

Supplementary Materials for

Sustained coral reef growth in the critical wave dissipation zone of a Maldivian atoll

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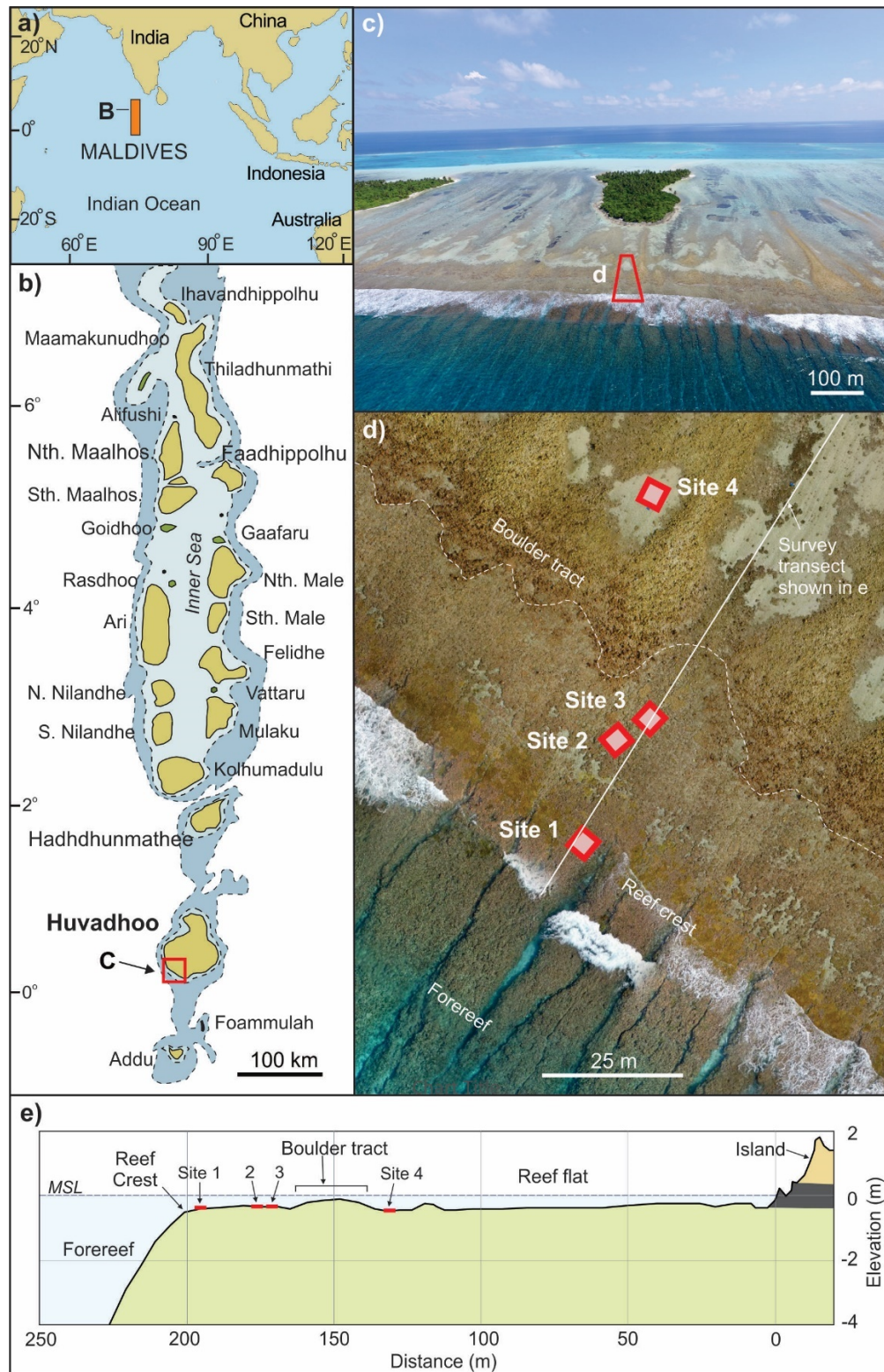
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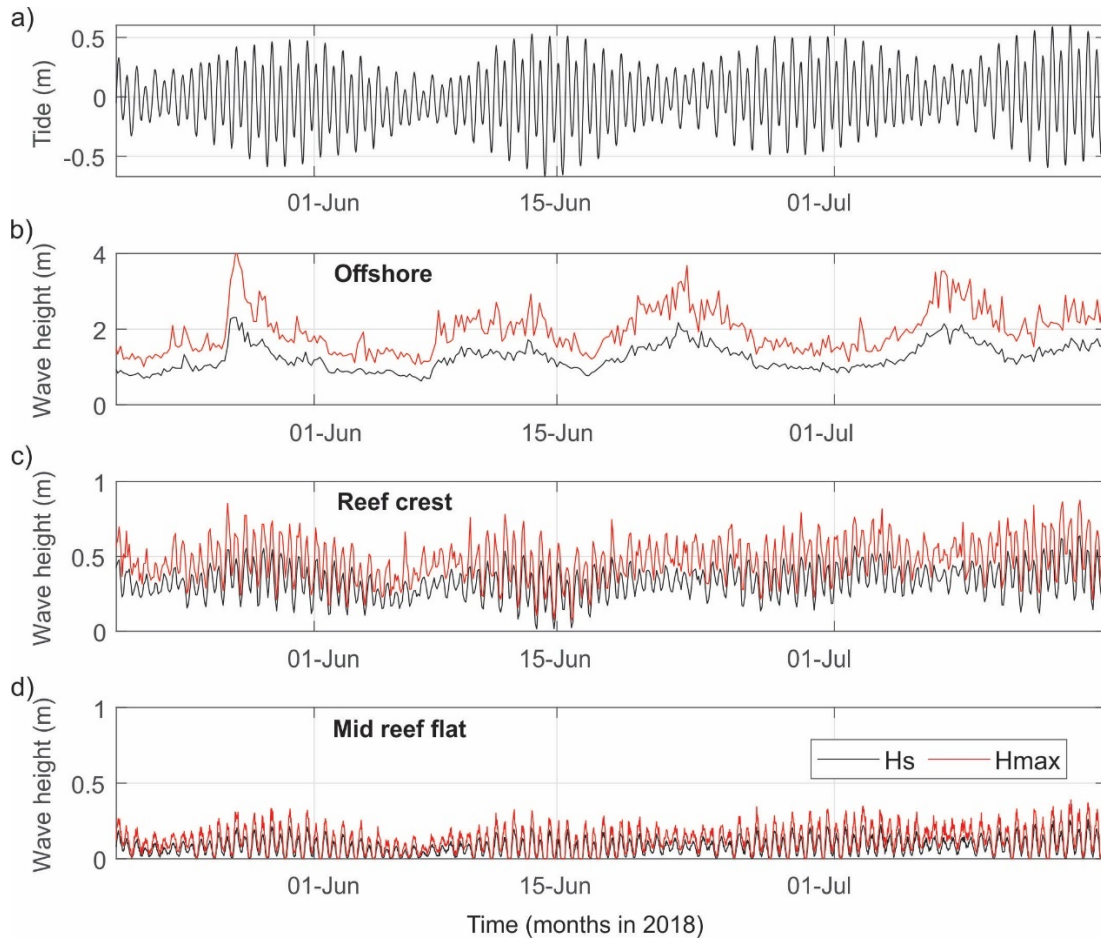
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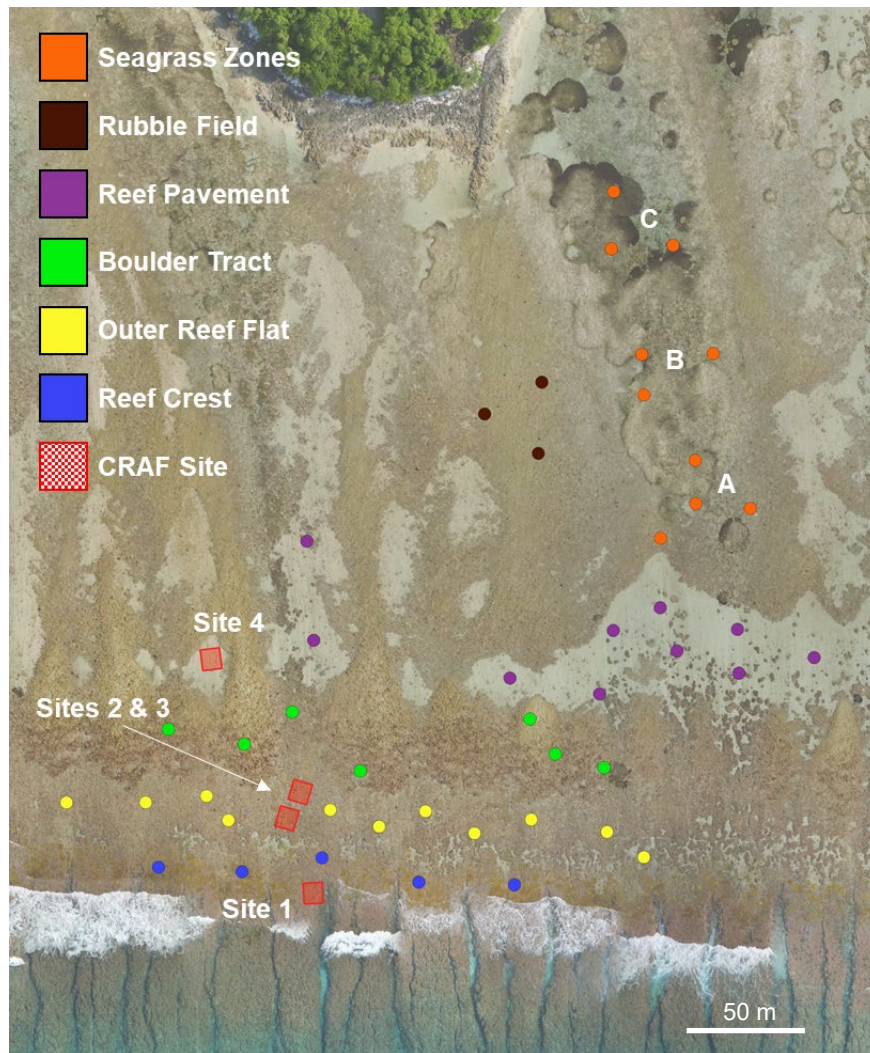
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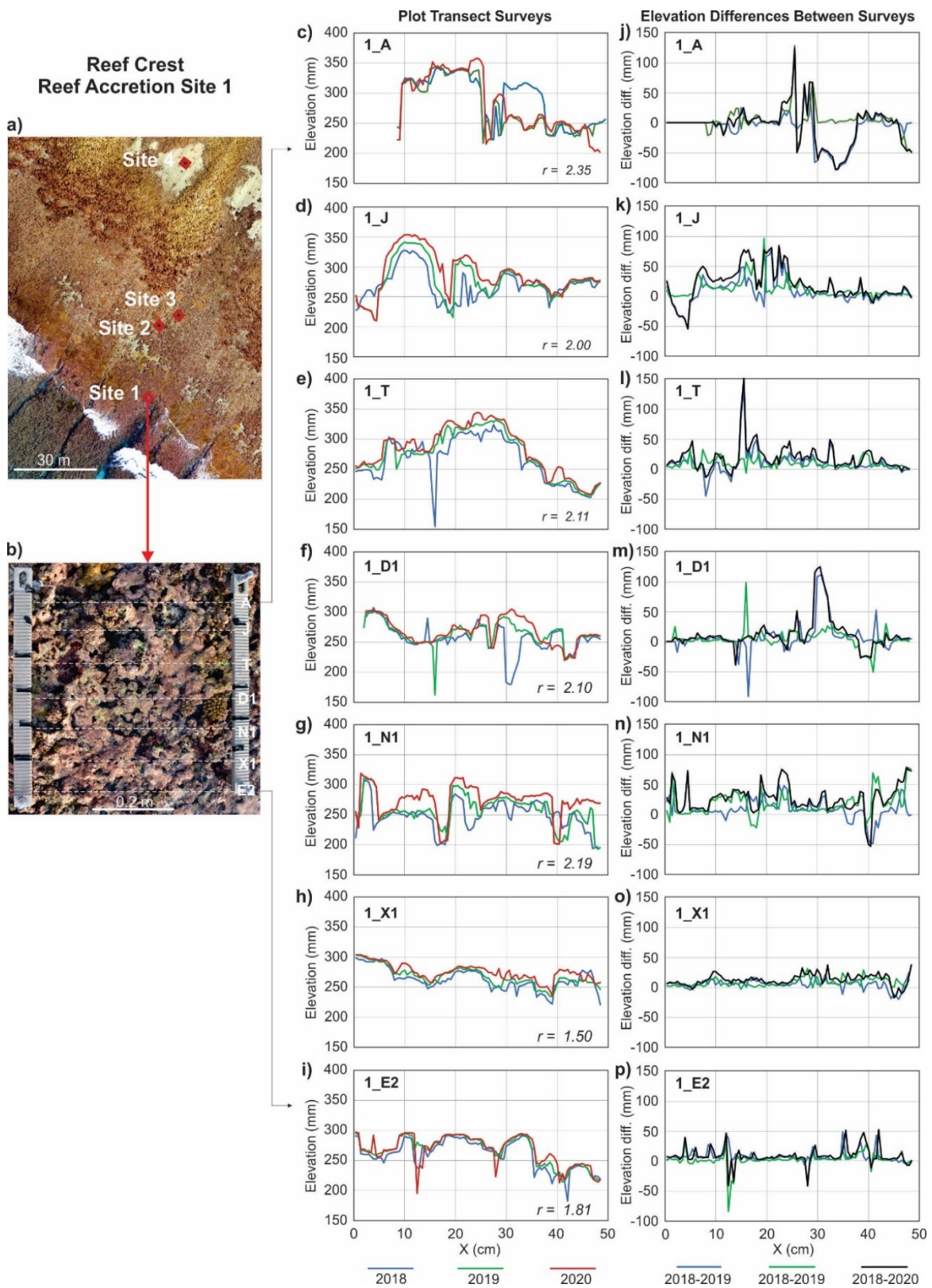
Supplementary Figure 1. Field location of the southwest Huvadhoo atoll, Maldives. a) Location of Maldives archipelago, central Indian Ocean. b) The Maldives archipelago. c) Oblique aerial photograph with a view across the exposed ocean reef crest and reef flat, note clear spur and groove pattern in the forereef. d) Vertical aerial photograph of the experimental site on the outer reef flat. White line denotes survey transect shown in e. Note the reef monitoring sites 1-4. e) Topographic survey from the upper forereef across the reef crest and reef flat to island. Source of photographs, author.



