# Rocky reef impacts of the 2016 Kaikōura earthquake: extended monitoring of nearshore habitats and communities to 3.5 years. New Zealand Aquatic Environment and Biodiversity Report...

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# Rocky reef impacts of the 2016 Kaikōura earthquake: extended monitoring of nearshore habitats and communities to 3.5 years

New Zealand Aquatic Environment and Biodiversity Report No. 253

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**Alestra, T.; Gerrity, S.; Dunmore, R.A.; Crossett, D.; Orchard, S.; Schiel, D.R. (2021). Rocky reef impacts of the 2016 Kaikōura earthquake: extended monitoring of nearshore habitats and communities to 3.5 years.**

***New Zealand Aquatic Environment and Biodiversity Report No. 253.* 46 p.**

The 7.8 magnitude Kaikōura earthquake in November 2016 caused extensive uplift along approximately 130 km of the north-eastern coastline of the South Island of New Zealand. This resulted in widespread mortality of marine organisms and alteration to the community structure and, in many places, the integrity of intertidal and subtidal rocky reefs. The disturbance adversely affected important taonga and habitat-forming species, such as pāua (*Haliotis iris*) and bull kelp (*Durvillaea* spp.), prompting an emergency ban on harvesting shellfish and seaweeds that is still in place. This report describes the results of nearshore reef surveys done at long-term monitoring sites between 2.5 and 3.5 years after the earthquake to assess the community structure and trajectories of recovery of rocky reef communities. A major goal of this work is to provide detailed information for underpinning informed decisions about re-opening fishery closures. The sites were first surveyed in 2017 as part of the Ministry for Primary Industries (MPI) Kaikōura Earthquake Marine Recovery Package. The new results included in this report relate to the fifth and fourth rounds of intertidal and subtidal surveys, respectively. These include (i) intertidal surveys done in November 2019 at 16 sites along the coastline between Oaro and Cape Campbell, encompassing uplift levels between approximately 0 and 6 metres; and (ii) subtidal surveys at 6 sites (2 around the Kaikōura Peninsula and 4 north of Kaikōura, in the Okiwi Bay/Waipapa Bay area) in mid-2019 and mid-2020, encompassing uplift levels between approximately 0.7 and 6 metres.

The results of these recent surveys are presented in the context of previous surveys to give a clear indication of the status and recovery of rocky reef communities. The intertidal surveys showed that three years after the earthquake all uplifted reefs were still largely unvegetated, with diverse algal communities found only in the lowest tidal zone. High intertidal areas had limpets and occasional ephemeral algae but remain barren. Similarly, the mid-tide zone had grazing invertebrates, occasional ephemeral algae, and occasional small recruits of large brown algae such as *Hormosira banksii*, but these algae were burned off in the warmer months. In the low intertidal zone, the presence and abundance of habitat-forming large brown algae (primarily *Durvillaea* spp., *Carpophyllum maschalocarpum*, *Cystophora* spp., and *Marginariella boryana*) varied across uplift levels, with the greatest abundance at control and low-uplift (under 1 m) sites and the lowest abundance at high-uplift (up to 6 m) sites. The major noteworthy features of algal changes in the low intertidal zone were: (i) bull kelp canopy cover remained low at most sites. Their pre-earthquake abundance (as detected by the initial surveys of uplifted areas immediately post-earthquake) was high in most places; (ii) in many places, bull kelp was replaced by other large brown algae, primarily *Carpophyllum maschalocarpum*, but also a suite of other low-shore fucoids; and (iii) over the last survey period, there was replacement of large brown algae by fleshy red algae in many places, so their recovery has been poor. In fact, there was a negative relationship between the covers of large brown algae and fleshy red algae, which accounted for 10% of the variability in the abundance of large brown algae across all sites in November 2019. Pre-earthquake data show that algal communities at medium- and high-uplift sites were not dominated by fleshy red algae before the earthquake. Fleshy reds most likely benefitted from the high mortality of large brown algae following the earthquake and their widespread expansion is now precluding recruitment of large brown algae.

Coralline algae, which play an important role in the settlement and early survival of invertebrates such as pāua and cat's eye snails (*Lunella smaragda*), were abundant in the low tidal zone at most sites. In contrast to the slow-recovering large algae, broadcast-spawners, especially a suite of limpets (mostly

*Cellana* spp.), recruited heavily within a couple of years post-earthquake. Their abundance was unrelated to the degree of uplift but was highly variable among sites. Community patterns, taking account of all the species encountered and their abundances, still showed a clear separation among sites depending on their degree of uplift. This is a clear indication that 'recovery' to pre-earthquake conditions is far from complete.

Subtidally, there was some recovery of seaweeds and invertebrates at Waipapa Bay, the area with the highest uplift and most evident earthquake damage, but there were extensive areas of bare rock still present. There were two striking differences compared with our earlier post-earthquake surveys: (i) there was a decrease in large brown algae at some sites around the Kaikōura Peninsula and at Okiwi Bay. This decline may have been due to altered wave dynamics following the uplift, marine heatwaves, and/or scour due to movement of cobble, gravel, or sand substrates; (ii) in at least one site, there was a replacement of stands of large brown algae by fleshy red algae (similar to that seen in the low intertidal zone in some areas). This has resulted in considerable amounts of drifting red algae in shallow areas, which may prove to be beneficial as food for passive grazers such as pāua.

The physical habitats themselves have continued to change. Intertidal reefs and boulder fields, which mostly comprise soft sedimentary rock, are continuing to erode and break up. Gravel movement and accumulation were evident in both the intertidal and subtidal zones, sometimes infilling large areas of reef and burying resident organisms. Shifts in sand and gravel can delay the recovery of benthic communities by scouring rock surfaces and smothering organisms and are indicative of a very dynamic physical environment. Reef erosion is no doubt contributing to the poor recovery of benthic communities in many areas.

This and related studies are showing a clear picture of the difficulties in resilience and recovery after a cataclysmic event. Decades of small-scale disturbance experiments along the coast of the South Island have shown that recovery can be very slow. For example, clearances of several square meters of large brown algal canopies can take up to 8 years to regain their original cover, and even longer for full communities to return. 'Resilience' usually means a quick recovery to a previous state. This is clearly not the case along the earthquake coast. 'Recovery' also implies a return to a previous state. This has not yet occurred. The major impediments to recovery are continuing changes to reef integrity, especially erosion and gravel movement, and poor connectivity between large brown algal populations. This is especially true for bull kelp, which have a very limited reproductive season and only short-range propagule dispersal except through drifting, reproductive adults. A slow recovery was expected, and further changes to algal-dominated communities are anticipated over the next few years. The recovery of bull kelp populations will be a clear signal that a major pre-earthquake configuration has returned.

This research has been presented regularly to local community groups, iwi, the commercial pāua fishing industry, and resource managers to facilitate a re-opening strategy for the Kaikōura coast.

# 1. INTRODUCTION

The 2016 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, Gerrity et al. 2020, Thomsen et al. 2020). The Kaikōura coastline is home to numerous taonga species which support customary, recreational, and commercial fisheries. It is important to monitor the health of the wider ecosystem, including abundance of biogenic habitats and seaweed communities, in addition to stock assessments. Extensive field surveys were done 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, etc.). It also established a baseline to gauge successional sequences and recovery dynamics. In summary, the initial research programme found that the coastline had undergone significant changes in the structure and function of rocky intertidal and subtidal algal and invertebrate communities and was experiencing variable states of recovery. Even small changes in tidal elevation as a result of coastal uplift affected habitat-forming algae and invertebrate abundance. Nearly all intertidal algal and invertebrate taxa experienced reduced abundance in the months and years following the earthquake compared with pre-earthquake levels. Although the subtidal communities were less affected, there was a significant decrease in the abundance of large brown algae, and an increase in newly emerged bare rock. In both intertidal and subtidal zones, erosion and the presence of mobile substrata such as gravel and sand likely inhibited recovery at some sites. Despite these impacts, clear signs of post-earthquake reproduction, settlement, and recruitment of pāua and large brown algae were documented, suggesting some potential for recovery.

The work done as part of the Kaikōura Earthquake Marine Recovery Package assessed the initial responses of rocky reef systems up to 16 months following the earthquake (to March 2018). To monitor long-term recovery trajectories and better understand the outcomes of this catastrophic event, further intertidal and subtidal surveys were carried out in late 2018/early 2019 (described by Alestra et al. 2020) and between late 2019 and mid-2020 (described in this report). The objectives of this research extension were to continue monitoring for the original objectives of the 2017 contract:

**Overall objective**

1. To quantify the impact of the Kaikōura earthquake on rocky reef intertidal and subtidal fauna and either quantify, or establish long-term monitoring sites to quantify, the recovery from the earthquake in order to inform future marine management decisions."

**Specific objectives**

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 in order 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 and specifically refer to relevant South Island iwi (Te Rūnanga o Kaikōura and Te Tau Ihu), and local community

This report provides an updated assessment of the state of intertidal (up to 3 years post-earthquake) and subtidal rocky reef communities (up to 3.5 years post-earthquake). This information will provide a context for management decisions, in particular those regarding the re-opening strategy for shellfish (especially pāua, *Haliotis* spp.) and seaweed harvest, which has been proposed for late 2021. This work will also contribute to a very limited pool of long-term studies about post-earthquake recovery of coastal systems worldwide. Although coastal uplift of this scale is unprecedented, studies from Chile (Barrientos & Ward 1990, Castilla & Oliva 1990, Jaramillo et al. 2012, Castilla et al. 2010, Castilla 1988) have documented catastrophic effects of seismic disturbances to coastal ecosystems. These studies consistently show a suite of severe immediate impacts of coastal uplift on marine communities, followed by a long recovery period of several years. As well, numerous disturbance studies by our group have shown that even local-scale disturbances to algal canopies can take 8 years to recover (e.g., Lilley & Schiel 2006, Schiel & Lilley 2007, Tait & Schiel 2011). This research provides quantitative survey data to improve our understanding of complex recovery dynamics which follow coastal uplift.

These extended surveys also provide added baselines and references for other research underway. This 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*", MBIE, UOCX1704).

## 2. METHODS

### 2.1 Survey design

Intertidal and subtidal surveys were done at a set of sites divided across eight locations which have been monitored since the earliest round of post-earthquake surveys in mid-2017 (Alestra et al. 2019, Figure 1). Replicate sites within each location were separated by at least 500 m. These sites were originally selected to encompass the length of the earthquake-impacted coastline and represent different levels of uplift (Alestra et al. 2019). Following the uplift categorisation used in previous reports (Alestra et al. 2019, 2020), the sites are divided into four uplift groups on the basis of uplift information obtained from GNS Science (K. Clark, personal communication) and our own calculations (Orchard et al., unpublished data): 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, Figure 1). Recent calculations by Gerrity et al. (2020) showed that rocky reefs occupy 48 km of the total length of the earthquake-impacted coastline (c.130 km). Three of the uplift categories used as part of the uplift categorisation are represented and account for 39 km of rocky reef habitat, whereas only 2 km experienced uplift beyond 4 m (Figure 2).

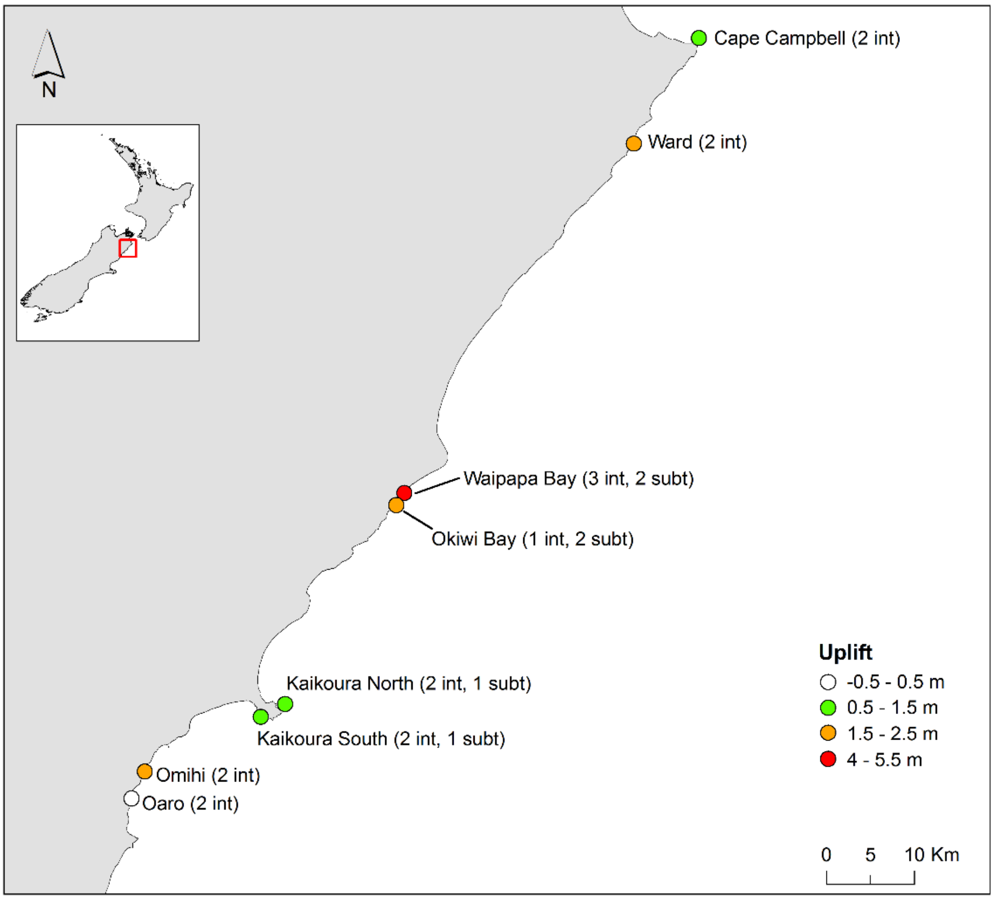


**Figure 1: The sites used for repeated intertidal and subtidal monitoring were divided across 8 locations displayed in this map. The information in parentheses indicates the number of intertidal (int) and subtidal sites (subt) per location. Different colours are used for the four uplift categories: control (white), low uplift (green), medium uplift (orange), high uplift (red).**

