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Rocky reef impacts of the Kaikōura earthquake: extended monitoring of nearshore habitats and communities – Year 1 results

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Contents

Executive Summary

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The 2016 7.8 magnitude Kaikōura earthquake caused extensive uplift of about 130 km of the north-eastern coastline of the South Island of New Zealand, which resulted in widespread mortality of many marine organisms and alteration to the structure of intertidal and subtidal rocky reefs. This report describes the results of nearshore reef surveys done at long-term monitoring sites between November 2018 and May 2019 to assess the trajectories of recovery of rocky reef communities. These surveys extended previous monitoring work done between 2017 and early 2018 as part of the Ministry for Primary Industries (MPI) Kaikōura Earthquake Marine Recovery Package, when the first post-earthquake surveys were carried out at these same sites. Overall, the results included in this report show that intertidal benthic communities are showing signs of recovery only in low zone areas, while subtidally there was little recovery in devegetated areas and previously abundant algal stands appear to have become more sparse and fragmented. Legacy effects of the earthquake and recovery trajectories remain highly variable across sites.

Follow-up intertidal surveys were done in November 2018 at 16 sites across the coastline between Oaro and Cape Campbell, and encompassing levels of uplift between approximately 0 and 6.5 metres. Subtidal surveys were done at 6 sites (2 around the Kaikōura Peninsula and 4 north of Kaikōura, in the Okiwi Bay/Waipapa Bay area) in April and May 2019. Subtidal sites encompassed levels of uplift between approximately 0.7 and 6.5 metres.

The results of intertidal surveys showed that two years after the earthquake the composition of intertidal benthic communities at all uplifted sites was still significantly different compared to non-uplifted control areas. This was because all uplifted reefs were still largely unvegetated, with diverse algal communities found only in the lowest tidal zone. In the low zone, habitat-forming large brown algae (primarily *Durvillaea* spp., *Carpophyllum maschalocarpum* and *Marginariella boryana*) were the dominant species at sites with low uplift (less than 1 m), while fleshy red algae dominated low zone areas at sites with medium and high uplift (between 1.5 and 6.5 m). Coralline algae, which play an important role in the life cycle of invertebrates such as pāua and cat's eye snails, were abundant in the low zone at most sites. The abundance of limpets, the most abundant large intertidal grazers along this coastline, was unrelated to the degree of uplift and highly variable among sites. Overall, these results show patterns of abundance of key intertidal algal and invertebrate taxa in line with those of our previous post-earthquake surveys. The November 2018 surveys also highlighted high variability among sites with similar degrees of uplift, confirming that earthquake impacts and trajectories of recovery cannot be predicted or assessed only on the basis of the magnitude of the uplift.

Subtidal surveys showed some recovery of seaweeds and invertebrates at Waipapa Bay, the area with the most evident earthquake damage, but there were extensive areas of bare rock still present. The most striking difference compared to previous post-earthquake surveys was the decrease in large brown algae at Okiwi Bay North, which may be related to changes in wave dynamics at this site. There were also shifts in sand/gravel distribution at Waipapa Bay and Okiwi Bay. Shifts in sand and gravel can scour rock surfaces and smother organisms, slowing the recovery of benthic communities, and are indicative of a very dynamic physical environment.

In summary, this updated assessment of the state of rocky reefs provided by extended intertidal and subtidal monitoring is extremely valuable given that the uplifted coastline is still very much in the early stages of recovery and presents a very dynamic physical environment. This work will inform management decisions, new research, also add to a very limited understanding of post-earthquake recovery of coastal systems worldwide.

1. INTRODUCTION

The 2016 Mw 7.8 Kaikōura earthquake caused extensive coastal uplift along about 130 km of coastline (Clark et al. 2017, Hamling et al. 2017), severely affecting highly productive nearshore ecosystems (Schiel et al. 2018, Schiel et al. 2019). Extensive field surveys were carried out between 2017 and 2018 as part of the Ministry for Primary Industries (MPI) Kaikōura Earthquake Marine Recovery Package to assess the impacts of the earthquake on rocky intertidal and shallow subtidal biogenic habitats (Alestra et al. 2019). This research provided a detailed assessment of the state of rocky reef systems along the uplifted coastline and of the impacts of the earthquake on species of ecological, cultural and/or commercial significance (e.g., pāua, bull kelp). It also established an important baseline to gauge successional sequences and recovery dynamics. While our previous work could only go as far as assessing the initial responses of rocky reef systems up to 16 months following the earthquake (March 2018), assessing their long-term recovery trajectories is particularly important to understand the ultimate outcome of this catastrophic event and inform management decisions.

Having established a wide range of intertidal and subtidal research sites along the uplifted coastline and gained considerable insight into the state of rocky reef systems in the early post-earthquake stages, we built on our previous work as part of this extended sampling programme. This report describes the research undertaken to extend the quantitative sampling of nearshore reef systems between November 2018 and May 2019. This study provides an updated assessment of the state of rocky reef habitats, which will inform the management of this valued coastline and also add to a very limited pool of long-term studies about post-earthquake recovery of coastal systems worldwide. It also represents an invaluable baseline and reference for another research programme funded by the Ministry for Business Innovation and Employment (MBIE), which uses a more holistic approach based on experimental work and wide-scale habitat mapping to tease out biological and physical mechanisms driving and underpinning the recovery of earthquake-affected reefs (Project title: "*Community concerns, key species and wahi taonga – recovery trajectories of the marine ecosystem from the Kaikōura earthquakes*", PI: David Schiel).

2. METHODS

2.1 Intertidal community surveys

Intertidal community surveys were done in November 2018, two years after the Kaikōura earthquake, at 16 sites across 8 locations (Figure 1). These were a subset of the sites used in the original MPI post-earthquake surveys (Alestra et al. 2019). Sites were divided into four uplift groups on the basis of uplift information obtained from GNS Science: control (C – no uplift); low uplift (L – 0.5 to 1 m); medium uplift (M – 1.5 to 2.5 m); high uplift (H – 4.5 to 6.5 m). Each uplift group included at least two sites. We used the same methodology as in previous post-earthquake sampling (Alestra et al. 2019). At each site, sampling was done along 30 m transects previously established within the current (i.e., post-earthquake) tidal elevation zones. There was one transect in each of the post-earthquake high, mid and low zones. Algae and invertebrates were identified to species level when feasible or to the finest possible taxonomic resolution and their abundances were recorded in ten haphazardly located 1 m^2 quadrats placed along each transect in each zone.

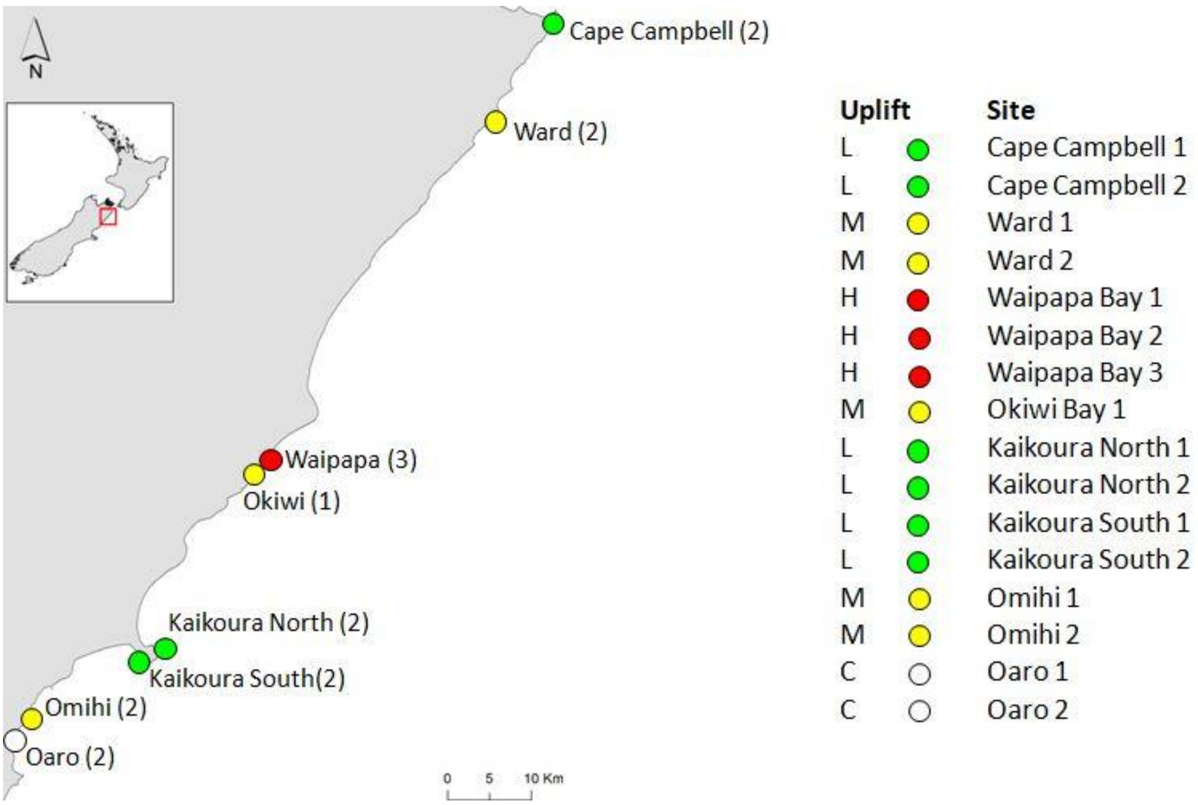

Figure 1: Sites used for repeated intertidal monitoring and their degrees of uplift. L = low uplift (green symbols), M = medium uplift (yellow symbols), H = high uplift (red symbols), C = control (white symbols). The sites are divided across 8 locations displayed on the map on the left. The numbers in brackets indicate the numbers of sites per location.

Data generated by the November 2018 surveys were analysed with univariate (ANOVA) and multivariate techniques (PERMANOVA) testing for differences among uplift groups and sites. To provide a comprehensive and easily understandable overview of the main patterns in intertidal community structure, the results included in this report mainly relate to broad taxonomic groups (i.e., groups of species sharing common morphological and life-history traits) and not to individual species.

These include:

- large brown algae, which are the dominant habitat-forming species along this coastline;
- fleshy red algae, which account for a large proportion of the diversity in intertidal algal communities;
- coralline red algae, which are also habitat-formers and an important invertebrate settlement substrate;
- limpets, which are the most abundant large intertidal grazers along this coastline.

2.2 Subtidal community surveys

Subtidal community surveys were done in April and May 2019, 29–30 months after the Kaikōura earthquake, at 6 sites selected across 4 locations: Waipapa Bay, Okiwi Bay, Kaikōura Peninsula North and South (Figure 2). The sites re-sampled in 2019 were a subset of the sites used in the original MPI post-earthquake surveys (Alestra et al. 2019) and included sites with little uplift (0.5–1 m) and no earthquake damage around the Kaikōura Peninsula, and sites with medium-high uplift (1.5–6.5 m) and moderate or significant earthquake damage in the Okiwi/Waipapa Bay area.

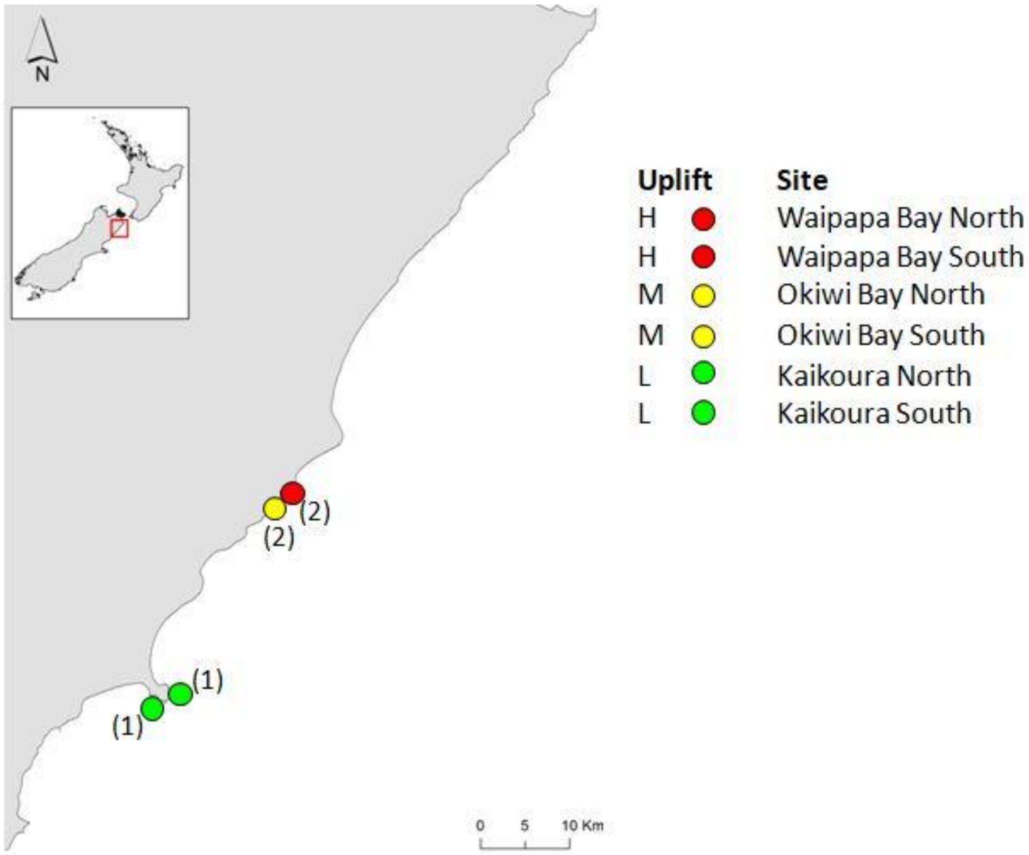

Figure 2: Sites used for repeated subtidal monitoring and their degrees of uplift. L = low uplift (green symbols), M = medium uplift (yellow symbols), H = high uplift (red symbols), C = control (white symbols). The sites are divided across 4 locations displayed on the map on the left. The numbers in brackets indicate the numbers of sites per location.