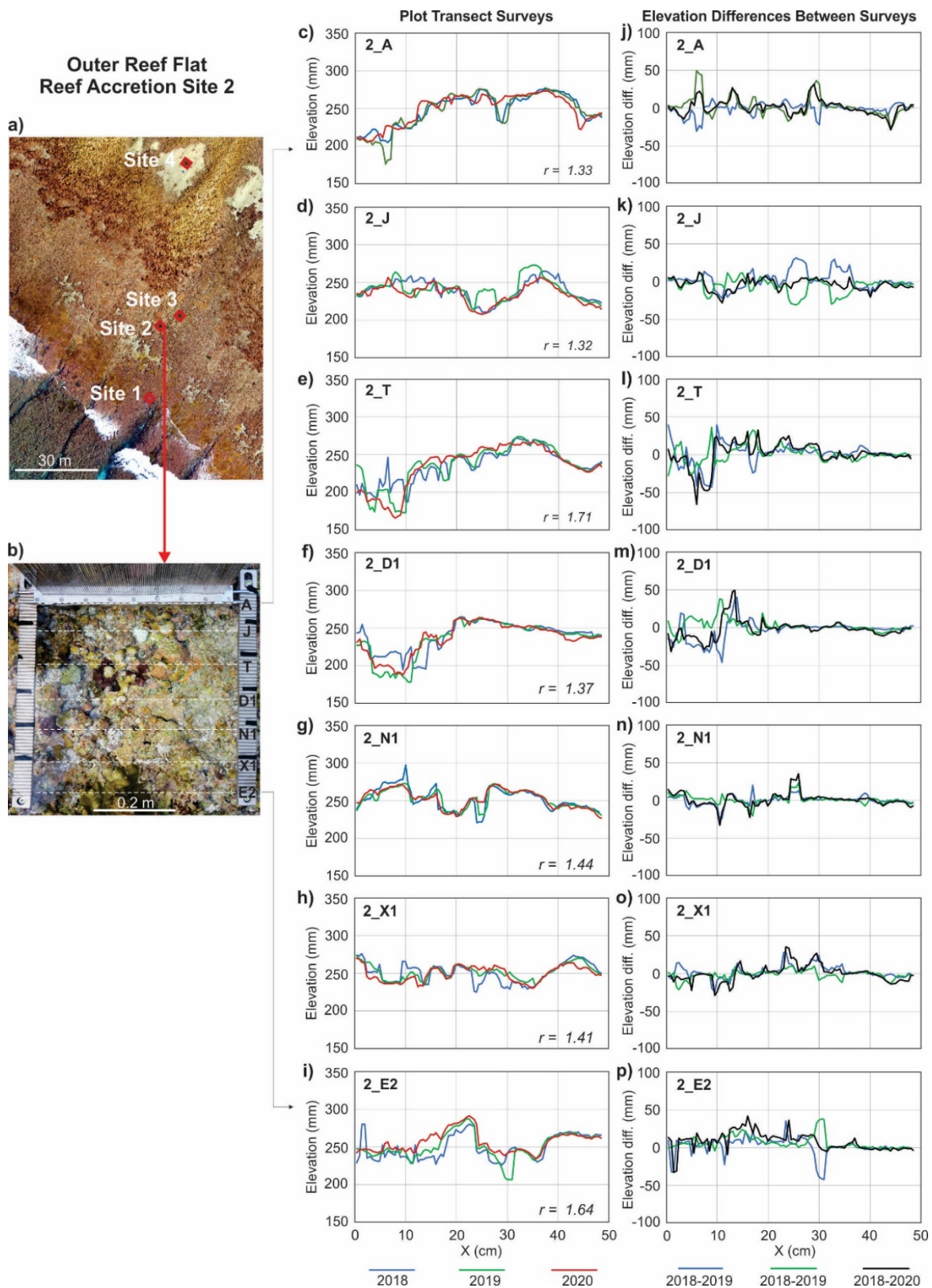
Supplementary Figure 2. Wave transformation across the Huvadhoon atoll reef rim at Keleihutta. Wave height was measured between May and July 2018 across the reef profile using wave sensors deployed on fore-reef slope (15 m water depth), the reef crest, and the central reef platform (locations shown in Figure 1a). a) Predicted tide and records. b-d) present significant (H_s) and maximum (H_{max}) wave heights offshore at the fore-reef (b), the reef crest (c) and, the central reef flat (d) respectively. Note, offshore significant wave height (H_s) was consistently above 1.0 m, with 3 discrete periods when wave heights exceeded 2.0 m. Wave height at the reef crest is influenced by water depth above the reef surface and is therefore strongly modulated by the tide, with a maximum high tide significant wave height around 0.5 m. Wave heights at the mid reef flat are further reduced, with H_s values at high tide typically below 0.25 m. Based on changes in H_s , 80% of incident energy is dissipated at the reef edge, through wave breaking. Further dissipation on the outer reef flat indicates only 10% of incident wave energy remains on the central reef platform.