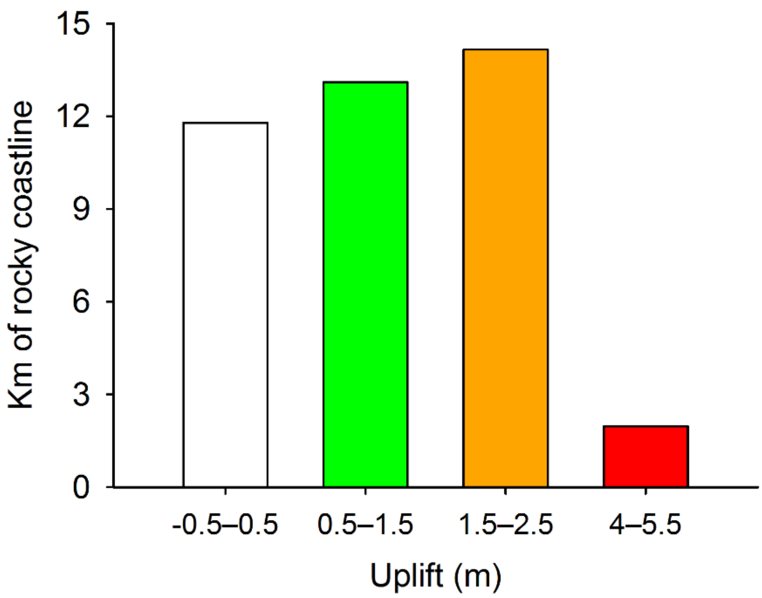


**Figure 2: Kilometres of rocky reef habitat that experienced uplift levels in line with our uplift characterisation system (white = control, green = low uplift, orange = medium uplift, red = high uplift).**

## 2.2 Intertidal community surveys

Intertidal community surveys were done in November 2019, three years after the Kaikōura earthquake, at 16 sites across 8 locations and encompassing the degrees of uplift (Figure 1). The methodology applied in previous post-earthquake sampling was used (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 (where present), and low tidal 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. Abundances were expressed as percentage cover for sessile organisms and as counts for mobile animals.

Data generated by the November 2019 surveys were analysed with univariate (ANOVA) and multivariate techniques (PERMANOVA) testing for differences among uplift groups and sites (Anderson et al. 2008, Clarke & Warwick 2001). 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.

In light of the opposite patterns of abundance of large brown and fleshy red algae in relation to uplift, the relationship between these two groups was explored three years after the earthquake. Using the November 2019 low zone data, a mixed-effects linear regression model was built, with the cover of large brown algae as a response variable and that of fleshy red algae as a fixed effect. Sites were treated as random effects to account for the spatial structure of the surveys and partition among- and within-site variability. Given the large variability in the data, a quantile regression model was used to perform the same analysis across five different quantiles and test whether the relationship remained stable across the entire range of the data. Waipapa Bay 1 was excluded from both regression analyses because both large brown and fleshy red algae were absent at this site three years after the earthquake.

## 2.3 Subtidal community surveys

Subtidal community surveys were done between May and July 2020, approximately 3.5 years after the Kaikōura earthquake, at 6 sites selected across 4 locations: Waipapa Bay, Okiwi Bay, and Kaikōura Peninsula North and South **(**Figure 1, Appendix 1). These sites encompassed degrees of uplift between 0.5 and 6 m. The low-uplift (around 0.6 m) sites 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, assessing algae, and sessile and mobile invertebrate community composition and abundances (Alestra et al. 2019). At each site:

- three 50 m transects perpendicular to the shore starting from the low tidal mark were re-surveyed. Subtidal transects were usually located directly offshore of intertidal transects and had been marked using GPS;
- substrate type and the abundance of all algae, sessile invertebrates, mobile invertebrates, and triplefin fish were recorded for 20 × 5 $m^2$ 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;
- the sizes of pāua (*Haliotis iris* and *Haliotis australis*) were measured using automated calipers that also recorded the depth of occurrence;

- the abundance of all large fish was recorded for 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);
- video footage was recorded 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 (63 out of 67) 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. SIMPER was used to identify taxa contributing to dissimilarity between communities. 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 0.6 with the PCO axes were displayed as vectors in the PCO plots.

# 3. RESULTS

## 3.1 Intertidal benthic community structure

Three years after the earthquake, intertidal reefs remained mostly bare, with algal communities surviving only in the lowest areas (Figure 3).

**Figure 3: Characteristic appearance of post-earthquake intertidal reefs, with extensive bare areas and algal cover confined to a narrow band in proximity of the low tide mark.**

As in previous years (Figures 4 A-D, F-I, K-N), 36 months after the earthquake most of the algal biomass was found in the post-earthquake low zone on uplifted reefs (Figure 4 O), whereas the high and the mid zones were generally devoid of algae (Figure 4 E, J). 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 can support diverse algal communities. However, under all levels of uplift, mid zone areas continued to be mostly unvegetated three years after the earthquake (Figure 4 J). In the low zone, algae were abundant in all uplift groups, and extensive covers of large brown algae characterised communities at the control and low-uplift sites, whereas fleshy red algae were more dominant at the medium- and high-uplift sites (Figure 4 O).

Multivariate analyses showed that in November 2019 there was a significant Uplift effect on benthic community composition in the post-earthquake high zone (Uplift: Pseudo-$F_{3,12}$ = 2.75, $P < 0.05$, Figure 5 A). However, these differences reflected occasional blooms in the abundance of ephemeral algae rather than a real earthquake legacy. In particular, the control and the low-uplift groups differed from the medium-uplift group because of higher covers of ephemeral green (*Ulva* spp.) and red algae (*Pyropia* spp.), respectively (Appendix 2 A). The 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-$F_{12,144}$ = 6.94, $P < 0.001$, Figure 5 A).

Long-lasting earthquake impacts were more evident in the post-earthquake mid zone, where abundant algal communities could only be found at the control sites (Appendix 2 B). As a result, the control group differed significantly from the low- and medium-uplift groups (Uplift: Pseudo-$F_{2,8}$ = 3.45, $P < 0.05$, Figure 5 B) and there was also significant variability in the structure of benthic communities among sites in the low- and medium-uplift groups (Pseudo-$F_{8,99}$ = 6.08, $P < 0.01$, Figure 5 B).

Finally, in the post-earthquake low zone, the composition of benthic communities was different in the low-uplift group (where large brown algae, particularly *Carpophyllum maschalocarpum*, were dominant) compared with the medium- and high-uplift groups (which were characterised by high covers of red algae: Uplift: Pseudo-$F_{3,12}$ = 1.93, $P < 0.01$, Figure 5 C, Appendix 2 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-$F_{12,144}$ = 10.08, $P < 0.01$, Figure 5 C). Waipapa Bay 1 was the only site almost completely devoid of algae in the low zone three years after the earthquake (Figure 5 C).

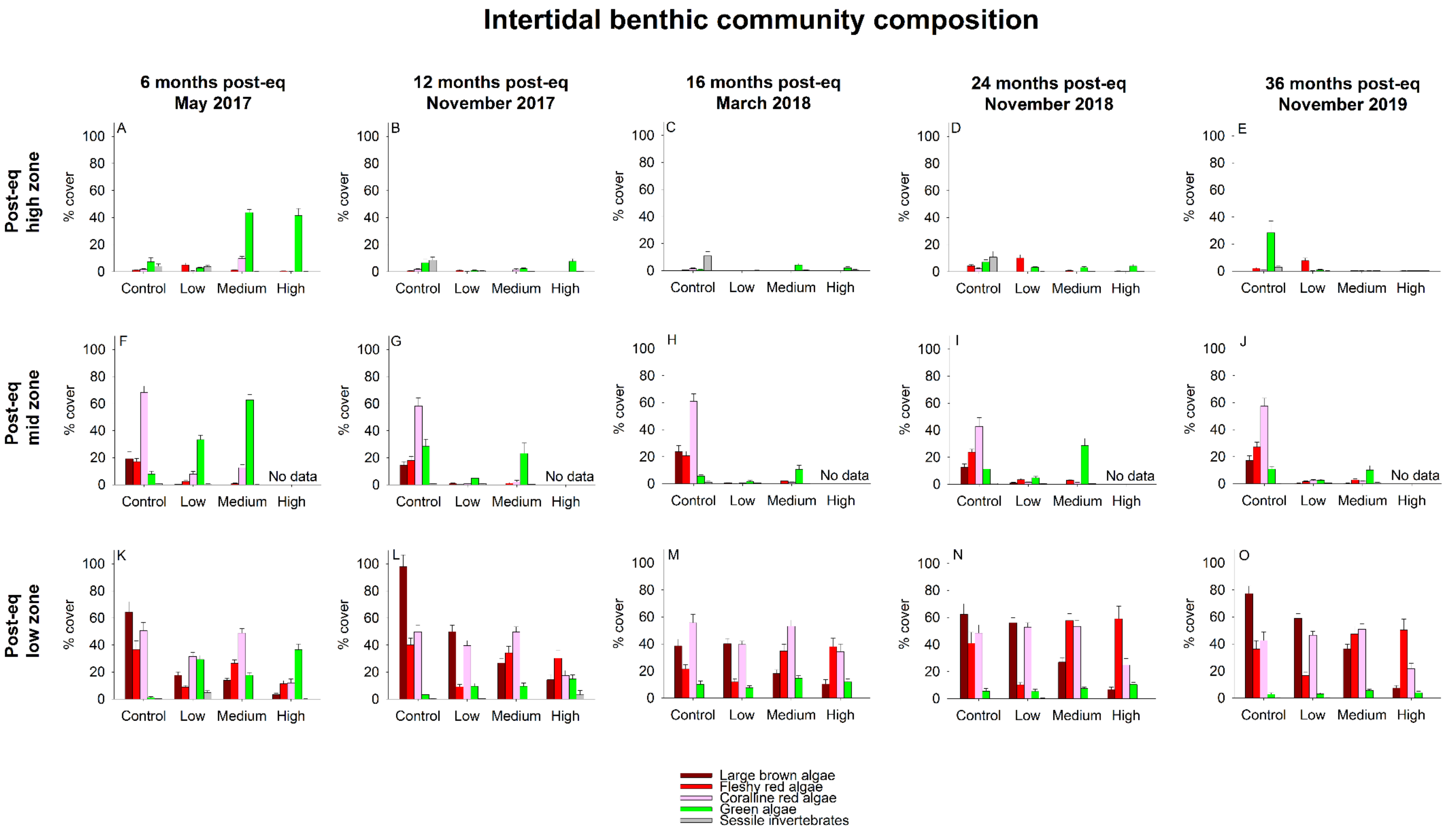


**Figure 4: Mean abundance of the main algal groups (+SE) and of sessile invertebrates across uplift levels 6, 12, 16, 24, and 36 months after the earthquake. Only the high and the low zone were sampled at high-uplift sites.**

