Title: Rocky reef impacts of the 2016 Kaikōura earthquake: extended monitoring of nearshore habitats and communities to 4.5 years

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1. EXECUTIVE SUMMARY

In November 2016, the 7.8 magnitude Kaikōura earthquake struck the North-Eastern section of New Zealand's South Island, causing varying degrees of uplift along 130 km of productive coastline. The uplift ranged from 0.5 m to over 6 m and resulted in widespread mortality across rocky intertidal and subtidal reefs, including mature algal forests and diverse invertebrate communities. Several taonga species of high cultural, ecological, and economic importance were severely affected, including rimurapa (bull kelp) and pāua (abalone), prompting an emergency ban on seaweed and shellfish harvesting that remains in effect nearly five years later. The integrity of newly exposed reefs was compromised by increased erosion rates and large-scale movement of gravels and sediments, further complicating the recovery dynamics. To quantify earthquake effects on community structure and chart recovery of the coastal ecosystem, a comprehensive monitoring programme was implemented in 2017 as part of the Ministry if Primary Industries (MPI) Kaikōura Earthquake Marine Recovery Package. Subsequent funding extensions have enabled continued monitoring of the coastal ecosystem as it undergoes ongoing physical and ecological changes. The growing data set, now with over 1 million entries, is source of fundamental informative for coastal managers, and represents one of the only known long-term studies of earthquake effects on coastal ecosystems.

This report details the latest results of nearshore community surveys, including intertidal surveys at 16 sites (completed in November 2020), and subtidal surveys at 6 sites (completed in March 2021). The sites, which cover a broad range of uplift degrees between 0.0 – 6.4 m, and span the 130 km of affected coastline, exhibit varying degrees of recovery, and are experiencing ongoing challenges. We compare the most recent data to long-term trends published in earlier reports (Alestra et al. 2019, 2020) and to baseline data collected immediately after the earthquake when communities were still intact, allowing a determination of how long recovery may take and what it may look like.

Intertidal Surveys:

Four years after the earthquake, high and mid zone areas of reefs affected by even low (< 1 m) degrees of uplift remain largely unvegetated and have shown little or no recovery towards pre-

earthquake conditions, either physically or biogenically. Other than intermittent seasonal blooms of ephemeral algae and isolated recruitment events of herbivorous invertebrates, there remains very low abundance of intertidal taxa here. Minimal re-establishment of the canopy-forming fucoid *Hormosira banksia* was short-lived, as hot summer conditions caused burn-off in the upper and mid zones.

The low tidal zone of intertidal reefs experienced the majority of biotic re-organisation over time, as these are predominantly underwater and remain suitable for algal and invertebrate communities. Low zones had diverse assemblages of habitat-forming large brown algae and other foliose red and green algae and associated invertebrates. Non-uplifted control sites had the greatest overall cover of algae, and high-uplift sites had the least, a legacy of the initial die-off. Percent cover of bull kelp/rimurapa (*Durvillaea* spp.), and other fucoids, especially *Carpophyllum maschalocarpum,* and *Cystophora* spp., was variable and depended on degree of uplift. Bull kelp has yet to recover to pre-earthquake levels at most sites, due largely to its replacement by other large brown algae and fast-growing foliose red algae. These have filled many areas formerly occupied by *Durvillaea* and have precluded bull kelp recruitment into those areas (e.g., pre-emptive competition). At highly disturbed northern sites the widespread replacement of bull kelp assemblages with other large brown algae and smaller foliose reds is remarkable and has lasting implications for coastal primary productivity and marine food web dynamics. Coralline algae, which serve as critical settlement substrate for marine gastropods including pāua, were abundant in the low zones but are far from recovering to pre-earthquake levels.

Intertidal reefs have been subjected to ongoing disturbances by erosion events, coastal floods, sudden influxes of gravel and sand, high air temperatures, and marine heatwaves. At a few sites we have witnessed months or years of recovery suddenly lost to an extreme event. The dynamics of this coastline are complex, and according to our data the changes are ongoing and may continue to be for years to come.

Subtidal Surveys:

Subtidal surveys were done by divers to assess subtidal reefs assemblages adjacent to the monitored intertidal sites. Repeat surveys of established transects followed the methods used in initial surveys. Subtidal monitoring 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 in 2019 – 2021 surveys compared to previous post-earthquake surveys was the decrease in large brown algae at some sites around the Kaikōura peninsula and at Okiwi Bay. This was primarily due to declines in *Marginariella boryana* and *Lessonia variegata*. The decrease in large brown algae may be due to effects of 2018 marine heatwaves, altered wave dynamics following the uplift, and/or scour due to movement of cobble, gravel, or sand substrates.

Conclusions:

The abiotic habitats continue to change along the coastline, further challenging the establishment of algal communities. Gravel movements and accumulation were evident both in the intertidal and subtidal zones, sometimes infilling large areas of reef. In the intertidal zone, ongoing reef erosion is also contributing to the poor recovery of benthic communities, effectively precluding secure attachment and recruitment of large algae. Sedimentary mudstone reefs, now mostly bare, continue to experience increased erosion rates from immersion followed by long periods of emersion, making them unsuitable for algal and invertebrate settlement. This is compounded in summer months when reef surface temperatures over 40 C cause die-offs of any established recruits. These factors are some of many contributing to the slow recovery of the Kaikōura region coastal ecosystem.

This work and other related research is showing a clear picture of the difficulties in resilience and recovery after a cataclysmic event. The slow and often interrupted recovery of coastal marine communities is consistent with findings from past experiments simulating disturbance, in which the re-establishment of dominant algae and their associated species can take close to a decade. This is especially true for slow-growing species such as bull kelp, which have a short reproductive season and long juvenile phase, and require some connectivity to parent populations.

This research has been presented frequently to local community groups, iwi, the commercial pāua fishing industry, and resource managers to facilitate a re-opening strategy for the Kaikōura coast. The work provides the detailed information that will underpin difficult management decisions around the re-opening of the shellfish and seaweed harvest and will inform future coastal management.

2. OBJECTIVES

See appended report.

3. METHODS

See appended report.

4. RESULTS

See appended report.

5. CONCLUSIONS

See appended report.

6. PUBLICATIONS

Not applicable.

7. DATA MANAGEMENT

Not applicable.

Fisheries New Zealand

Tini a Tangaroa

Rocky reef impacts of the 2016 Kaikōura earthquake: extended monitoring of nearshore habitats and communities to 4.5 years

Year 1 - Draft interim report on findings to date.

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Gerrity, S.
Dunmore, R.A.
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New Zealand Government

EXECUTIVE SUMMARY

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***New Zealand Aquatic Environment and Biodiversity Report No.* . 46 pp.**

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1. INTRODUCTION

The 2016 magnitude 7.8 (M_w) Kaikōura earthquake was the most powerful experienced in over 150 years, uplifting around 130 km coastline up to 6.4 m (Clark et al. 2017, Hamling et al. 2017). This cataclysmic event greatly affected the ecosystem of the productive nearshore zone of Kaikōura's coastline (Schiel et al. 2018, Schiel et al. 2019, Gerrity et al. 2020, Thomsen et al. 2020). Numerous taonga species inhabiting intertidal and subtidal areas were affected, upending customary, commercial, and recreational fisheries, and compromising ecosystem structure and function.

A monitoring programme was established in 2017 to quantify the earthquake effects on intertidal and subtidal rocky reef communities. The sampling methodology had been established decades earlier by the Marine Ecology Research Group from the University of Canterbury, and this allowed comparison of pre- and post-earthquake conditions. The initial work following the earthquake, funded in part by the Ministry for Primary Industries (MPI) Kaikōura Earthquake Marine Recovery Package, assessed the immediate impacts on rocky reef communities and early recovery trajectories (Alestra et al. 2019, Alestra et al 2020). The research extensively detailed the state of the rocky reef systems and the overall impacts of the earthquake on the ecologically, culturally, or commercially significant species (e.g., bull kelp, pāua, etc.). A continuation of funding has allowed for extended sampling as the coastline continues to experience ongoing changes, with the following objectives.

Overall objective

1. To assess the recovery of rocky intertidal and subtidal communities affected by the 2016 Kaikōura earthquake and coastal uplift disturbance

Specific objectives

Original monitoring programme (to 2020)

1. Determine the impact of the Kaikōura earthquake on rocky reef systems, this may also include sub-lethal responses where methodologies to test this exist.
2. Assess long-term monitoring sites to quantify the recovery from the earthquake to inform future marine management decisions.
3. Compare impacts across the range of uplift and habitats impacted on the rocky shore.
4. Continue monitoring sediment cover to suggest causation between short-term uplift and potentially longer-term increased sedimentation as a result of the Kaikōura earthquake.
5. Where possible include local participation in the recovery package work specifically refer to relevant South Island iwi (Te Rūnanga o Kaikōura and Te Tau Ihu), and local community.

Objectives from November 2020 onwards

1. Repeat three annual surveys of 16 intertidal areas across degrees of uplift.
2. Repeat three annual surveys of 6 subtidal sites across degrees of uplift.
3. Assess the recovery of nearshore rocky reef communities.

This report provides an update on the state of Kaikōura's intertidal (up to 4.5 years post-earthquake) and subtidal rocky reef communities (up to 4 years post-earthquake). This information is aimed at informing and underpinning coastal management decisions, particularly the re-opening strategy for shellfish and seaweed harvest, by providing a holistic assessment of the recovery and state of the nearshore coastal ecosystem. This work has global significance and will significantly add to the limited understanding of long-term recovery dynamics following cataclysmic events.

These surveys also provide added baselines and references for another research project. This uses an experimental approach and wide-scale habitat mapping to tease out biological and physical processes 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*", MBIE, UOCX1704, ending in January 2022).

2. METHODS

2.1 Survey design

Intertidal and subtidal surveys were done sequentially across eight locations since the earliest round of pre-earthquake surveys in mid-2017 (Alestra et al. 2019, Figure 1). Locations were selected to encompass a range of vertical uplift degrees, including non-uplifted control sites, and span the 130 km of affected coastline (See Alestra et al. 2019). Where possible, at least two sites separated by c. 500 m were nested within each location. Each site was in one of four uplift groups: control (C – no uplift); low uplift (L – 0.5 to 1.5 m); medium uplift (M – 1.5 to 2.5 m); high uplift (H – 4 to 5.5 m), based on uplift information obtained from GNS Science (K. Clark, personal communication) and our own calculations (Orchard et al., unpublished data). Of the c. 130 km of earthquake-impacted coastline, rocky reefs comprised 48 km (Gerrity et al. 2020). The control, low, and medium uplift categories account for 39 km of rocky reef, with 2 km of reef experiencing high uplift (Figure 2).

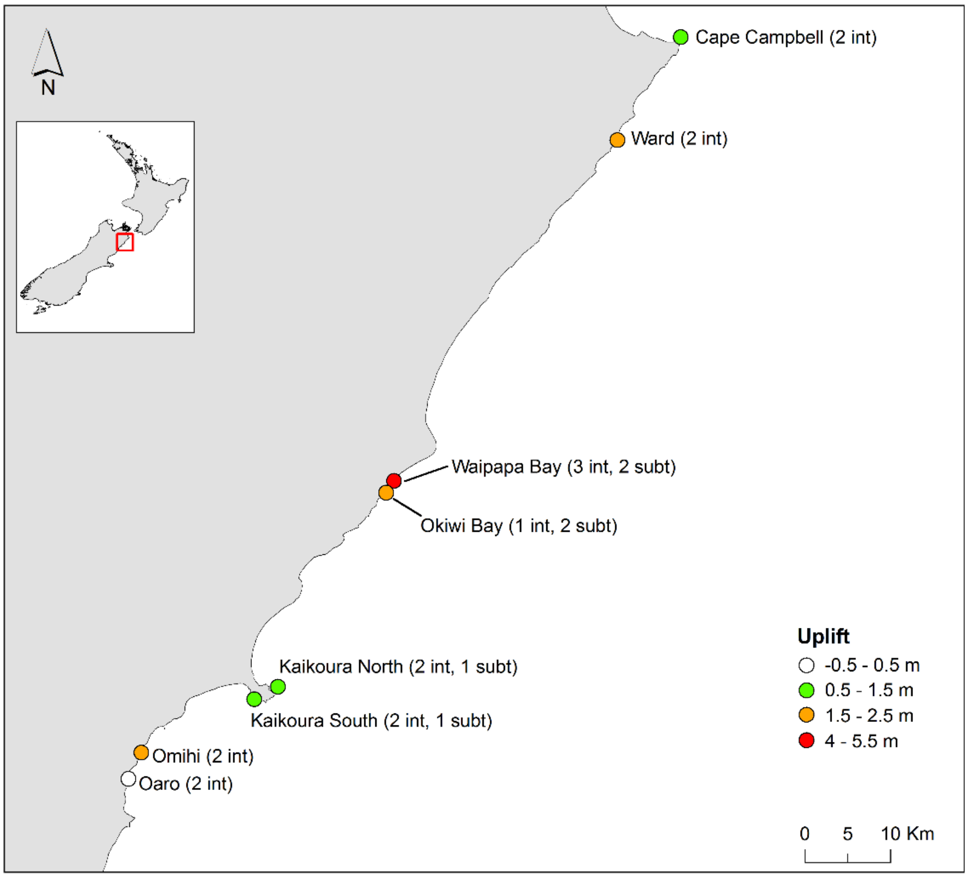

Figure 1: Sites of repeated intertidal (16 sites) and subtidal (8 sites) monitoring were at 8 locations. The number of intertidal (int) and subtidal sites (subt) per location are shown in brackets. Different colours are used for the four uplift categories: control (white), low uplift (green), medium uplift (orange), high uplift (red).

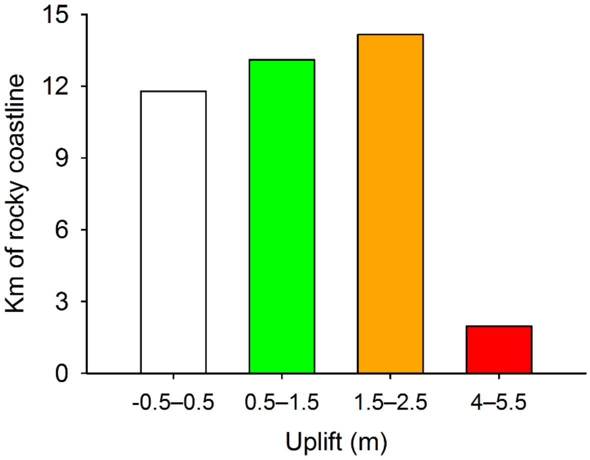

Figure 2: Kilometres of rocky reef that experienced uplift levels based on our uplift characterisations (white = control, green = low uplift, orange = medium uplift, red = high uplift)

2.2 Intertidal community surveys

The sixth round of intertidal community surveys were completed in November 2020 at all 16 sites across the 8 locations (Figure 1), using methods described in Alestra et al. 2019. At each site, samples were taken in each of the previously established 30 m transects (one at each of the post-earthquake low, mid, and high tidal zones (where present)). All algal and invertebrate species were identified down to the lowest taxonomic resolution, with percent cover recorded for sessile species such as algae and counts recorded for mobile invertebrates. Along the transect in each zone the abundances of all taxa in 10 haphazardly placed 1 m^2 quadrats were recorded.

Data collected in November 2020 was analysed with univariate (ANOVA) and multivariate (PERMANOVA) techniques testing for differences between sites, uplift groups, and significant changes between the 2019 and 2020 sampling periods (Anderson et al. 2008, Clark & Warwick, 2001). The results included in this report focus on broad taxonomic groupings (i.e., groups of species with shared morphological and life-history traits) rather than species-specific analyses.

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 and subtidal 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.

To visualise differences between communities, principal coordinates analyses (PCO) and multidimensional scaling (MDS) plots with R correlates greater than 0.6 are used to visualise similarity or lack of it, between uplift levels and sites (Kruskal & Wish, 1978; Anderson & Willis, 2003).

2.3 Subtidal community surveys

Subtidal community surveys were done between April and May 2021, around 4.5 years after the Kaikōura earthquake, at 6 sites across 4 locations: Waipapa Bay, Okiwi Bay, Kaikōura Peninsula North and South (Figure 1). These sites encompassed degrees of uplift between 0.5 and 5.5 m. The low-uplift sites (around 0.6 m) around the Kaikōura Peninsula had no earthquake damage (Alestra et al. 2019, 2020) and were considered as controls. Sampling followed the methodology of previous surveys, including the assessment of 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 with 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 or gravel. 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/gravel-dominated quadrats resulted in a reduction in the number of replicates, although most transects (49 out of 55) 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, 4 levels), Site (random, nested within Uplift, 6 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 greater than 0.5 with the PCO axes were displayed as vectors in the PCO plots. SIMPER was used to explore differences in sites between years.

3. RESULTS

3.1 Intertidal community structure

Similar to previous sampling events (Figure 3 A-E, G-K, M-Q), 48 months after the earthquake, intertidal algal cover was greatest in the low zone across all uplift levels (Figure 3R) and was very low at uplifted sites in mid and high zones (Figures 3 F, L), as it had been through time. Although algal abundance is typically low in the high intertidal zone due to environmental stressors, the mid zone should support diverse and abundant communities. The persistent low cover of algae recorded at uplifted mid zone sites compared to control sites shows a distinct lack of recovery to pre-earthquake conditions. Other than subtle shifts in algal community structure, little has changed since our previous sampling event in 2019 (Figure 3). The low zone contains the vast majority of algal biomass and is consistently characterized by high covers of large brown, fleshy red, and coralline algae. Algal composition in the low zone differs among uplift groups, with a shift from brown-dominated communities in the control and low uplift groups, to a greater proportion of fleshy red algae at the more uplifted sites. Finally, the percent cover of sessile invertebrates (e.g., barnacles, mussels) was very low, as expected, as these are predominantly algal-dominated reefs.

Some variability in community composition is typical on intertidal reefs, but significant earthquake effects on algal composition were detected. Multivariate analysis showed that in November 2020, uplift had a significant effect on intertidal community composition in the post-earthquake high zone (Uplift: Pseudo-$F_{3,12} = 2.42$, $P < 0.05$, Figure 4 A). Similar to 2019 results, the community composition of the 2020 high zone displayed blooms of ephemeral algal species, namely red (*Pyropia* spp.) and green algae (*Ulva* spp.) (Appendix 1 A). The medium- and high-uplift groups differed from the control group and the low- and medium-uplift differed from one another (Appendix 1 A). The medium- and high-uplift groups did not significantly differ. There was also significant variability in benthic community structure among the sites within each uplift group (Pseudo-$F_{12,144} = 4.96$, $P < 0.01$, Figure 4 A).

In the mid zone abundant algal communities were only found at the control sites. Analyses of community composition found a significant effect of uplift (Uplift: Pseudo-$F_{2,8} = 2.62$, $P < 0.01$) with the control group significantly differing from both the low- and medium-uplift groups (Appendix 1 B). There was also significant variability in benthic community structure among sites in the low- and medium-uplift groups (Pseudo-$F_{8,99} = 9.37$, $P < 0.01$, Figure 4 B).

In the post-earthquake low zone, benthic community composition was significantly different between the low-uplift group, which was dominated by large brown algae, and the medium- and high-uplift groups, which had more coralline and red algae (Uplift: Pseudo-$F_{3,12} = 2.43$, $P < 0.01$, Figure 5 C, Appendix 1 C). The medium- and high-uplift sites also differed, with coralline crusts being dominant in the medium- and the red alga *Polysiphonia mullerii* dominant in the high-uplift sites (Appendix 1 C). There was significant site-by-site variability across uplift degrees as well (Pseudo-$F_{12,144} = 7.66$, $P < 0.01$, Figure 4 C). Waipapa Bay, which has been heavily inundated with sediment and gravel, was the only site nearly devoid of algae in the low zone four years after the earthquake (Figure 4 C).