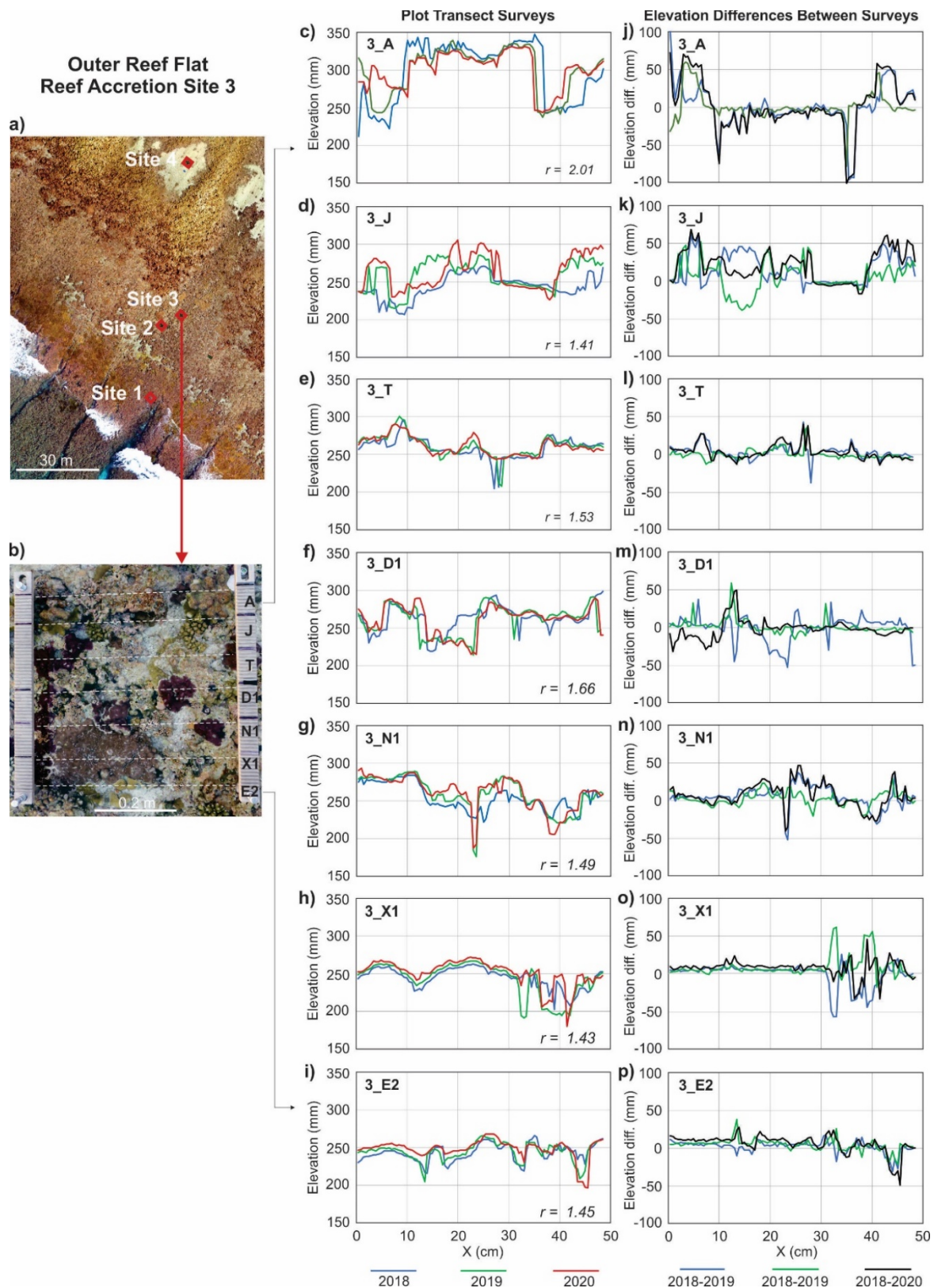
Supplementary Figure 3. Location of ecological surveys (PITs) to characterize ecological zones on the Keleihutta central to outer reef flat. Coloured points denote survey locations. Source image, author.