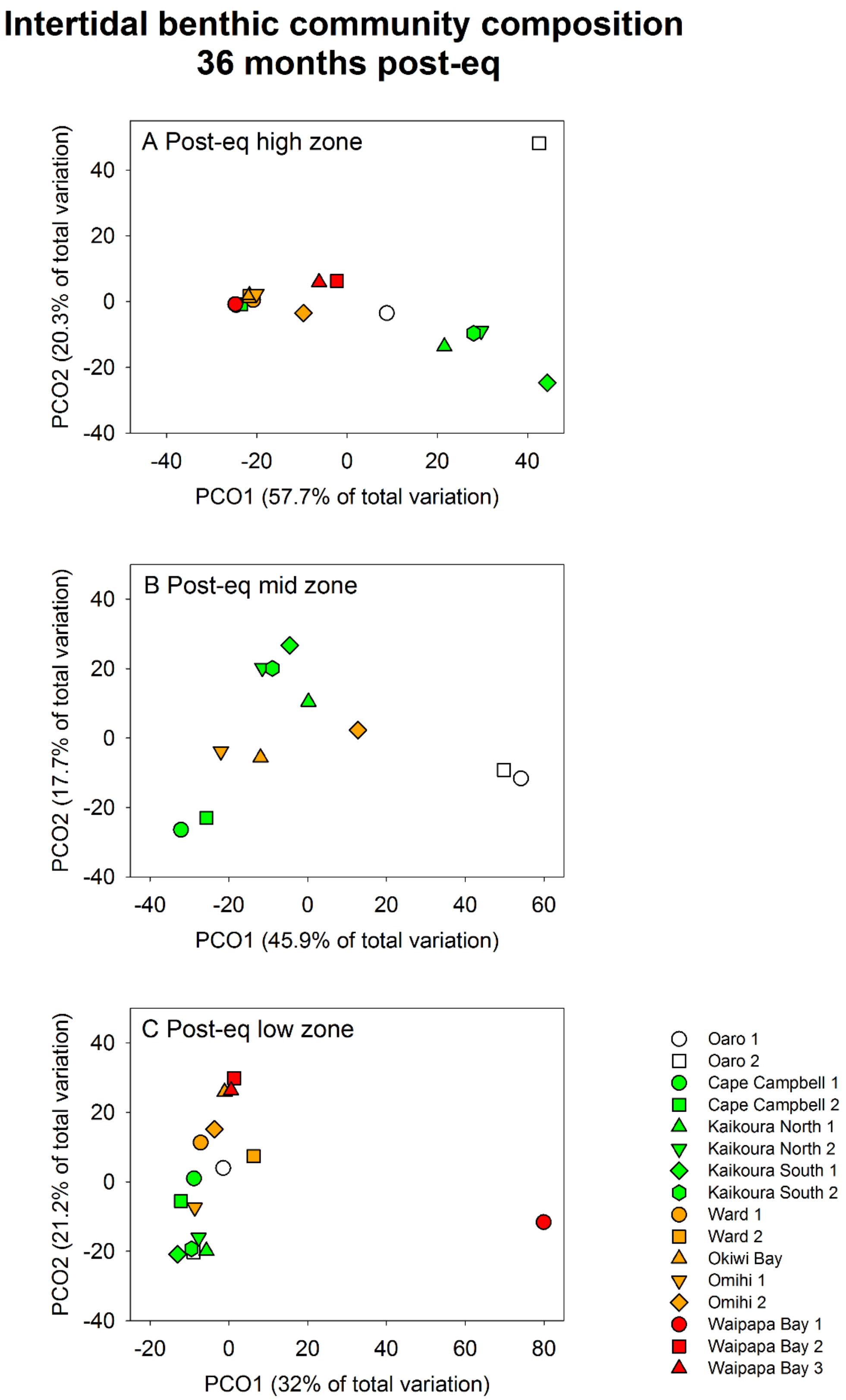


**Figure 5: Principal coordinates analysis (PCO) plots showing differences in the composition of benthic communities in the post-earthquake high (A), mid (B), and low zones (C) across sites with different degrees of uplift 36 months after the earthquake. The symbols represent the centroid of each site 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 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 three years after the earthquake, Sections 3.2.1, 3.2.2, and 3.2.4 describe the recovery of brown and red algae in the post-earthquake low zone. Section 3.2.3 describes the relationship between large brown algae and fleshy red algae. Section 3.2.5 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, *Carpophyllum maschalocarpum* was the most abundant species of large brown algae three years after the earthquake (about 25% average cover across all sites), followed by *Cystophora scalaris*, *Durvillaea* spp., and *Marginariella boryana* (which had average covers between 3 and 5% across all sites). In November 2019, the abundance of large brown algae decreased with increasing uplift across the four groups, which all differed from each other (Uplift: $F_{3,12} = 48.53$, $P < 0.001$, Figure 6). The control group had the highest average cover of large brown algae (77%), followed by the low-uplift group (59%), the medium-uplift group (36%), and the high-uplift group (7%). These results are in line with those from previous sampling dates, showing a steady increase in the abundance of large brown algae in the low- and medium-uplift groups, and a lack of recovery in the high-uplift group. The extended time series also shows that the low-uplift group has maintained abundances of large brown algae in line with pre-earthquake levels across two consecutive years, and that the control sites are recovering after high mortality during the hot summer and heat wave of 2017–2018 (Figure 6).

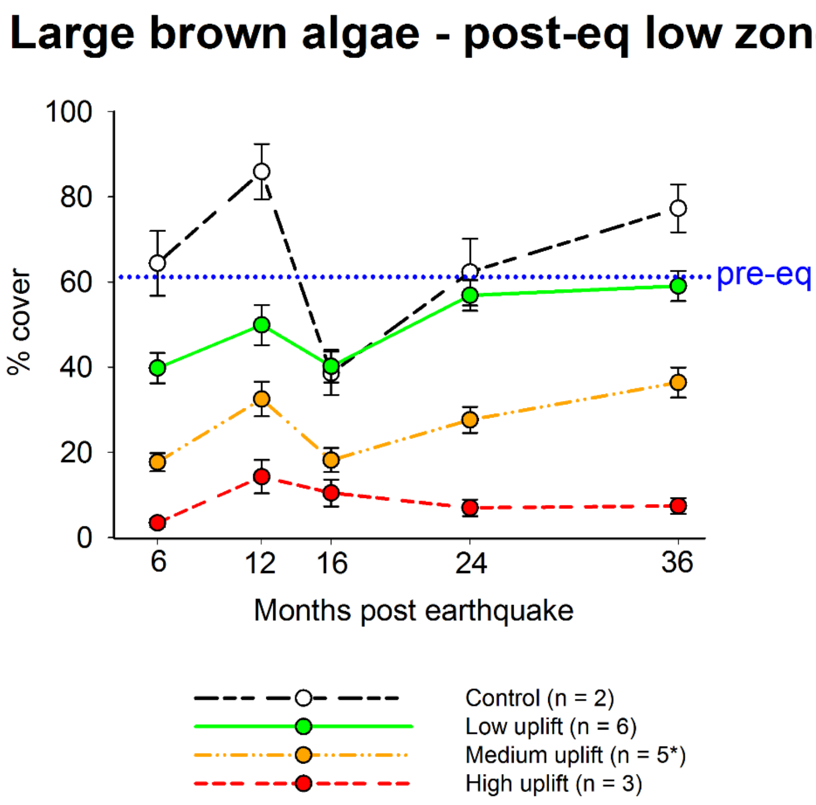


**Figure 6: Time series of the mean percentage cover (±SE) of large brown algae per square metre in the post-earthquake low zone across uplift levels. The dotted blue line indicates the average abundance of large brown algae in the pre-earthquake low zone across sites sampled in November 2016 (see Alestra et al. 2019). n = number of sites in each uplift group. *n = 5 after 12 months.**

Three years after the earthquake, the different sites within each group had a similar cover of large brown algae (Site: $F_{12,144}$ = 0.94, P = 0.51, Figure 7). All low-uplift sites had a cover of large brown algae greater than 48% (Figure 7 B), whereas all medium- and high-uplift sites were below this (Figure 7 C, D). As in previous sampling events, Waipapa Bay 1 was the only site where large brown algae were completely absent (Figure 7 D). Comparisons with pre-earthquake data show that the low-uplift sites have returned or are close to covers in line with pre-earthquake abundances (Figure 7 B), whereas medium- and high-uplift sites are still well below pre-earthquake levels (Figure 7 C, D).

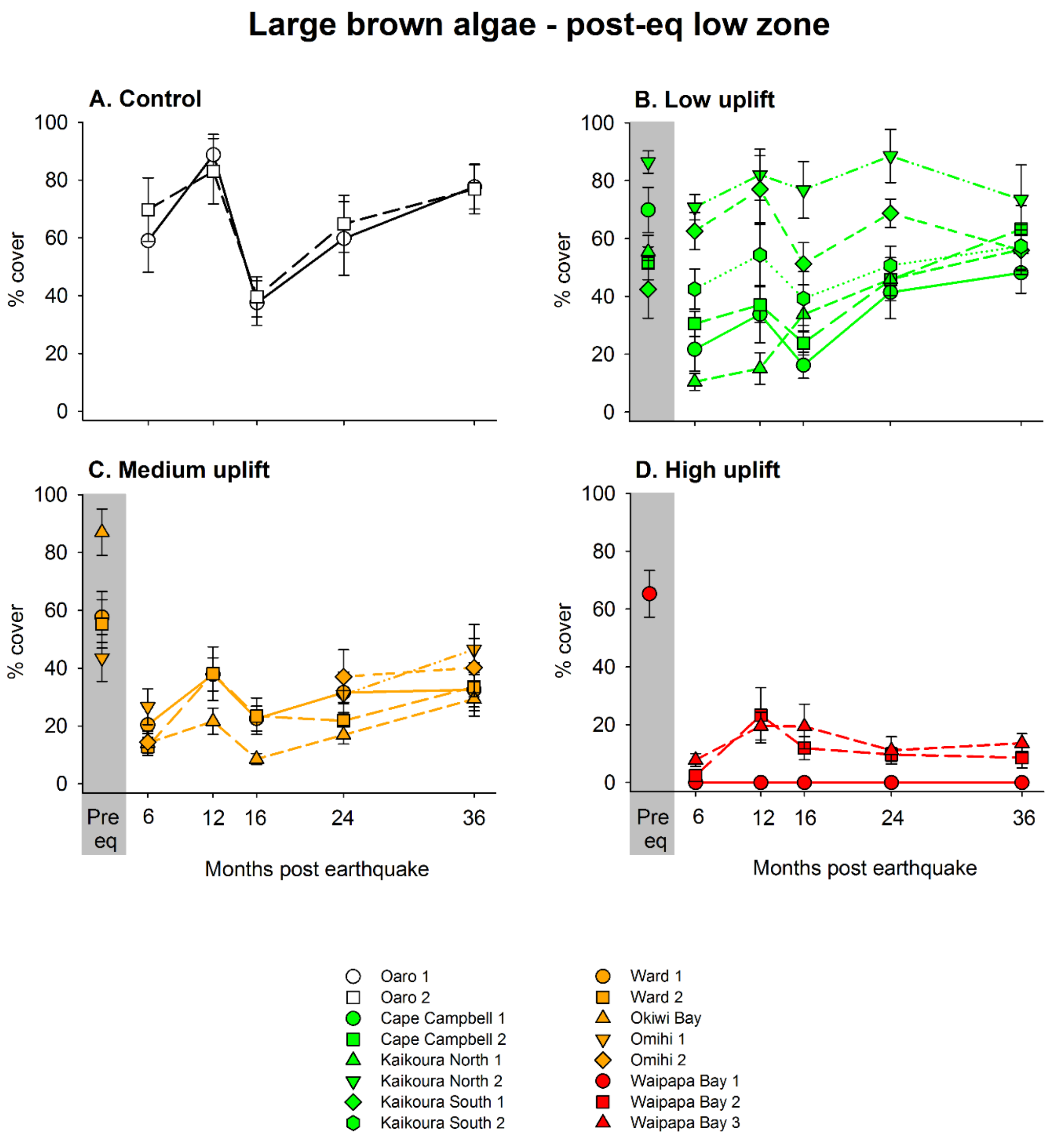


**Figure 7: Time series of the mean percentage cover (±SE) of large brown algae per square metre in the post-earthquake low zone across sites with no (A), low (B), medium (C), and high uplift (D). For the sites sampled in November 2016 (see Alestra et al. 2019), the average abundance of large brown algae 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 post-earthquake assemblages of large brown algae are no longer dominated by bull kelp (*Durvillaea* spp.) but instead other species of fucoids (primarily *Carpophyllum maschalocarpum*) represent the vast majority of large brown algal cover in November 2019 (Figures 8 and 9).

**Figure 8: Large brown algae assemblages dominated by bull kelp (*Durvillaea poha* in the top picture) and mixed fucoids (mainly *Carpophyllum maschalocarpum* in the bottom picture).**

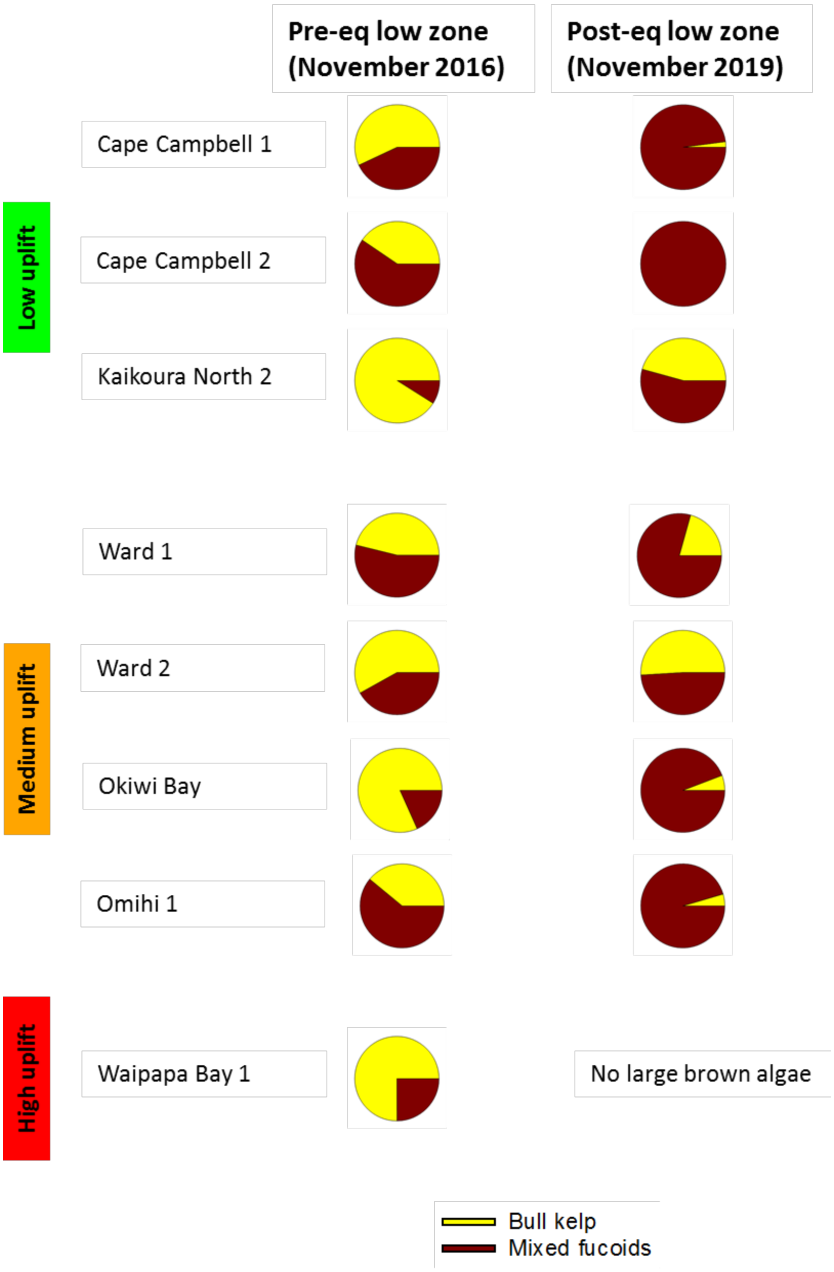


**Figure 9: Changes in the relative abundance of bull kelp (*Durvillaea* spp.) and other species of fucoids (mixed fucoids - primarily *Carpophyllum maschalocarpum*, *Cystophora scalaris, Marginariella boryana*, and *Lessonia variegata*) in the pre- (November 2016) and post-earthquake low zone (November 2019).**

Shifts in the composition of large brown algae assemblages resulted from a post-earthquake decline in the abundance of bull kelp combined with a simultaneous increase in the cover of mixed fucoids. Most sites had declining abundances of bull kelp following the earthquake (Figure 10), with no sign of recovery in the area of highest uplift, where bull kelp was completely extirpated (Figure 10 D). At the same time, the cover of mixed fucoids increased at almost all sites (Figure 11), particularly where there was no or low uplift (Figure 11 A and B). Three years after the earthquake, the abundance of mixed fucoids decreased with increasing uplift across the four groups (Uplift: $F_{3,12} = 23.4$, $P < 0.001$) and was highest in the control group (65%) and lowest in the high-uplift group (7%, Figure 11). Whereas for bull kelp, there were no significant differences among uplift levels in November 2019 (Uplift: $F_{3,10} = 0.86$, $P = 0.48$), although it remained absent in the high-uplift group, and its cover ranged between 9 and 12% in the others (Figure 10).