When looking at dissimilarities between community compositions across all zones there are clear differences between each of the uplift groups (Figure 5 A). Diversity of species was highest in the low-uplift group with a broad array of brown algae driving dissimilarity between this group and the control, medium-, and high-uplift groups. The key drivers of this dissimilarity are the brown algae *Colpomenia* spp., *Carpophyllum maschalocarpum*, *Cystophora scalaris*, *C. torulosa*, and *Macrocystis pyrifera* (Figure 5 B). The medium- and high-uplift groups share a similar assortment of species, with the mid-uplift group higher in diversity. Fleshy and foliose red algae are driving dissimilarity for these sites with *Polysiphonia mullerii*, *Gigartina* spp., *Cladhymenia* spp., and *Chondria macrocarpa* having the most influence (Figure 5 B). The dissimilarity between the control and each of the other uplift groups is still notable, indicating that uplift has affected community composition on recovering intertidal reefs.

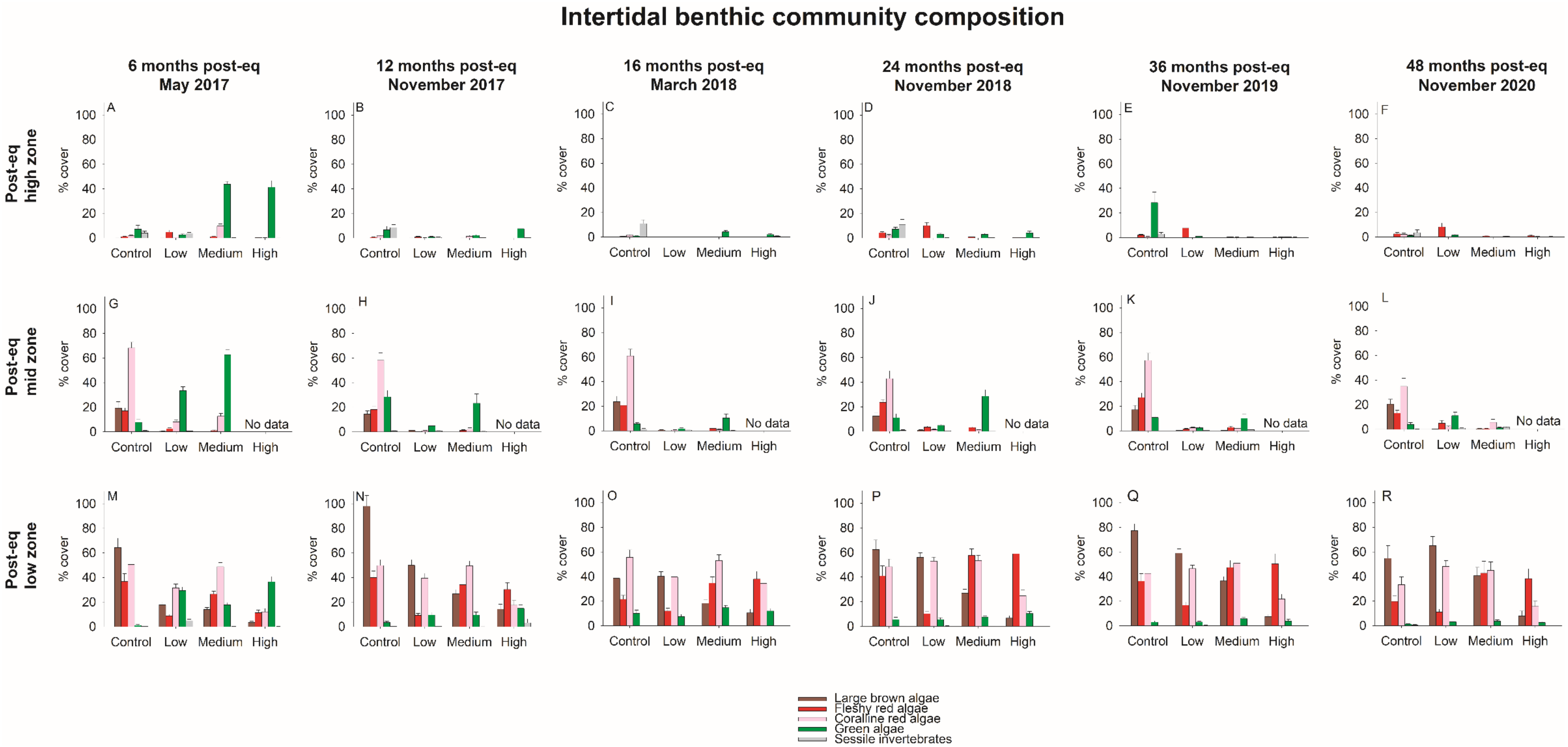

Figure 3: Abundance of the main algal groups and of sessile invertebrates across uplift levels 6, 12, 16, 24, 36 and 48 months after the earthquake. Only the high and the low tidal zones were sampled at high-uplift sites.

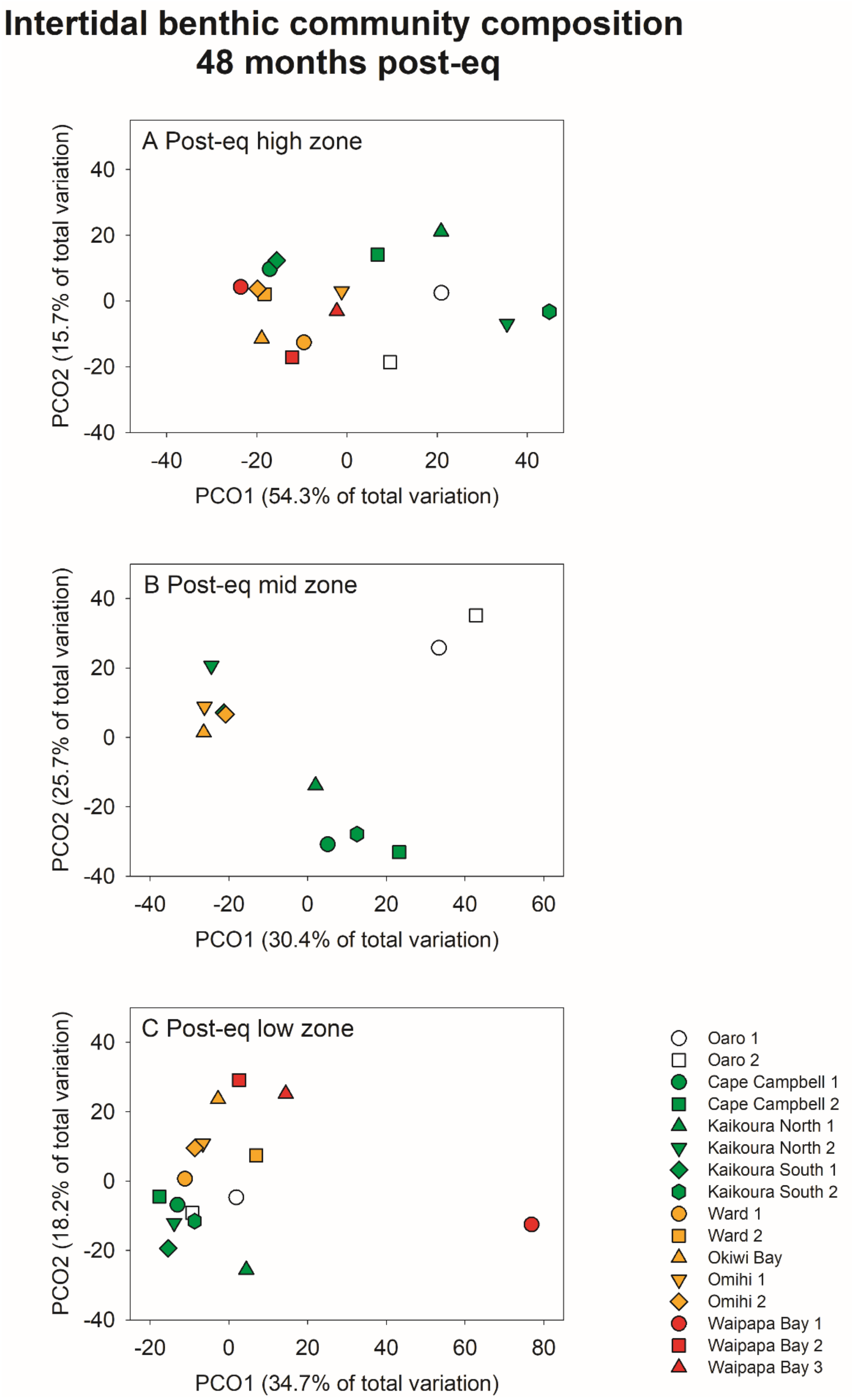

Figure 4: Principal coordinates analysis (PCO) plots showing differences in the composition of benthic communities in the post-earthquake high (A), mid (B) and low zone (C) across sites with different degrees of uplift 48 months after the earthquake. The symbols represent the centroid of each site and the colours the different levels of uplift (white = no uplift, green = low uplift, yellow = medium uplift, red = high uplift). Sites are ordered north to south within each uplift group. Only the high and the low tidal zones were sampled at high-uplift sites.

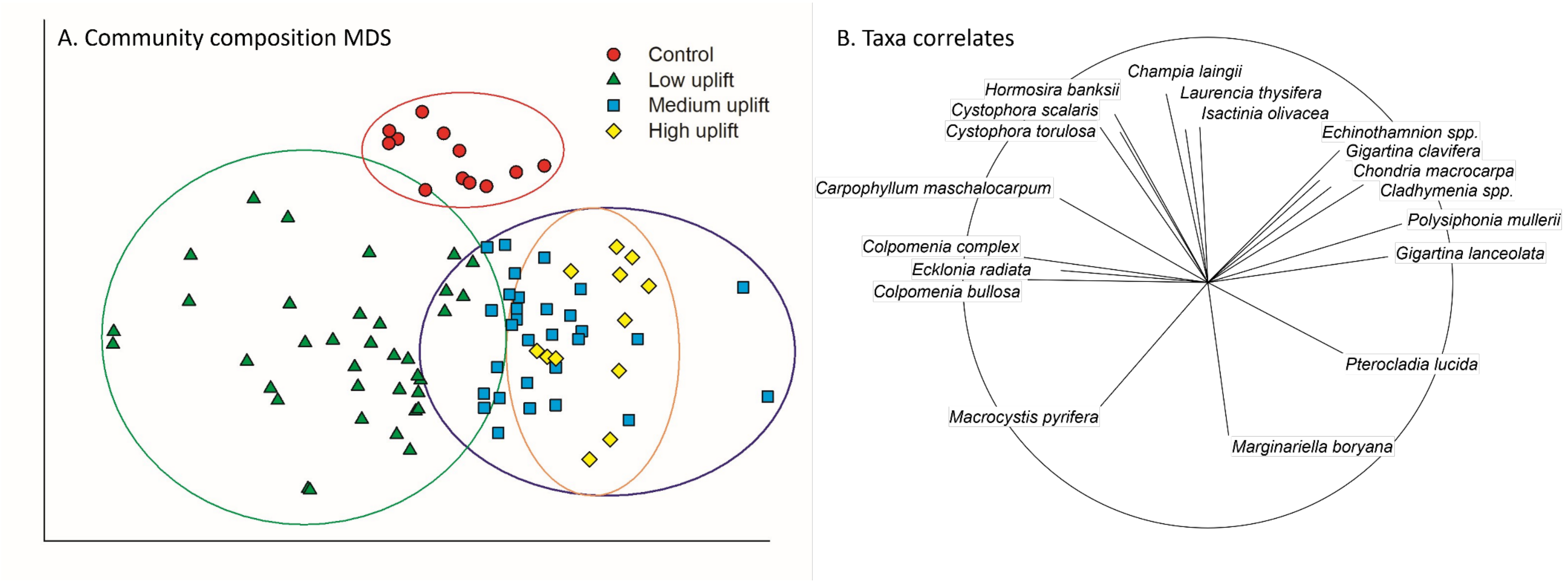

Figure 5: (A) Community composition across all zones. Each symbol represents the average of all quadrats within a site for each year. Red symbols represent control sites, green low-uplift, blue medium-uplift, and yellow high-uplift sites. (B) Shows taxa with an r correlate > 0.60.

3.2. Abundance of key intertidal taxa

Because there was very limited recovery of algae in the high and mid zones of uplifted reefs, sections 3.2.1, 3.2.2, and 3.2.3, focus on the abundance of key taxa in the low zones of sites, including brown algae, fleshy red algae, and coralline red algae. Section 3.2.4 focuses on temporal trends in the abundance of the main intertidal grazers (limpets) across all tidal zones.

3.2.1. Large brown algae

In the post-earthquake low zone, the abundance of large brown algae decreased with increasing uplift across the control and uplift groups, with all groups significantly differing from one another (Uplift: $F_{3,156} = 14.57$, $P < 0.01$, Figure 6). The most abundant species were *Carpophyllum maschalocarpum*, contributing c. 25% average cover across all sites, followed by *Durvillaea* spp., *Cystophora scalaris,* and *Marginariella boryana,* which each contributed between 3-5% average cover. The low-uplift sites had the highest average large brown algal cover (65%), followed by the control (55%), medium-uplift (40%), and the high-uplift sites (8%; Figure 6). There was no statistically significant difference in large brown algal cover across sites between 2019 and 2020 ($F_{1,312} = 0.632$, $P = 0.73$). These trends are consistent with previous years. With the extended time series, we see a sustained but slow increase of large brown algae cover at low-uplift sites towards pre-earthquake levels, suggesting recovery there.

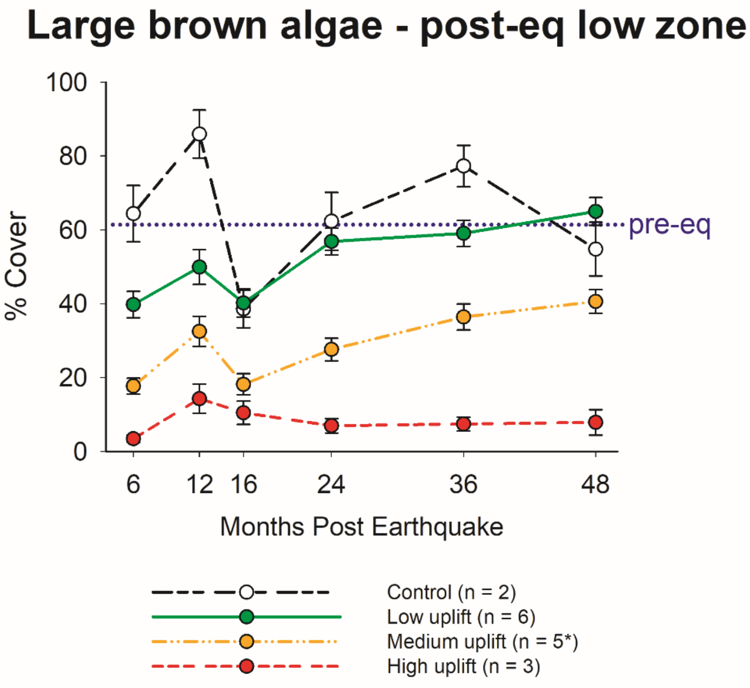

Figure 6: Time series of the mean percentage cover (±SE) of large brown algae per m^2 in the post-earthquake low zone across uplift levels. The dotted blue line indicates the average abundance of large brown algae in the pre-earthquake low zone across sites sampled in November 2016 (see Alestra et al. 2019). n = number of sites in each uplift group. *n = 3 after 12 and 16 months.

Comparisons with pre-earthquake data show that brown algal cover in low-uplift sites has returned to covers similar to what was found pre-earthquake (Figure 7 B), while medium- and high-uplift sites remain well below pre-earthquake levels (Figure 7 C, D).

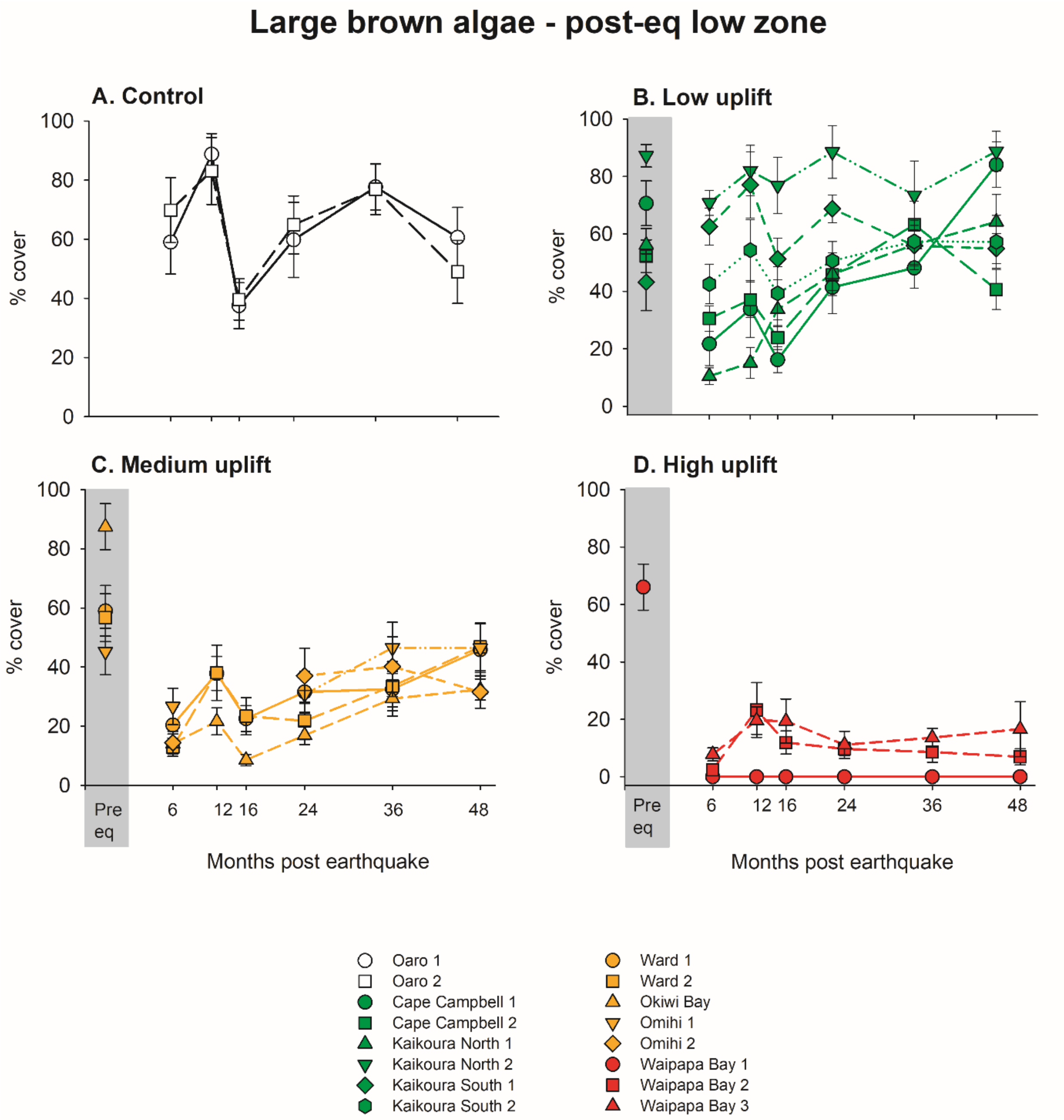

Figure 7: Time series of the mean percentage cover (±SE) of large brown algae per m^2 in the post-earthquake low zone across sites with no (A), low (B), medium (C) and high uplift (D). For the sites sampled in November 2016 (see Alestra et al. 2019), the average abundance of large brown algae in the pre-earthquake low zone is displayed in the grey panels. At Omihi 1 and 2 (panel C) the low zone could not be sampled 12 and 16 months after the earthquake.