Sampling followed the methodology of previous surveys, assessing algae, and sessile and mobile invertebrate community composition and abundances (Alestra et al. 2019). At each site, we:

- re-surveyed three 50 m transects perpendicular to the shore starting from the low tidal mark. Subtidal transects were usually located directly offshore of intertidal transects and had been marked using GPS;
- recorded substrate type and the abundance of all algae, sessile invertebrates, mobile invertebrates and triplefin fish in 20 × 5m^2 sections along each transect (each section was 1 m either side of the transect, and 2.5 m in length). Taxa were usually identified to species level and when this was not achievable they were given descriptive names;
- measured the sizes of pāua (*Haliotis iris* and *Haliotis australis*) using automated calipers that also recorded the depth of occurrence;
- recorded the abundance of all large fish in 5 × 20 m^2 sections along each transect (each section was 1 m either side of the transect, 2 m above the seafloor and 10 m in length);
- collected video footage along transects.

As for previous surveys, subtidal data were filtered to include only quadrats with at least 50% rock coverage (cobble, boulder or bedrock). This was done to eliminate the large variability in communities due to some transects having extensive areas of sand. By eliminating the sandy/gravel quadrats, a more accurate comparison of the rocky reef communities between transects, sites and uplift could be made. The removal of the sand-dominated quadrats resulted in a reduction in the number of replicates, although most transects (45 out of 49) still had at least 10 quadrats per transect. Numbers of quadrats per site used in analyses are provided in Appendix 1.

Differences in subtidal community structure and grouped taxa with respect to uplift, site and transect were analysed statistically using a distance-based permutational analysis (PERMANOVA). The PERMANOVA design had four factors; Uplift (fixed, 3 levels: low, medium, high), Survey (fixed, 3 levels), Site (random, nested within Uplift, 20 levels) and Transect (random, nested within Site, 3 levels). Data were square-root transformed to de-emphasise the influence of abundant organisms, and analyses were based on Bray-Curtis similarities. For the Bray-Curtis similarity matrices, a dummy variable of 0.01 was used so that double zero data were treated as 100% similar. To visualise the differences between communities, principal coordinates analyses (PCO) were run on the resemblance matrices created from distances among centroids for the unique Site/Transect and Site combinations. Taxa that had a correlation more than 0.6 with the PCO axes were displayed as vectors in the PCO plots.

3. RESULTS

3.1 Intertidal benthic community structure

As in previous sampling (Figure 3 A-C, E-G, I-K), 24 months after the earthquake most of the algal biomass was found in the post-earthquake low zone on uplifted reefs (Figure 3 L), whereas the high and the mid zones were generally devoid of algae (Figure 3 D, H). Low algal abundance in the high zone is typical of rocky intertidal habitats because physical conditions in this area are too harsh for most seaweeds, but the mid zone environment is generally known to support complex and diverse algal communities. However, under all levels of uplift, mid zone areas continued to be mostly unvegetated two years after the earthquake (Figure 3 H). In the low zone, algae were abundant in all uplift groups, with large covers of large brown algae characterizing communities at the control and low-uplift sites, while fleshy red algae were more dominant at the mid- and high-uplift sites (Figure 3 L).

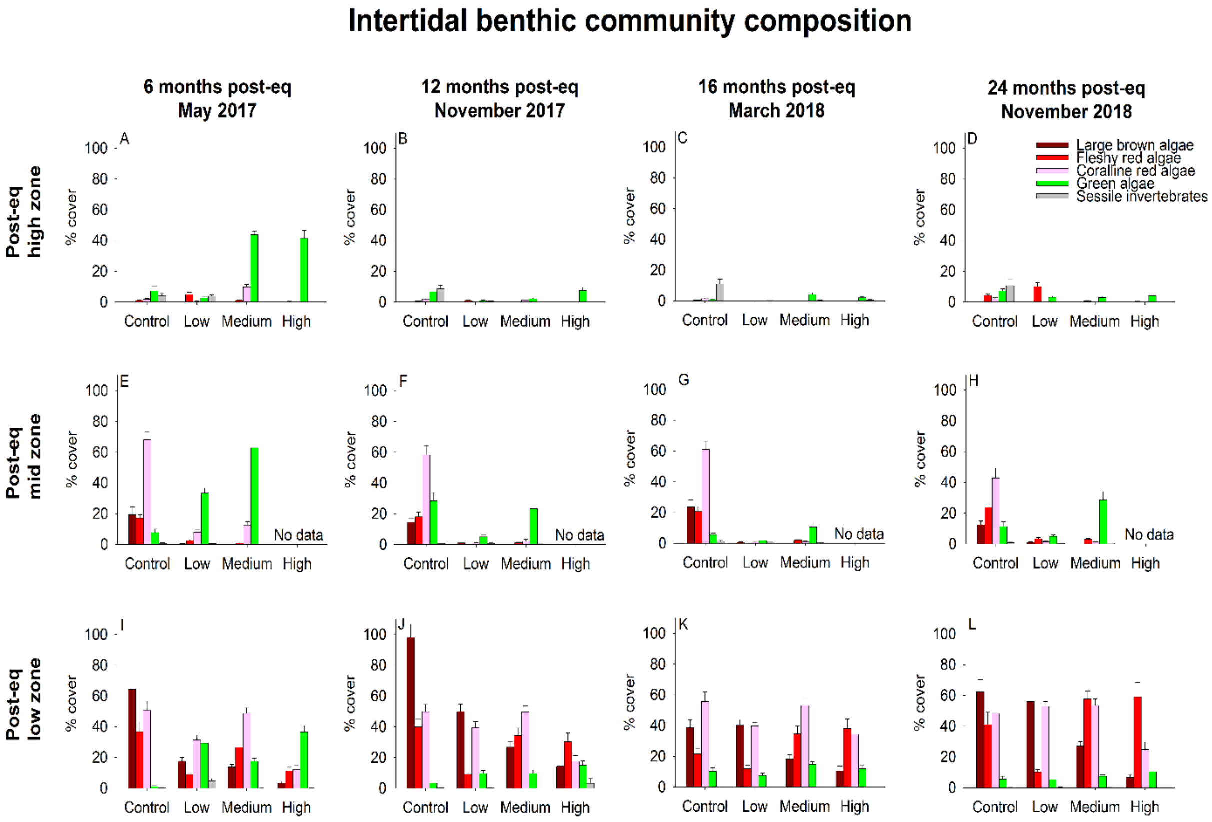

Figure 3: Abundance of the main algal groups and of sessile invertebrates across uplift levels 6, 12, 16 and 24 months after the earthquake.

Multivariate analyses showed that, in November 2018, benthic community composition in the post-earthquake high zone differed between the controls and the three other groups (Uplift: Pseudo-$F_{3,12} = 2.32$, $P < 0.05$, Figure 4 A). The low-, medium- and high-uplift groups did not differ from each other and there was significant variability in the structure of benthic communities among sites within each uplift group (Pseudo-$F_{12,144} = 7.5$, $P < 0.001$, Figure 4 A). Similarly to the high zone, two years after the earthquake benthic communities in the post-earthquake mid zone were different in the controls compared to the low- and medium-uplift groups which did not differ from each other (Uplift: Pseudo-$F_{2,8} = 2.66$, $P < 0.05$, Figure 4 B). There was also significant variability in the structure of benthic communities among sites in the low- and medium-uplift groups (Pseudo-$F_{8,99}$ = 10.1, $P < 0.001$, Figure 4 B). Finally, in the post-earthquake low zone, the composition of benthic communities was different in the low-uplift group compared to the medium- and high-uplift groups (Uplift: Pseudo-$F_{3,12}$ = 2.42, $P < 0.01$, Figure 4 C). No other groups differed from the others and there was significant variability in the structure of benthic communities among sites within each uplift group (Pseudo-$F_{12,144}$ = 9.19, $P < 0.001$, Figure 4 C). Results of SIMPER tests, showing the taxa driving the differences in benthic community composition highlighted by multivariate analyses are included in Appendix 2.

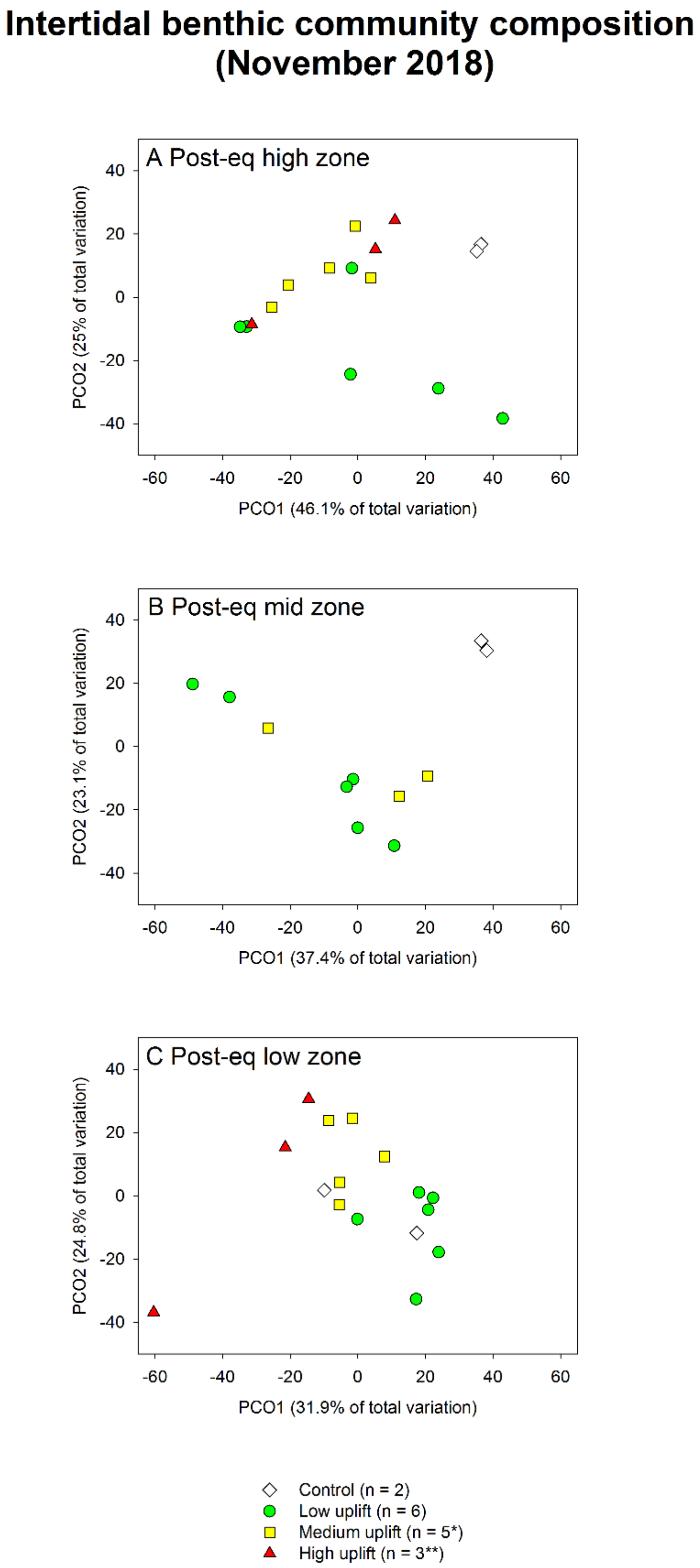

Figure 4: Principal coordinates analysis (PCO) plots showing differences in the composition of benthic communities in the post-earthquake high (A), mid (B) and low zone (C) across sites with different degrees of uplift 24 months after the earthquake. Symbols represent the centroid of each site. n = number of sites in each uplift group. *n = 3 after 12 and 16 months in all panels; ** n = 0 in panel B because only the high and the low zone were sampled at high-uplift sites.

3.2 Abundance of key intertidal taxa

Because there was very limited recovery of algae in the post-earthquake high and mid zones of uplifted reefs two years after the earthquake, Sections 3.2.1, 3.2.2 and 3.2.3 describe the recovery of brown and red algae in the post-earthquake low zone. Section 3.2.4 focuses on temporal trends in the abundance of the main intertidal grazers (limpets) across all tidal zones.

Large brown algae

In the post-earthquake low zone, *Durvillaea* spp., *Carpophyllum maschalocarpum* and *Marginariella boryana* were the most abundant species of large brown algae two years after the earthquake. In November 2018, the control and low-uplift groups had the highest cover of large brown algae (between 56–62%) and the high-uplift group the lowest (6%; Uplift: $F_{3,12} = 12.52$, $P < 0.001$, Figure 5). These results are in line with those of previous sampling dates, showing a faster recovery of large brown algae at low-uplift sites. The extended time series also shows that the abundance of large brown algae at control sites seems to be bouncing back after large mortality during the hot summer of 2017–2018 (Figure 5). Two years after the earthquake, there was also significant variability among sites in all groups except controls ($F_{12,144} = 3.42$, $P < 0.001$, Figure 6). All low-uplift sites had cover of large brown algae greater than 40%, while all medium- and high-uplift sites were below this. As in previous sampling events, Waipapa Bay 1 was the only site where large brown algae were completely absent (Figure 6). Comparisons between March and November 2018 surveys showed a large increase in the % cover of large brown algae at all low-uplift sites (Table 1).

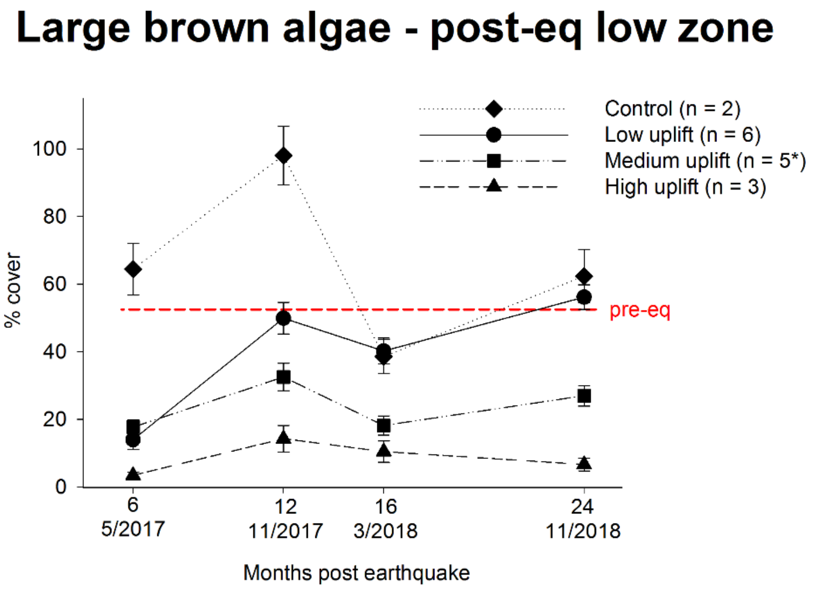

Figure 5: Time series of the mean percentage cover (±SE) of large brown algae per m^2 in the post-earthquake low zone across uplift levels. The dashed red line indicates the average abundance of large brown algae in the pre-earthquake low zone across sites sampled in November 2016 (see Alestra et al. 2019). n = number of sites in each uplift group. *n = 3 after 12 and 16 months.