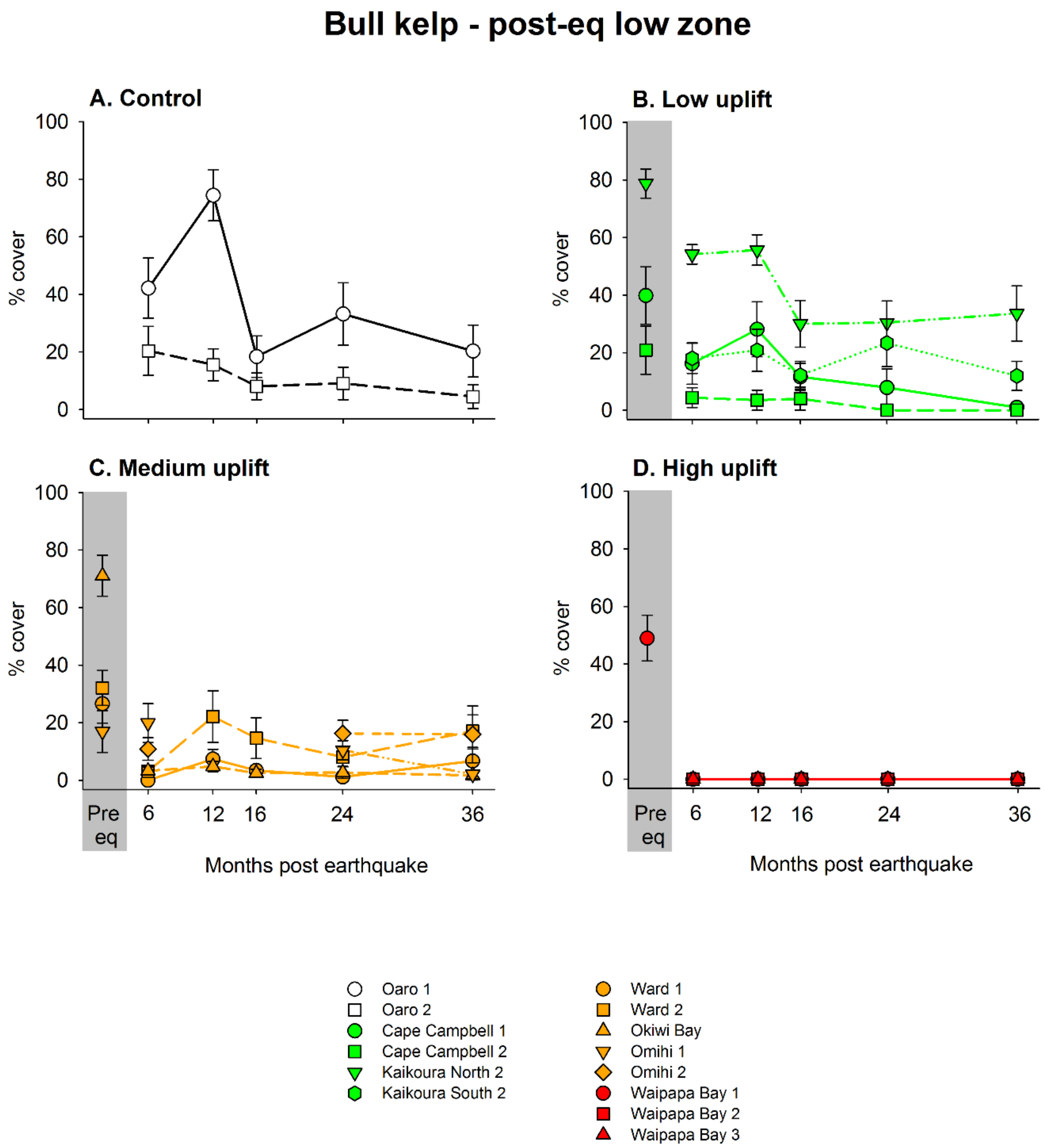


**Figure 10: Time series of the mean percentage cover (±SE) of bull kelp (*Durvillaea* spp.) per square metre in the post-earthquake low zone across sites with no (A), low (B), medium (C), and high uplift (D). For the sites sampled in November 2016 (see Alestra et al. 2019), the average abundance of 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.**

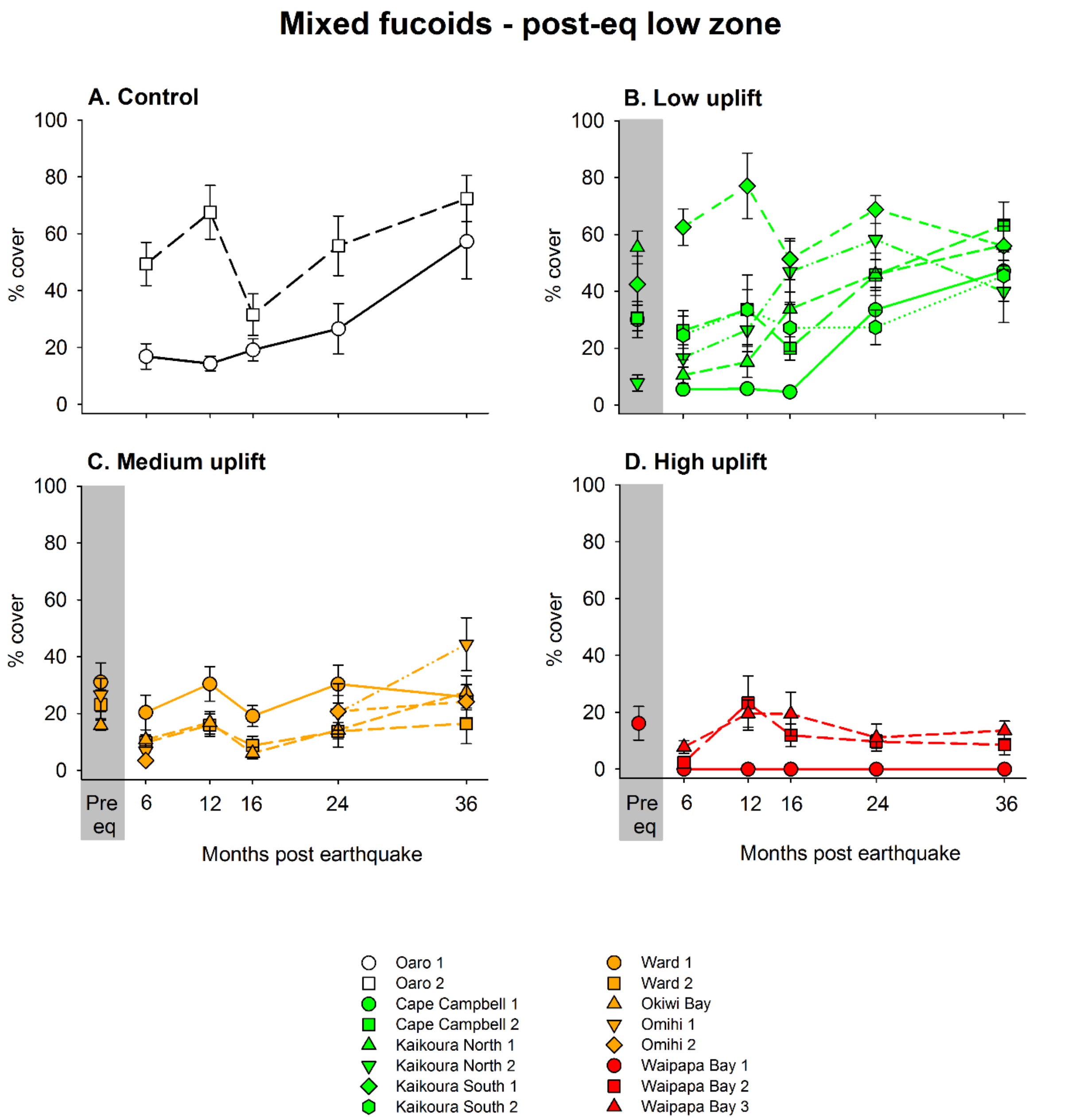


**Figure 11: Time series of the mean percentage cover (±SE) of mixed fucoids (primarily *Carpophyllum maschalocarpum*, *Cystophora scalaris*, *Marginariella boryana*, and *Lessonia variegata*) per square metre in the post-earthquake low zone across sites with no (A), low (B), medium (C), and high uplift (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

In November 2019, the medium- and high-uplift groups had the highest cover of fleshy red algae in the post-earthquake low zone (47% and 50%, respectively) and the low-uplift group had the lowest (17%, Figure 12), but the analysis could not detect significant differences among uplift groups (Uplift: $F_{3,12} = 1.93$, $P = 0.18$) because these were outweighed by the large variability among sites within all groups ($F_{12,144} = 8.15$, $P < 0.001$, Figure 13). These patterns are in line with those of previous years, with high abundances of fleshy red algae in areas with uplift between 1.5 and 5.5 m, although their cover did not increase as steadily between 2018 and 2019 at many medium- and high-uplift sites (Figure 13).

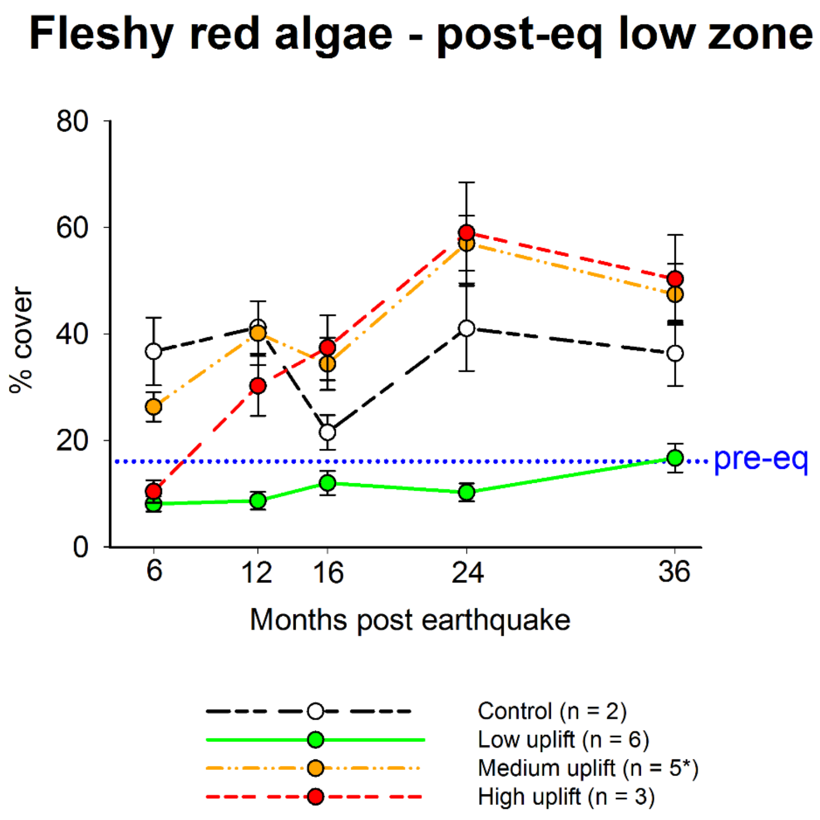


**Figure 12: Time series of the mean percentage cover (±SE) of fleshy red algae per square metre in the post-earthquake low zone across uplift levels. The dotted blue line indicates the average abundance of fleshy red algae in the pre-earthquake low zone across sites sampled in November 2016 (see Alestra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