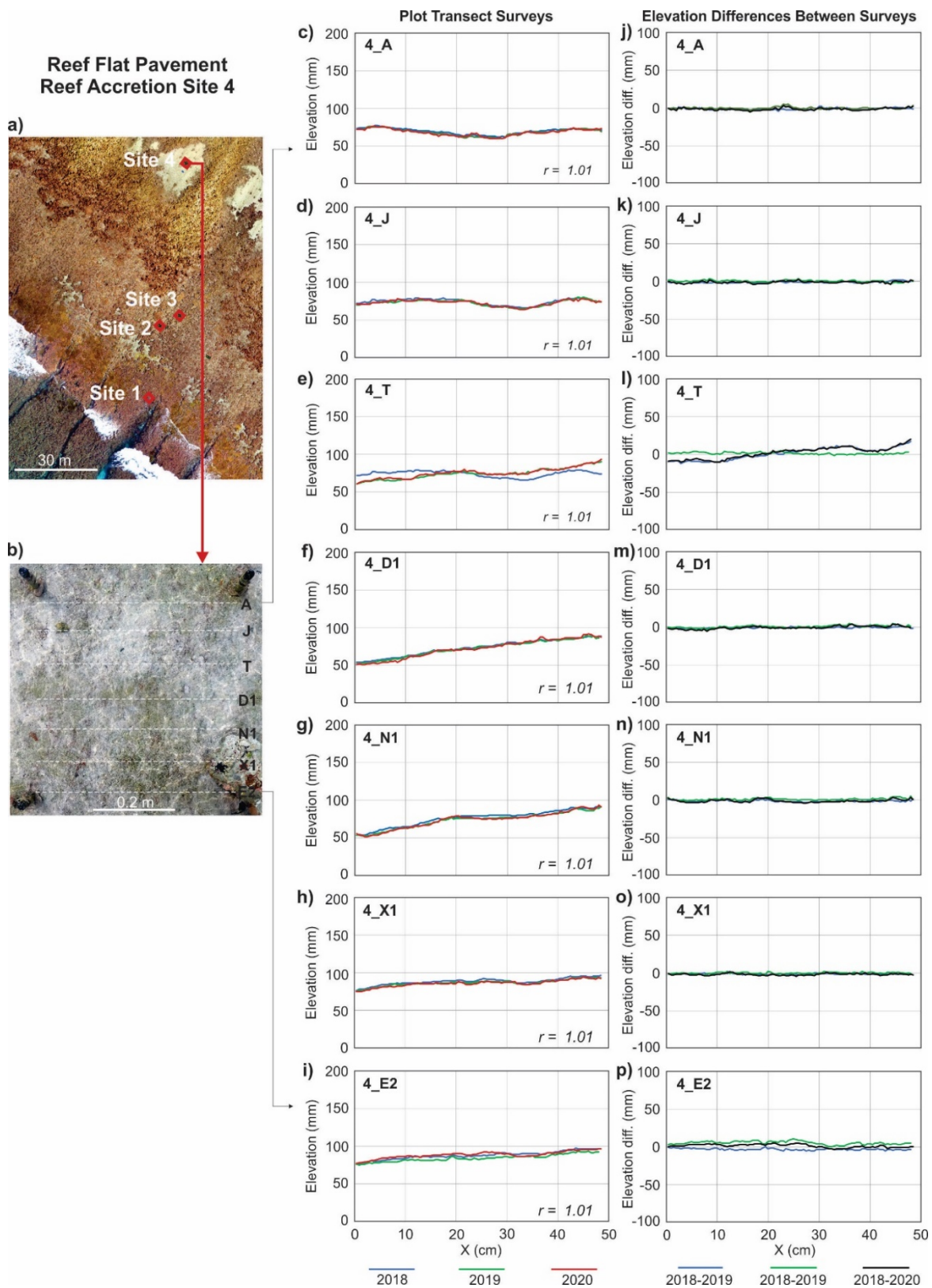
Supplementary Figure 4. Summary coral reef accretion frame (CRAF) data on the outer reef crest (Site 1) 2018-2020, Keleihutta reef flat, Huvadhoo atoll, Maldives. a) Location of measurement site on reef flat. b) Image of CRAF plot. c-i) Yearly observations of reef surface topography along transects. j-p) Differences between measurements on each transect.



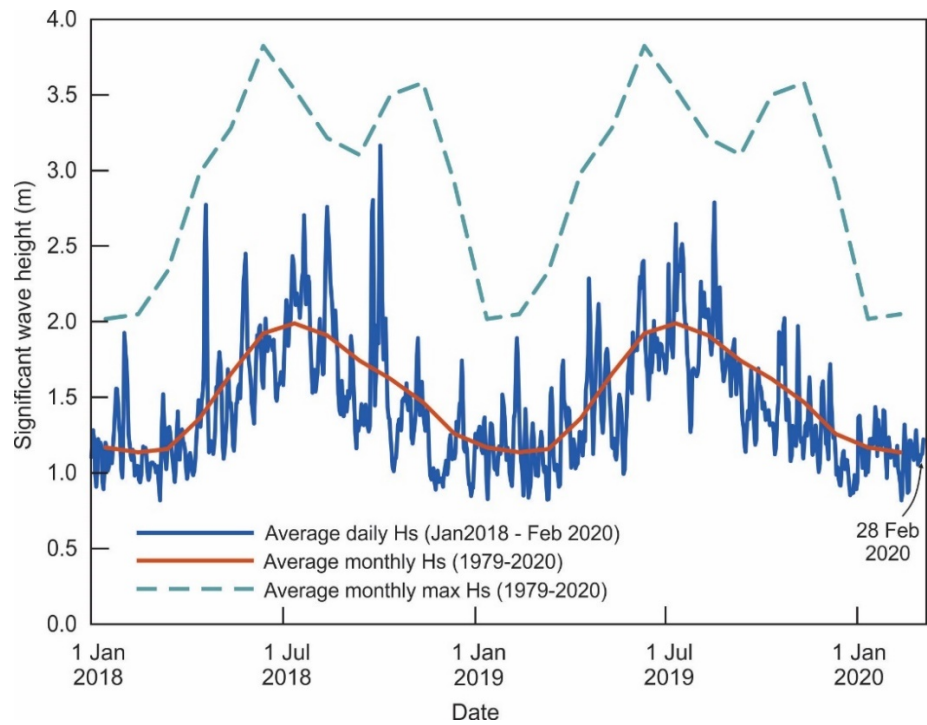
Supplementary Figure 5. Summary coral reef accretion frame (CRAF) data on the outer reef flat (Site 2), 2018-2020, Keleihutta reef flat, Huvadho atoll, Maldives. a) Location of measurement site on reef flat. b) Image of CRAF plot. c-i) Yearly observations of reef surface topography along transects. j-p) Differences between measurements on each transect.