Comparisons with pre-earthquake data also show that assemblages of large brown algae are no longer dominated by bull kelp (*Durvillaea* spp.), but rather a mixture of fucoid and laminarian species, primarily *Carpophyllum maschalocarpum* (Figure 8). This is true for both the post-earthquake low-uplift and medium-uplift sites in November 2020 (Figure 9 A, B). Note that the highest-uplift site is not displayed as the one site sampled pre-earthquake (Waipapa bay 1) is now bare.

Figure 8: Large brown algae assemblages dominated by bull kelp (*Durvillaea poha* in the top picture) and a mix of fucoid and laminarian species (mainly *Carpophyllum maschalocarpum* in the bottom picture).

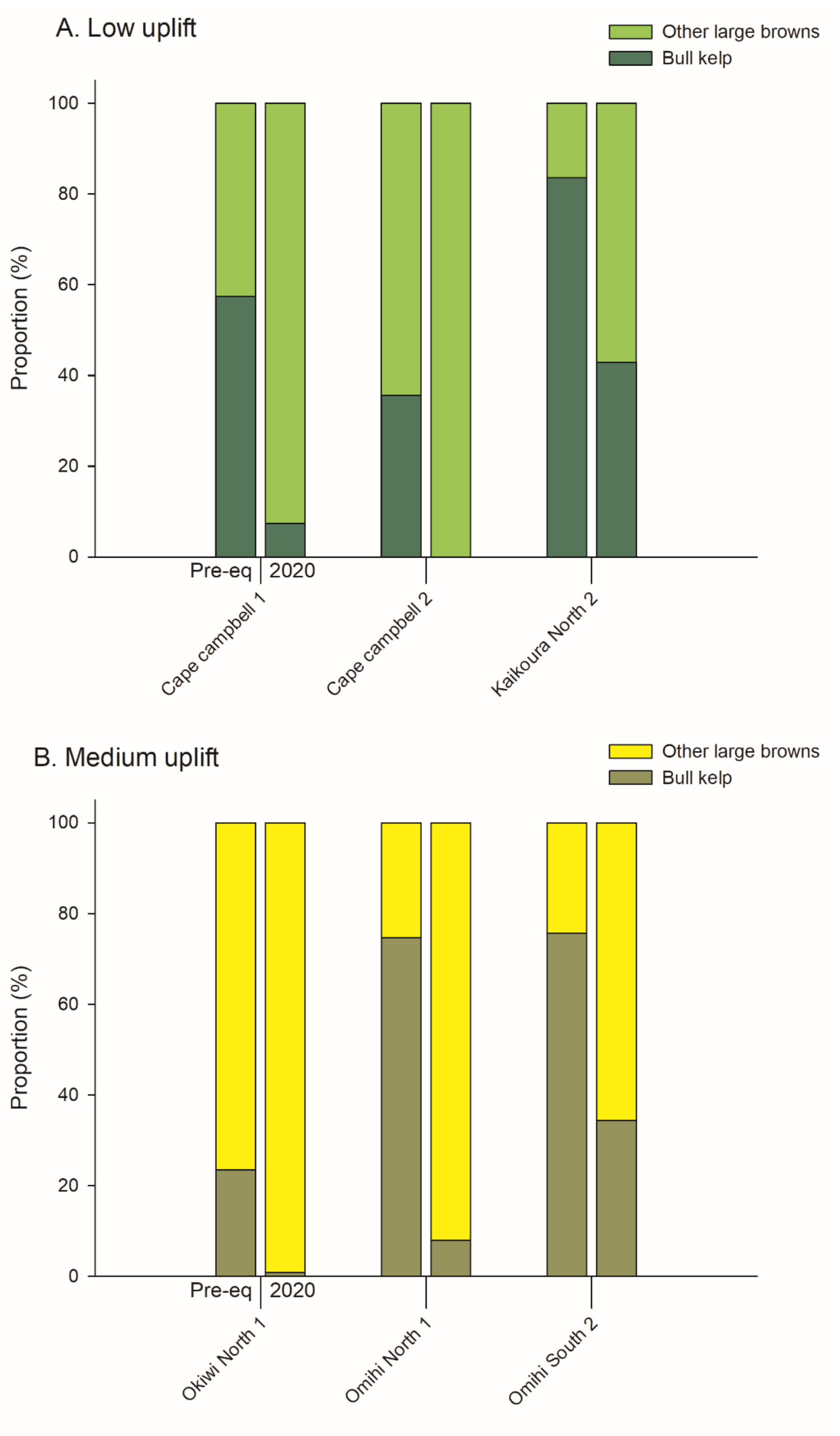

Figure 9: Changes in the relative proportions of bull kelp (*Durvillaea* spp.) and other species of large brown algae (primarily *Carpophyllum maschalocarpum*, *Cystophora scalaris*, *Marginariella boryana*, and *Lessonia variegata*) in the low zones of sites with (A) low- and (B) medium-uplift pre- (November 2016) and post-earthquake (November 2020).

Following the earthquake, bull kelp cover declined significantly at most sites, and populations were further affected by the 2017 marine heatwave (Thomsen et al. 2019). To date, high-uplift sites have showed no signs of recovery (Figure 10 D) and control, low- and medium- uplift sites have maintained relatively low covers of bull kelp ranging from 8% to 11% (Figure 10 A, B, C). Significant differences were found between all uplift-groups ($F_{3,156} = 4.80$, $P < 0.01$) and there were no significant changes in bull kelp cover between 2019 and 2020 ($F_{1,312} = 0.55$, $P = 0.64$), suggesting some stabilization (but not recovery).

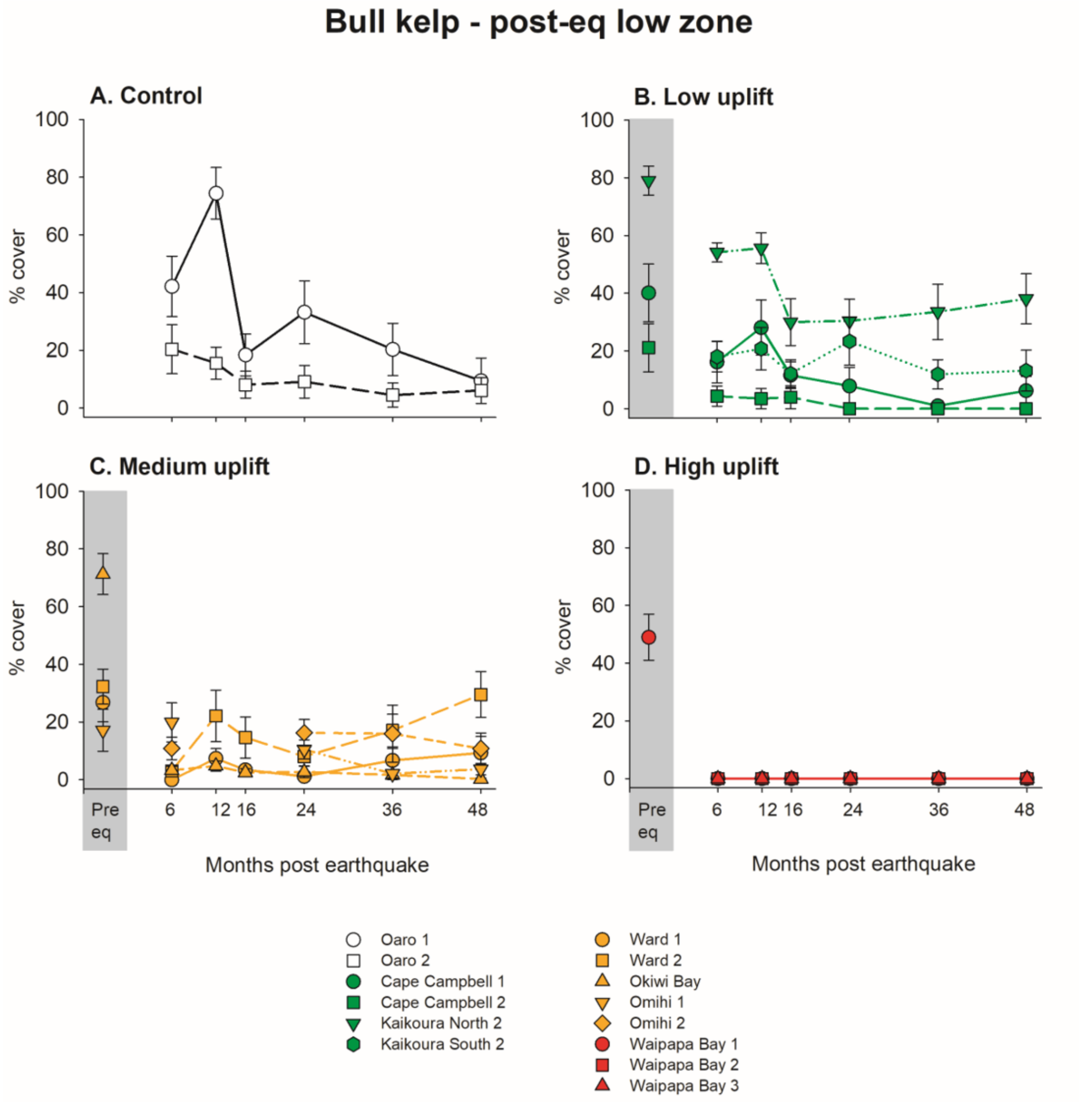

Figure 10: Time series of the mean percentage cover (±SE) of bull kelp (*Durvillaea* spp.) per m^2 in the post-earthquake low zone across sites with no (A), low (B), medium (C) and high uplift (D). For the sites sampled in November 2016 (see Alestra et al. 2019), the average abundance of bull kelp in the pre-earthquake low zone is displayed in the grey panels. At Omihi 1 and 2 (panel C) the low zone could not be sampled 12 and 16 months after the earthquake. Kaikōura North 1 and South 1, where bull kelp was not present both before and after the earthquake, are not included in this figure.

The abundance of other large brown algae (excluding *Durvillaea*) has been stable or increasing since the earthquake at almost all sites (Figure 11). Abundances were relative to uplift degree, with average covers being highest in the low- (55%), control (47%) and medium-uplift sites (30%) and lowest in the high-uplift sites (8%) (Figure 11). Four years after the earthquake, the canopy covers of other large brown algae significantly differed between uplift levels ($F_{3,156} = 14.0$, $P < 0.01$) and there were no significant differences between 2019 and 2020 ($F_{1,312} = 0.82$, $P = 0.54$).

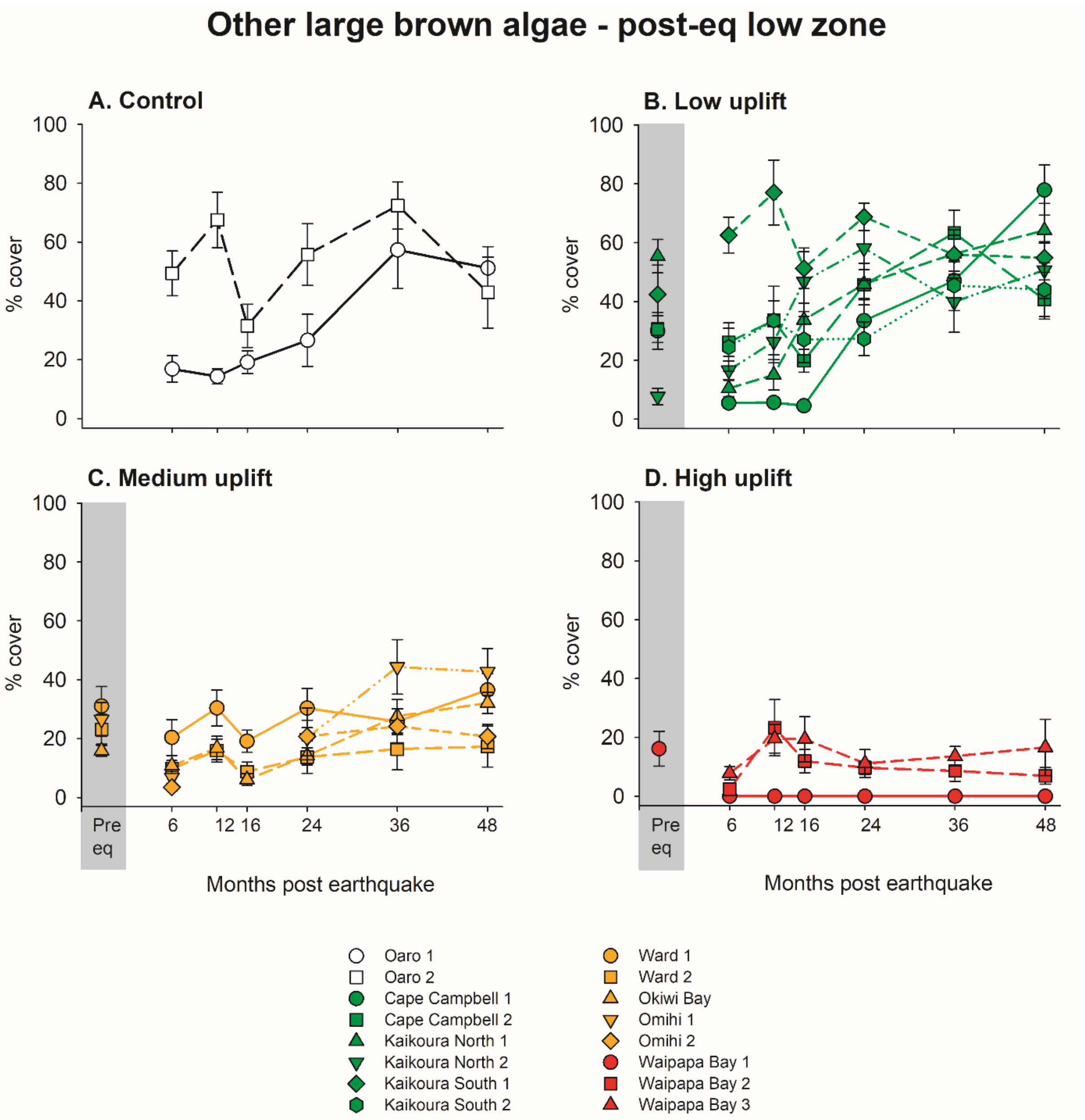

Figure 11: Time series of the mean percentage cover (±SE) of other large brown algae species excluding *Durvillaea* spp. (primarily *Carpophyllum maschalocarpum*, *Cystophora scalaris*, *Marginariella boryana* and *Lessonia variegata*) per m^2 in the post-earthquake low zone across sites with no (A), low (B), medium (C) and high uplift (D). For the sites sampled in November 2016 (see Alestra et al. 2019), the average abundance of mixed fucoids in the pre-earthquake low zone is displayed in the grey panels. At Omihi 1 and 2 (panel C) the low zone could not be sampled 12 and 16 months after the earthquake.

3.2.2. Fleshy red algae

There was a general decrease in the cover of red algae between 2019 and 2020 (Figure 12). The greatest decreases occurred at the control sites, from 36% to 20%, followed by high-uplift (50% to 38%), low-uplift (17% to 11%), and medium-uplift (47% to 43%). These were statistically significant differences between uplift groups in 2020 ($F_{3,156} = 2.42$, $P < 0.01$) and between 2019 and 2020 for the low-uplift sites ($F_{1,312} = 1.96$, $P < 0.05$). There was also considerable variability between sites within uplift groups (Figure 13) but also a clear trend for decreases in red algal cover between 2019 and 2020, except for one site at Waipapa where there was no red algal cover.

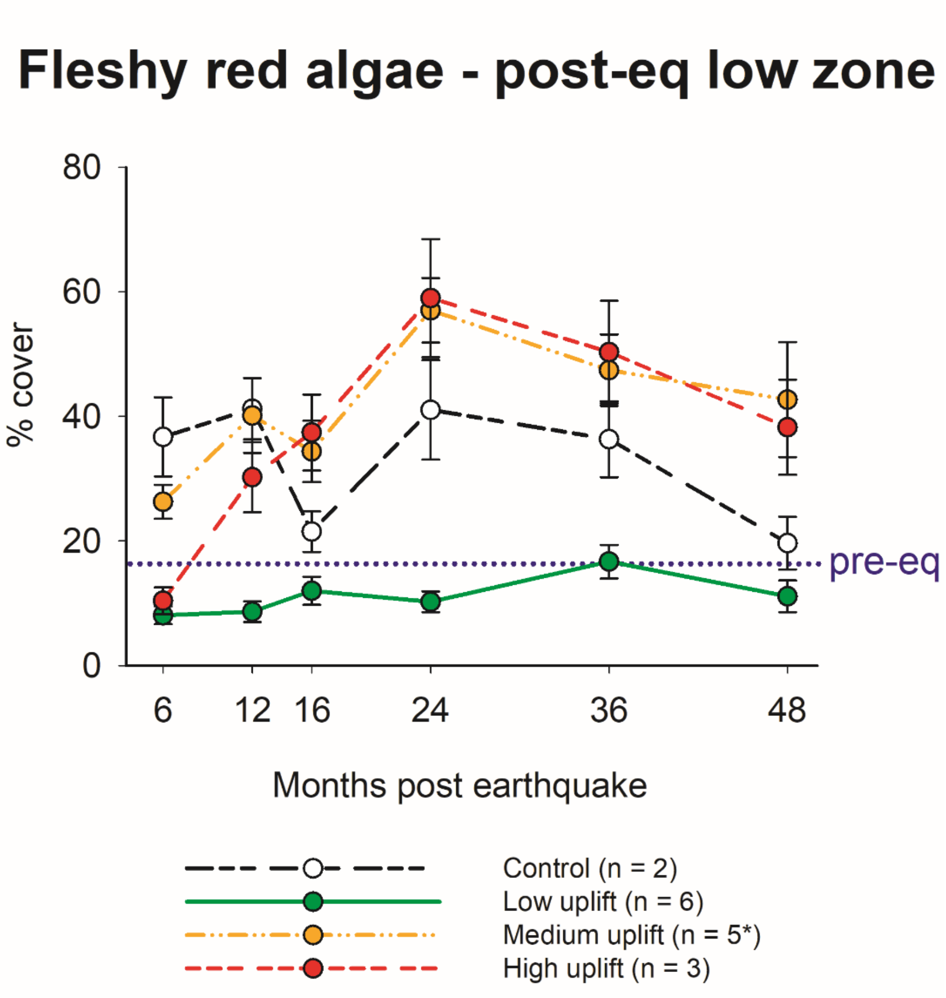

Figure 12: Time series of the mean percentage cover (±SE) of fleshy red algae (based on m^2 quadrats) in the post-earthquake low zone across uplift levels. The dotted blue line indicates the average abundance of fleshy red algae in the pre-earthquake low zone across sites sampled in November 2016 (see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