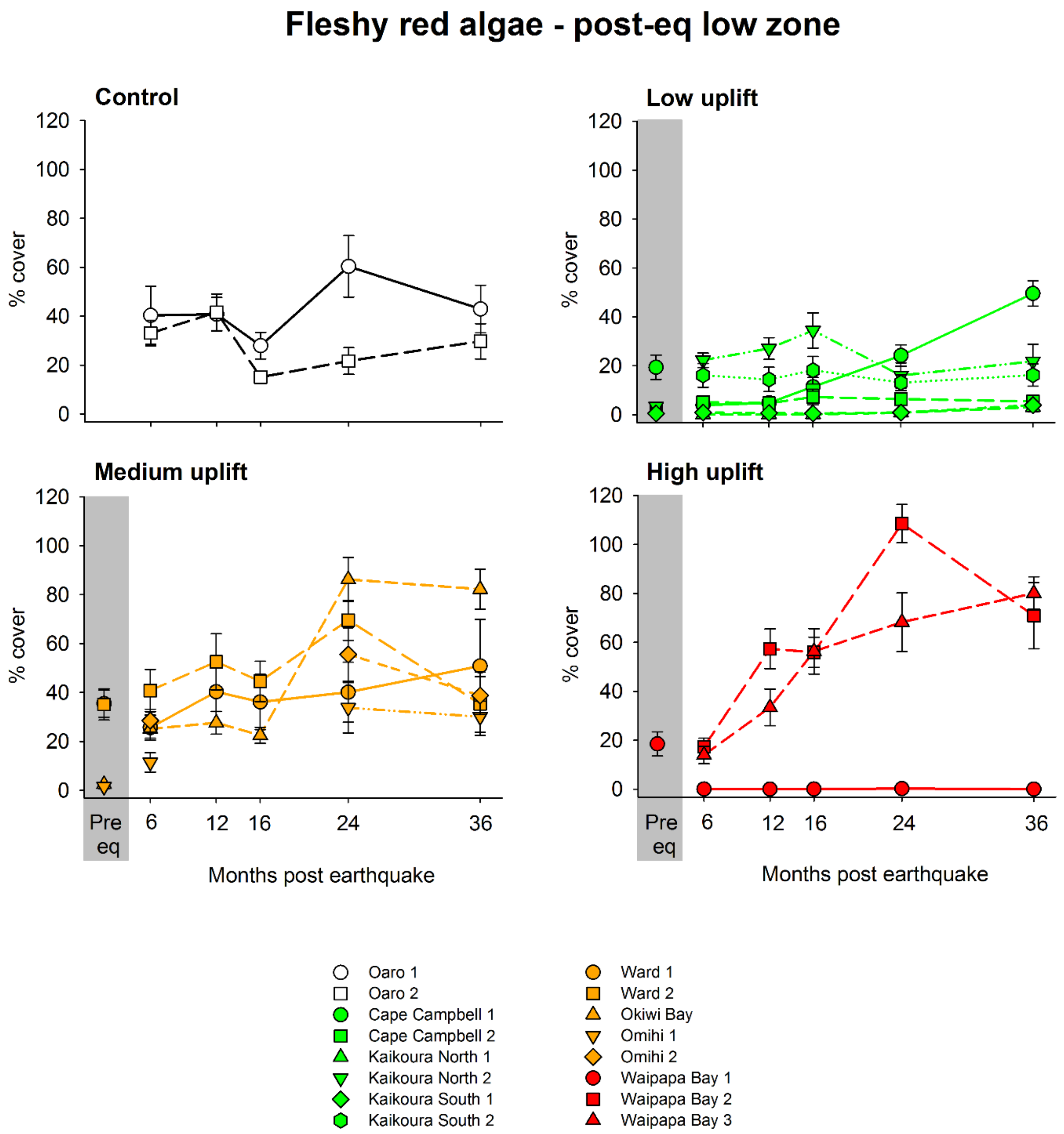


**Figure 13: Time series of the mean percentage cover (±SE) of fleshy red algae per square metre in the post-earthquake low zone across sites with no (A), low (B), medium (C), and high uplift (D). For the sites sampled in November 2016 (see Alestra et al. 2019), the average abundance of fleshy red algae 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 Relationship between large brown algae and fleshy red algae

Regression analysis highlighted a negative relationship between the cover of large brown algae and that of fleshy red algae (slope: -0.26, $P < 0.001$, Figure 14 A). This relationship accounted for 10% of the variability in the abundance of large brown algae in November 2019. The whole model (accounting also for site by site differences) explained 36% of the variability in the abundance of large brown algae. Quantile regression analyses confirmed the presence of a strong negative relationship between the two groups across five different quantiles (q10 slope -0.25, $P < 0.001$; q25 slope -0.35, $P < 0.001$; Q50 slope -0.41, $P < 0.001$; q75 slope -0.44, $P < 0.001$; q90 slope -0.4, $P < 0.01$, Figure 14 B).

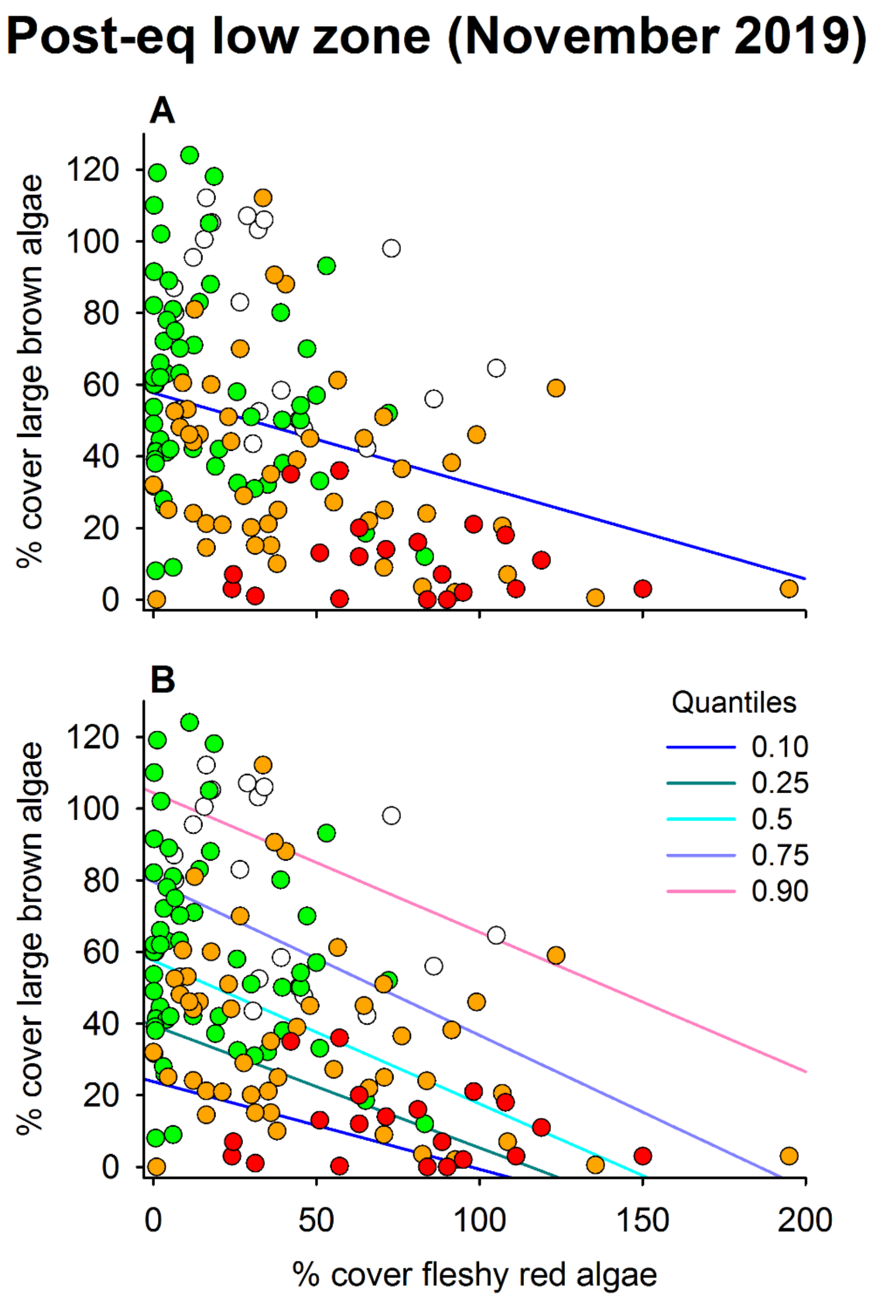


**Figure 14: Relationship between the abundance of large brown and fleshy red algae three years after the earthquake estimated through mixed effects (A) and quantile regression models (B). Regression lines are displayed for significant relationships. Symbol colours indicate different levels of uplift (white = no uplift, green = low uplift, yellow = medium uplift, red = high uplift). Data from Waipapa Bay 1, where both large brown and fleshy red algae were not present in November 2019, were not included in this analysis.**

### 3.2.4 Coralline red algae

In November 2019, control, low-, and medium-uplift groups had similar covers of coralline red algae (between 43–51%), whereas the mean for the high-uplift group was 22% (Figure 15). However, the analysis found no significant differences among uplift groups ($F_{3,12}$ = 1.96, P = 0.17). The extended time series shows a slight decline in the abundance of coralline algae between 24 and 36 months post-earthquake, with all groups remaining below the pre-earthquake baseline (Figure 15). In November 2019, there was also significant variability among sites in all groups, but the two control sites did not differ significantly from each other ($F_{12,144}$ = 7.35, P < 0.001). Across all sites, the cover of corallines remained stable or declined between 2018 and 2019. Waipapa Bay 1 was the only site where coralline algae were completely absent (Figure 16).

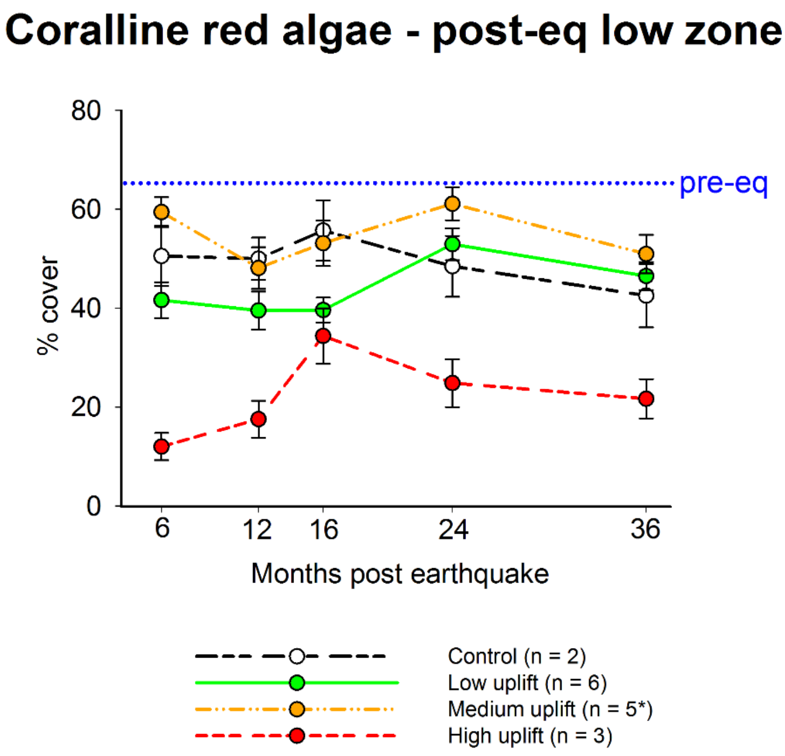


**Figure 15: Time series of the mean percentage cover (±SE) of coralline red algae per square metre in the post-earthquake low zone across uplift levels. The dotted blue line indicates the average abundance of coralline red algae in the pre-earthquake low zone across sites sampled in November 2016 (see Alestra et al. 2019). n = number of sites in each uplift group. *n = 5 after 12 months.**

