamics of coral cover on the great barrier reef (1995-2009). *Plos One* 6: e17516.
- Ouillon, S., Douillet, P., Lefebvre, J.P., Le Gendre, R., Jouon, A., Bonneton, P., Fernandez, J.M. *et al.* 2010. Circulation and suspended sediment transport in a coral reef lagoon: the south-west lagoon of new caledonia. *Marine Pollution Bulletin* 61: 269–296.
- Plagányi, É.E., Babcock, R.C., Rogers, J., Bonin, M., and Morello, E.B. 2020. Ecological analyses to inform management targets for the culling of crown-of-thorns starfish to prevent coral decline. *Coral Reefs* 39: 1483–1499.
- Pratchett, M.S., Cowan, Z.L., Nadler, L.E., Caballes, C.F., Hoey, A.S., Messmer, V., Fletcher, C. S. *et al.* 2017a. Body size and substrate type modulate movement by the western pacific crown-of-thorns starfish, *acanthaster solaris*. *Plos One* e0180805, 12. <https://doi.org/10.1371/journal.pone.0180805>.
- Pratchett, M., Caballes, C., Wilmes, J., Matthews, S., Mellin, C., Sweatman, H., Nadler, L. *et al.* 2017b. Thirty years of research on Crown-of-Thorns starfish (1986–2016): scientific advances and emerging opportunities. *Diversity* 9: 41.
- Pratchett, M.S. 2005. Dynamics of an outbreak population of *acanthaster planci* at lizard island, northern great barrier reef (1995-1999). *Coral Reefs* 24: 453–462.
- Pratchett, M.S., Caballes, C.F., Rivera-Posada, J.A., and Sweatman, H.P.A. 2014. Limits to understanding and managing outbreaks of Crown-of-Thorns starfish (*Acanthaster* spp.). *Oceanogr. Mar. Biol. Annu. Rev.* 52: 133–199.
- Pratchett, M.S., and Cumming, G.S. 2019. Managing cross-scale dynamics in marine conservation: pest irruptions and lessons from culling of crown-of-thorns starfish (*Acanthaster* spp.). *Biological Conservation* 238: 108211.
- Pratchett, M.S., Schenk, T.J., Baine, M., Syms, C., and Baird, A.H. 2009. Selective coral mortality associated with outbreaks of *acanthaster planci* l. in bootless bay, papua new guinea. *Marine Environmental Research* 67: 230–236.
- Richer de Forges, B. 1991. Le benthos des fonds meubles des lagons de Nouvelle-Calédonie.
- RORC. 2019. Réseau d'Observation des Récifs Coralliens de Nouvelle-Calédonie (RORC) : Campagne de suivi 2018-2019.
- RORC. 2018. Réseau d'Observation des Récifs Coralliens de Nouvelle-Calédonie (RORC) : Campagne de suivi 2017-2018.
- RORC. 2016. Réseau d'Observation des Récifs Coralliens de Nouvelle-Calédonie (RORC) : Campagne de suivi 2015-2016. ADL Nouméa.
- RORC. 2014. Réseau d'Observation des Récifs Coralliens de Nouvelle-Calédonie (RORC) : Campagne de suivi 2013-2014. ADL Nouméa.
- Saponari, L., Montalbetti, E., Galli, P., Strona, G., Seveso, D., Dehnert, I., and Montano, S. 2018. Monitoring and assessing a 2-year outbreak of the corallivorous seastar *acanthaster planci* in ari atoll, republic of maldives. *Environmental Monitoring and Assessment* 190: 344.
- Sulu, R., Cumming, R., Wantiez, L., Kumar, L., Mulipola, A., Lober, M., Sauni, S. *et al.* 2002. Status of coral reefs in the southwest pacific region to 2002: fiji, nauru, new caledonia, samoa, solomon islands, tuvalu and vanuatu, in: Status of Coral Reefs of the World: 2002. Australian Institute of Marine Science, pp. 180–201.
- Suzuki, G., Kai, S., and Yamashita, H. 2012. Mass stranding of crown-of-thorns starfish. *Coral Reefs* 31: 821–821, 31. <https://doi.org/10.1007/s00338-012-0906-z>.
- Tkachenko, K.S., Huan, N.H., Thanh, N.H., and Britayev, T.A. 2020. Extensive coral reef decline in nha trang bay, vietnam: *acanthaster planci* outbreak: the final event in a sequence of chronic disturbances. *Mar. Freshw. Res.* <https://doi.org/10.1071/MF20005>.
- Vanhatalo, J., Hosack, G.R., and Sweatman, H. 2017. Spatiotemporal modelling of crown-of-thorns starfish outbreaks on the great bar-

- rier reef to inform control strategies. *Journal of Applied Ecology* 54: 188–197.
- Wantiez, L. 2008. Coral reefs of new caledonia in 2006: status report and monitoring network. *Rev. Ecol.- Terre Vie* 63: 117–132.
- Westcott, D.A., Fletcher, C.S., Kroon, F.J., Babcock, R.C., Plagányi, E.E., Pratchett, M.S., and Bonin, M.C. 2020. Relative efficacy of three approaches to mitigate Crown-of-Thorns starfish outbreaks on australia's great barrier reef. *Scientific Reports* 10: 12594.
- Wilmes, J.C., Schultz, D.J., Hoey, A.S., Messmer, V., and Pratchett, M.S. 2020. Habitat associations of settlement-stage crown-of-thorns starfish on australia's great barrier reef. *Coral Reefs* 39: 1163–1174.
- Zann, L., Brodie, J., and Vuki, V. 1990. History and dynamics of the Crown-of-Thorns starfish *acanthaster-planci* (L) in the suva area, fiji. *Coral Reefs* 9: 135–144.

Handling Editor: Henn Ojaveer