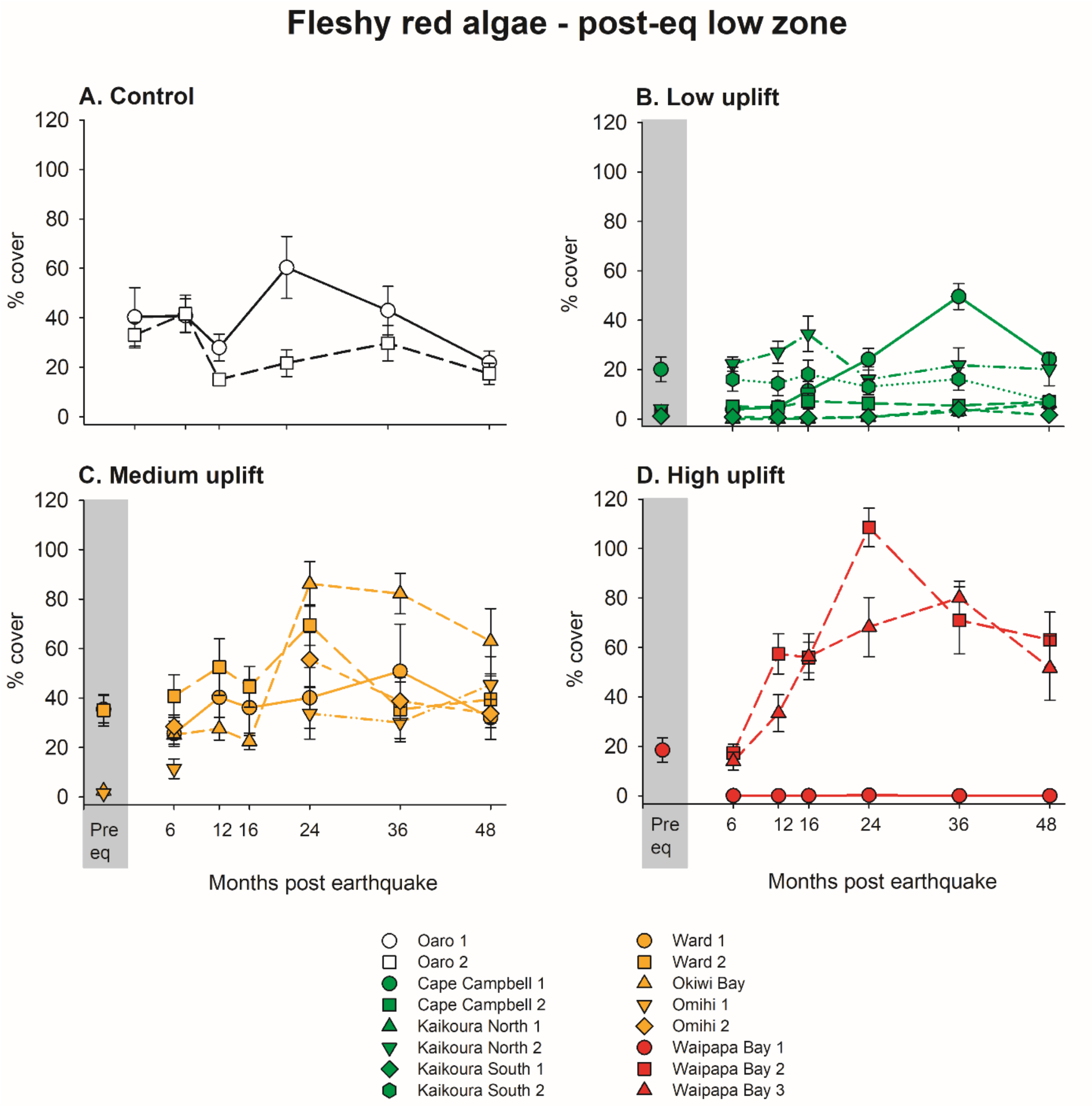

Figure 13: Time series of the mean percentage cover (±SE) of fleshy red algae (on a per m^2 basis) in the post-earthquake low zone across sixteen sites with no (A), low (B), medium (C) and high uplift (D). For the sites sampled in November 2016 (see Alestra et al. 2019), the average abundance of fleshy red algae in the pre-earthquake low zone is displayed in the grey panels. At Omihi 1 and 2 (panel C) the low zone could not be sampled 12 and 16 months after the earthquake.

3.2.3. Proportion change in large brown algae and fleshy red algae

At some uplifted sites the proportions of dominant algal species have shifted notably over the past 4 years, with fleshy red algae increasing in abundance relative to large brown algae (Figure 14 and 15). This was found particularly at northern sites with low and medium uplift (high-uplift sites are either lacking sufficient recovery or were not sampled pre-earthquake).

Figure 14: Large brown algae assemblages dominated by *Carpophyllum maschalocarpum* (top picture) and fleshy red algae (mainly *Gigartina* species in the bottom picture).

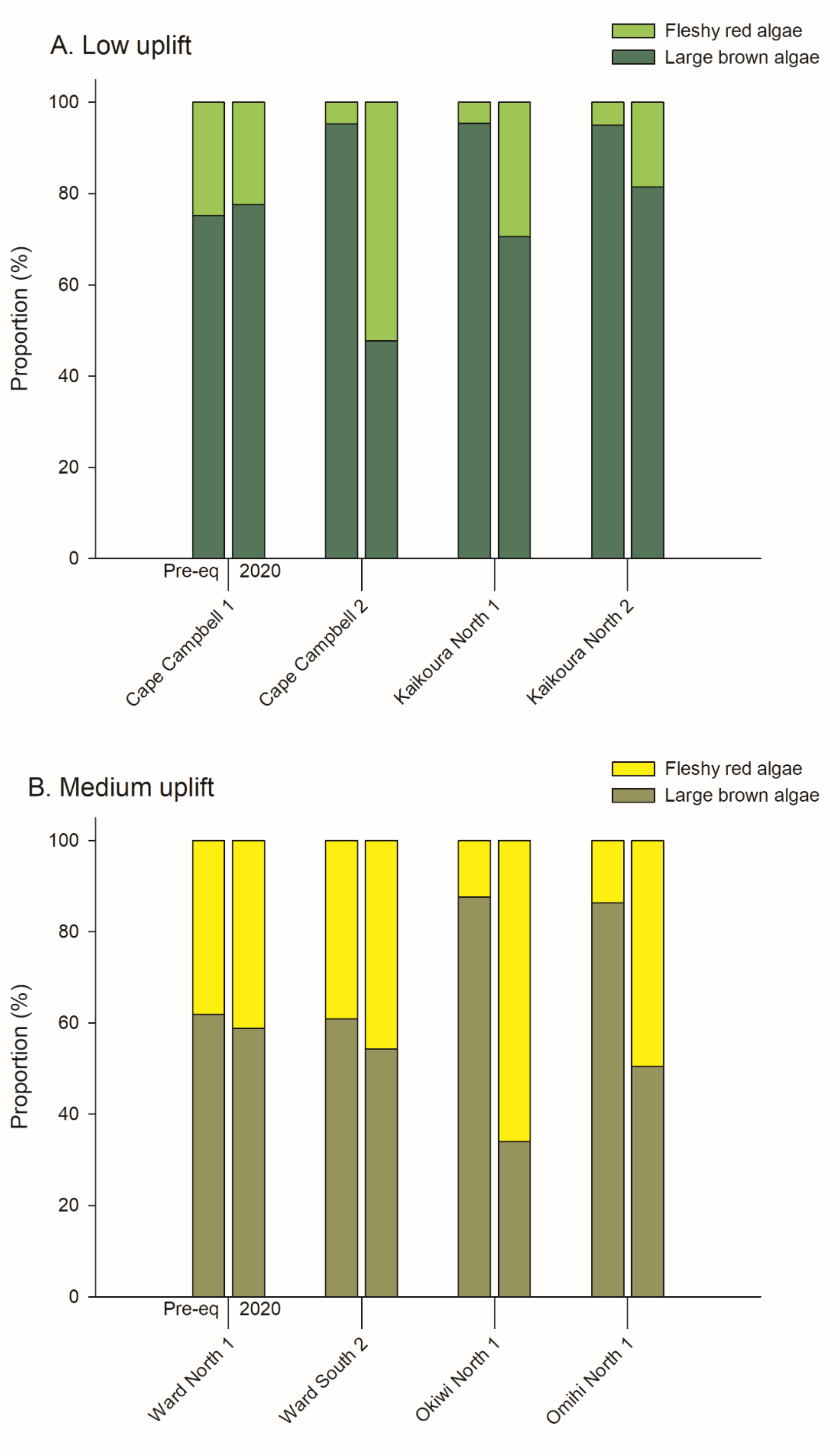

Figure 15: Changes in the relative proportions large brown and fleshy red algae in the low zones of sites with (A) low- and (B) medium-uplift pre- (November 2016) and post-earthquake (November 2020).

3.2.4. Coralline red algae

In 2020, low- and medium-uplift sites had similar mean covers of coralline red algae, at 48% and 45% respectively, followed by control (33%) and high-uplift sites (16%) (Figure 16). There were significant differences between uplift groups in 2020 ($F_{3,156}$ = 18.6, P = 0.13). Comparisons of cover in 2019 and 2020 show no significant differences between years ($F_{1,312}$ = 1.72, P < 0.05). Coralline algae remain well below pre-earthquake levels, with all but the low-uplift sites showing a gradual decline since 24 months post-earthquake. There was considerable site-to-site variation within uplift groups (Figure 17) and Waipapa Bay 1 was the only site where coralline algae were absent (Figure 17 D).

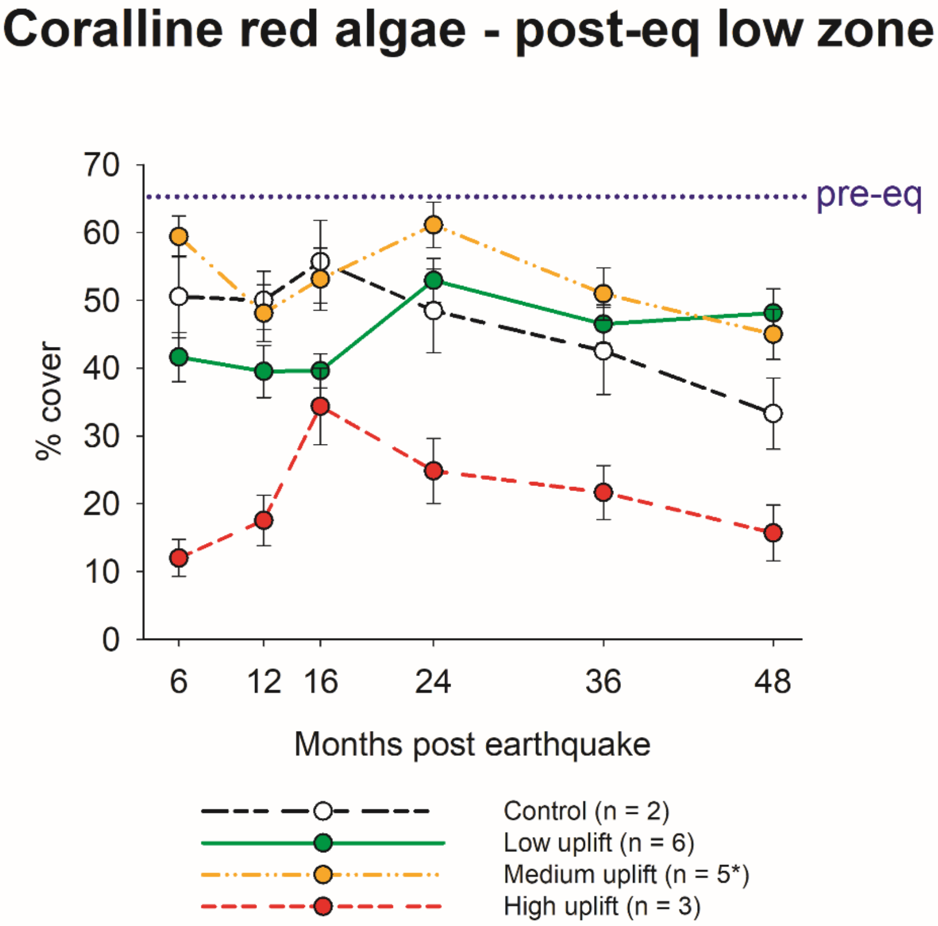

Figure 16: Time series of the mean percentage cover (±SE) of coralline red algae per m^2 in the post-earthquake low zone across uplift levels. The dotted blue line indicates the average abundance of coralline red algae in the pre-earthquake low zone across sites sampled in November 2016 (see Alestra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

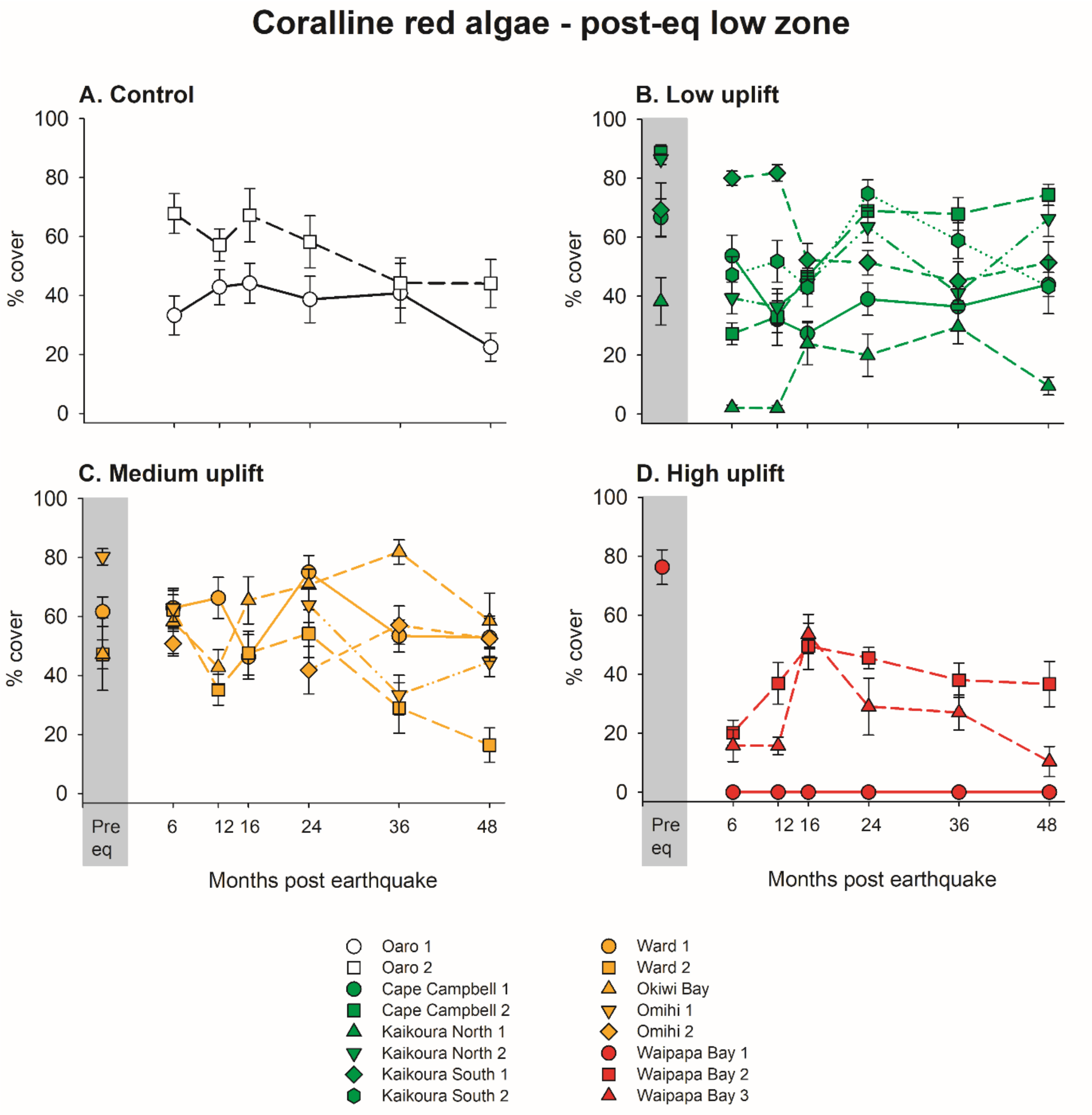

Figure 17: Time series of the mean percentage cover (±SE) of coralline red algae per m^2 in the post-earthquake low zone across sites with no (A), low (B), medium (C) and high uplift (D). For the sites sampled in November 2016 (see Alestra et al. 2019), the average abundance of coralline red algae in the pre-earthquake low zone is displayed in the grey panels. At Omihi 1 and 2 (panel C) the low zone could not be sampled 12 and 16 months after the earthquake.

3.2.5. Limpets

In 2020, the medium-uplift group had the greatest limpet densities at 63 per m^2, followed by the high uplift group (26 per m^2), and low and control groups (c. 14 m^2) (Figure 18). These differences between uplift levels were significant ($F_{3,426} = 6.9$, $P < 0.01$). Within uplift groups, there was a significant increase among sites between 2019 and 2020 within the medium-uplift group ($F_{3,312} = 11.1$, $P < 0.01$) (Figure 19). This increase was largely attributed to one site (Okiwi bay) having counts > 200 per m^2 (Figure 19 C). At most sites, the density of limpets is similar to pre-earthquake levels (Figure 19).

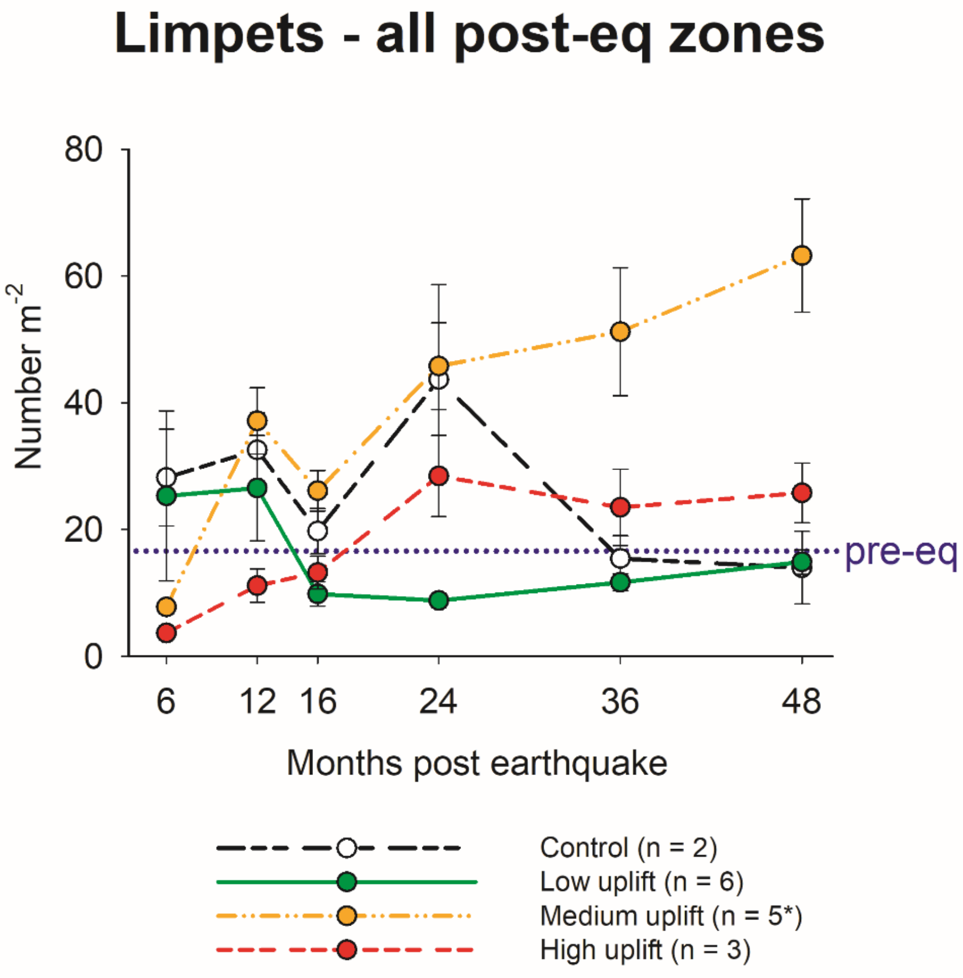

Figure 18: Time series of the mean number (±SE) of limpets per m^2 across uplift levels. The dotted blue line indicates the average abundance of limpets across sites sampled in November 2016 (see Alestra et al. 2019).