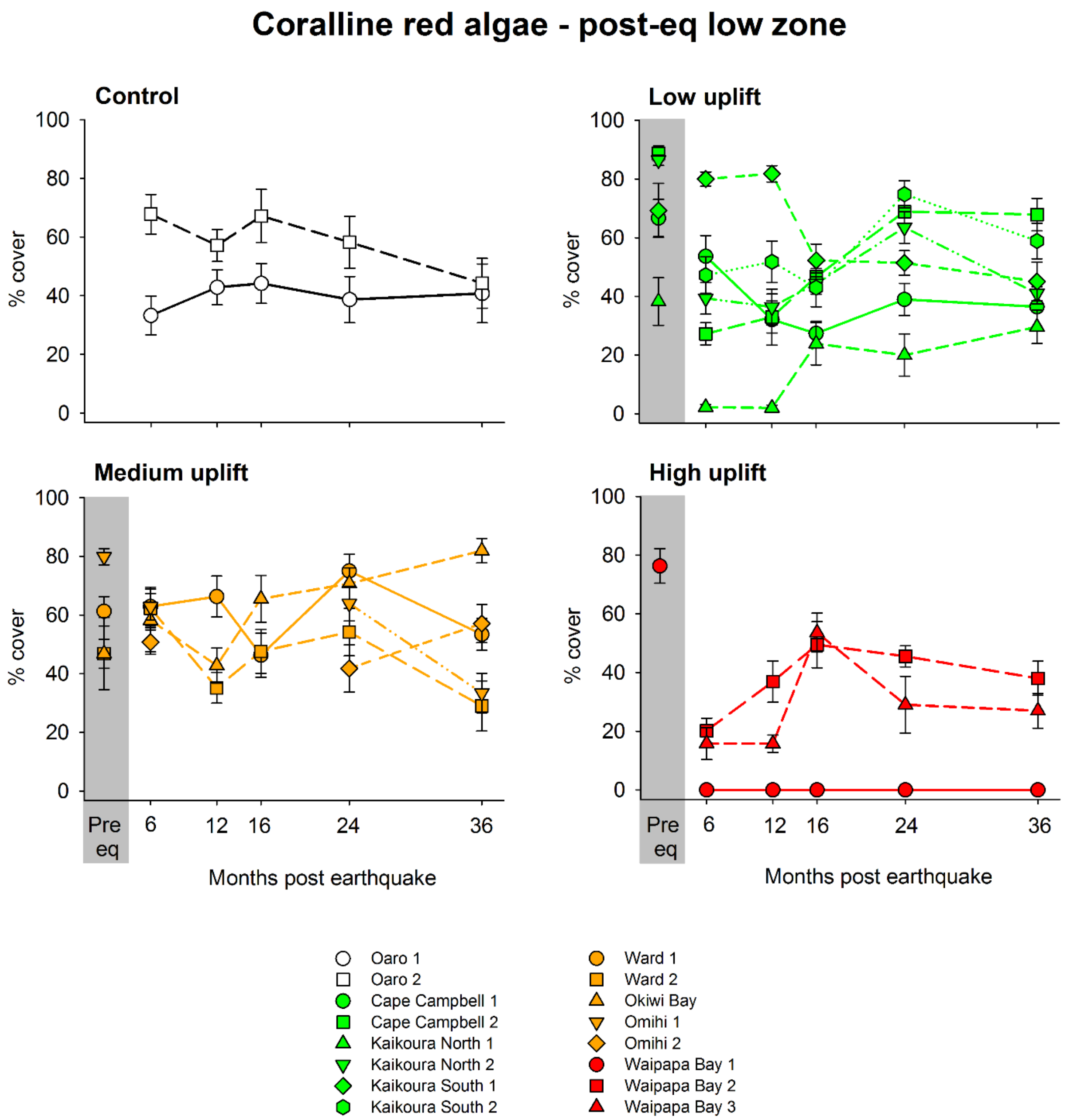


**Figure 16: Time series of the mean percentage cover (±SE) of coralline red algae per square metre in the post-earthquake low zone across sites with no (A), low (B), medium (C), and high uplift (D). For the sites sampled in November 2016 (see Alestra et al. 2019), the average abundance of coralline 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 November 2019, the medium-uplift group had limpet densities over 50 per m$^2$, whereas limpet abundances in all other groups were between 12 and 24 individuals per m$^2$ (Figure 17). However, the analysis found no significant differences among uplift groups ($F_{3,12} = 1.54$, $P = 0.25$) and significant differences among sites in all groups ($F_{12,144} = 6.91$, $P < 0.001$, Figure 18). High limpet densities in the medium-uplift group were due to very high numbers at a single site (Okiwi Bay, Figure 18 C). The drop in limpet numbers in the control group (Figure 17) did not reflect a widespread decline in the abundance of all limpet species, but simply the absence of large clusters of *Siphonaria* spp. in November 2019 at one of the Oaro sites (Figure 18 A).

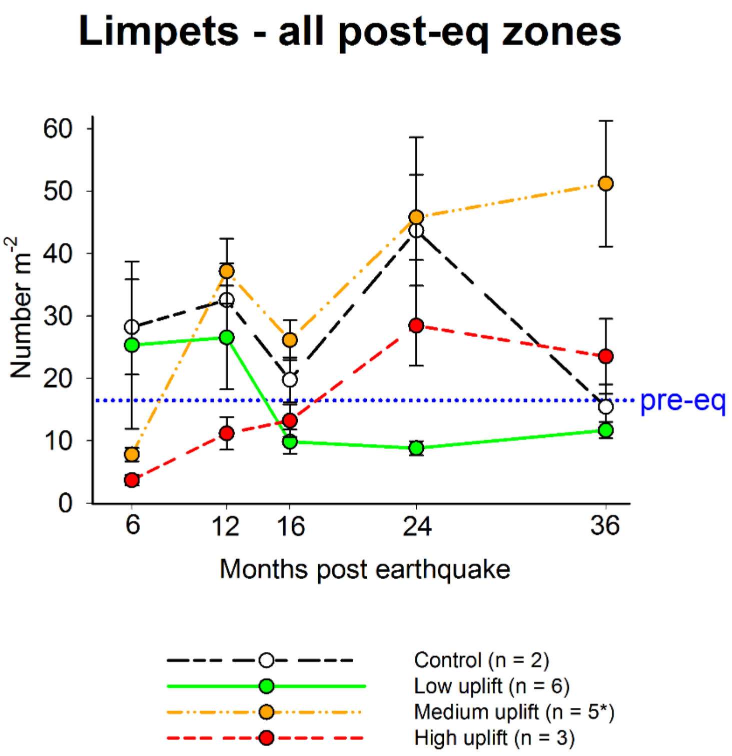


**Figure 17: Time series of the mean number (±SE) of limpets per square metre across uplift levels. The dotted blue line indicates the average abundance of limpets across sites sampled in November 2016 (see Alestra et al. 2019). n = number of sites in each uplift group. *n = 5 after 12 months.**

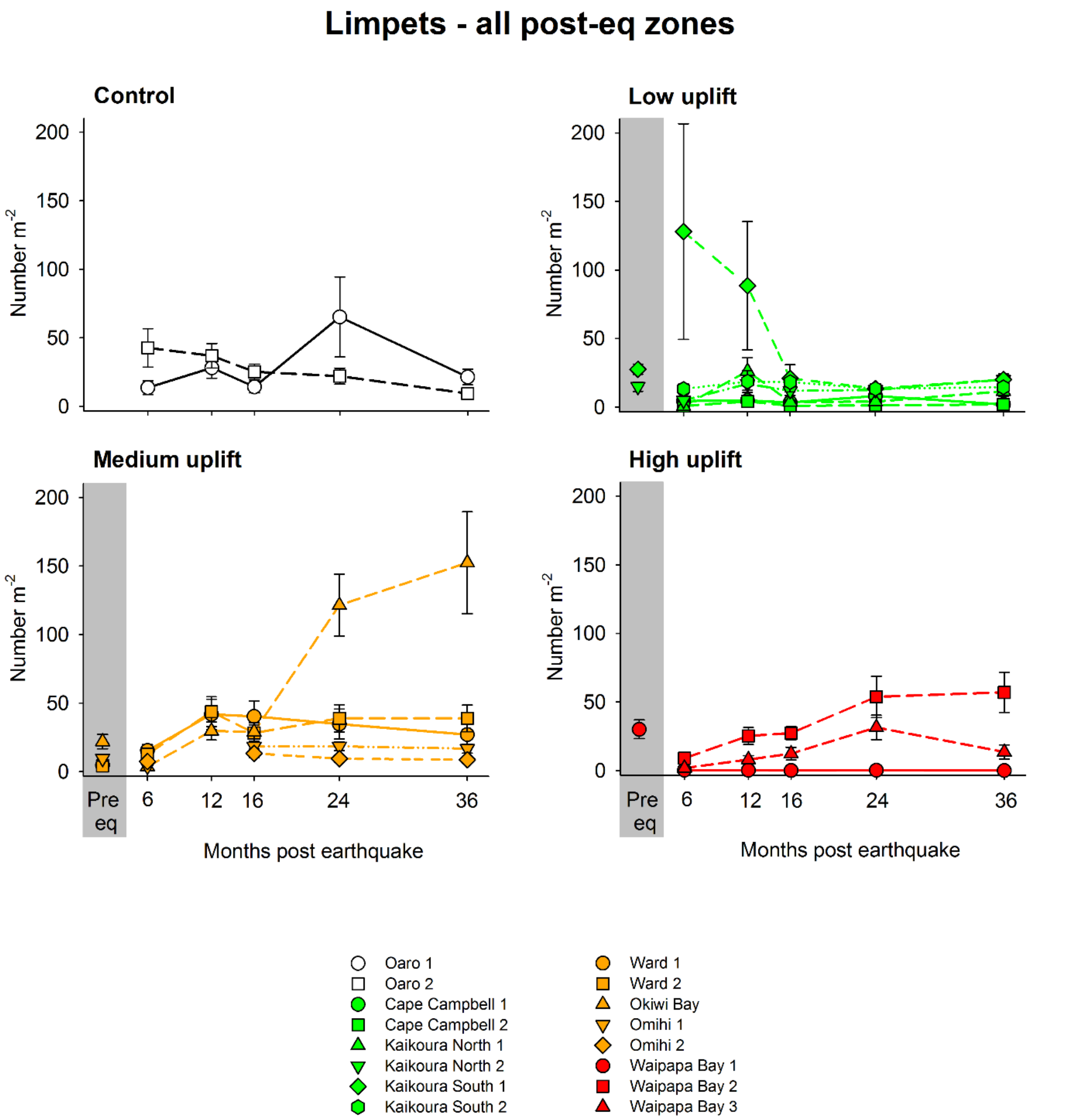


**Figure 18: Time series of the mean number (±SE) of limpets per square metre across sites with no (A), low (B), medium (C), and high uplift (D). For the sites sampled in November 2016 (see Alestra et al. 2019), the average abundance of limpets is displayed in the grey panels. At Omihi 1 and 2 (panel C) the low zone could not be sampled 12 and 16 months after the earthquake.**

## 3.3 Subtidal community structure

General observations during the 2020 subtidal surveys showed minor recovery of seaweeds and invertebrates at Waipapa Bay (Figure 19), and a decrease in the abundance of large brown algae around the Kaikōura Peninsula and at Okiwi Bay (Figure 20). 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 three and a half years after the earthquake.

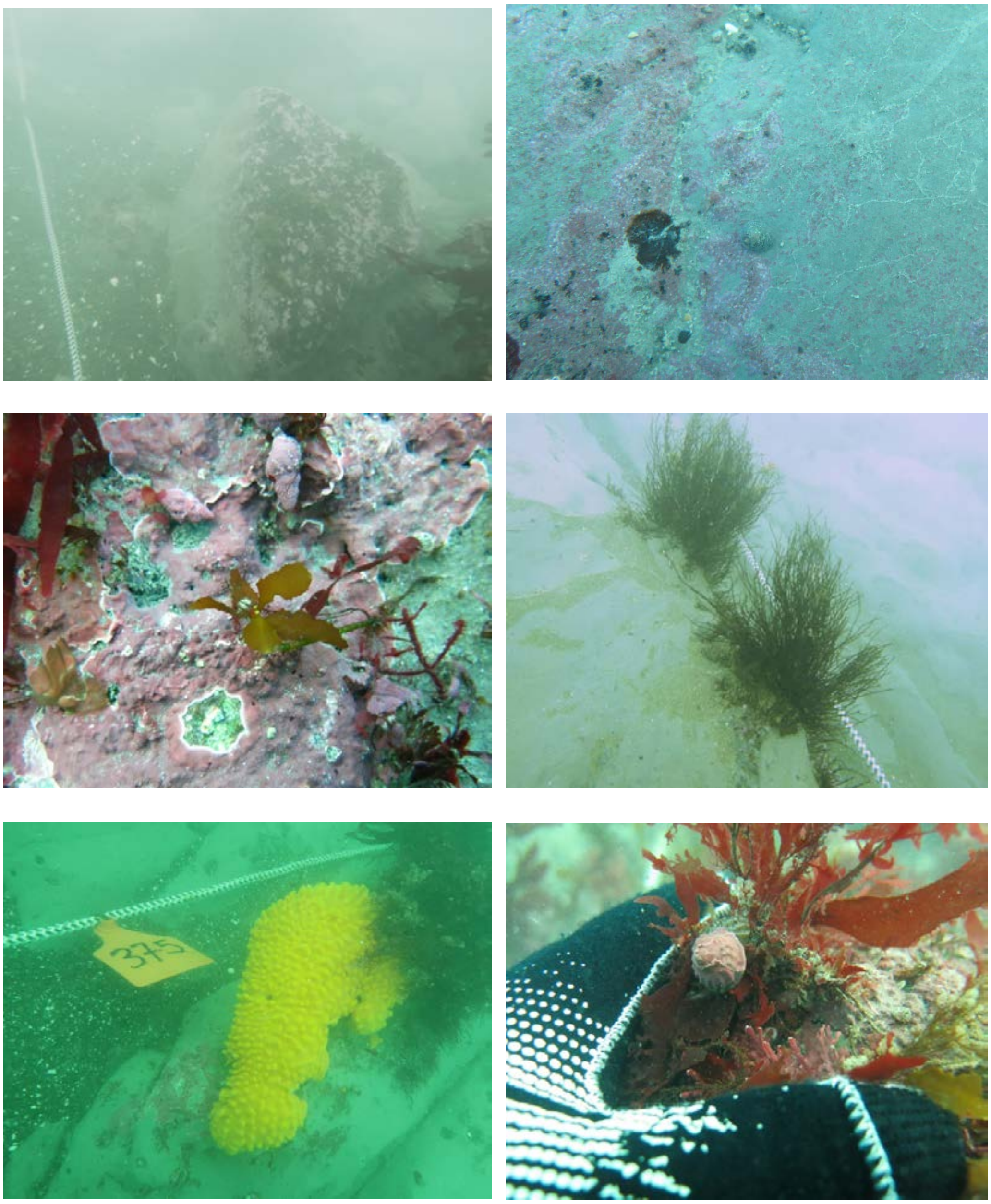


**Figure 19: Examples of recruitment of encrusting coralline and encrusting red algae (top), brown (*Landsburgia quercifolia*) and red algae (middle), and sessile and mobile invertebrates (bottom) at Waipapa Bay. Photos taken in July 2020.**

**Figure 20: Subtidal landscape at Okiwi Bay North (Transect 1), showing an area dominated by large brown algae in 2017 (top) and by red algae in 2020 (bottom).**