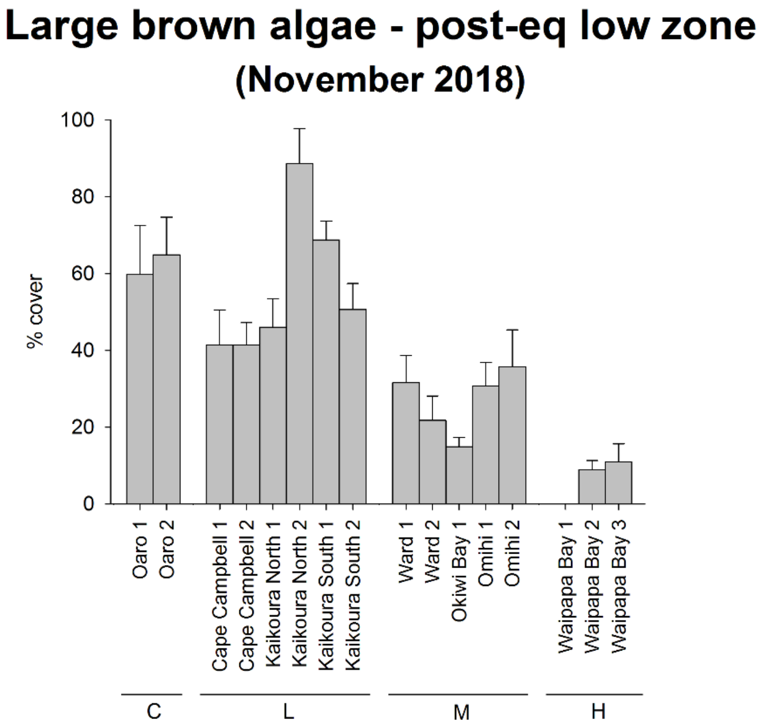

Figure 6: Mean percentage cover (+SE) of large brown algae per m^2 in the post-earthquake low zone 24 months after the earthquake. C = control (no uplift), L = low uplift, M = medium uplift, H = high uplift. Sites are ordered north to south within each uplift group.

Table 1: Change in the % cover of large brown algae at each site between March and November 2018. C = control (no uplift), L = low uplift, M = medium uplift, H = high uplift. Sites are ordered north to south within each uplift group. Positive values showing increase in the cover of large brown algae are highlighted in bold. NA = data not available for the Omihi sites, where the low zone was not sampled in March 2018.

Uplift	Site	Change in % cover
C	Oaro 1	+22%
C	Oaro 2	+25%
L	Cape Campbell 1	+25%
L	Cape Campbell 2	+18%
L	Kaikōura north 1	+12%
L	Kaikōura north 2	+12%
L	Kaikōura south 1	+17%
L	Kaikōura south 2	+11%
M	Ward 1	+9%
M	Ward 2	-2%
M	Okiwi Bay 1	+6%
M	Omihi 1	NA
M	Omihi 2	NA
H	Waipapa Bay 1	0%
H	Waipapa Bay 2	-3%
H	Waipapa Bay 3	-8%

Fleshy red algae

In November 2018, the medium- and high-uplift groups had the highest cover of fleshy red algae in the post-earthquake low zone (around 58%) and the low-uplift group the lowest (10%; Uplift: $F_{3,12} = 3.56$, $P < 0.05$, Figure 7). These results are in line with those of March 2018 and highlight a steady increase in the abundance of fleshy red algae in areas with uplift between 1.5 and 6.5 m, while there was little change where the uplift was less than 1 m. The extended time series also showed an increase in the abundance of fleshy red algae at control sites, where it had dropped significantly between November 2017 and March 2018 (Figure 7). In November 2018, there was also significant variability among sites in all uplift groups ($F_{12,144} = 11.99$, $P < 0.001$, Figure 8). The high-uplift group included both the site with the highest cover of fleshy red algae (108% at Waipapa Bay 2) and the one with the lowest (0.2% at Waipapa Bay 1, Figure 8). Comparisons between the March and November 2018 surveys showed an increase in the % cover of fleshy red algae at all control, medium- and high-uplift sites aside from Waipapa Bay 1 (Table 2).

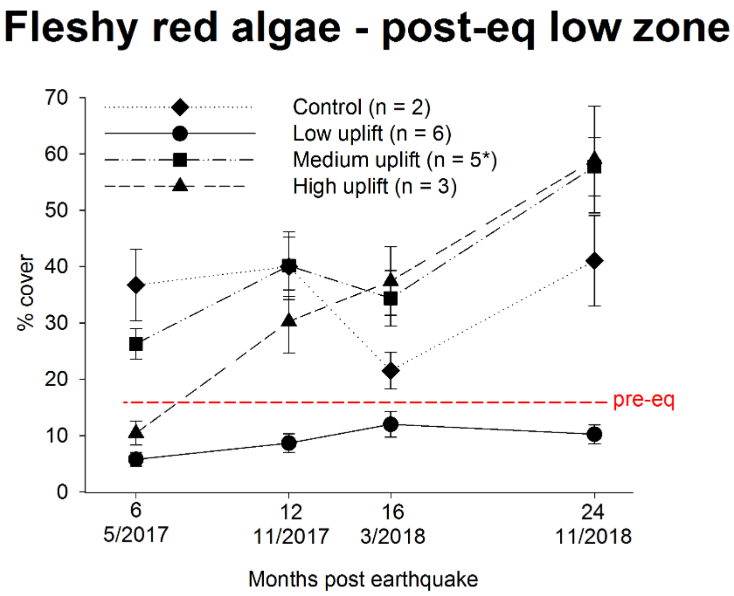

Figure 7: Time series of the mean percentage cover (±SE) of fleshy red algae per m^2 in the post-earthquake low zone across uplift levels. The dashed red line indicates the average abundance of fleshy red algae in the pre-earthquake low zone across sites sampled in November 2016 (see Alestra et al. 2019). n = number of sites in each uplift group. *n = 3 after 12 and 16 months.

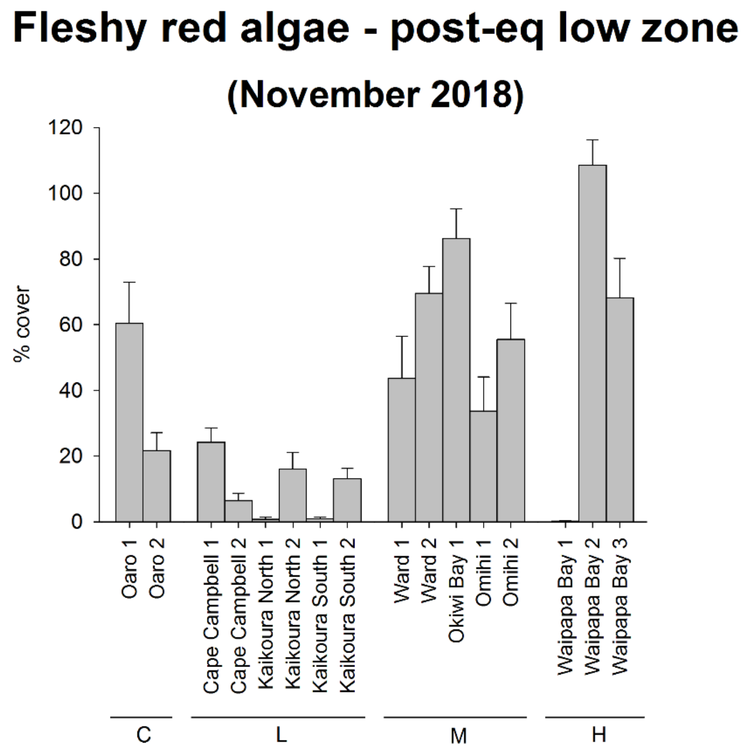

Figure 8: Mean percentage cover (+SE) of fleshy red algae per m^2 in the post-earthquake low zone 24 months after the earthquake. C = control (no uplift), L = low uplift, M = medium uplift, H = high uplift. Sites are ordered north to south within each uplift group.

Table 2: Change in the % cover of fleshy red algae at each site between March and November 2018. C = control (no uplift), L = low uplift, M = medium uplift, H = high uplift. Sites are ordered north to south within each uplift group. Positive values showing increase in the cover of fleshy red algae are highlighted in bold. NA = data not available for the Omihi sites, where the low zone was not sampled in March 2018.

Uplift	Site	Change in % cover
C	Oaro 1	+32%
C	Oaro 2	+7%
L	Cape Campbell 1	+13%
L	Cape Campbell 2	-1%
L	Kaikōura north 1	+1%
L	Kaikōura north 2	-18%
L	Kaikōura south 1	0%
L	Kaikōura south 2	-5%
M	Ward 1	+8%
M	Ward 2	+25%
M	Okiwi Bay 1	+64%
M	Omihi 1	NA
M	Omihi 2	NA
H	Waipapa Bay 1	0%
H	Waipapa Bay 2	+53%
H	Waipapa Bay 3	+12%

Coralline red algae

In November 2018, control, low- and medium-uplift groups had similar covers of coralline red algae in the low zone (between 49–53%), while these species had around 25% cover in the high-uplift group (Figure 9). However, the analysis found no significant differences among uplift groups ($F_{3,12} = 1.54$, $P = 0.26$). The extended time series shows that between March and November 2018 the abundance of coralline algae was stable in the medium-uplift group, increased in the low-uplift group, and decreased in the control and high-uplift groups (Figure 9). In November 2018, there was also significant variability among sites in all uplift groups ($F_{12,144} = 8.93$, $P < 0.001$). Waipapa Bay 1 was the only site were coralline algae were completely absent (Figure 10). Comparisons between the March and November 2018 surveys showed large increases in the abundance of coralline algae at several sites across the low- and medium-uplift groups. Waipapa Bay 3 was the only site showing a large decline in the cover of corallines between March and November 2018 (Table 3).

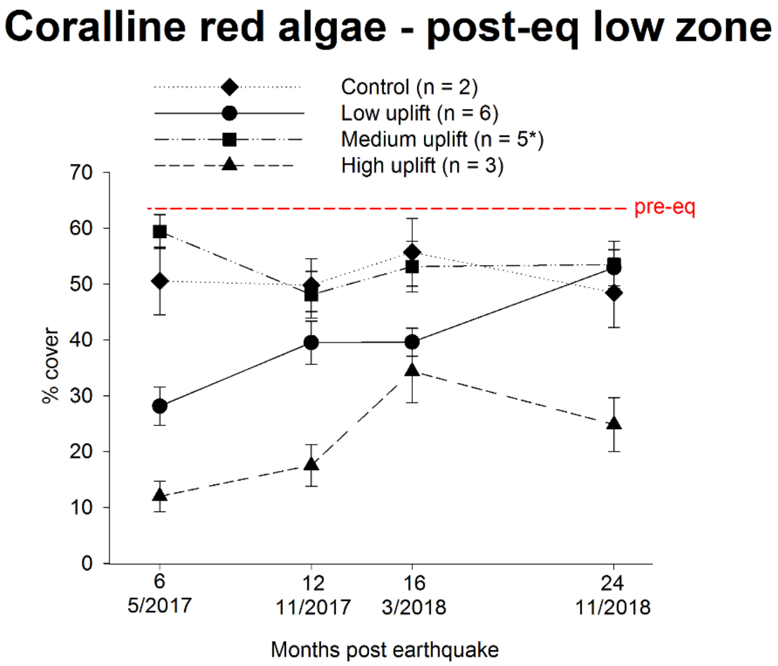

Figure 9: Time series of the mean percentage cover (±SE) of coralline red algae per m^2 in the post-earthquake low zone across uplift levels. The dashed red line indicates the average abundance of coralline red algae in the pre-earthquake low zone across sites sampled in November 2016 (see Alestra et al. 2019). n = number of sites in each uplift group. *n = 3 after 12 and 16 months.

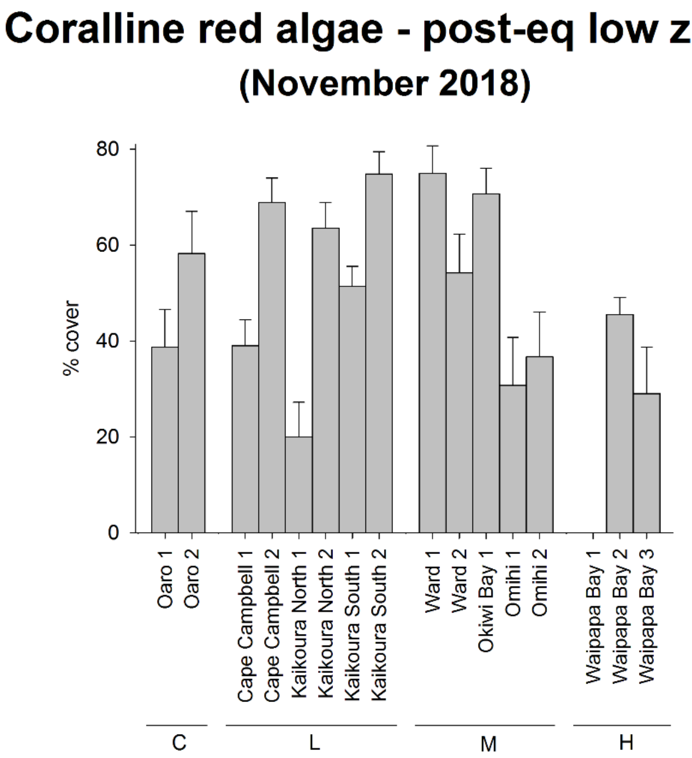

Figure 10: Mean percentage cover (+SE) of coralline red algae per m^2 in the post-earthquake low zone 24 months after the earthquake. C = control (no uplift), L = low uplift, M = medium uplift, H = high uplift. Sites are ordered north to south within each uplift group.

Table 3: Change in the % cover of coralline red algae at each site between March and November 2018. C = control (no uplift), L = low uplift, M = medium uplift, H = high uplift. Sites are ordered north to south within each uplift group. Positive values showing increase in the cover of coralline red algae are highlighted in bold. NA = data not available for the Omihi sites, where the low zone was not sampled in March 2018.