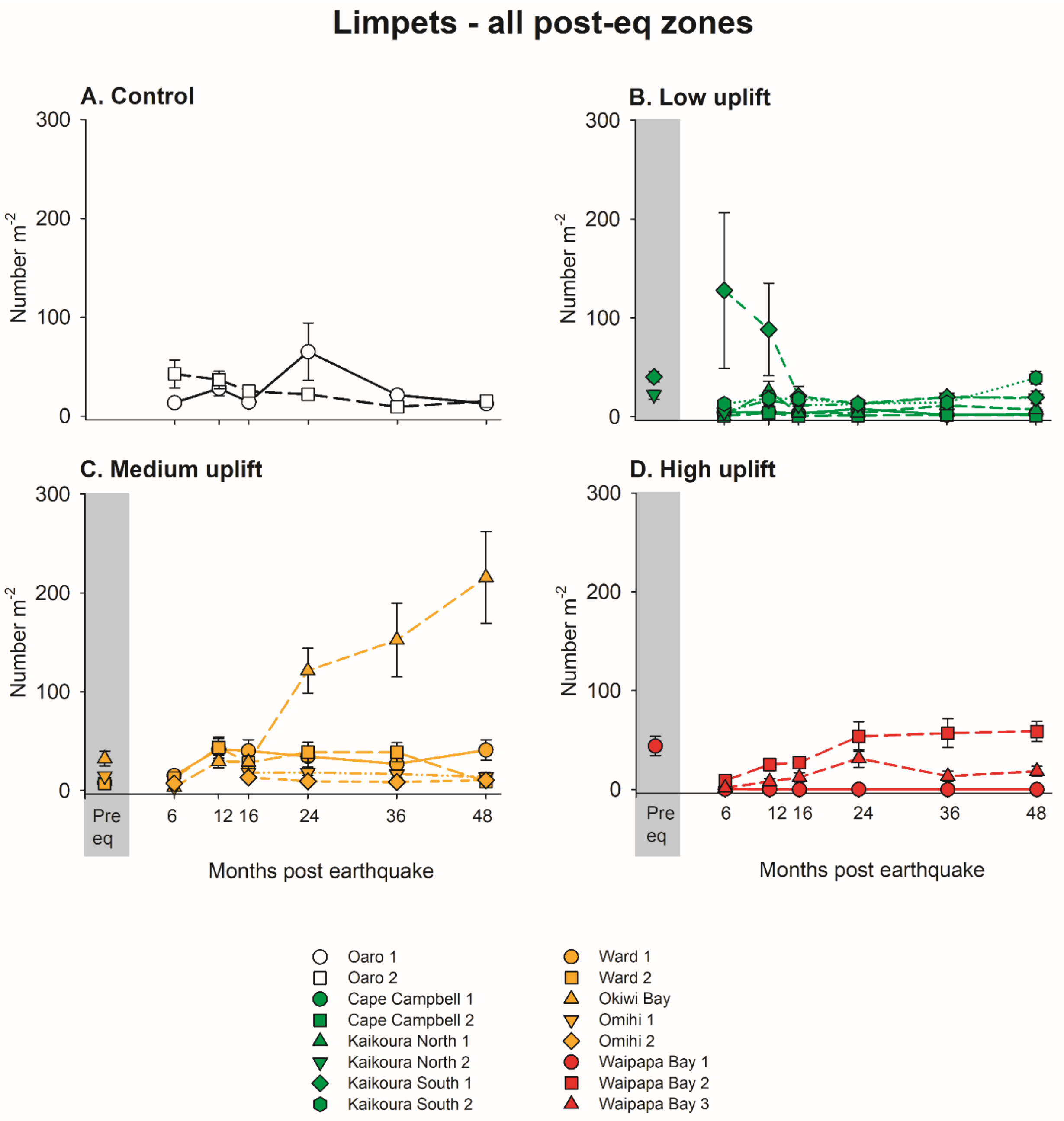

Figure 19: Time series of the mean number (±SE) of limpets per m^2 across sites with no (A), low (B), medium (C) and high uplift (D). For the sites sampled in November 2016 (see Alestra et al. 2019), the average abundance of limpets is displayed in the grey panels. At Omihi 1 and 2 (panel C) the low zone could not be sampled 12 and 16 months after the earthquake.

3.3. Subtidal community structure

The 2021 subtidal surveys showed minor recovery of seaweeds and invertebrates at Waipapa Bay (Figure 20). Previous surveys documented a decline in large brown algae around the Kaikōura peninsula and at Okiwi Bay. The 2021 surveys showed a slight increase in abundance of large brown algae around the Kaikōura peninsula, but large brown algal abundance at Okiwi Bay remained low. Percentage cover of non-encrusting red algae continued to increase at Okiwi Bay. There were shifts in sand and gravel distribution in some transects at Okiwi Bay South and Waipapa Bay (Figure 21), and an overall decline in algae at one cobble-dominated site (Okiwi Bay South T1). Sites at Waipapa Bay still had large areas of bare rock that had not been recolonised four and a half years after the earthquake.

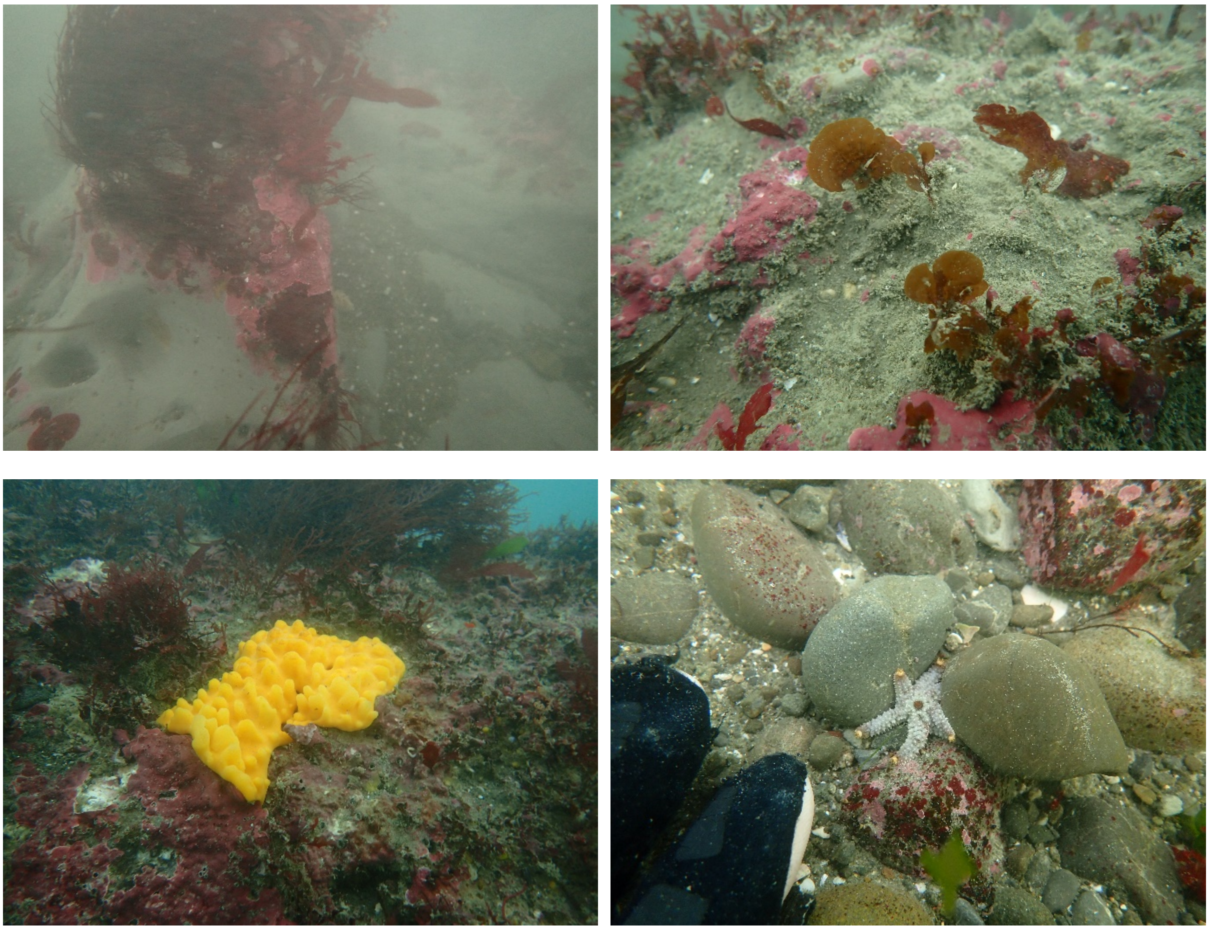

Figure 20: Examples of recruitment of algae (top), and sessile and mobile invertebrates (bottom) at Waipapa Bay. Photos taken in April 2021.

Figure 21: Examples of sand covering algae at Waipapa Bay North (top left), evidence of scour from gravel movement at Waipapa Bay South (top right), and gravel amongst cobble and boulders at Okiwi Bay South (bottom).

There were changes in substrate cover (using all data and not filtered to only include quadrats with ≥50% rock) at some Waipapa and Okiwi Bay sites (Figure 22). The changes mainly related to the movement of sand and gravel at some sites (Figure 23). Waipapa Bay North and South sites had declines in sand cover in 2019 and increases in 2020 and 2021. This was particularly evident at Waipapa Bay North in 2021 (Figure 23) and reduced the number of quadrats along two transects available for the community analyses (which only used quadrats with ≥50% rock) (Appendix 2). Gravel cover also fluctuated, particularly at the south sites. The increase in bedrock in 2018 at Waipapa Bay South sites is due to sand and gravel cover decreasing and exposing bedrock, and also due to the addition of a new transect in 2018 (Figure 22). Okiwi South sites also had fluctuations in sand and gravel cover since 2017 (Figure 23), and increases in cobble (Figure 22).

Percentage covers of some algal groups across sites changed between surveys. There was a decline in large brown algal cover at Kaikōura Peninsula and Okiwi Bay sites after 2018, and an increase in red non-encrusting algae at Okiwi Bay sites (Figure 24). The decline in large brown algae was mostly driven by decreases in abundances of *Marginariella boryana* and *Lessonia variegata* (Figure 25). Percentage cover of large brown algae has remained low at Okiwi Bay sites, but has increased at Kaikōura Peninsula sites in 2020 and 2021. While encrusting/turfing algae cover was similar through time at Kaikōura Peninsula and Okiwi Bay sites, slight increases were seen at Waipapa Bay sites, along with an increase in red non-encrusting algae (Figure 24). Some recruitment of large brown algae was observed at Waipapa Bay, but this was not noticeable in the plots due to the small sizes of the recruits. The main species of large brown algae present at Waipapa sites between 2017-2021 were *Landsburgia quercifolia* and *Carpophyllum maschalocarpum*, with a few individuals of *Ecklonia radiata*, *Cystophora retroflexa*, *Cystophora scalaris* and *Cystophora platylobium* also present at times. *L. variegata* and *M. boryana* were present in 2017 and 2018 but were practically absent from 2019-2021 (Figure 25). The ephemeral green alga Ulva sp. had higher percentage cover at Okiwi Bay South in 2020 and 2021, and at Waipapa Bay South in 2018, 2020 and 2021 (Figure 24).

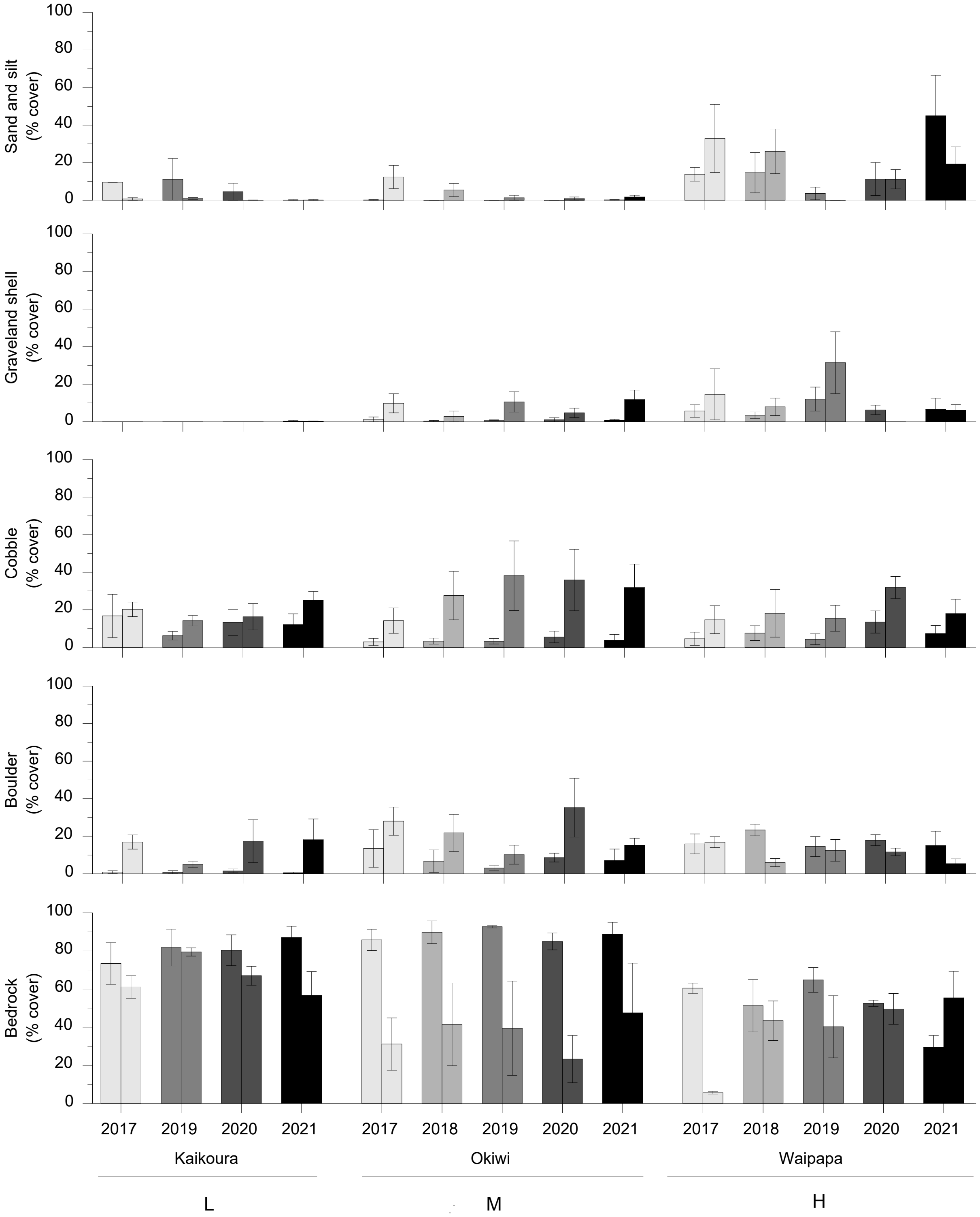

Figure 22: Mean percentage cover of substrate types per 5 m^2 quadrat at the six sites surveyed between 2017-2021. For each pair of bars, the left bar refers to the northern site and the right bar to the southern site. L=Low, M=Medium, H=High. N = 20. Data are averaged over 3 transects; error bars represent 1 ±SE.

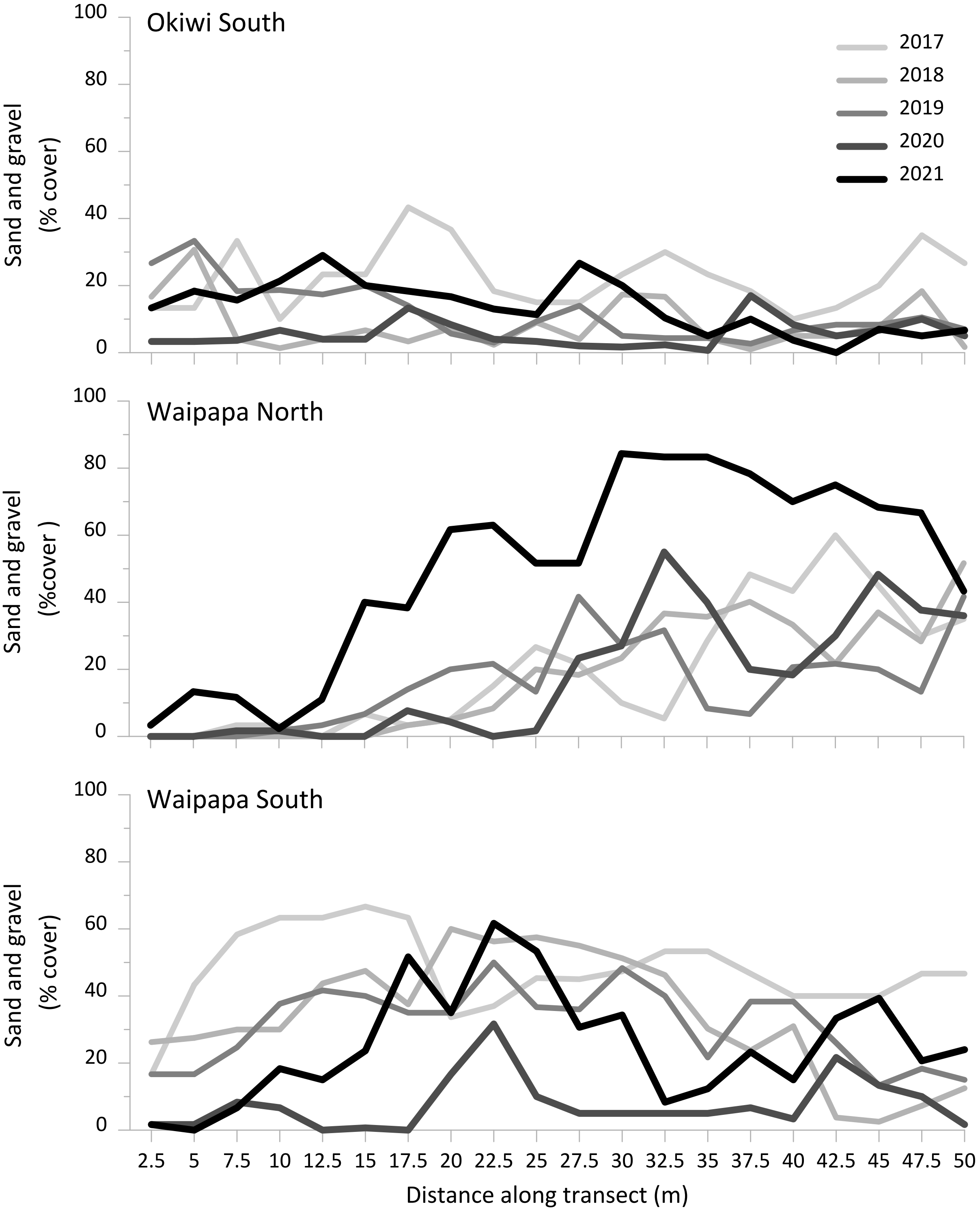

Figure 23: Mean percentage cover of sand/gravel substrate per 5 m^2 quadrat along transects at Okiwi South, Waipapa North and Waipapa South sites surveyed between 2017-2021. N = 3. Data are averaged over 3 transects, error bars are not shown for clarity of the plots.