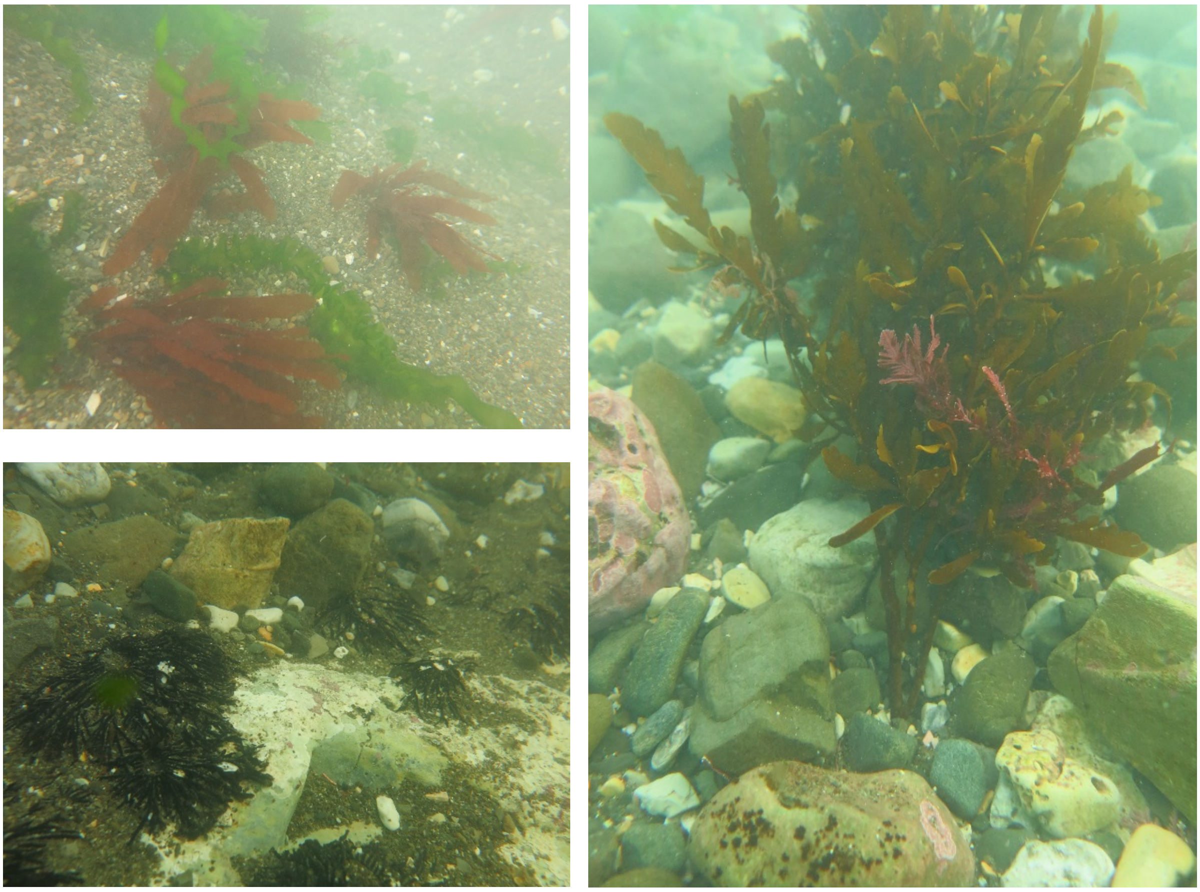

**Figure 21: Examples of gravel and cobble covering algae at Okiwi Bay South (top and right), and remnant holdfasts of *Marginariella boryana* (bottom left). Photos taken in May 2019.**

There were changes in substrate cover (using all data and not filtered to only include quadrats with at least 50% rock – see page 7 of this report) at some Waipapa Bay and Okiwi Bay sites. The changes mainly related to the movement of sand and gravel at the sites. Waipapa Bay North and South sites had declines in sand cover in 2019 and increases in 2020. Gravel cover also fluctuated, particularly at the south sites. The increase in bedrock at Waipapa Bay South sites is due to sand and gravel cover decreasing and exposing bedrock, and due to the addition of a different transect in 2018 (Figure 22). Okiwi South sites also had declines in sand cover since 2017 (from a mean of 13% to 1%) and increases in cobble (from 14% to 36%). These results agree with observations during the surveys. Other changes in abundances could be related to slight differences in the positioning of transects.

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 through time, and an increase in red non-encrusting algae at Okiwi Bay sites (Figure 23). Means of large brown algae declined from 54% to 33% and from 32% to 12% at Kaikōura and Okiwi Bay sites, respectively, whereas red non-encrusting algae increased from 15% to 32% at Okiwi Bay sites. Although encrusting/turfing algae cover was similar through time at Kaikōura and Okiwi Bay sites, increases were seen at Waipapa Bay sites (14% to 38%), along with an increase in red non-encrusting algae (6% to 19%). Some recruitment of large brown algae was seen around Waipapa Bay, but this was not noticeable in the plots due to the small sizes of the recruits (Figure 19). Ephemeral green algae (*Ulva* sp.) had a greater percentage cover at Okiwi Bay South in 2020 and at Waipapa Bay South in 2018 and 2020 (Figure 23).

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 (Figure 24). The high numbers of mobile invertebrates at Waipapa Bay South in 2017 skewed results and were due to a large number of rock lobsters along one transect, but overall numbers of other mobile invertebrates increased through time.

Numbers of Cook’s turban shells (*Cookia sulcata*) and both species of pāua (*Haliotis iris, H. australis*) increased (Figure 25). Numbers of both pāua species also increased at Okiwi Bay sites (means of 0.06 to 0.26 and 0 to 0.09 for *H. iris* and *H. australis* respectively), and kina increased at the Kaikōura South site (from a mean of 0.6 to 1.5).

Sessile invertebrate cover increased at Kaikōura North (1% to 2%), and this was driven by increases in sponges and ascidians. There were small increases in sponges and ascidians at Waipapa North and South, respectively (Figure 24).

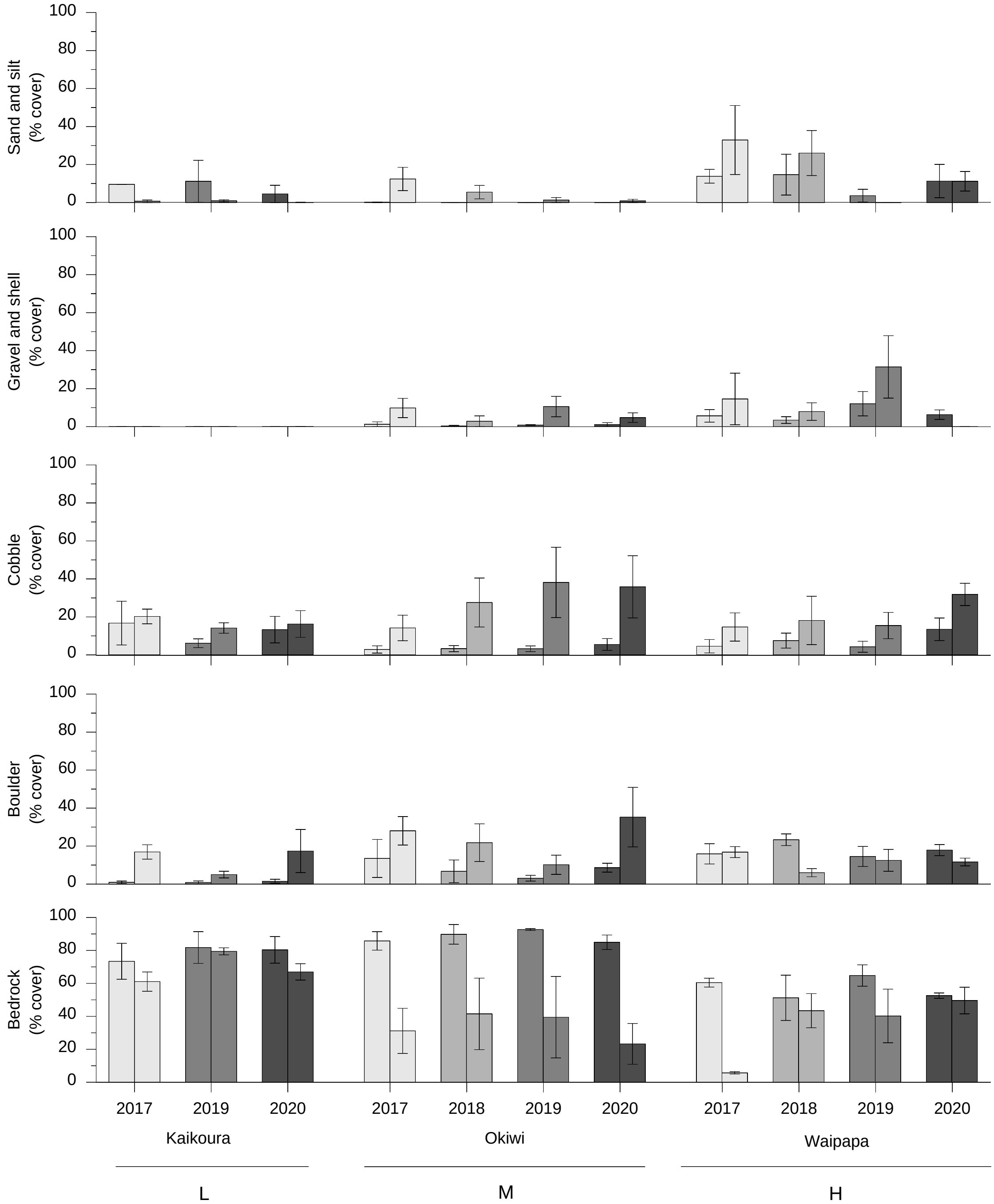


**Figure 22: Mean percentage cover of substrate types per 5-m² quadrat at the six sites surveyed between 2017 and 2020. For each pair of bars, the left bar refers to the northern site and the right bar to the southern site, with locations of the sites labelled below the x-axis. L=Low, M=Medium, H=High. 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.**

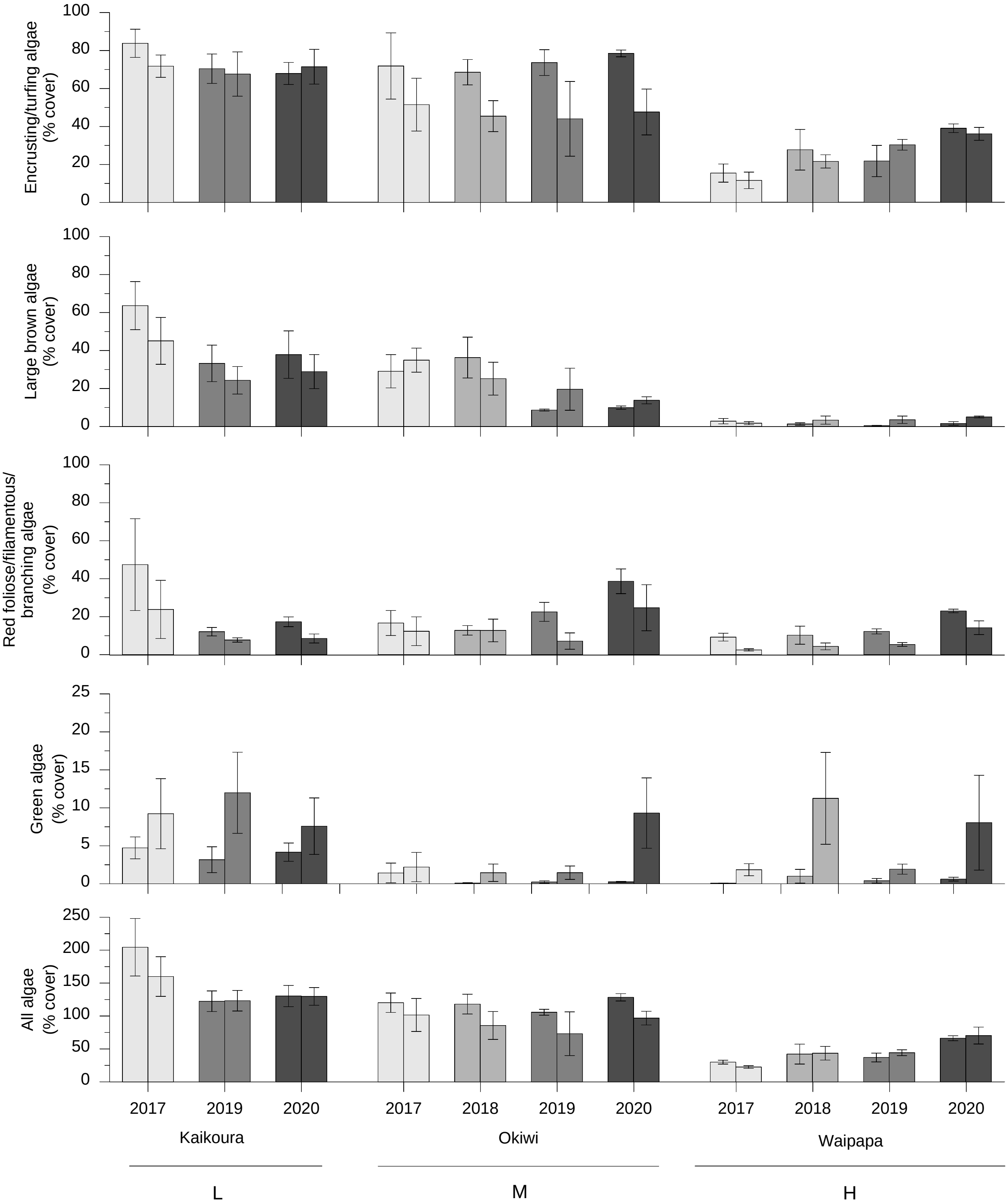


**Figure 23: Mean percentage cover of algae per 5-m² quadrat at the six sites surveyed between 2017 and 2020. For each pair of bars, the left bar refers to the northern site and the right bar to the southern site. Data were filtered to only include quadrats with at least 50% rock substrate (cobble, boulder, 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 different scales for 'green' and 'all algae' plots.**