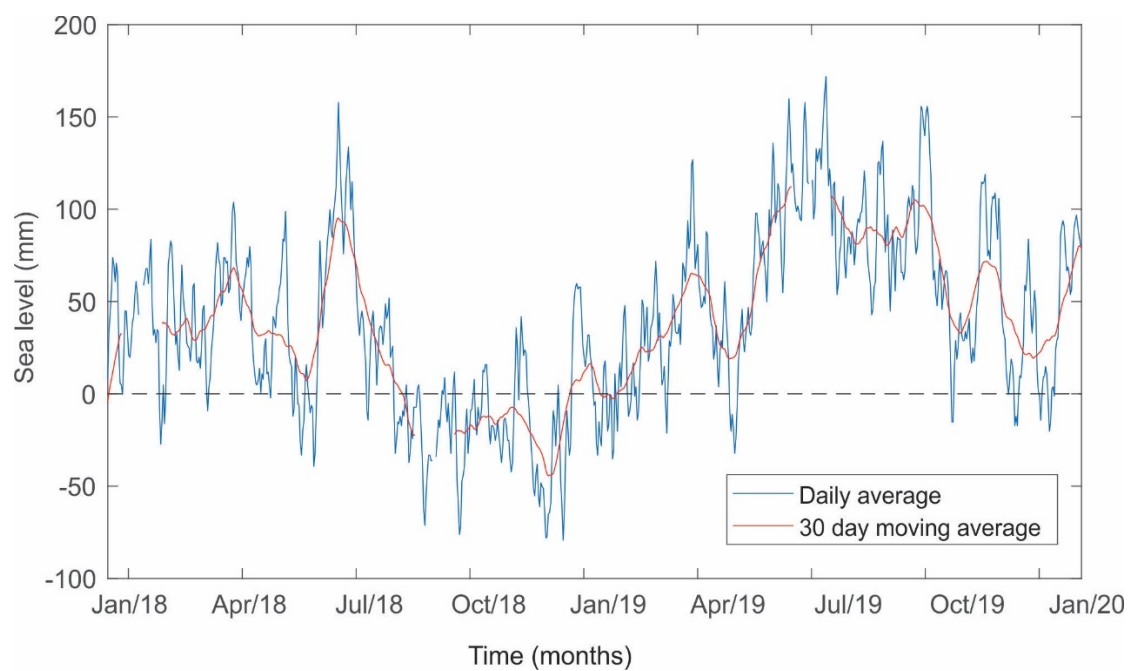
Supplementary Figure 6. Summary coral reef accretion frame (CRAF) data on the outer reef flat (Site 3), 2018-2020, Keleihutta reef flat, Huvadhoo atoll, Maldives. a) Location of measurement site on reef flat. b) Image of CRAF plot. c-i) Yearly observations of reef surface topography along transects. j-p) Differences between measurements on each transect.



Supplementary Figure 7. Summary of coral reef accretion frame (CRAF) data on the reef flat (Site 4), 2018-2020, Keleihutta reef flat, Huvadhoo atoll, Maldives. a) Location of measurement site on reef flat. b) Image of CRAF plot. c-i) Yearly observations of reef surface topography along transects. j-p) Differences between measurements on each transect.



Supplementary Figure 8. Summary wave characteristics impacting the Southwest margin of Huvadhoο atoll. All data derived from the global wave hindcast model Wave Watch 3 (WW3)¹ offshore of Huvadhoο (74° E; 0° N). Average daily Hs values (blue line) are presented for the duration of CRAF measurement period. Note, average monthly Hs (gold line) and average monthly maximum Hs (blue dashed line) are calculated from the 40-year dataset (1979-2020).



Supplementary Figure 9. Tide gauge data from Gan, southern Maldives from January 2018 to January 2020 (source: [Data and Station Information for GAN II \(psmsl.org\)](#)).

Supplementary Table 1. Benthic cover types (as %) for key calcifying reef habitats located across the outer to mid reef flat at Keleihutta, Huvadhoo Atoll. Locations of central and outer reef flat survey sites are shown in Supplementary Figure 3.

Location			Reef Crest		Outer Reef Flat		Central Reef Flat			
Experimental sites			Reef crest (CRAF 1) <i>n</i> = 5		ORF (CRAF 2 & 3) <i>n</i> = 11		Boulder Tract <i>n</i> = 7		Reef Pavement (CRAF 4) <i>n</i> = 10	
			Mean	SE	Mean	SE	Mean	SE	Mean	SE
Benthic cover	<i>Living Cover</i>									
	Coral	All genera	14.00	1.00	27.91	2.36	3.86	2.25	8.50	1.51
	Octocoral	<i>Heliopora</i> spp.	0.60	0.60	0.64	0.31	0.00	0.00	0.00	0.00
		Articulate & encrusting	30.80	3.29	32.91	3.23	2.14	2.14	3.10	1.59
	Macroalgae	<i>Halimeda</i> spp.	2.60	1.40	1.36	0.54	0.43	0.30	0.60	0.36
	Zoanthid	<i>Palythoa</i> spp.	50.20	5.25	1.55	0.53	0.00	0.00	0.00	0.00
	Other living	Seagrass & turf algae	1.80	0.73	7.00	2.55	2.57	2.57	1.10	1.10
	<i>Non living cover</i>									
	Dead Coral		0.00	0.00	8.09	3.42	1.71	1.71	3.50	1.45
	Pavement		0.00	0.00	7.91	2.04	0.00	0.00	70.90	3.80
	Sand		0.00	0.00	1.73	0.70	5.00	1.79	0.80	0.47
	Rubble with CCA		0.00	0.00	1.27	0.59	18.00	7.51	4.80	1.98
	Rubble		0.00	0.00	9.64	2.51	66.29	12.81	6.70	1.84
	Rugosity		1.19	0.02	1.21	0.02	1.30	0.02	1.14	0.04
Coral	Genera	<i>Acropora</i>	4.80	0.86	5.36	0.78	0.71	0.57	0.90	0.69
		<i>Coscinaria</i>	0.00	0.00	0.00	0.00	0.14	0.14	0.00	0.00
		<i>Favia</i>	0.00	0.00	0.27	0.19	0.00	0.00	0.50	0.40
		<i>Favites</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.10
		<i>Goniastrea</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.20
		<i>Isopora</i>	0.00	0.00	2.27	0.78	1.14	0.99	0.80	0.33
		<i>Leptastrea</i>	0.20	0.20	0.18	0.18	0.00	0.00	0.40	0.22
		<i>Pavona</i>	0.20	0.20	0.09	0.09	0.00	0.00	0.30	0.15
		<i>Platygyra</i>	1.60	0.81	1.73	0.62	0.00	0.00	0.10	0.10
		<i>Pocillopora</i>	1.00	0.32	1.73	0.43	0.00	0.00	0.90	0.69
		<i>Porites</i>	6.20	1.24	16.27	2.09	1.86	0.91	4.30	1.22
	Growth form	Branching	2.00	0.71	0.82	0.55	0.00	0.00	0.10	0.10
		Digitate	Not observed							
		Columnar	0.00	0.00	0.00	0.00	0.29	0.29	0.20	0.20
		Corymbose	1.20	0.80	0.18	0.18	0.00	0.00	0.00	0.00
		Encrusting	6.40	1.40	17.91	2.33	1.71	0.89	4.10	1.12
		Massive	0.00	0.00	2.09	0.64	0.43	0.43	1.40	0.79
		Submassive	1.00	0.32	2.09	0.46	0.71	0.71	1.90	0.90