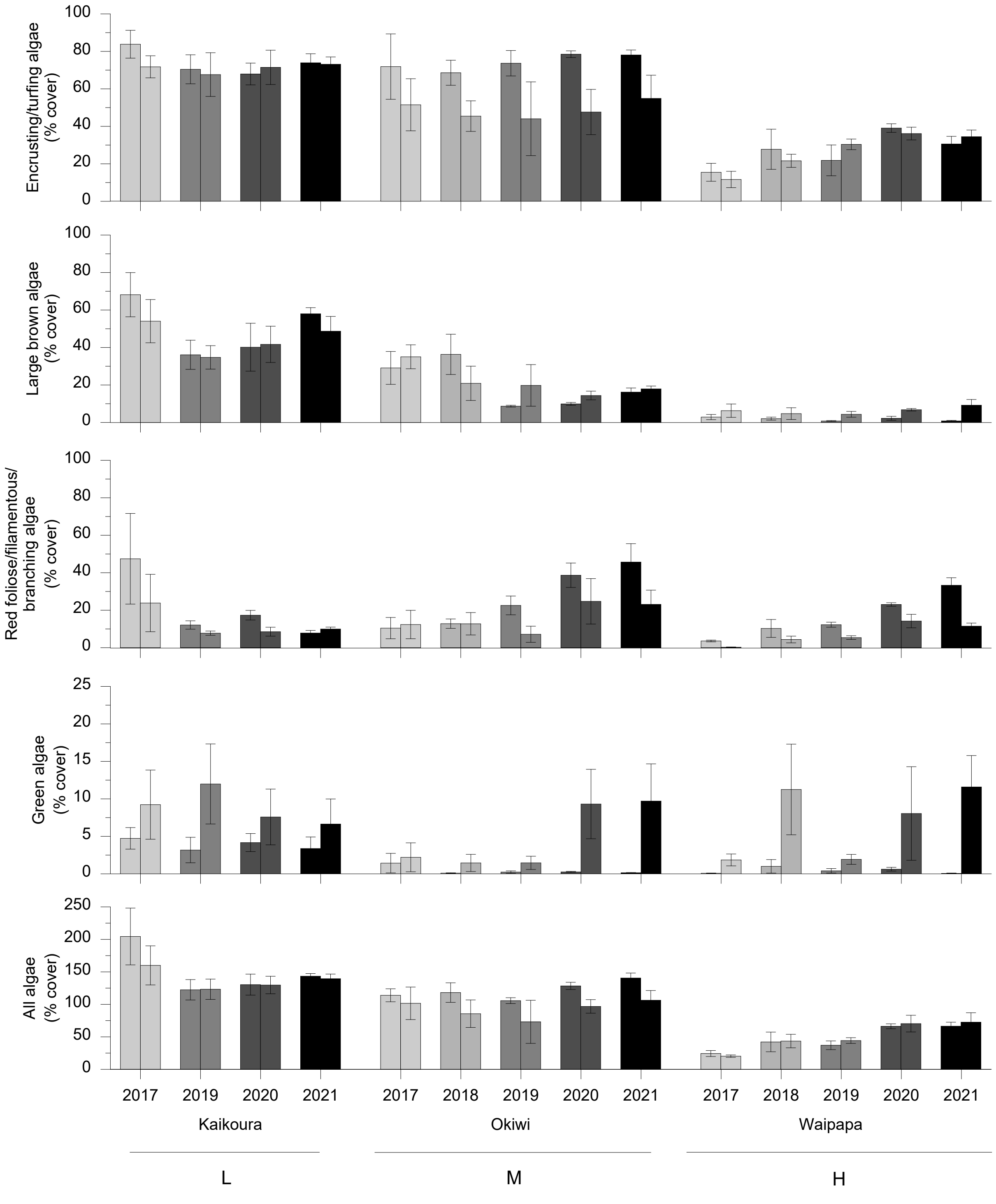

Figure 24: Mean percentage cover of algae per 5 m^2 quadrat at the six sites surveyed between 2017 – 2021. For each pair of bars, the left bar refers to the northern site and the right bar to the southern site. L=Low, M=Medium, H=High. Data were filtered to only include quadrats with ≥50% rock substrate (cobble, boulder, or bedrock) (n=variable and noted in Appendix 2). 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 ±SE. Note different scales for green and all algae plots.

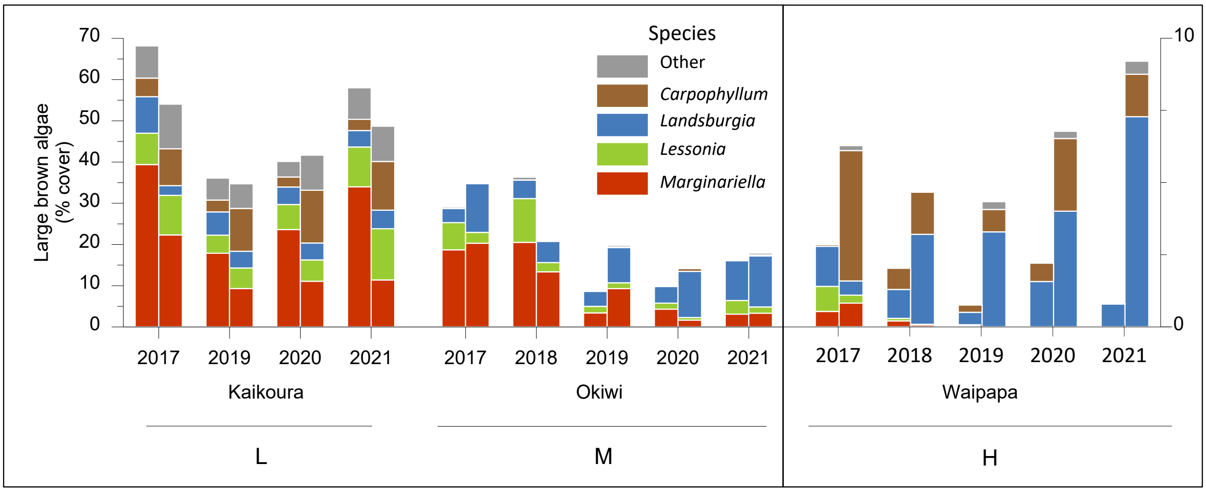

Figure 25: Mean percentage cover of large brown algal species per 5 m^2 quadrat at the six sites surveyed between 2017 – 2021. The "Other" species category included *Ecklonia radiata*, *Macrocystis pyrifera*, *Cystophora retroflexa*, *Cystophora scalaris* and *Cystophora platylobium*, but species present varied between sites. For each pair of bars, the left bar refers to the northern site and the right bar to the southern site. L=Low, M=Medium, H=High. Data were filtered to only include quadrats with ≥50% rock substrate (cobble, boulder, or bedrock) (n=variable and noted in Appendix 2). 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 ±SE. Note different scales for Kaikōura/Okiwi and Waipapa sites.

There were no clear trends in mobile invertebrate abundances through time at Kaikōura and Okiwi Bay sites, but Waipapa Bay sites showed increases in numbers up to 2020, with a slight decrease in 2021 comparable to 2019 abundances (Figure 26). The high numbers of mobile invertebrates at Waiapapa Bay South in 2017 skewed results and were due to a large number of crayfish along one transect, but overall numbers of other mobile invertebrates have increased through time. For example, numbers of cook's turban shells increased over time and numbers of sea stars increased at Waipapa South (Figure 27). Numbers of both pāua species increased at Okiwi Bay sites, and yellow foot pāua increased at the Kaikōura North (rahui) site. Kina increased at the Kaikōura South site in 2019 and 2020, but in 2021 were at similar abundances to 2017.

Sessile invertebrate cover increased at Kaikōura North until 2020, and this was driven by increases in sponges and ascidians. There were small increases in sponges and ascidians at Waipapa Bay sites until 2020, and a decline in 2021 (particularly at Waipapa North) (Figure 26). The decline at Waipapa North may be associated with an increase in sand and gravel there (Figure 23).

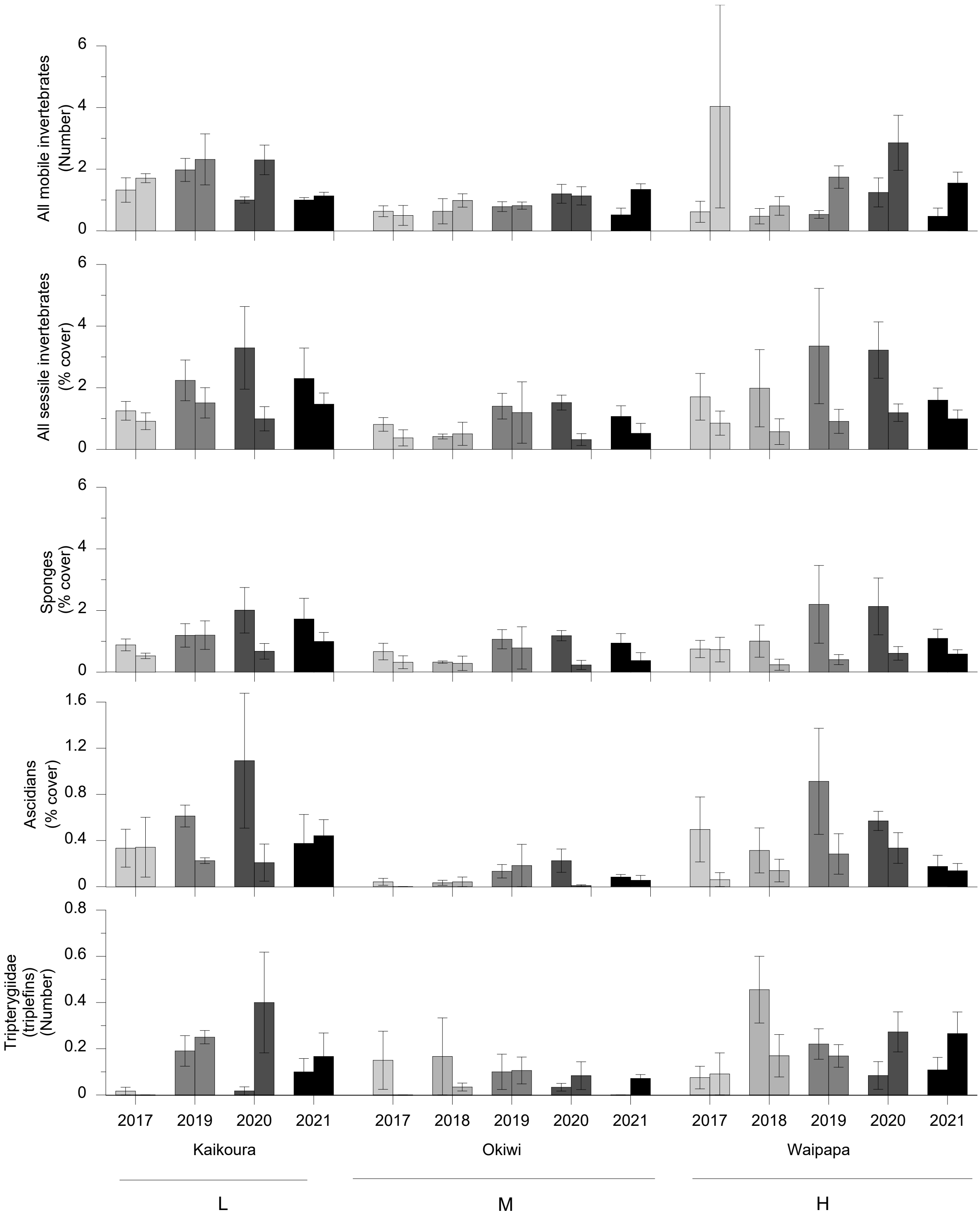

Figure 26: Mean percentage cover of sessile invertebrates, sponges and ascidians, and numbers of mobile invertebrates and triplefins per 5 m^2 quadrat at the six sites surveyed between 2017 - 2021. For each pair of bars, the left bar refers to the northern site and the right bar to the southern site. L=Low, M=Medium, H=High. Data were filtered to only include quadrats with ≥50% rock substrate (cobble, boulder or bedrock) (n=variable and noted in Appendix 2). 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 ±SE. Note change in scales.

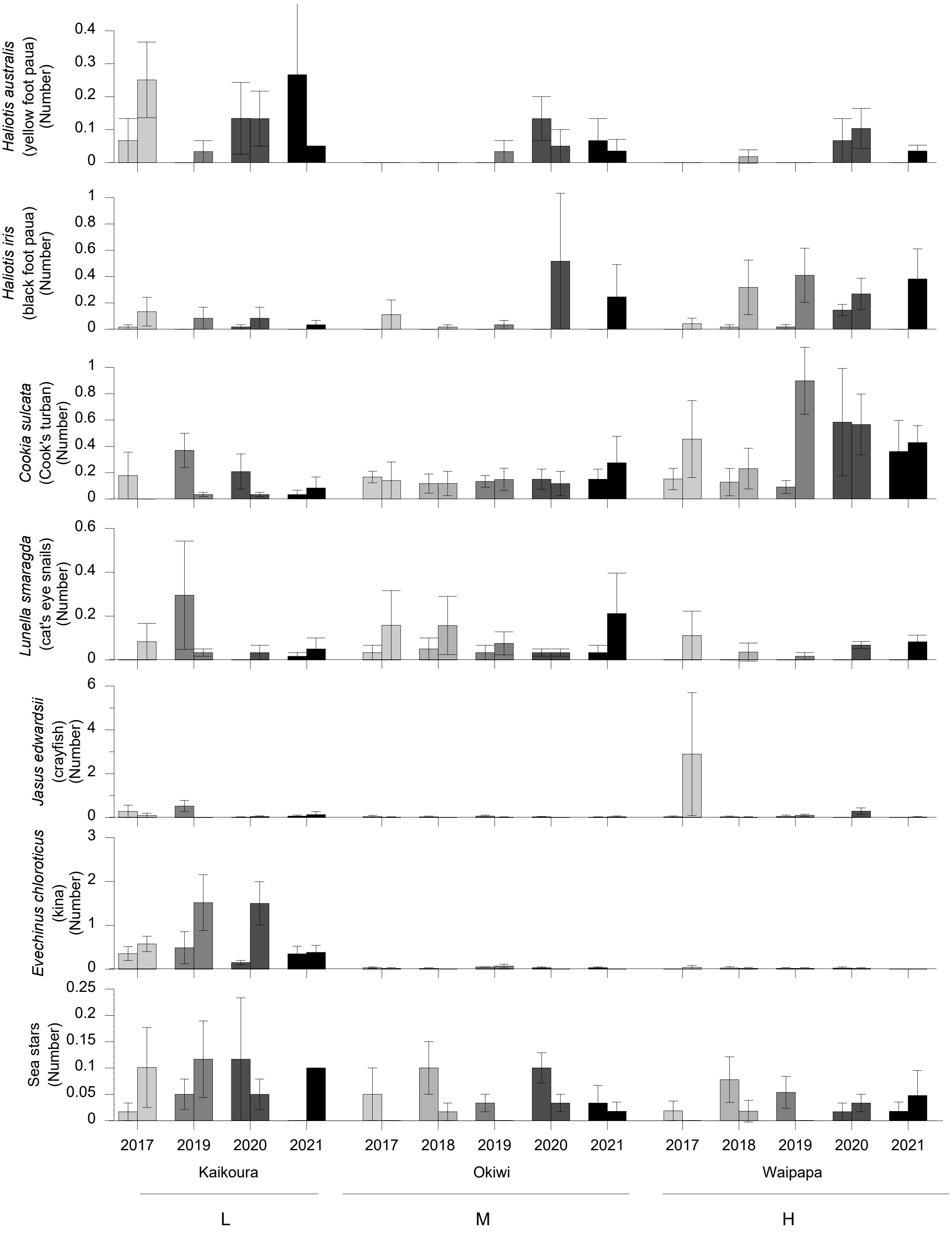

Figure 27: Mean number of selected mobile invertebrates per 5 m^2 quadrat at the six sites surveyed between 2017 - 2021. For each pair of bars, the left bar refers to the northern site and the right bar to the southern site. Uplift areas: L=Low, M=Medium, H=High. Data were filtered to only include quadrats with ≥50% rock substrate (cobble, boulder, or bedrock) (n=variable and noted in Appendix 2). 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 ±SE. Note change in scales.

Permanova analysis for the subtidal community data showed the very high amount of temporal and spatial variabilty, with all terms significant (Table 1). Site and Transect were highly significant (P < 0.001) and this indicates there was spatial variability at small (between transects) and large (between sites) scales. The Survey × Site(Uplift) and Survey x Transect (Site(Uplift)) interaction terms were also highly significant, indicating that one or more sites and transects changed differently from each other between surveys.

Principle coordinate analysis (PCO) of distance between centroids for the Site combinations showed the degree of change in communities between surveys (Figure 28). Okiwi Bay north and south, and Waipapa Bay south communities changed the most between surveys. Communities at Okiwi Bay sites (particularly south sites) had a directional change towards the right of the plot (Figure 28). The communites on the right side had less brown algae, and more red algae than the communities on the left side of the plot. Communities at Waipapa Bay showed directional change from the top to the bottom of the plot and this was primarily driven by increases in several different taxa (i.e. recruitment and recovery of algal and invertebrate populations).

SIMPER analysis showed that the differences between surveys at Okiwi North were primarily driven by a reduction in some large brown algae (*Margineriella 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, and some large brown algae (*M. boryana*, *Landsburgia quercifolia* and *Lessonia variegata*), and increases in some red foliose algal taxa. The increase in the green alga *Ulva* sp. also contributed to the dissimilarity between communities in 2020 and 2021, and previous years.

Changes in Waipapa Bay communities were indicative of the recruitment and recovery at these sites, and reflected the increases in a variety of algal taxa. Waipapa Bay South sites were dissimilar between surveys primarily due to an increase in encrusting coralline and encrusting red algae, *Ulva* sp., some red foliose algal taxa and some brown algae (*L. quercifolia*, *Halopteris* spp. and *Zonaria* sp.), and a decrease in the brown alga *Carpophyllum maschalocarpum*. The large difference in the Waipapa Bay South 2017 communities and subsequent surveys was due to a high number of crayfish recorded in one transect in 2017. Communities at Waipapa North were dissimilar through time due to increases in encrusting corallines, red encrusting algae, some red foliose algal taxa and and an encrusting orange sponge.