Uplift	Site	Change in % cover
C	Oaro 1	-5%
C	Oaro 2	-9%
L	Cape Campbell 1	+12%
L	Cape Campbell 2	+22%
L	Kaikōura north 1	-4%
L	Kaikōura north 2	+19%
L	Kaikōura south 1	-1%
L	Kaikōura south 2	+32%
M	Ward 1	+29%
M	Ward 2	+7%
M	Okiwi Bay 1	+5%
M	Omihi 1	NA
M	Omihi 2	NA
H	Waipapa Bay 1	0%
H	Waipapa Bay 2	-4%
H	Waipapa Bay 3	-25%

Limpets

In November 2018, control and medium-uplift groups had similar limpet densities (43–45 individuals per m^2), whereas limpet abundances were around 28 and 9 individuals per m^2 in the high- and low-uplift groups, respectively (Figure 11). However, the analysis found no significant differences among uplift groups ($F_{3,12} = 1.6$, $P = 0.24$). The extended time series shows that between March and November 2018 the abundance of limpets increased under almost all uplift levels, the only exception being the low-uplift group (Figure 11). In November 2018, there was also significant variability among sites in the control, medium- and high-uplift groups ($F_{12,144} = 7.02$, $P < 0.001$, Figure 12). A comparison between March and November 2018 showed large increases in the density of limpets at several medium- and high-uplift sites and also at one of the controls (Table 4).

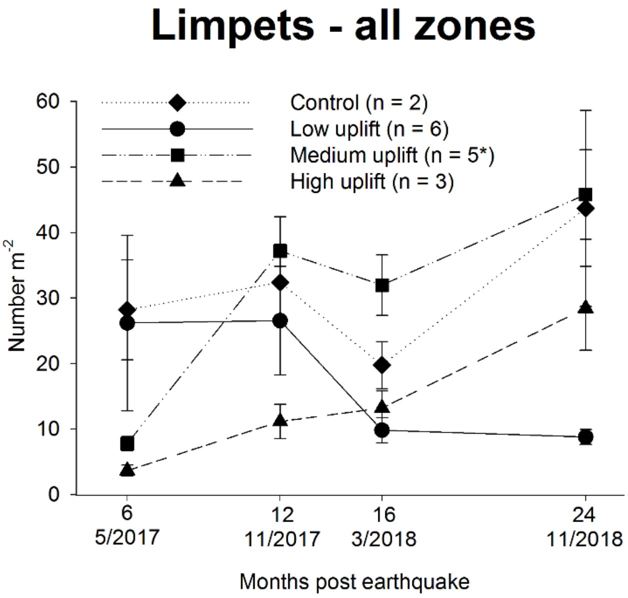

Figure 11: Time series of the mean number (±SE) of limpets per m^2 in all post-earthquake zones across uplift levels. n = number of sites in each uplift group. *n = 3 after 12 and 16 months.

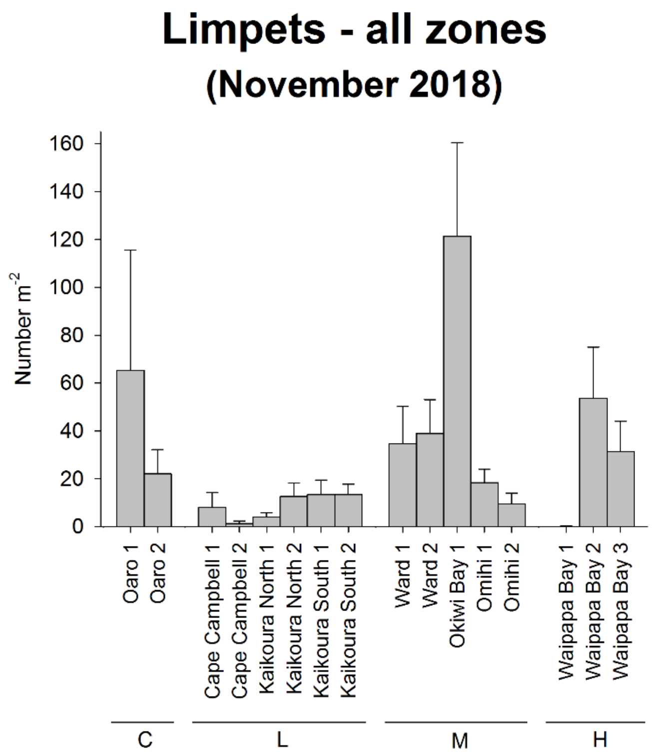

Figure 12: Mean number (+SE) of limpets per m^2 in all post-earthquake zones 24 months after the earthquake. C = control (no uplift), L = low uplift, M = medium uplift, H = high uplift. Sites are ordered north to south within each uplift group.

Table 4: Change in limpet density per m^2 at each site between March and November 2018. C = control (no uplift), L = low uplift, M = medium uplift, H = high uplift. Sites are ordered north to south within each uplift group. Positive values showing increase in the density of limpets are highlighted in bold. NA = data not available for the Omihi sites, where the low zone was not sampled in March 2018.

Uplift	Site	Change in density m^{-2}
C	Oaro 1	+51
C	Oaro 2	-3
L	Cape Campbell 1	+5
L	Cape Campbell 2	0
L	Kaikōura north 1	0
L	Kaikōura north 2	+1
L	Kaikōura south 1	-8
L	Kaikōura south 2	-5
M	Ward 1	-6
M	Ward 2	+11
M	Okiwi Bay 1	+92
M	Omihi 1	NA
M	Omihi 2	NA
H	Waipapa Bay 1	0
H	Waipapa Bay 2	+26
H	Waipapa Bay 3	+19

3.3 Subtidal community structure

The 2019 subtidal surveys showed minor recovery of seaweeds and invertebrates at Waipapa Bay (Figure 13), and a decrease in the abundance of large brown algae at Okiwi Bay North (Figure14). There were shifts in sand and gravel distribution at Okiwi Bay South (Figure 15), and an overall decline in algae at one cobble-dominated site (Okiwi Bay South T1). Sites at Waipapa Bay still had areas of bare rock that had not been recolonised, around two and a half years after the earthquake.

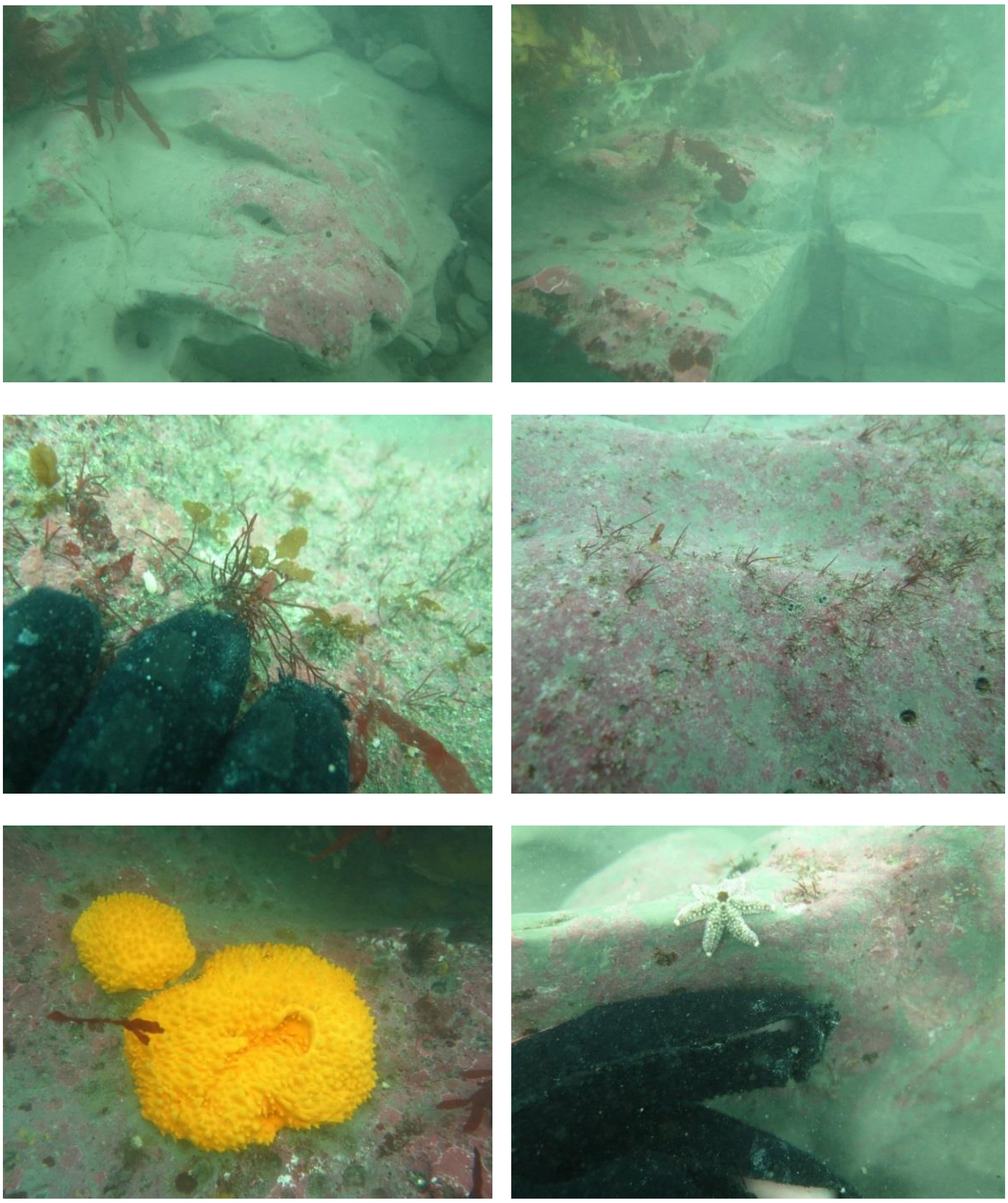

Figure 13: Examples of recruitment of encrusting coralline and encrusting red algae (top), brown (*Landsburgia quercifolia*) and red algae (middle), and sessile and mobile invertebrates (bottom) at Waipapa Bay. Photos taken in May 2019.

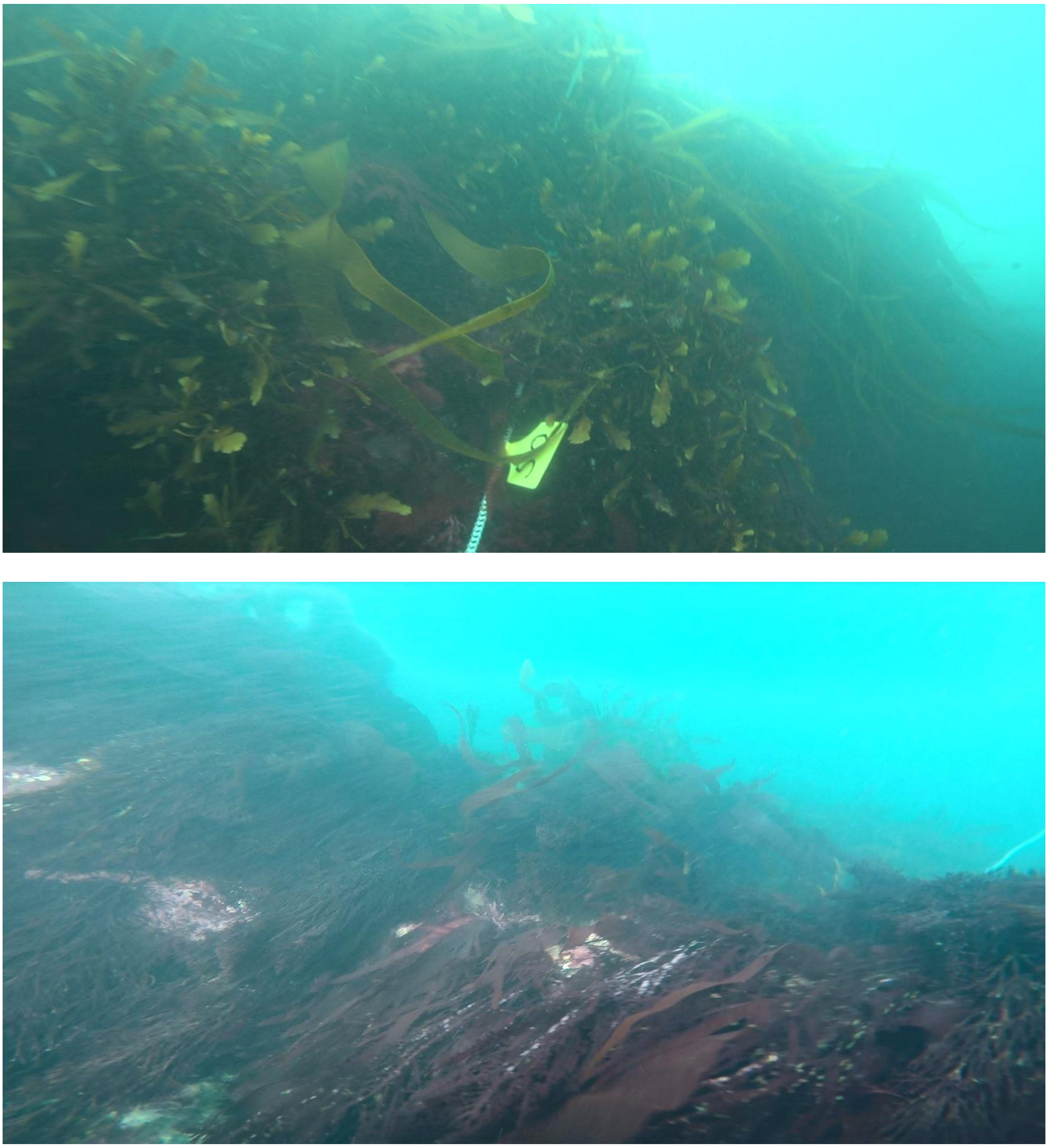

Figure14: Subtidal landscape at Okiwi Bay North Transect 1, showing a community dominated by large brown algae in 2017 (top) and by red algae in 2019 (bottom).

Figure 15: Examples of gravel and cobble covering algae at Okiwi Bay South (top and right), and remnant holdfasts of *Marginariella boryana* (bottom left). Photos taken in May 2019.