NB: *M* = mean, *SE* = standard error, *n* = number of 10 m PITs surveyed within each reef habitat.

Supplementary Table 2. Benthic cover types (as %) for key calcifying reef habitats located across the mid to inner reef flat at Keleihutta, Huvadhoo Atoll. Locations are shown in Supplementary Figure 3.

Location		Central Reef Flat								Inner Reef Flat			
		Rubble Field <i>n</i> = 3		Seagrass Zones <i>n</i> = 10						Microatoll Patch <i>n</i> = 4		Channel <i>n</i> = 3	
				A <i>n</i> = 4		B <i>n</i> = 3		C <i>n</i> = 3					
		M	SE	M	SE	M	SE	M	SE	M	SE	M	SE
<i>Living Cover</i>													
Coral	All genera	10.0	4.6	3.0	2.7	6.3	2.3	7.3	3.7	20.5	2.7	18.3	1.2
Octocoral	<i>Heliopora</i> spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
CCA	Articulate & encrust.	0.3	0.3	1.0	0.7	0.7	0.7	0.0	0.0	0.8	0.3	0.0	0.0
Macroalgae	<i>Halimeda</i> spp.	0.3	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.6
Zoanthid	<i>Palythoa</i> spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Other living	algae	2.0	2.0	46.0	3.5	68.0	0.6	67.7	16.5	17.8	1.9	27.0	6.1
<i>Non-living cover</i>													
Dead Coral		1.3	1.3	0.5	0.3	17.0	3.2	3.7	2.7	15.0	6.0	31.3	3.5
Pavement		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.5	6.5	16.3	9.2
Sand		4.0	2.7	22.3	2.1	3.0	0.6	1.0	1.0	22.5	3.5	0.0	0.0
Rubble - CCA		20.7	9.1	10.5	2.4	0.0	0.0	0.0	0.0	5.8	2.8	0.0	0.0
Rubble		61.3	11.8	16.8	2.3	5.0	1.7	20.3	12.1	11.3	5.5	5.0	2.7
Rugosity		1.15	0.03	1.12	0.01	1.21	0.06	1.19	0.09	1.21	0.04	1.31	0.07
By genera	<i>Acropora</i>	0.7	0.7	0.3	0.3	0.0	0.0	1.3	0.9	0.8	0.8	0.0	0.0
	<i>Goniastrea</i>	0.3	0.3	0.0	0.0	0.0	0.0	0.3	0.3	0.0	0.0	0.0	0.0
	<i>Isopora</i>	1.7	1.7	0.3	0.3	0.0	0.0	2.3	1.5	0.0	0.0	0.0	0.0
	<i>Pavona</i>	0.3	0.3	0.0	0.0	0.7	0.7	0.0	0.0	0.0	0.0	0.7	0.7
	<i>Porites</i>	7.0	1.7	2.5	2.5	5.7	2.9	3.3	2.0	19.8	2.1	17.8	1.9
By growth form	Branching	0.0	0.0	0.3	0.3	0.0	0.0	1.0	1.0	6.3	2.2	9.7	2.3
	Digitate	0.7	0.7	0.0	0.0	0.0	0.0	0.3	0.3	0.0	0.0	0.0	0.0
	Columnar	1.0	1.0	0.0	0.0	0.0	0.0	1.0	1.0	0.0	0.0	0.0	0.0
	Corymbose	Not observed.											
	Encrusting	1.7	1.2	0.3	0.3	0.7	0.7	1.7	0.9	0.0	0.0	1.0	1.0
	Massive	3.3	2.9	2.5	2.5	2.7	1.76	1.0	1.0	14.3	2.3	5.3	0.3
	Submassive	3.3	1.2	0.0	0.0	3.0	1.53	2.3	2.3	0.0	0.0	2.3	1.9

NB: *M* = mean, *SE* = standard error, *n* = number of 10 m PITs surveyed within each reef habitat.

Supplementary Table 3. Results of statistical analysis of differences in CRAM measurements using the post hoc Dunn test (with Bonferroni adjustment)² of total reef elevation change (mm) for the two year observational period 2018-2020 comparing between CRAM sites. Sites with significant difference are shown in bold.

CRAM Zone Comparisons	Z value	<i>P</i> unadjusted	<i>P</i> adjusted
CS1-CS2	17.5	1.411e ⁻⁶⁸	8.468e⁻⁶⁸
CS1-CS3	8.031	9.691e ⁻¹⁶	5.814e⁻¹⁵
CS1-CS4	20.44	6.74e ⁻⁹³	4.044e⁻⁹²
CS2-CS3	9.549	1.308e ⁻²¹	7.85e⁻²¹
CS2-CS4	2.968	0.002997	0.01798
CS3-CS4	12.52	6.015e ⁻³⁶	3.609e⁻³⁵

Supplementary Note 1. Ecological Characteristics of the Keleihutta Reef Flat

A sampling strategy was designed to capture information on the ecological characteristics of the reef flat, with a focus on outer reef locations where the coral reef accretion frame (CRAF) monitoring sites are located. Benthic surveys were undertaken at 53 locations across the Keleihutta reef flat in February 2018. Quantitative measurements of benthic cover were made using a Point Intercept Transect (PIT) methodology, where observations of benthic cover were recorded at 10 cm intervals along a 10 m tape³⁻⁶. Sampling sites were established in the vicinity of each CRAF monitoring site, and replicate PITs were located along-reef (parallel to the reef crest) at spacings of ~5-10 m. Using this approach, ecological data were collected along 5 replicate PITs within the reef crest zone (representative of monitoring Site 1); 11 replicate PITs within the outer reef flat zone (representative of monitoring Site 2 and Site 3); and 10 replicate PITs at the transition between the outer and central reef flat on coral reef pavement (as representative of CRAF Site 4). Benthic surveys were also undertaken within the boulder tract zone (7 PITs) and across 6 inner reef locations where living benthic communities were observed (28 PITs). The sites at which PIT surveys were undertaken across central and outer reef locations are shown in Supplementary Figure 3. In total, 5,300 observations of benthic cover were recorded across 530 m of the reef flat using this sampling method.