Table 1: PERMANOVA results for epibiota community data. P values: * < 0.05, ** < 0.01, * < 0.001.**

Source	df	SS	MS	Pseudo-F	P(perm)
Uplift	2	4.78E+05	2.39E+05	4.4802	0.0195*
Survey	4	1.16E+05	28 925	2.2602	0.0001***
Site(Uplift)	3	1.72E+05	57 466	2.8885	0.0002***
Uplift × Survey	7	99 174	14 168	1.4699	0.0233*
Transect (Site(Uplift))	13	2.71E+05	20 884	23.958	0.0001***
Survey × Site(Uplift)	11	1.08E+05	7 787	1.5212	0.0005***
Survey×Transect(Site(Uplift))	44	2.91E+05	6 618.7	7.5929	0.0001***
Res	1 448	1.26E+06	871.69		

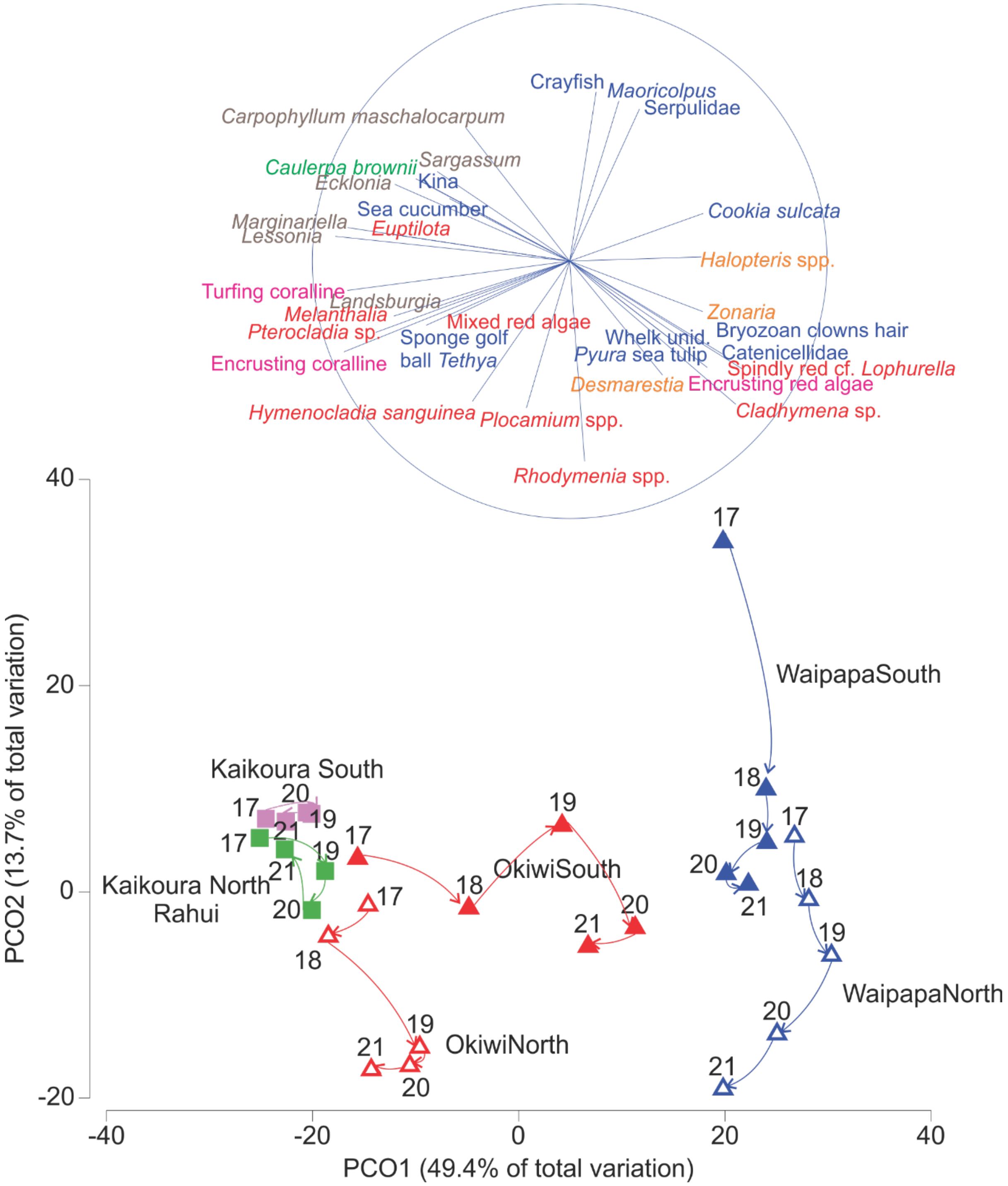

Figure 28: Principal coordinates analysis (PCO) of distance among centroids for the six sites surveyed between 2017 – 2021, based on a Bray-Curtis similarity matrix of community assemblage data. Vector overlay shows taxa with > 0.5 correlation.

As in previous surveys, few mobile reef fish (excluding triplefins) were seen in 2021 (Figure 29). The exception was at Kaikōura South, which had averages of 41, 18 and 30 fish along the transects in 2019, 2020 and 2021 respectively. The other sites had averages of fewer than 10 fish (Figure 29). Banded wrasse (*Pseudolabrus fucicola*) and spotties (*Notolabrus celidotus*) were the most abundant fish species. Other fish observed (in order of decreasing abundance) were butterfish (*Odax pullus*), blue moki (*Latridopsis ciliaris*), marblefish (*Aplodactylus arctidens*), blue cod (*Parapercis colias*), and red moki (*Cheilodactylus spectabilis*).

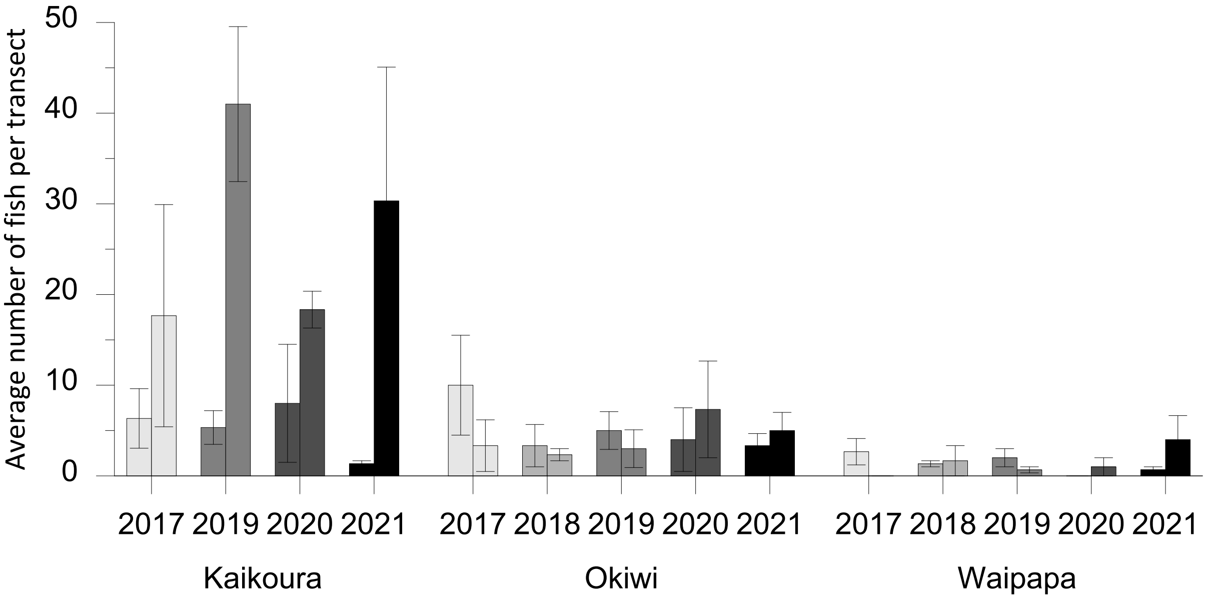

Figure 29: Average abundances of fish at each site during each survey. In each pair of bars, the left bar refers to the northern site and the right bar to the southern site. N = 3 transects. Error bars represent 1 ±SE. Transects were 50 m in length, and the area surveyed was 1 m either side of the transect, and 2 m above the transect.

Most black foot and yellow foot pāua (*Haliotis iris* and *Haliotis australis*) were recorded in around 0.5 – 3.5 m depths (Figure 30). Numbers of black foot pāua were stable through time at Kaikōura, and yellow foot pāua were abundant at the northern (rahui) site in 2021 (see Figure 27). There were higher numbers of both species at Okiwi Bay in 2020 and 2021 than in previous years. An apparent increase in black foot pāua at Waipapa Bay after 2017 was largely driven by the addition of a transect at Waipapa Bay South which had several pāua. A few yellow foot pāua were observed in 2020 and 2021 at Waipapa Bay after being virtually absent between 2017- 2019 (Figure 30).

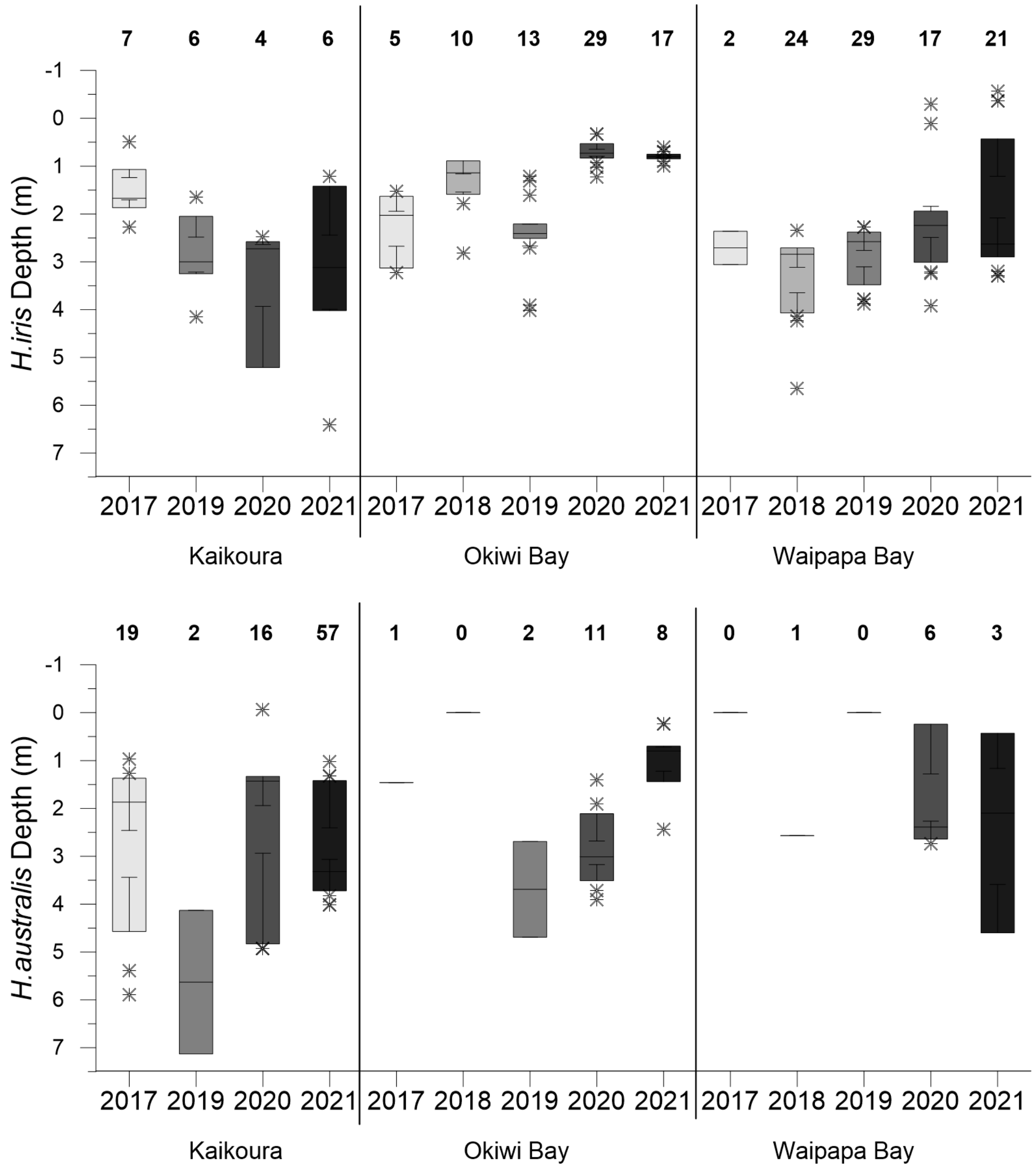

Figure 30: Box-whisker plots showing the depth distribution of *Haliotis iris* (black foot pāua, top) and *Haliotis australis* (yellow foot pāua, bottom) at each location through time Data from sites at each location were combined due to low numbers of pāua (n = 6 transects). Numbers of pāua encountered are at the top of each plot.

4. DISCUSSION

This research is a continuation of the previous work done on the Kaikōura Earthquake Marine Recovery Project (Alestra et al. 2019) and provides an updated assessment on the state of the uplifted intertidal and subtidal rocky reefs along the Kaikōura coastline. Findings from the most recent surveys show that long-lasting impacts of the earthquake are still evident even after four years of recovery time. In intertidal areas, only the low tidal zone has shown appreciable re-establishment of habitat-forming algae. The mid- and upper tidal zones are largely barren of algae, except for some small, short-lived ephemeral species such as sea lettuce. Limpets dominate some sites, which no doubt contributes to the paucity of even short-lived ephemeral algae in the mid and upper tidal zones. These zones have continuing high temperatures during summer, often exceeding 40ºC, which is beyond the thermal tolerance of large algae. The recruitment of desiccation-resistant *Hormosira banksii* that we have seen on the lower margins of the mid-tidal zone in some sites, such as Wairepo Reef Kaikōura, where it was dominant for many decades, is burned off during the hot days of summer. This perennial fucoid has therefore become more of a seasonal ephemeral species, and it has not become abundant enough to support its former lush communities. Bull kelp, *Durvillaea poha/antarctica*, remains sparse on most reefs, mainly due to poor population connectivity, little recruitment, and pre-emptive competition with dense red algae and other large brown algae that have covered its normal zone of dominance. There has been continued erosion of the soft sedimentary reefs, which also reduces effective recruitment of large algae because of unstable rock surfaces on which to attach. The movement of gravel and sand along the coastline has not only scoured parts of the low intertidal zone, such as at Waipapa, but has alternately buried and exposed inshore rocks subtidally affecting algal recruitment and persistence. Experimental outplants of juvenile fucoid and laminarian algae have also been greatly affected by sand and gravel. There has been some reduction in red algal cover in the shallow portions of reefs, and a returning dominance of large brown algae in some areas. Nevertheless, some previously abundant algal stands have become sparser and more fragmented. Altogether, there is no doubt that the degree of initial coastal uplift has continued to affect recovery of these reefs. Uplifted subtidal rock did not replace the vast intertidal platforms lost in the earthquake, and there remains an overall deficit of algal cover compared to pre-earthquake conditions. Concurrent investigations focussing on processes will help clarify the changes in food web structure along this coastline and the consequences of a massive loss in standing stock of algae and its primary productivity.

4.1. Intertidal rocky reefs

Intertidal reefs are still undergoing numerous stressors from the earthquake. The most prominent ones are continued erosion of soft sedimentary rocks, significant movement of sand and gravel that both scours and buries rocky reef, a changed intertidal reef topography, which is now near-vertical compared to the wide intertidal platforms covered in algae pre-earthquake, and the prolonged high temperatures experiences in the mid and upper intertidal zones, which effectively preclude annual survival of any new recruitment that might have occurred during the cooler months. These are essentially non-manageable stressors that are part of the continuing physical and ecological re-configuration of the rocky reefs along 130 km of coastline.

Large brown algal species, primarily fucoids and especially *Carpophyllum maschalocarpum*, and *Cystophora* spp., are steadily increasing at most low and medium uplift sites, although far less so at high uplift sites. The exception is the bull kelp *Durvillaea poha/antarctica*, which remains far below its original cover at most sites. As the extensive experimental work of Schiel (2019, and unpublished) has shown, bull kelp take in the order of 8-10 years to recover from clearances of only a few square meters, even when surrounded by reproductive adults. They do not recruit well into red algal turfs, and they have relatively short dispersal distances as propagules. Combined with a short reproductive season of only around 2 months, this yields a relatively low probability of effective recruitment even by drift plants. *Durvillaea* is also known to be greatly affected by grazing from butterfish (*Odax pullus*) (Taylor and Schiel 2005), which has also affected subtidal algae in the recovering areas around Kaikōura.

The traction and pre-emptive competition for space from red algae seems to be diminishing slowly through time. As red algae decrease, there has been some expansion of large brown algae. The initial shift to red algae coincided with the severe marine heat wave elevated air temperatures in the summer of 2017-2018. Brown algae declined precipitously after this, and remaining populations of bull kelp were hit particularly hard. Recovery of large brown algae has been a slow process. However, it is clear that at least the low zone in low- and medium uplift sites are showing some recovery. Unfortunately, these zones are now very narrow topographically, compared to the vast intertidal platforms pre-earthquake, so there remains a large biomass deficit along the coastline. This has likely had impacts on primary productivity and the carbon sources of the coastal food web. Both of these are being examined in related studies.

As a concurrent study to this monitoring, it is worth noting that pāua (*Haliotis iris*) populations are recovering well. Recruitment seems to be occurring annually at most sites under investigation and growth rates are also good. There is a large biomass of pāua of >125 mm (shell length) in the accessible low intertidal zone along much of the coastline. In fact, these numbers of large pāua have rarely, if ever, been seen in the intertidal zones of coastal southern New Zealand since the early 1970s. These pāua are those that were propelled upwards by the earthquake and others that grew to harvestable size since the ban on fishing. It will be interesting to see how long these last after the recreational fishery is opened (which is expected to occur in late 2021).

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 the emergence of bare rock at some sites (Alestra et al. 2019).

The 2019 - 2021 surveys, 2.5 to 4.5 years after the earthquake, showed minor recovery of seaweeds and invertebrates at Waipapa Bay. In particular, there were increases in encrusting red algae and corallines, and recruitment of red and brown foliose algae. Sessile invertebrates such as sponges, and ascidians also increased in cover. Despite this recovery, extensive areas of bare rock were still present. At Kaikōura Peninsula and Okiwi Bay sites, the most striking difference in 2019 was a decrease in cover of large brown algae. This was primarily due to declines in *Marginariella boryana* and *Lessonia variegata*. While large brown algal cover increased in 2020 and 2021 at Kaikōura sites, cover remained low at Okiwi Bay sites. This decrease in large brown algae has also been observed at other sites included in the original Kaikōura Earthquake Marine Recovery Project (Alestra et al. 2019), which were recently re-sampled as part of our MBIE research. Reasons for this decline are unclear, but it may be due to a combination of effects of intense marine heatwaves of 2018, altered wave dynamics as a result of the uplift, extreme wave events, and/or scour due to movement of cobble, gravel or sand substrates.

There were shifts in sand/gravel distribution at Waipapa Bay and Okiwi Bay South. 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. We have observed small recruits of large brown algae, but only of some species (*Landsburgia quercifolia* and *Carpophyllum maschalocarpum*). These recruits were very small and therefore did not contribute to changes in the cover of large brown algae.