Analysis of the whole data set (without removing quadrats with less than 50% rock) showed changes in substrate cover at Waipapa and Okiwi Bay. Waipapa Bay North and South had declines in sand cover in 2019, and Waipapa Bay South had an increase in gravel and bedrock cover (Figure 16). Okiwi South also had declines in sand and boulder cover since 2017 and increases in gravel and cobble cover.

There was a decline in the total algal cover at Okiwi Bay sites between 2017 and 2019, while algal cover at Kaikōura and Waipapa Bay sites was relatively stable between years (Figure 17). Changes in the percentage cover of different algae groups varied between sites. While encrusting/turfing algae cover was similar through time at Kaikōura and Okiwi Bay, slight increases were seen at Waipapa Bay. There were noticeable declines in large brown algae at the Kaikōura and Okiwi Bay sites. The cover of green algae increased significantly in Kaikōura and also at one of the Waipapa Bay sites (Figure 17).

Generally, sessile and mobile invertebrate cover did not differ between surveys at Kaikōura and Okiwi Bay. Sessile invertebrate cover at Waipapa Bay North increased in 2018 and declined in 2019. These changes were driven by variation in sponge and ascidian cover (Figure 18). Mobile invertebrate numbers at Waipapa Bay South increased in 2018 and declined in 2019 (but numbers were higher in 2019 than in 2017). This peak was driven by an increase in numbers of lobsters and Cook's Turban shell *Cookia sulcata* (Figure 19).

Although there were generally low numbers of mobile invertebrates along transects, a few individual taxa showed increases through time (Figure 19). Numbers of black-foot pāua and Cook's turban shells increased at the Waipapa Bay sites, and yellow-foot pāua and sea urchins increased at Kaikōura North and South sites respectively.

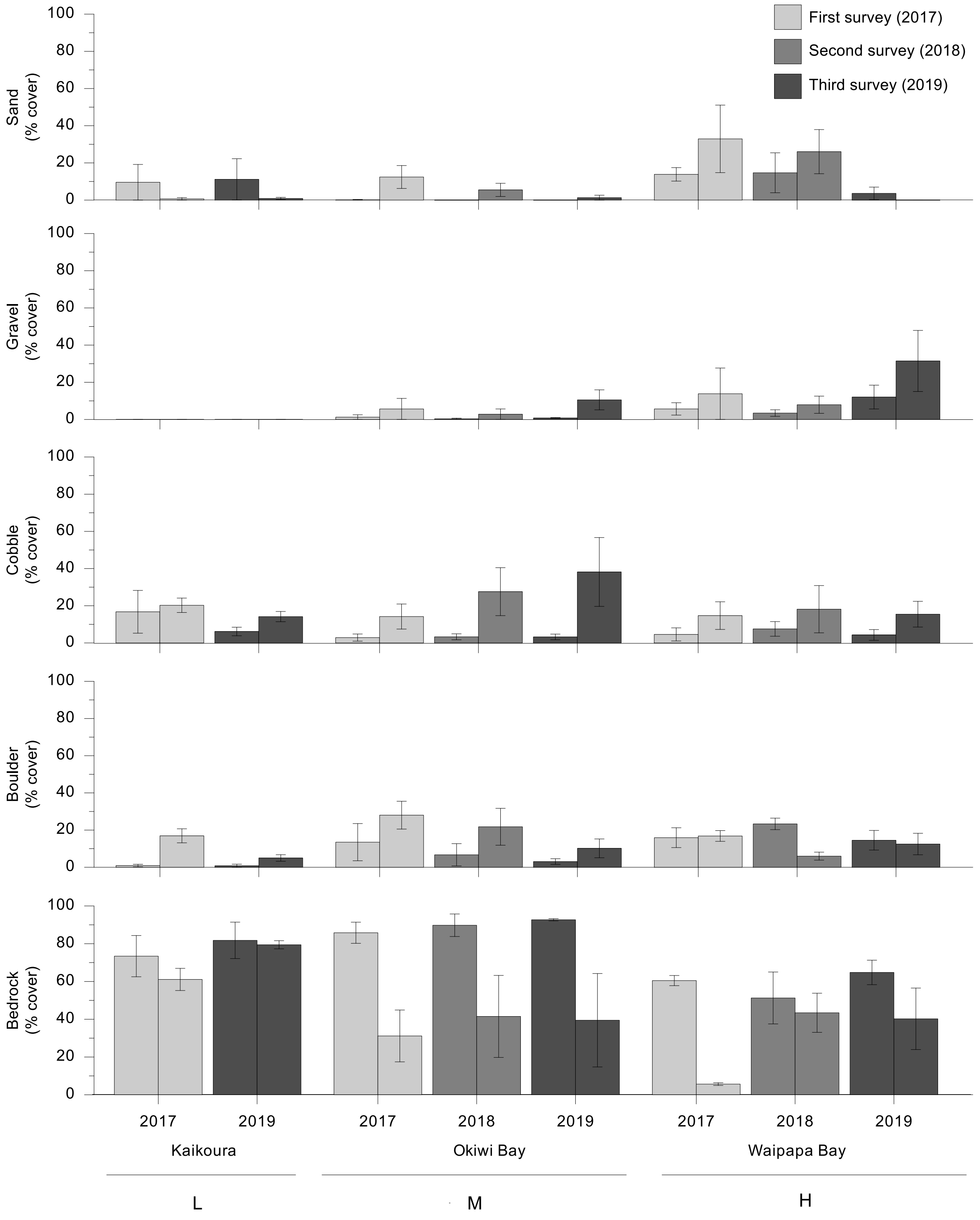

Figure 16: Mean percentage cover of substrate types per 5 m^2 quadrat at each site surveyed in 2017, 2018 (at Okiwi and Waipapa Bays only) and 2019. For each pair of bars, the left bar refers to the northern site and the right bar to the southern site. C=Control, L=Low, M=Medium, H=High. N = 20. Data are averaged over 3 transects with the exception of 2018 surveys at Waipapa South, where data are averaged over 4 transects; error bars represent 1 s.e.

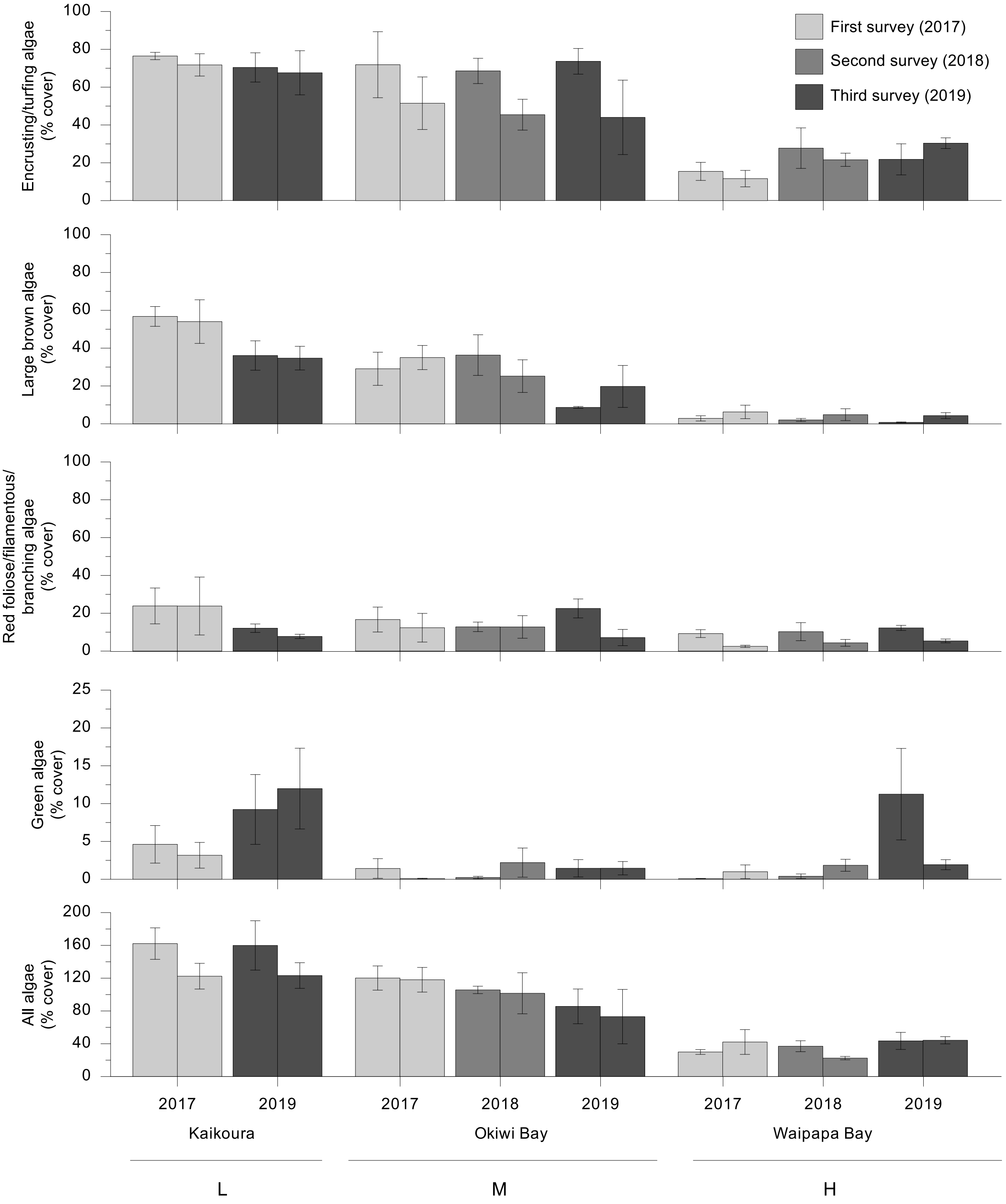

Figure17: Mean percentage cover of algae per 5 m^2 quadrat at each site surveyed in 2017, 2018 (at Okiwi and Waipapa Bays only) and 2019. For each pair of bars, the left bar refers to the northern site and the right bar to the southern site. C=Control, L=Low, M=Medium, H=High. Data were filtered to only include quadrats with ≥50% rock substrate (cobble, boulder or bedrock). The number of quadrats used in the analysis varied and is noted in Appendix 1. Data are averaged over 3 transects with the exception of 2018 surveys at Waipapa South, where data are averaged over 4 transects; error bars represent 1 s.e. Note different scales for green and all algae plots.

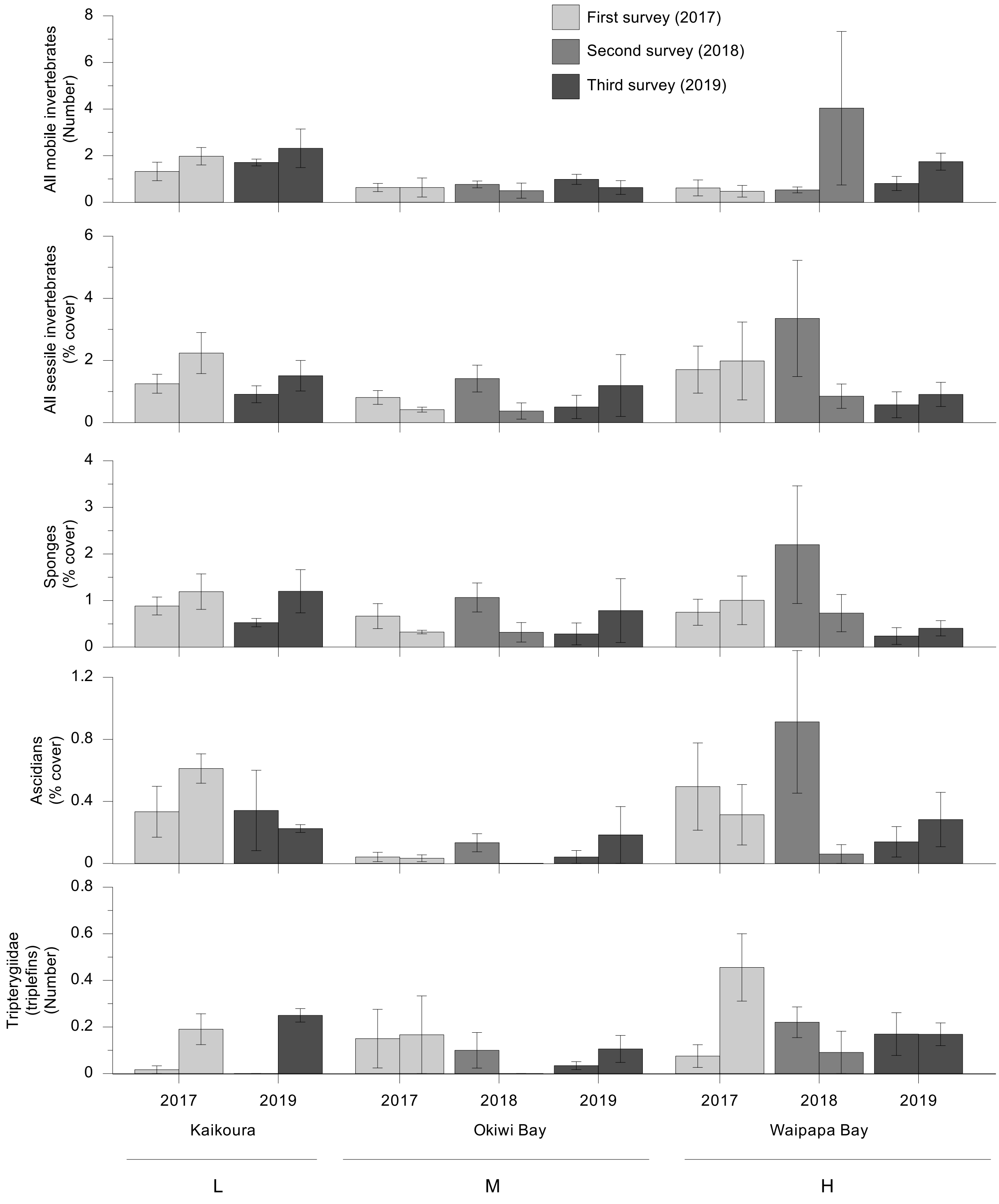

Figure 18: Mean percentage cover of sessile invertebrates, sponges and ascidians, and abundance of mobile invertebrates and triplefins per 5 m^2 quadrat at each site surveyed in 2017, 2018 (at Okiwi and Waipapa Bays only) and 2019. For each pair of bars, the left bar refers to the northern site and the right bar to the southern site. C=Control, L=Low, M=Medium, H=High. Data were filtered to only include quadrats with at least 50% rock substrate (cobble, boulder or bedrock). N = variable and noted in Appendix 1. Data are averaged over 3 transects with the exception of 2018 surveys at Waipapa South, where data are averaged over 4 transects; error bars represent 1 s.e. Note change in scales.