Along each PIT living cover was identified to the lowest taxonomic level (e.g., scleractinian corals to the genera), and colony morphology of hard corals were recorded. Abiotic substrate types were also classified (e.g., sand, rubble, reef pavement). Substrate rugosity was measured using the standard chain method⁷⁻⁸, where rugosity ($d1/d2$) is calculated as the total cumulative reef surface distance ($d1$) divided by the equivalent linear distance ($d2$). Three rugosity measurements were recorded for each PIT, totalling 159 measurements on the reef flat.

Estimates of percentage benthic cover were calculated for each PIT replicate as:

$$\frac{\text{No. of observations of a benthic substrate type}}{\text{Total number of observations}} \times 100 = \% \text{ cover}$$

The PIT methodology employed provided for a standardized total number of observations (100) at each replicate location and therefore no further transformation of data was undertaken. Mean and standard error were calculated for each benthic substrate type by survey location.

Benthic Cover

Benthic cover summary data is provided in Supplementary Table 1 (reef crest and outer reef zones) and Supplementary Table 2 (central to inner reef flat zones).

The wave-dominated reef crest and outer reef flat zones exhibited relatively high scleractinian and crustose coralline algae (CCA) cover. At the reef crest, encrusting zoanthids (non-calcifiers) are the dominant cover type, accounting for 50.2% of the reef surface on average, while CCA and living coral accounted for 30.8% and 14.0% respectively. On the outer reef flat zone, mean percent coral cover was higher (27.9%) and CCA was the dominant cover type (mean: 32.9%). Observations of zoanthid cover were spatially constrained to the reef crest zone, and minimal zoanthid cover was observed within the outer reef flat zone (mean 1.6%). Observations of benthic cover in the reef crest zone are representative of CRAF Site 1, while observations of benthic cover in the outer reef flat zone are representative of CRAF Sites 2 and 3.

Immediately lagoonward of the boulder tract zone, the reef substrate was comprised predominantly of smooth coral/algal pavement (mean 70.9%), with some discrete patch coral gardens (mean 8.5%). The results from benthic surveys of this part of the reef flat are representative of the habitat underlying CRAF Site 4.

At surveyed locations across the central reef flat, mean percent coral cover was generally low ($\leq 10.0\%$) and spatially variable (range = 3.0% to 10.0%). Mean CCA cover was also low across the central and inner reef substrate ($\leq 1.0\%$),

except for areas of concentrated rubble and boulder deposits (Supplementary Tables 1 and 2). The seaward margin of the central reef flat was characterised by rubble deposits (~82%), and some living coral cover (10%), while there were discrete areas of living benthos surveyed across the mid to inner reef flat dominated by seagrass meadows growing atop a thin layer of sand (mean range: 46% to 68%).

The inner reef flat immediately southeast of Keleihutta Island is characterised by intertidal pools and channels, and these exhibited a relatively high percentage of living coral cover (mean of 18.3% to 20.5%), similar in magnitude to the percent cover of living coral on the outer reef flat zone. At inner reef locations, patch coral gardens grew alongside seagrass, reef pavement and deposits of sand and rubble (Supplementary Table 2). Consequently, within these areas, coral cover was not indicative of consolidated reef framework but rather existed as patches of living coral growing on top of reef pavement.

The inner reef pond and channel areas exhibited the highest percent cover of dead coral (mean: 15.0% to 31.3%). However, juvenile and re-sheeting corals were observed in the dead gardens, suggesting that cyclical patterns of mortality and renewal were occurring in this area.

The reef flat surface exhibited a consistently low level of structural complexity across all zones (mean range: 1.12 to 1.31).

Coral community structure

The dominant coral community members recorded at all surveyed reef flat locations were *Porites*, *Acropora* and *Isopora* species. The percent cover of *Porites* far exceeded all other coral genera (16.3%), and therefore the presence or absence of *Porites* species strongly influenced the total percent coral cover recorded within each reef flat zone. Coral community diversity was greatest within the reef pavement zone, at the transition between the outer reef flat and central reef flat, where 10 coral genera were recorded. Coral diversity was also relatively high within the outer reef flat zone (8 genera recorded) and the reef crest zone (6 genera recorded). Diversity was generally low across central to inner reef flat survey locations (Supplementary Table 2).

Within the high energy reef crest zone, *Porites* (6.2%), *Acropora* (4.8%) and *Platygyra* (1.6%) were the dominant coral genera, collectively accounting for 90% of total coral cover (14%). Coral communities were dominated by encrusting growth morphologies (6.4%), with some corymbose (1.2%), branching (2.0%) and submassive (1.0%) morphotypes also recorded at this location. Coral communities located within the outer reef flat zone were dominated by *Porites* species (16.3%), and encrusting growth forms (17.9%). The outer reef flat hosted the highest percent cover of *Acropora* species (5.4%) and relatively high *Isopora* cover (2.3%). The highest percent cover of *Platygyra* and *Pocillopora* species (1.7% respectively) was also recorded within this zone. The reef crest and outer reef zones hosted the highest percent cover of encrusting coral species across the reef flat of 6.4% and 17.9% respectively. The reef pavement zone exhibited relatively low coral cover on average (10%), but the highest diversity of genera. Across the central reef flat, coral communities were dominated by massive and sub-massive *Porites* species. However, the percent cover of branching corals increased toward the inner reef flat, where branching cover was highest within the microatoll patch and channel zones (6.3% and 9.7% respectively).

Supplementary References

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