4.3 Conclusions

The surveys presented in this report provide an updated assessment of the state of nearshore reef communities along the uplifted coastline. This work augments an extensive body of information that had never been previously available for this region. The data generated in this report and related studies has fed into public information and has helped underpin the concerns and management options for tāngata whenua and a wide range of user groups, including recreational harvesters, commercial fishers, tourist operators, citizens' groups, and local residents. These reports have been the basis of numerous end-user interactions (around 400 during the past year) from the research team, including many public talks. The complexity of impacts, recovery and the issues involved in human usages of the large coastline affected by the earthquake have had considerable public interest. By understanding the continuing natural stressors affected recovery of the coastal ecosystem, it puts into focus the manageable stressors that have accrued in this altered ecosystem. Damaged catchments, pedestrian and vehicular traffic, damage to coastal dune reformation, effects on recovering species, and potential opening of harvesting and the pāua fishery, have all come into focus as we collectively work through the issues of the resilience of the coastal ecosystem and sustainability of activities. This monitoring work has provided an invaluable compendium of data and understanding to underpin the process-oriented work in other related research, such as the MBIE coastal recovery programme. Together they will continue to provide a context and baseline for near-future issues of fisheries, usage, and coastal recovery.

6. References

Alestra, T.; Gerrity, S.; Dunmore, R.A.; Marsden, I.D.; Pirker, J.G.; Schiel, D.R. (2019). Rocky reef impacts of the Kaikōura earthquake: quantification and monitoring of nearshore habitats and communities. *New Zealand Aquatic Environment and Biodiversity Report No. 212*. 120 p.

Alestra, T.; Gerrity S.; Dunmore R.A.; Schiel, D.R. (2020). Rocky reef impacts of the Kaikōura earthquake: extended monitoring of nearshore habitats and communities – Year 1 results. Prepared for the Ministry for Primary Industries. *New Zealand Fisheries Assessment Report 2020/01*. 40 p.

Alestra, T.; Gerrity, S.; Dunmore, R.A.; Crosset, D.; Orchard, S.; Schiel, D.R. (2021). Rocky reef impacts of the Kaikōura earthquake: extended monitoring of nearshore habitats and communities to 3.5 years. *New Zealand Aquatic Environment and Biodiversity Report No. 253*. 46 p.

Anderson, M.J.; Gorley, R.N.; Clarke, R.K. (2008). PERMANOVA+ for PRIMER: Guide to software and statistical methods. Bretonside Copy, Plymouth, UK

Anderson, M.J.; Willis, T.J. (2003). Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. *Ecology 84(2):* 511-525.

Barrientos, S.E.; Ward, S.N. (2020). The 1960 Chile earthquake: inversion for slip distribution from surface deformation. *Geophysics Journal International 103*: 589-598.

Castilla, J.C. (1988). Earthquake-caused coastal uplift and its effects on rocky intertidal kelp communities. *Science 242(4877)*: 440–443.

Castilla, J.C.; Manríquez, P.H.; Camaño, A. (2010). Effects of rocky shore coseismic uplift and the 2010 Chilean mega-earthquake on intertidal biomarker species. *Marine Ecology Progress Series 418*: 17–23.

Castilla, J.C.; Oliva, D. (1990). Ecological consequences of coseismic uplift on the intertidal kelp belts of *Lessonia nigrescens* in central Chile. *Estuarine, Coastal and Shelf Science 31(1)*: 45–56.

Clark, K.J.; Nissen, E.K.; Howarth, J.D.; Hamling, I.J.; Mountjoy, J.J.; Ries, W.F.; Jones, K.J.; Goldstien, S.; Cochran, U.A.; Villamor, P.; Hreinsdóttir, S.; Litchfield, N.J.; Mueller, C.; Berryman, K.R.; Strong, D.T. (2017). Highly variable coastal deformation in the 2016 Mw7.8 Kaikōura earthquake reflects rupture complexity along a transpressional plate boundary. *Earth and Planetary Science Letters 474*: 334–344.

Clarke, K.R.; Warwick, R.M. (2001) Change in marine communities: An approach to statistical analysis and interpretation (2nd edition). PRIMER-E Ltd., Plymouth, UK

Gerrity, S.; Alestra, T.; Fishman, H.S.; Schiel, D.R. (2020). Earthquake effects on abalone habitats and populations in southern New Zealand. *Marine Ecology Progress Series 656*: 153–161. DOI: https://doi.org/10.3354/meps13458

Jaramillo, E.; Dugan, J.E.; Hubbard, D.M.; Melnick, D.; Manzano, M.; Duarte, C.; Campos, C.; Sanchez, R. (2012). Ecological implications of extreme events: footprints of the 2010 earthquake along the Chilean coast. *PloS One 7(5)*: e35348.

Kruskal, J.B.; Wish, M. (1978). Multidimensional scaling. Sage Publications, Beverley Hills, California, USA.

Lilley, S.A.; Schiel, D.R (2006). Community effects following the deletion of a habitat-forming alga from rocky marine shores. *Oecologia 148 (4)*: 672681.

Schiel, D.R. (2019). Experimental analyses of diversity partitioning in southern hemisphere algal communities. *Oecologia*, *190* (1),179-193.

Schiel, D.R.; Alestra, T.; Gerrity, S.; Orchard, S.; Dunmore, R.A.; Pirker, J.G.; Lilley, S.A.; Tait, L.W.; Thomsen, M.S. (2019). The Kaikōura earthquake in southern New Zealand: loss of connectivity of marine communities and the necessity of a cross-ecosystems perspective. *Aquatic Conservation: Marine and Freshwater Ecosystems 29 (9)*: 1520–1534.

Schiel, D.R.; Gerrity, S.; Alestra, T.; Pirker, J.G.; Marsden, I.D.; Dunmore, R. A.; Tait, L.W.; South, P.M.; Taylor, D.I.; Thomsen, M.S. (2018). Kaikōura earthquake: Summary of impacts and changes in nearshore marine communities. *In*: Shaky Shores – Coastal impacts & responses to the 2016 Kaikōura earthquakes. *New Zealand Coastal Society, Special Publication 3*. 44 p.

Schiel, D.R.; Lilley, S.A. (2011). Impacts and negative feedbacks in community recovery over eight years following removal of habitat-forming macroalgae. *Journal of Experimental Marine Biology and Ecology 407*: 108–115.

Taylor, D.I.; Schiel, D.R. (2005). Self-replacement and community modification by the southern bull kelp Durvillaea antarctica. *Marine Ecology Progress Series*, *288*, 87-102.

Tait, L.W.; Schiel, D.R. (2011). Legacy effects of canopy disturbance on ecosystem functioning in macroalgal assemblages. *PLOS ONE 6*: e26986

Thomsen, M.S.; Metcalfe, I.; Siciliano, A.; South, P.M.; Gerrity, S.; Alestra, T.; Schiel, D.R. (2020). Earthquake-driven destruction of an intertidal habitat cascade. *Aquatic Botany 164*: 103217.

Thomsen, M.S.; Mondardini, L.; Alestra, T.; Gerrity, S.; Tait, L.; South, P.M.; Lilley, S.A.; Schiel, D.R. (2019). Local extinction of Bull Kelp (*Durvillaea* spp.) due to a marine heatwave. *Frontiers in Marine Science 6*: 1-10.

7. APPENDICES

Appendix 1: 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) in November 2019. For each test, the taxa contributing to up to 90% of the dissimilarity between groups are listed.

A) Post-earthquake high zone

	Low-uplift vs Medium-uplift – Average dissimilarity = 90.32				
Taxa	Average abundance Low-uplift	Average abundance Medium-uplift	Average dissimilarity	Contribution %	Cumulative contribution%
Pyropia spp.	8.08	0.75	39.89	44.16	44.16
Ulva spp.	1.36	0.01	11.39	12.61	56.77
Limnoperna pulex	0.01	0.22	8.94	9.89	66.66
Enteromorpha spp.	0.15	0.02	6.54	7.24	73.90
Encrusting algae	0.18	0.10	4.67	5.17	79.07
Mytilus galloprovincialis	0.03	0.07	3.41	3.78	82.84
Coralline paint	0.11	0.06	3.13	3.47	86.31
Chamaesipho columna	0.04	0.06	2.97	3.29	89.60
Ectocarpus spp.	0.15	0.01	2.19	2.42	92.02

	Control vs Medium-uplift – Average dissimilarity = 91.89				
Taxa	Average abundance Control	Average abundance Medium-uplift	Average dissimilarity	Contribution %	Cumulative contribution%
Pyropia spp.	1.86	0.75	18.97	20.65	20.65
Chamaesipho columna	2.98	0.06	16.29	17.72	38.37
Coralline turf	1.91	0.01	14.97	16.29	54.66
Ulva spp.	0.84	0.01	8.59	9.35	64.01
Limnoperna pulex	0.36	0.22	6.85	7.46	71.47
Enteromorpha spp.	0.26	0.02	4.50	4.90	76.36
Encrusting algae	0.17	0.10	4.18	4.54	80.91
Coralline paint	0.26	0.06	3.81	4.14	85.05
Ceramium spp.	0.31	0.00	2.81	3.06	88.11
Aulacomya maoriana	0.06	0.01	2.41	2.63	90.73

Taxa	Control vs High-uplift – Average dissimilarity = 93.41				
	Average abundance Control	Average abundance High-uplift	Average dissimilarity	Contribution %	Cumulative contribution%
Pyropia spp.	1.86	0.87	16.05	17.19	17.19
Chamaesipho columna	2.98	0.04	15.87	16.99	34.18
Coralline turf	1.91	0.02	15.07	16.14	50.31
Ulva spp.	0.84	0.09	9.59	10.26	60.58
Coralline paint	0.26	0.23	5.67	6.07	66.65
Limnoperna pulex	0.36	0.08	5.66	6.06	72.71
Encrusting algae	0.17	0.19	4.85	5.19	77.90
Enteromorpha spp.	0.26	0.01	4.52	4.84	82.74
Ceramium spp.	0.31	0.03	3.25	3.48	86.22
Aulacomya maoriana	0.06	0.04	3.19	3.42	89.64
Mytilus galloprovincialis	0.07	0.12	2.95	3.15	92.79

B) Post earthquake mid zone

Taxa	Control vs Low-uplift – Average dissimilarity = 93.00				
	Average abundance Control	Average abundance Low-uplift	Average dissimilarity	Contribution %	Cumulative contribution%
Coralline turf	33.00	0.44	31.43	33.80	33.80
Hormosira banksii	15.94	0.09	16.27	17.50	51.29
Ulva spp.	3.95	10.78	10.50	11.29	62.58
Gelidium caulacantheum	6.25	0.15	6.44	6.92	69.50
Pyropia spp.	0.00	4.54	3.88	4.17	73.68
Ralfsia verrucosa	0.00	2.70	2.68	2.89	76.56
Coralline paint	1.78	1.58	2.64	2.84	79.40
Cystophora scalaris	2.00	0.00	2.59	2.79	82.19
Encrusting algae	0.51	1.76	1.95	2.10	84.29
Carpophyllum maschalocarpum	1.43	0.13	1.81	1.94	86.24
Gigartina lanceolata	1.32	0.00	1.62	1.74	87.98
Echinothamnion spp.	1.41	0.00	1.57	1.68	89.67
Cystophora torulosa	1.10	0.03	1.40	1.51	91.17

	Control vs Medium-uplift – Average dissimilarity = 96.21				
Taxa	Average abundance Control	Average abundance Medium-uplift	Average dissimilarity	Contribution %	Cumulative contribution%
Coralline turf	33.00	0.23	35.60	37.01	37.01
Hormosira banksii	15.94	0.00	18.64	19.38	56.38
Gelidium caulacantheum	6.25	0.03	7.55	7.85	64.24
Coralline paint	1.78	5.34	6.08	6.32	70.56
Ulva spp.	3.95	0.71	5.30	5.51	76.07
Cystophora scalaris	2.00	0.01	3.04	3.16	79.23
Carpophyllum maschalocarpum	1.43	0.32	2.19	2.28	81.51
Echinothamnion spp.	1.41	0.22	1.94	2.02	83.53
Gigartina lanceolata	1.32	0.00	1.89	1.97	85.50
Encrusting algae	0.51	1.58	1.84	1.91	87.41
Cystophora torulosa	1.10	0.00	1.63	1.69	89.11
Chamaesipho spp.	0.04	1.25	1.56	1.62	90.73

C) Post earthquake Low zone

	Low-uplift vs Medium-uplift – Average dissimilarity = 67.44				
Taxa	Average abundance Low-uplift	Average abundance Medium-uplift	Average dissimilarity	Contribution %	Cumulative contribution%
Carpophyllum maschalocarpum	42.45	15.36	11.78	17.47	17.47
Coralline paint	39.58	35.24	10.58	15.70	33.17
Coralline turf.	7.55	9.10	3.69	5.47	38.64
Echinothamnion spp.	1.30	9.86	3.54	5.26	43.90
Durvillaea willana	7.02	3.84	3.27	4.85	48.75
Durvillaea poha	2.38	6.76	3.05	4.53	53.28
Encrusting algae	7.91	2.13	2.73	4.05	57.32
Marginariella boryana	2.83	6.94	2.71	4.02	61.34
Halopteris spp.	6.12	1.56	2.38	3.53	64.87
Polysiphonia mullerii	0.32	6.61	2.18	3.23	68.10
Ulva spp.	3.01	3.68	1.94	2.88	70.99
Red turf/filaments	1.53	4.54	1.88	2.79	73.77
Pterocladia lucida	1.75	4.51	1.77	2.62	76.39
Cystophora scalaris	3.81	1.21	1.74	2.58	78.98
Lessonia variegate	1.77	3.74	1.61	2.39	81.37
Gelidium microphyllum	0.78	3.50	1.30	1.93	83.29
Landsburgia quercifolium	0.85	2.53	1.02	1.51	84.81
Chondria macrocarpa	1.20	2.06	0.89	1.32	86.13
Gigartina Lanceolata	0.05	2.56	0.88	1.30	87.42
Cladhymenia spp.	1.34	1.21	0.74	1.09	88.52
Macrocystis pyrifera	1.77	0.00	0.64	0.95	89.47
Ectocarpus spp.	0.90	0.82	0.59	0.88	90.34

	Low-uplift vs High-uplift – Average dissimilarity = 85.41				
Taxa	Average abundance Low-uplift	Average abundance High-uplift	Average dissimilarity	Contribution %	Cumulative contribution%
Carpophyllum maschalocarpum	42.45	7.37	20.21	23.66	23.66
Coralline paint	39.58	15.67	17.89	20.95	44.61
Polysiphonia mullerii	0.32	22.73	8.76	10.26	54.87
Encrusting algae	7.91	1.49	4.19	4.90	59.77
Coralline turf	7.55	0.02	3.69	4.32	64.09
Echinothamnion spp.	1.30	8.87	3.60	4.22	68.31
Halopteris spp.	6.12	0.38	3.45	4.04	72.35
Durvillaea willana	7.02	0.00	3.09	3.62	75.97
Ulva spp.	3.01	2.48	2.55	2.98	78.95
Cystophora scalaris	3.81	0.00	2.25	2.63	81.59
Marginariella boryana	2.83	0.00	1.30	1.53	83.11
Chondria macrocarpa	1.20	1.71	1.08	1.26	84.38
Cladhymenia spp.	1.34	1.51	1.04	1.21	58.59
Durvillaea poha	2.38	0.00	0.96	1.13	86.72
Glossophora kunthii	0.79	1.46	0.93	1.09	87.80
Macrocystis pyrifera	1.77	0.00	0.92	1.07	88.88
Pterocladia lucida	1.75	0.35	0.90	1.05	89.93
Lessonia variegata	1.77	0.00	0.86	1.01	90.94

	Medium-uplift vs High-uplift – Average dissimilarity = 83.04				
Taxa	Average abundance Medium-uplift	Average abundance High-uplift	Average dissimilarity	Contribution %	Cumulative contribution%
Coralline paint	35.24	15.67	16.91	20.37	20.37
Polysiphonia mullerii	6.61	22.73	9.71	11.69	32.06
Carpophyllum maschalocarpum	15.36	7.37	9.11	10.97	43.03
Echinothamnion spp.	9.86	8.87	7.23	8.71	51.74
Coralline turf	9.10	0.02	4.56	5.49	57.22
Durvillaea poha	6.76	0.00	3.88	4.67	61.89
Marginariella boryana	6.94	0.00	3.35	4.04	65.93
Ulva spp.	3.68	2.48	2.49	3.00	68.93
Pterocladia lucida	4.51	0.35	2.25	2.71	71.65
Red turf/filaments	4.54	0.03	2.19	2.64	74.29
Durvillaea willana	3.84	0.00	2.04	2.46	76.75
Lessonia variegate	3.74	0.00	1.87	2.26	79.00
Gelidium microphyllum	3.50	0.00	1.63	1.96	80.96
Chondria macrocarpa	2.06	1.71	1.44	1.74	82.70
Landsburgia quercifolium	2.53	0.49	1.32	1.58	84.28
Gigartina lanceolate	2.56	0.33	1.30	1.56	85.84
Encrusting algae	2.13	1.49	1.22	1.47	87.31
Rhodymenia spp.	1.12	1.61	1.00	1.20	88.51
Cladhymenia spp.	1.21	1.51	0.94	1.13	89.64
Gigartina clavifera	1.49	0.03	0.84	1.01	90.65

Appendix 2: Subtidal site details with degree of uplift, location, maximum and average depth and number of quadrats used in analyses for each survey time.

									Number of quadrats used in analyses (>50% rock)				
							Max. depth (m)	Ave. depth (m)	Number of quadrats used in analyses (>50% rock)				
Site	**Transect**	**Uplift**	**Transect start**		**Transect end**				**2017**	**2018**	**2019**	**2020**	**2021**
Kaikōura North Rahui	T1	L	-42.4155	173.7089	-42.4153	173.7093	7.0	5.3	15		14	19	20
	T2	L	-42.413	173.7073	-42.4134	173.7072	7.0	4.5	20		20	20	20
	T3	L	-42.4135	173.7063	-42.4132	173.7065	5.7	2.0	20		20	20	20
Kaikōura South S2	T1	L	-42.4355	173.6921	-42.4356	173.6926	4.6	2.6	20		20	20	20
	T2	L	-42.4352	173.6929	-42.4351	173.6926	6.8	4.1	20		20	20	20
	T3	L	-42.4347	173.6926	-42.435	173.6931	7.3	5.6	19		20	20	20
Okiwi Bay North	T1	M	-42.2171	173.8726	-42.5209	173.509	5.5	3.9	20	20	20	20	20
	T2	M	-42.2178	173.8717	-42.218	173.872	4.2	2.4	20	20	20	20	20
	T3	M	-42.2181	173.8716	-42.2183	173.872	5.4	2.9	20	20	20	20	20
Okiwi Bay South	T1	M	-42.2189	173.8665	-42.2194	173.8665	4.1	2.1	18	20	20	20	19
	T2	M	-42.2189	173.869	-42.219	173.8696	3.8	2.2	12	19	17	20	19
	T3	M	-42.2191	173.8697	-42.2194	173.8701	5.4	3.3	19	20	20	20	18
Waipapa Bay North	T1	H	-42.2044	173.8794	-42.2045	173.8798	4.5	3.5	18	20	19	19	19
	T2	H	-42.205	173.8798	-42.205	173.8803	5.5	4.4	18	20	18	13	6
	T3	H	-42.2056	173.8796	-42.2057	173.8802	6.1	5.3	17	12	18	20	7
Waipapa Bay South	T1	H	-42.2092	173.8758	-42.2097	173.8758	2.8	1.7	6	5			
	T2	H	-42.2099	173.8762	-42.2103	173.8763	3.8	2.9	8	20	20	20	19
	T3	H	-42.2096	173.8774	-42.21	173.8778	4.9	3.6	11	14	7	20	14
	T1b	H								20	19	19	19