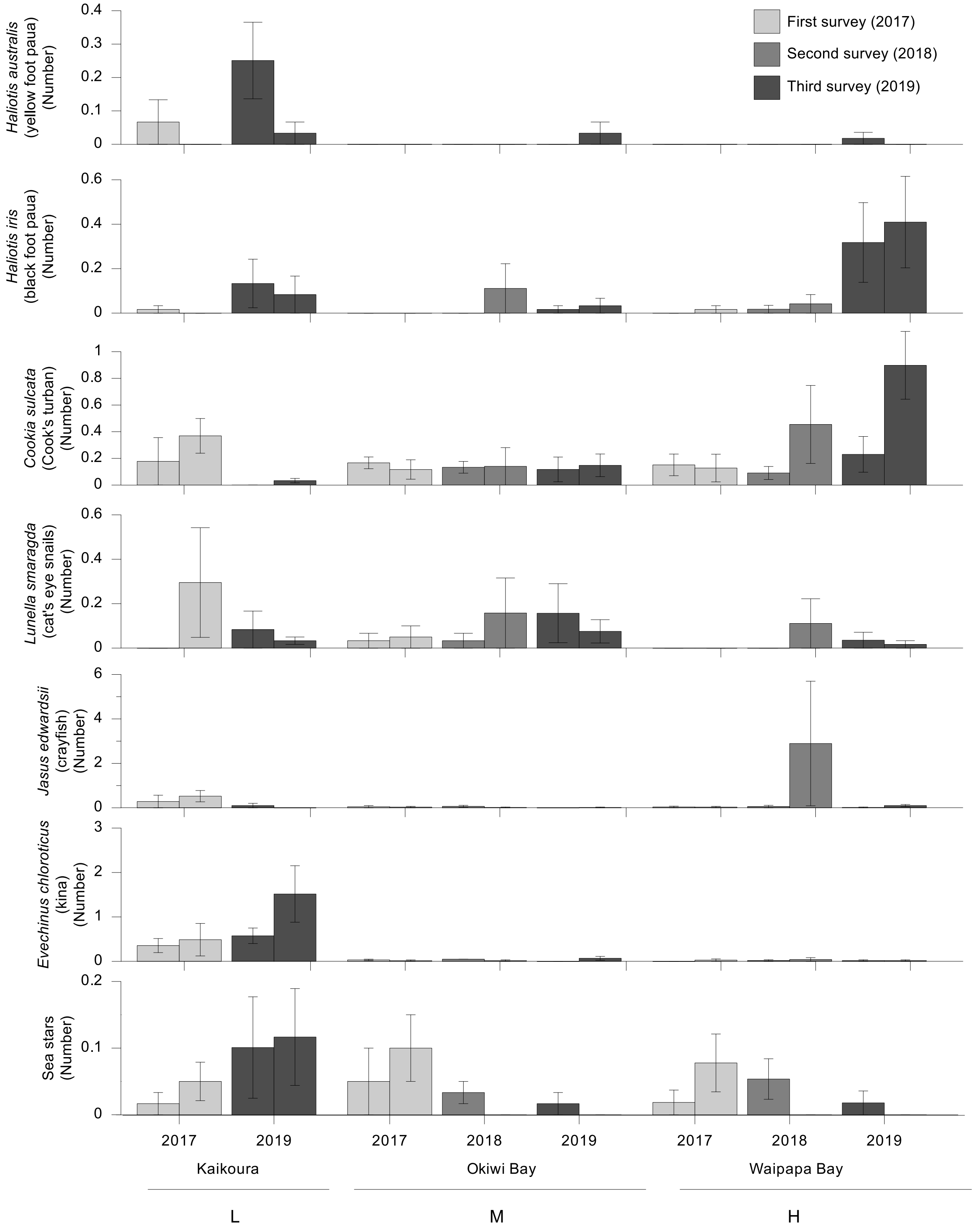

Figure19: Average abundances of selected mobile per 5m^2 quadrat at each site surveyed in 2017, 2018 (at Okiwi and Waipapa Bays only) and 2019. For each pair of bars, the left bar refer to the northern site and the right bar to the southern site. C=Control, L=Low, M=Medium, H=High. Data were filtered to only include quadrats with at least 50% rock substrate (cobble, boulder or bedrock). N = variable and noted in Appendix 1. Data are averaged over 3 transects with the exception of 2018 surveys at Waipapa South, where data are averaged over 4 transects; error bars represent 1 s.e. Note change in scales.

PERMANOVA analysis showed significant differences among uplift levels, surveys, sites and transects (Table 5). This indicates that there was high spatial variability both at small (between transects) and large (between sites) scales, but also that communities with different degrees of uplift were significantly different from each other and that communities differed between surveys. The Survey × Transect (Site(Uplift)) interaction indicates that one or more transects changed differently from others between surveys.

Principle coordinate analysis (PCO) of distance among site centroids showed that communities at Okiwi Bay North and South, and Waipapa Bay South changed the most between surveys (Figure 20). SIMPER analysis showed that the differences between surveys at Okiwi North were primarily driven by a reduction in some large brown algae (*Marginariella boryana* and *Lessonia variegata*), and an increase in several red algal taxa. Differences in surveys at Okiwi Bay South were primarily driven by a reduction in encrusting and turfing corallines, red encrusting algae, some large brown algae (*M. boryana*, *Landsburgia quercifolia* and *Lessonia variegata*), and some red algal taxa. Waipapa Bay South sites were dissimilar between surveys primarily due to an increase in encrusting coralline and encrusting red algae, *Ulva* sp., and some brown algae (*L. quercifolia* and *Halopteris* spp.), and a decrease in the brown alga *Carpophyllum maschalocarpum*. PCO of all sites and surveys showed that the Okiwi Bay sites have moved towards the right of the plot, with communites characterized by less brown algae and more red algae and bare space than the communities on the left side of the plot (Figure 21).

PERMANOVA on individual taxa showed that Transect and the Survey × Transect (Site(Uplift)) interaction were nearly always significant (Table 6), confirming the high spatial and temporal variability in this system. Encrusting algae, all foliose algae, large brown algae and brown foliose algae were significantly different between different levels of uplift.

Table 5: PERMANOVA results for epibiota community data. P values: * < 0.05, ** < 0.01, * < 0.001.**

Source	df	SS	MS	Pseudo-F	P(perm)
Uplift	2	3.08E+05	1.54E+05	5.3478	0.0042**
Survey	2	48 287	24 144	2.6791	0.0034**
Site(Uplift)	3	94 141	31 380	1.9843	0.0053**
Uplift × Survey	3	29 905	9 968.5	1.0942	0.3797
Transect (Site(Uplift))	13	2.11E+05	16 250	17.702	0.0001***
Survey × Site(Uplift)	5	46 555	9 311	1.271	0.1118
Survey × Transect (Site(Uplift))	20	1.53E+05	7 643.4	8.3267	0.0001***
Res	814	7.47E+05	917.94		

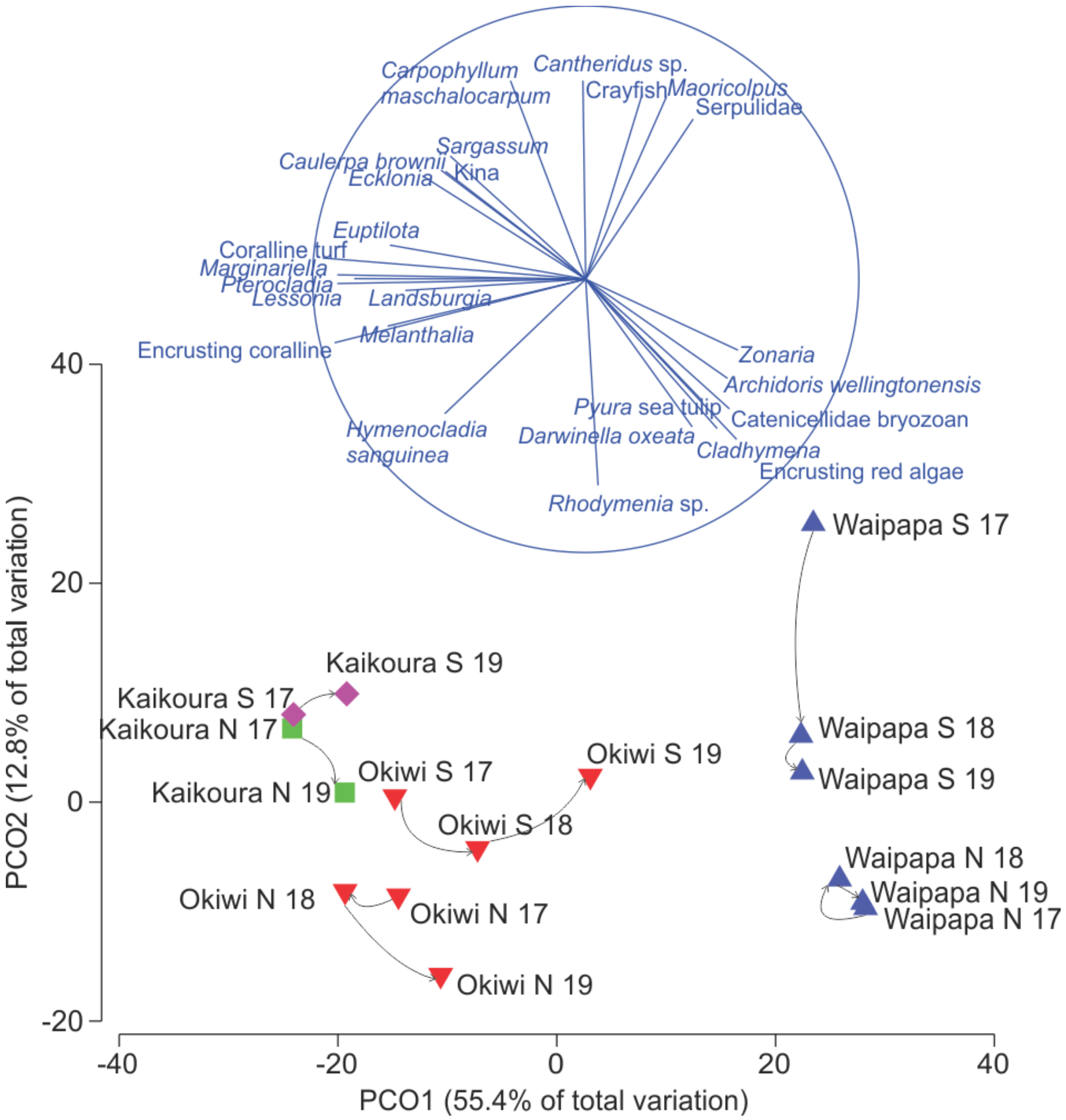

Figure 20: Principal coordinates analysis (PCO) of distance among centroids for Site-Year grouping factor, based on a Bray-Curtis similarity matrix of community assemblage data. Vector overlay shows taxa with > 0.6 correlation.

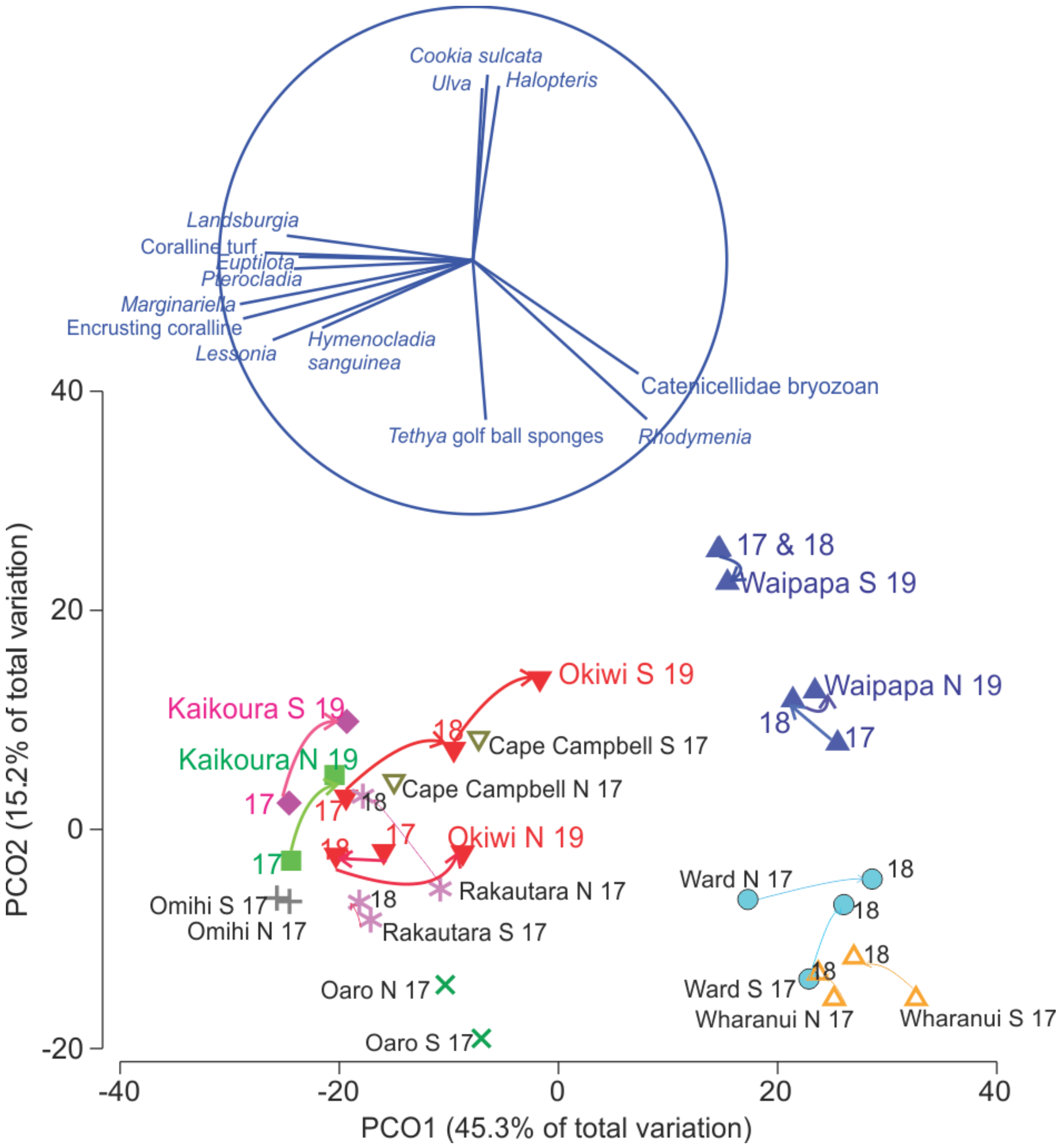

Figure 21: Principal coordinates analysis (PCO) of distance among centroids for Site-Year grouping factor for all sites, based on a Bray-Curtis similarity matrix of community assemblage data. Vector overlay shows taxa with > 0.6 correlation.

Table 6. Summary of PERMANOVA results for the whole epibiota community data, and grouped taxa. P values: * < 0.05, ** < 0.01, * < 0.001.**

Source	Whole community data	Sessile invertebrates	Mobile invertebrates	Sponges	Ascidians	Sea stars	Snails, limpets, chitons, pāua	All encrusting algae	All foliose algae	Large brown algae	Brown foliose algae	Red foliose algae	Green foliose algae	Triplefins
Uplift	**							*	***	***	***			
Survey	**	**		**	*	*								
Site(Uplift)	**													
Uplift × Survey														
Transect (Site(Uplift))	***	***	***	***	***	**	***	***	***	***	***	***	***	
Survey ×Site(Uplift)														
Survey × Transect (Site(Uplift))	***	***	***	***	***			***	***	***	***	***	***	***

As in previous surveys, few mobile reef fish (excluding triplefins) were seen in the 2019 survey (Figure 22). The exception was at Kaikōura South, which had averages of 18 and 41 fish along the transects in 2017 and 2019 respectively. The other sites had averages of fewer than 10 fish (Figure 22). Banded wrasse (*Pseudolabrus fucicola*) and spotties (*Notolabrus celidotus*) were the most abundant fish species. Other fish observed (in order of decreasing abundance over all sites) were blue moki (*Latridopsis ciliaris*), butterfish (*Odax pullus*), blue cod (*Parapercis colias*), marblefish (*Aplodactylus arctidens*) and red moki (*Cheilodactylus spectabilis*).

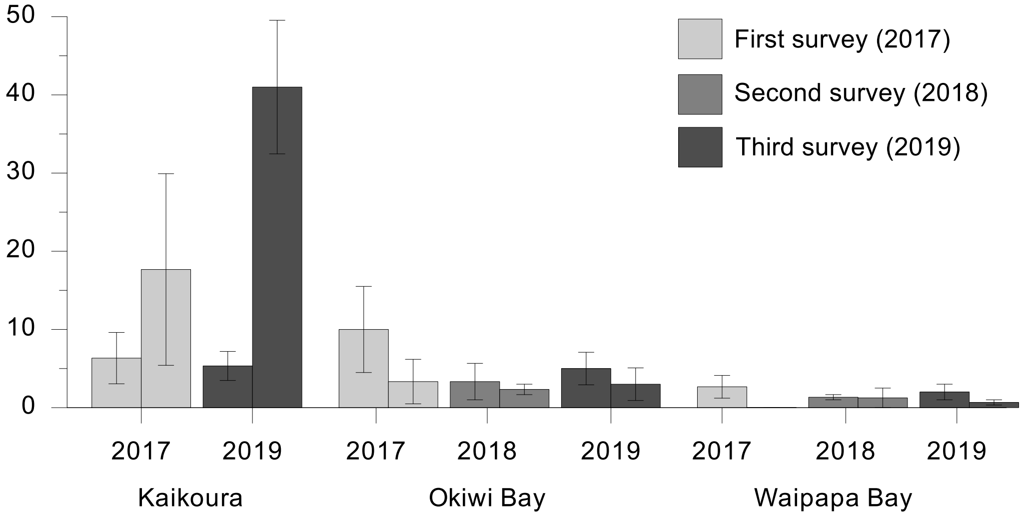

Figure 22: Average abundances of fish at each site during each survey. In each pair of bars, the left bar refers to the northern site and the right bar to the southern site. N = 3 transects, with the exception of second surveys at Waipapa Bay South, where n = 4. Error bars represent 1 s.e. Transects were 50 m in length, and the area surveyed was 1 m either side of the transect, and 2 m above the transect.

A total of 14, 34 and 48 black foot pāua (*Haliotis iris*) were recorded during the subtidal surveys at Okiwi and Waipapa Bay sites in 2017, 2018 and 2019. Sample sizes were too low for the data to be distributed normally and hence do not give an accurate representation of size distribution (Figure 23). However, the data do give an indication of the general sizes measured at each location. Some small black foot pāua were present at Kaikōura and Okiwi Bay in 2019, but the rest had an average size of 143 mm overall.

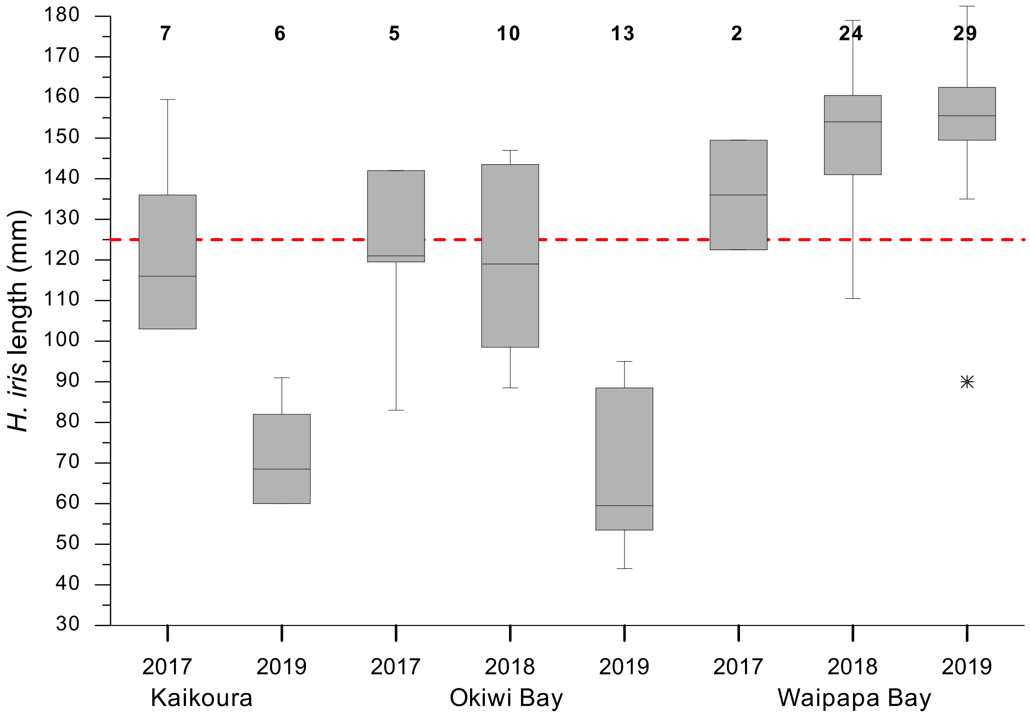

Figure 23: Box-whisker plots showing *Haliotis iris* (black foot pāua) size distributions at each location through time. Sample counts are at the top of each plot. The red dashed line represents the legal harvesting size of 125 mm.

4. DISCUSSION

This research extends our previous work (Alestra et al. 2019) done as part of the Kaikōura Earthquake Marine Recovery Package and provides an updated assessment of the state of rocky reef systems impacted by the coastal uplift.

4.1 Intertidal rocky reefs

The monitoring of intertidal reefs was extended to end of 2018, two years post-earthquake. The latest surveys showed that the biogenic structure of uplifted reefs is still significantly altered by the impact of the earthquake. Under all degrees of uplift, large portions of intertidal reefs were almost entirely devoid of algal cover, with most algae surviving only in low intertidal zone areas. These results confirm that mid tidal zone areas, which used to support lush and diverse algal communities before the earthquake (Schiel 2004, Schiel 2006) are now resistant to algal colonization, most likely because the unvegetated reefs erode very quickly and heat up significantly at low tide (Schiel at al. 2018, 2019, Alestra et al. 2019). The reduced cover of coralline algae, which are known to maintain reef complexity and reduce erodibility (Bosence 1983, Steneck 1986) is probably a critical factor driving high erosion rates. To promote the revegetation of uplifted reefs, as part of our MBIE research we are now testing whether artificial habitat amelioration, through the installation of shade cloth canopies and the creation of artificial water basins, could facilitate the recovery of seaweed communities.

In line with the results of previous sampling, most sites in the low intertidal zone hosted abundant and diverse algal communities. Large brown algae dominated low zone communities in areas of low uplift (less than 1m) at Cape Campbell and around the Kaikōura Peninsula. The November 2018 surveys showed that the abundance of large brown algae is increasing more rapidly in low-uplift areas compared to all other uplifted sites. Between March and November 2018, large brown algae also showed signs of recovery at the control sites in the Oaro area, where they experienced high mortality during the hot summer 2017–2018 (Alestra et al. 2019, Thomsen et al. 2019).

The abundance of fleshy red algae followed an opposite trend to that of large brown algae. As in previous surveys, two years after the earthquake red algae were more abundant in areas with medium- and high-uplift along the northern part of the coastline than at low-uplift sites. The reduced abundance of large brown algae at medium- and high-uplift sites may have facilitated the proliferation of red algae. Although these species account for most of the diversity of post-earthquake low zone communities at medium- and high-uplift sites, it is possible that they may be contributing to delay or prevent the recovery of larger, habitat-forming brown algae. The recovery of algal canopies following disturbances can be inhibited by the proliferation of low-lying, turf-forming algae (O’Brien & Scheibling 2018) and assessing the interactions between large brown and fleshy red algae is required to understand the potential for natural and/or assisted recovery of large habitat-forming brown algae at medium and high-uplift sites.

Encrusting and turf-forming coralline algae were abundant in the low zone at most sites, with percentage covers generally above 30%. These species play an important role in the life cycle of many taonga invertebrates, for example inducing the settlement of pāua larvae (Morse & Morse 1984), and acting as nurseries for juvenile cat’s eye snails (Robinson 1992).

Patterns of abundance of limpets across all intertidal zones were unrelated to the degree of uplift and highly variable across sites. However, limpet densities were lower at low-uplift sites than elsewhere, possibly because these sites consist mostly of flat mudstone platforms with limited availability of microhabitats (i.e., cracks, holes, channels, pools) providing shelter from the harsh post-earthquake physical environment.

Overall, the patterns of abundance of key intertidal algal and invertebrate taxa across uplift levels observed in November 2018 are in line with those shown by previous post-earthquake surveys. The November 2018 surveys also highlighted high variability among sites with similar degrees of uplift, confirming that earthquake impacts and trajectories of recovery cannot be predicted only on the basis of the magnitude of the uplift.

4.2 Subtidal rocky reefs

Previous subtidal surveys in 2017 and 2018 showed significant effects of the earthquake on shallow subtidal communities at sites with high uplift (Waipapa Bay), and minor effects at sites with medium uplift (Ward, Wharanui and Okiwi Bay). The most obvious effects were on the abundances of understory algae (encrusting and turfing coralline algae, and red and brown encrusting algae), large brown algae (laminarian and fucoid algae such as *Lessonia variegata*, *Marginariella boryana*, *Landsburgia quercifolia*), and on the presence of newly-emerged rock at some sites (Alestra et al. 2019).

The 2019 surveys showed minor recovery of seaweeds and invertebrates at Waipapa Bay. In particular, there was an increase in encrusting red algae and corallines, and recruitment of red and brown foliose algae. Despite this recovery, there were some extensive areas of bare rock still present. The most striking difference compared to previous surveys was the decrease in large brown algae at Okiwi Bay North, which may be related to changes in wave dynamics at this site. There were some shifts in sand/gravel distribution at Waipapa Bay and Okiwi Bay South transects. The shifts in sand and gravel can scour rock surfaces, slowing recovery of these habitats, and are indicative of a very dynamic physical environment. In addition, the reduced propagule supply of large brown algae at Waipapa Bay could reduce the amount of recruitment. As part of our MBIE research, we are currently transplanting large brown algae collected from unaffected locations to facilitate the recovery of these species at Waipapa Bay

4.3 Conclusions

The surveys and resulting data presented in this report provide an updated assessment of the state of nearshore reef environments along the uplifted coastline. This work augments a comprehensive and extensive body of information that had never been previously available for this region. Extending the monitoring of rocky reef habitats is extremely valuable given that the uplifted coastline is very much in the early stages of recovery and presents a very dynamic physical environment. In addition, post-earthquake recovery and resulting management implications are of great interest and concern among the various coastline user groups, including customary and recreational harvesters, commercial fishers, tourist operators, citizens' groups, tangata whenua and local residents. Longer time series will allow a better assessment of recovery trajectories and can also be helpful in characterizing the impacts of other local (e.g., floods, sedimentation, pedestrian and vehicle traffic) and global stressors (e.g., heatwaves) on the delicate equilibrium of the post-earthquake ecosystem. Finally, this work sets the context for new research such as our MBIE programme and for important management decisions, particularly regarding a range of human uses and the reopening of the pāua fishery.

5. ACKNOWLEDGMENTS

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7. APPENDICES

Appendix 1: Subtidal site details with degree of uplift, location, maximum and average depth, visibility and number of quadrats used in analyses for each survey time.

Site	Transect	Uplift	Transect start		Transect end		Max. depth (m)	Ave. depth (m)	Visibility (m)		Number of quadrats used in analyses (>50% rock)		
									2017	2018	2017	2018	2019
Oaro North	T1	C	-42.517	173.5109	-42.5171	173.5114	5.4	4.8	1		10		
	T2	C	-42.5171	173.5106	-42.5173	173.5112	5.0	4.6	1		2		
	T3	C	-42.517	173.5091	-42.5171	173.5097	2.2	1.9	2		20		
Oaro South	T1	C	-42.5208	173.5085	-42.5209	173.509	5.1	3.9	2.5		20		
	T2	C	-42.5211	173.5085	-42.5212	173.5091	5.3	3.7	2		19		
	T3	C	-42.5212	173.5082	-42.5213	173.5088	4.7	3.2	2		20		
Cape Campbell North	T1	L	-41.7222	174.2808	-41.7223	174.2813	4.3	3.0	1–2		19		
	T2	L	-41.7226	174.2808	-41.7228	174.2813	4.5	3.7	1–2		19		
	T3	L	-41.723	174.2805	-41.7231	174.281	4.4	3.0	1–2		19		
Cape Campbell South	T1	L	-41.7409	174.2774	-41.741	174.2779	6.2	4.6	2–5		16		
	T2	L	-41.7414	174.2773	-41.7415	174.2778	6.2	4.2	2		17		
	T3	L	-41.742	174.2772	-41.7423	174.2775	6.2	4.4	2		18		
Kaikōura North Rahui	T1	L	-42.4155	173.7089	-42.4153	173.7093	7.0	5.3	5		15		14
	T2	L	-42.413	173.7073	-42.4134	173.7072	7.0	4.5	5		20		20
	T3	L	-42.4135	173.7063	-42.4132	173.7065	5.7	2.0	5		20		20
Kaikōura North Wairepo	T1	L	-42.4192	173.7124	-42.4191	173.7128	4.5	3.2	4		18		
	T2	L	-42.4207	173.7147	-42.4203	173.7151	4.3	2.3	4		14		
	T3	L	-42.419	173.7117	-42.4186	173.7119	3.8	2.8	4		18		
Kaikōura South S1	T1	L	-42.4326	173.6903	-42.4325	173.6898	6.3	4.0	4		20		
	T2	L	-42.4331	173.6901	-42.433	173.6897	7.2	5.2	4		15		
	T3	L	-42.4333	173.6902	-42.4332	173.6897	7.8	5.8	4		20		
Kaikōura South S2	T1	L	-42.4355	173.6921	-42.4356	173.6926	4.6	2.6	5		20		20
	T2	L	-42.4352	173.6929	-42.4351	173.6926	6.8	4.1	5		20		20
	T3	L	-42.4347	173.6926	-42.435	173.6931	7.3	5.6	5		19		20
Ward North	T1	M	-41.8436	174.189	-41.8438	174.1894	7.1	5.9	1	1–2	11	15	

			Transect start		Transect end		Max. depth (m)	Ave. depth (m)	Visibility (m)		Number of quadrats used in analyses (>50% rock)		
Site	Transect	Uplift							2017	2018	2017	2018	2019
	T2	M	-41.844	174.1885	-41.8442	174.1889	7.8	5.9	1–1.5	1–2	20	20	
	T3	M	-41.8441	174.1881	-41.8443	174.1886	7.3	5.8	1	2	19	17	
Ward South	T1	M	-41.8486	174.1847	-41.8488	174.1852	9.0	6.4	3	2	15	11	
	T2	M	-41.8494	174.1843	-41.8496	174.1847	9.0	6.9	3–5	3	16	17	
	T3	M	-41.8501	174.1837	-41.8503	174.1842	9.1	7.1	2.5–3	3	19	15	
Wharanui North	T1	M	-41.9294	174.0993	-41.9297	174.0998	5.2	3.9	3	0.5–1	19	17	
	T2	M	-41.9298	174.0991	-41.93	174.0996	5.5	4.1	3	2	20	19	
	T3	M	-41.9301	174.0989	-41.9303	174.0993	5.2	4.0	3	1	15	14	
Wharanui South	T1	M	-41.935	174.0944	-41.9353	174.0948	4.1	3.1	2–2.5	1–1.5	18	18	
	T2	M	-41.9354	174.0942	-41.9357	174.0946	4.0	2.9	2	1	17	18	
	T3	M	-41.9357	174.0937	-41.936	174.0941	3.9	2.5	2	1–1.5	18	18	
Okiwi Bay North	T1	M	-42.2171	173.8726	-42.5209	173.509	5.5	3.9	1–2	1.5	20	20	20
	T2	M	-42.2178	173.8717	-42.218	173.872	4.2	2.4	4	2	20	20	20
	T3	M	-42.2181	173.8716	-42.2183	173.872	5.4	2.9	4	2	20	20	20
Okiwi Bay South	T1	M	-42.2189	173.8665	-42.2194	173.8665	4.1	2.1	1		18	20	20
	T2	M	-42.2189	173.869	-42.219	173.8696	3.8	2.2	1	2	12	19	17
	T3	M	-42.2191	173.8697	-42.2194	173.8701	5.4	3.3	5	2.5	19	20	20
Rakautara North	T1	M	-42.2638	173.8111	-42.2638	173.8116	5.5	3.5	2.5	0.75–1	20	20	
	T2	M	-42.2622	173.8123	-42.2623	173.8128	8.1	5.5	2.5	0.5–1	20	12	
	T3	M	-42.2616	173.8128	-42.262	173.8132	6.5	5.0	2.5	1	20	20	
Rakautara South	T1	M	-42.2685	173.8053	-42.2687	173.8058	5.0	3.3	2.5	1	20	20	
	T2	M	-42.2683	173.8057	-42.2684	173.8062	6.2	4.5	2.5	2–2.5	20	20	
	T3	M	-42.2674	173.8071	-42.2676	173.8075	6.3	3.6	2.5		19		
Omihi North	T1	M	-42.4868	173.5278	-42.4869	173.5283	3.7	2.5	3		20		
	T2	M	-42.4849	173.53	-42.4851	173.5303	6.8	4.4	3		20		
	T3	M	-42.4908	173.5255	-42.4909	173.526	4.1	3.1	3		20		
Omihi South	T1	M	-42.493	173.5238	-42.4931	173.5244	4.4	3.5	2.5		20		
	T2	M	-42.4934	173.5235	-42.4936	173.524	3.4	2.6	2.5		20		
	T3	M	-42.4936	173.524	-42.4938	173.524	5.4	4.2	2.5		20		
Waipapa Bay North	T1	H	-42.2044	173.8794	-42.2045	173.8798	4.5	3.5	1–1.5	2.5	18	20	19
	T2	H	-42.205	173.8798	-42.205	173.8803	5.5	4.4	1.5	2.5	18	20	18

Site	Transect	Uplift	Transect start		Transect end		Max. depth (m)	Ave. depth (m)	Visibility (m)		Number of quadrats used in analyses (>50% rock)		
									2017	2018	2017	2018	2019
	T3	H	-42.2056	173.8796	-42.2057	173.8802	6.1	5.3	1.5-2.5	2.5	17	12	18
Waipapa Bay South	T1	H	-42.2092	173.8758	-42.2097	173.8758	2.8	1.7	0.5	0.5	6	5	
	T2	H	-42.2099	173.8762	-42.2103	173.8763	3.8	2.9	0.5	0.5	8	20	20
	T3	H	-42.2096	173.8774	-42.21	173.8778	4.9	3.6	2	1.5	11	14	7
	T1b	H										20	19

Appendix 2: Results of SIMPER tests for each pair of uplift groups with significantly different benthic community composition in the post-earthquake high (A), mid (B) and low zone (C). For each test, the taxa contributing to up to 90% of the dissimilarity between groups are listed.

A) Post-earthquake high zone

Control vs Low-uplift - Average dissimilarity = 92.06

Taxa	Average abundance - Control	Average abundance - Low-uplift	Average dissimilarity	Contribution %	Cumulative contribution %
Chamaesipho columna	10.53	0.08	25.19	27.37	27.37
Ulva sp.	7.11	0.7	22.45	24.39	51.75
Pyropia/Porphyra complex	2.33	10.04	21.36	23.2	74.95
Articulated coralline algae	2.01	0	7.86	8.54	83.49
Ceramium spp.	1.38	0	5.73	6.22	89.71
Encrusting algae (red crust)	1.19	0.04	2.72	2.95	92.66

Control vs Medium-uplift - Average dissimilarity = 88.60

Taxa	Average abundance - Control	Average abundance - Medium-uplift	Average dissimilarity	Contribution %	Cumulative contribution %
Chamaesipho columna	10.53	0.08	27.25	30.76	30.76
Ulva sp.	7.11	2.31	23.86	26.93	57.68
Pyropia/Porphyra complex	2.33	0.37	9.72	10.97	68.65
Articulated coralline algae	2.01	0	8.63	9.75	78.4
Ceramium spp.	1.38	0.04	6.29	7.09	85.49
Encrusting algae (red crust)	1.19	0	2.89	3.26	88.76
Encrusting algae (black crust)	0.1	0.68	2.8	3.15	91.91

Control vs High-uplift - Average dissimilarity = 90.57

Taxa	Average abundance - Control	Average abundance - High-uplift	Average dissimilarity	Contribution %	Cumulative contribution %
Chamaesipho columna	10.53	0.04	25.29	27.93	27.93
Ulva sp.	7.11	3.94	23.92	26.41	54.33
Pyropia/Porphyra complex	2.33	0.13	8.55	9.43	63.77
Encrusting algae (black crust)	0.1	3.29	8.16	9.01	72.78
Articulated coralline algae	2.01	0.01	7.87	8.69	81.47
Ceramium spp.	1.38	0.2	5.79	6.39	87.86
Encrusting algae (red crust)	1.19	1.77	4.98	5.5	93.36

B) Post-earthquake mid zone

Taxa	Control vs Low-uplift - Average dissimilarity = 93.79				
	Average abundance - Control	Average abundance - Low-uplift	Average dissimilarity	Contribution %	Cumulative contribution %
Articulated coralline algae	41.25	0.28	35.68	38.04	38.04
Gelidium caulacantheum	12.45	0.04	12.68	13.52	51.56
Ulva sp.	11.21	3.61	10.09	10.76	62.32
Hormosira banksii	9.66	0.52	7.74	8.26	70.58
Polysiphonia strictissima	4.14	0.05	3.64	3.88	74.46
Encrusting algae (red crust)	0.15	3.78	3.32	3.54	77.99
Pyropia/Porphyra complex	0	3.14	2.8	2.99	80.98
Encrusting coralline algae	1.35	1.1	1.85	1.97	82.95
Encrusting algae (black crust)	0	2.15	1.69	1.8	84.75
Ceramium spp.	1.17	0	1.5	1.6	86.35
Carpophyllum maschalocarpum	1.21	0.37	1.42	1.52	87.86
Champia novae-zelandiae	1.4	0	1.34	1.42	89.28
Cystophora scalaris	1.19	0.05	1.25	1.33	90.62

Taxa	Control vs Medium-uplift - Average dissimilarity = 88.12				
	Average abundance - Control	Average abundance - Medium-uplift	Average dissimilarity	Contribution %	Cumulative contribution %
Articulated coralline algae	41.25	0.22	31.97	36.28	36.28
Ulva sp.	11.21	28.11	19.3	21.9	58.18
Gelidium caulacantheum	12.45	1.17	10.58	12.01	70.18
Hormosira banksii	9.66	0	7.1	8.05	78.24
Polysiphonia strictissima	4.14	0.07	3.25	3.68	81.92
Encrusting algae (black crust)	0	1.73	1.38	1.57	83.48
Encrusting coralline algae	1.35	0.94	1.31	1.48	84.97
Ceramium spp.	1.17	0.01	1.3	1.48	86.45
Champia novae-zelandiae	1.4	0	1.19	1.35	87.8
Cystophora scalaris	1.19	0	1.09	1.24	89.04
Carpophyllum maschalocarpum	1.21	0	1.04	1.18	90.21

C) Post-earthquake low zone

Taxa	Low-uplift vs Medium-uplift - Average dissimilarity = 67.44				
	Average abundance - Low-uplift	Average abundance - Medium-uplift	Average dissimilarity	Contribution %	Cumulative contribution %
Carpophyllum maschalocarpum	33.62	8.72	9.37	13.89	13.89
Encrusting coralline algae	37.2	40.94	8.99	13.33	27.22
Streblocladia muelleriana	0.24	17.82	5.71	8.47	35.69
Articulated coralline algae	15.74	12.54	5.08	7.54	43.23
Durvillaea willana	7.25	6.09	3.62	5.37	48.6
Encrusting algae (black crust)	9.99	1.31	3.41	5.05	53.65
Ulva sp.	5.38	7.45	3.26	4.83	58.49
Echinothamnion hystrix	1.97	8.95	3.13	4.64	63.13
Marginariella boryana	5	6.68	2.88	4.27	67.4
Red filamentous turf	1.9	6.67	2.52	3.74	71.14
Chondria macrocarpa	1.06	6.37	2.2	3.26	74.4
Halopteris sp.	3.82	2.03	1.42	2.11	76.5
Pterocladia lucida	1.21	3.77	1.4	2.07	78.58
Lessonia variegata	1.87	2.56	1.32	1.95	80.53
Durvillaea poha	2.95	1.02	1.15	1.7	82.23
Dictyota spp.	2.1	0.94	0.81	1.2	83.43
Cystophora scalaris	2.1	0.12	0.77	1.15	84.58
Sarcothalia lanceata	0.07	2.25	0.74	1.1	85.68
Glossophora kunthii	0.95	1.62	0.72	1.06	86.74
Landsburgia quercifolia	0.91	1.51	0.69	1.03	87.77
Colpomenia bullosa	1.83	0	0.65	0.96	88.74
Ectocarpus spp.	1.11	1.15	0.62	0.92	89.66
Cladhymenia oblongifolia	0.1	1.69	0.55	0.82	90.48

	Low-uplift vs High-uplift - Average dissimilarity = 82.63				
Taxa	Average abundance - Low-uplift	Average abundance - High-uplift	Average dissimilarity	Contribution %	Cumulative contribution %
Encrusting coralline algae	37.2	24.77	13.95	16.88	16.88
Carpophyllum maschalocarpum	33.62	6.03	13.49	16.33	33.21
Streblocladia muelleriana	0.24	31.43	10.39	12.58	45.79
Articulated coralline algae	15.74	0.08	7.19	8.7	54.49
Ulva sp.	5.38	9.17	4.99	6.04	60.53
Encrusting algae (black crust)	9.99	0.79	4.79	5.79	66.32
Chondria macrocarpa	1.06	13.37	4.43	5.36	71.68
Durvillaea willana	7.25	0	2.9	3.51	75.19
Echinothamnion hystrix	1.97	5.6	2.36	2.86	78.06
Marginariella boryana	5	0	2.19	2.65	80.7
Halopteris sp.	3.82	0.08	1.81	2.19	82.89
Pterocladia lucida	1.21	2.64	1.18	1.42	84.32
Durvillaea poha	2.95	0	1.13	1.37	85.69
Cystophora scalaris	2.1	0.02	1.03	1.25	86.94
Dictyota spp.	2.1	0.2	0.95	1.14	88.09
Colpomenia bullosa	1.83	0	0.91	1.1	89.19
Glossophora kunthii	0.95	1.78	0.89	1.08	90.26