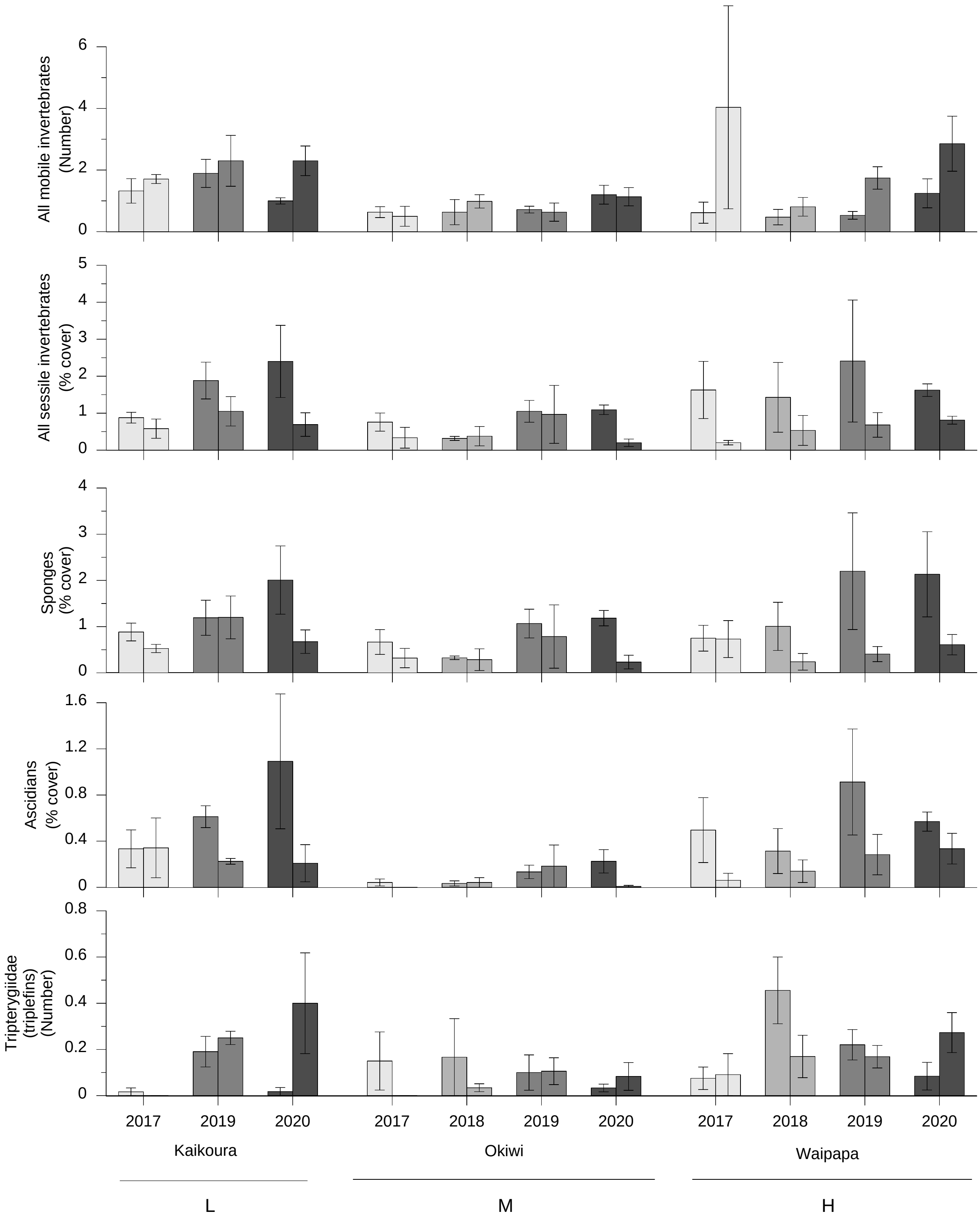


**Figure 24: Mean percentage cover of sessile invertebrates, sponges, and ascidians, and numbers of mobile invertebrates and triplefins per 5-m² quadrat at the six sites surveyed between 2017 and 2020. For each pair of bars, the left bar refers to the northern site and the right bar to the southern site. 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.**

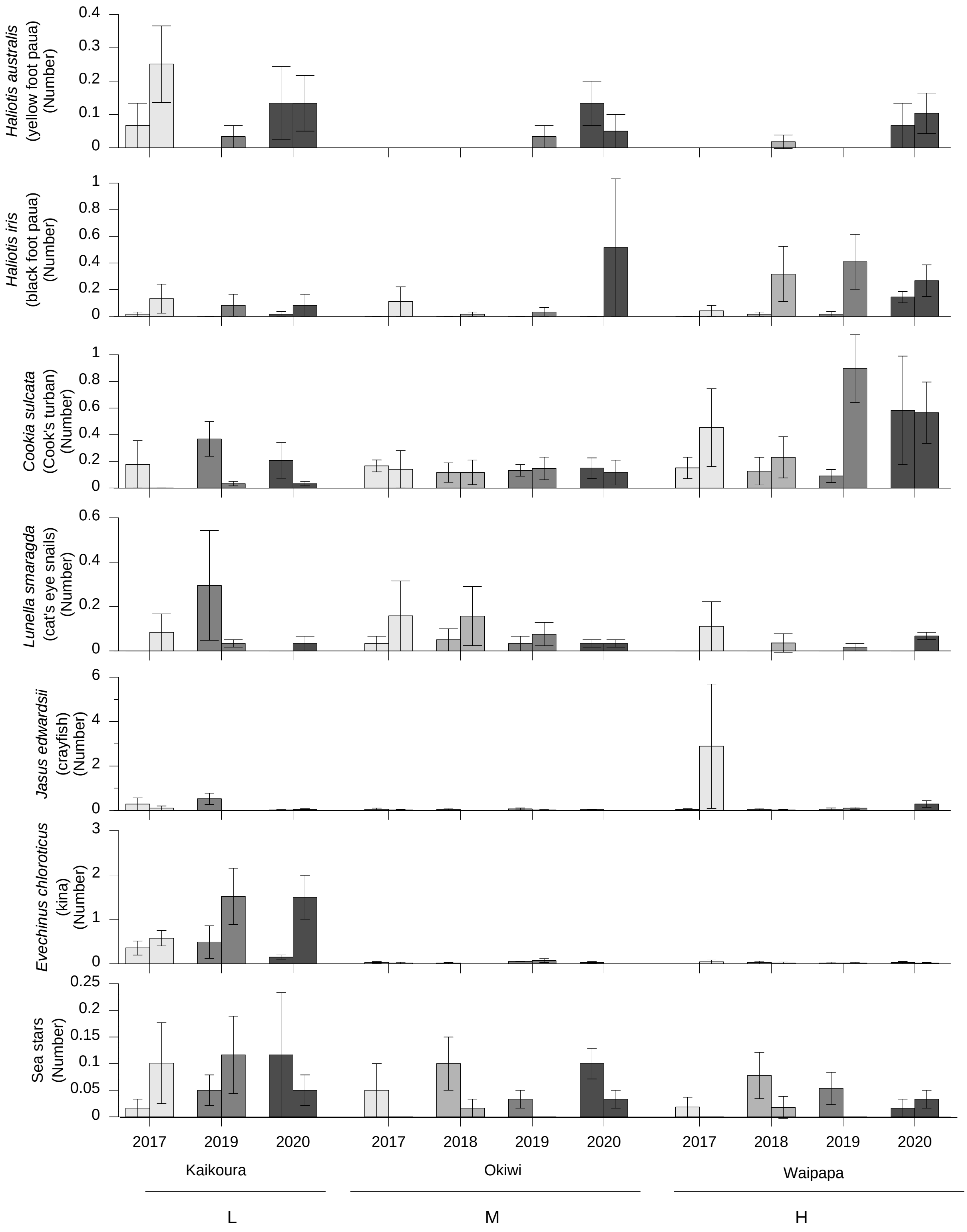


**Figure 25: Mean number of selected mobile invertebrates per 5-m$^2$ quadrat at the six sites surveyed between 2017 and 2020. For each pair of bars, the left bar refers to the northern site and the right bar to the southern site. Data were filtered to only include quadrats with at least 50% rock substrate (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 for the subtidal community data showed that Site was significant and Transect was highly significant (P < 0.001) (Table 1). This indicates there was spatial variability at small (between transects) and large (between sites) scales. The Survey x Transect (Site(Uplift)) interaction term was also highly significant, indicating that one or more transects changed differently from each other between surveys.

Principle coordinate analysis of distance between centroids for the Site combinations showed the degree of change in communities between surveys (Figure 26). 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 26). 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 (*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 foliose algal taxa. The increase in the green alga *Ulva* sp. also contributed to the dissimilarity between communities in 2020 and previous years.

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*. 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 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 | 1.29E+05 | 6 4401 | 4.3998 | 0.0763 |
| Survey | 3 | 28 373 | 9 457.8 | 2.2602 | 0.0600 |
| Site(Uplift) | 3 | 47 077 | 15 692 | 3.12 | 0.0270* |
| Uplift × Survey | 5 | 34 408 | 6 881.5 | 1.6259 | 0.1407 |
| Transect (Site(Uplift)) | 13 | 68 220 | 5 247.7 | 12.894 | 0.0001*** |
| Survey × Site(Uplift) | 8 | 34 276 | 4 284.5 | 1.3252 | 0.1584 |
| Survey×Transect(Site(Uplift)) | 32 | 1.06E+05 | 3 326.2 | 8.1729 | 0.0001*** |
| Res | 1 146 | 4.66E+05 | 406.98 | | |

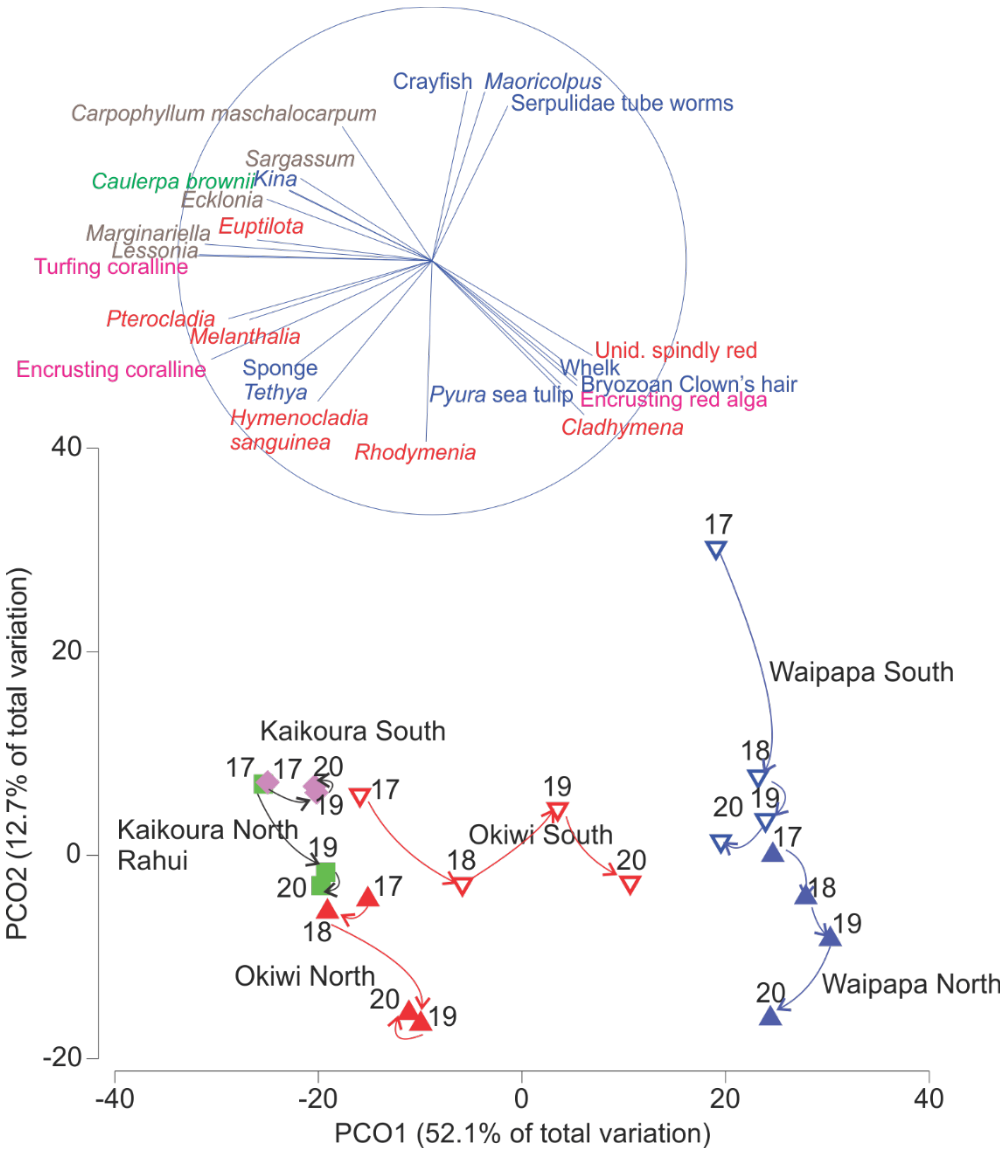


**Figure 26: Principal coordinates analysis (PCO) of distance among centroids for the six sites surveyed between 2017 and 2020, based on a Bray-Curtis similarity matrix of community assemblage data. Vector overlay shows taxa with > 0.6 correlation.**

As in previous surveys, few mobile reef fish (excluding triplefins) were seen in 2019 and 2020 (Figure 27). The exception was at Kaikōura South, which had means of 41 and 18 fish along the transects in 2019 and 2020, respectively. The other sites had averages of fewer than 10 fish (Figure 27). Banded wrasse (*Pseudolabrus fucicola*) and spotties (*Notolabrus celidotus*) were the most abundant fish species. Other fish observed (in order of decreasing abundance) were blue moki (*Latridopsis ciliaris*), butterfish (*Odax pullus*), blue cod (*Parapercis colias*), marblefish (*Aplodactylus arctidens*), and red moki (*Cheilodactylus spectabilis*).

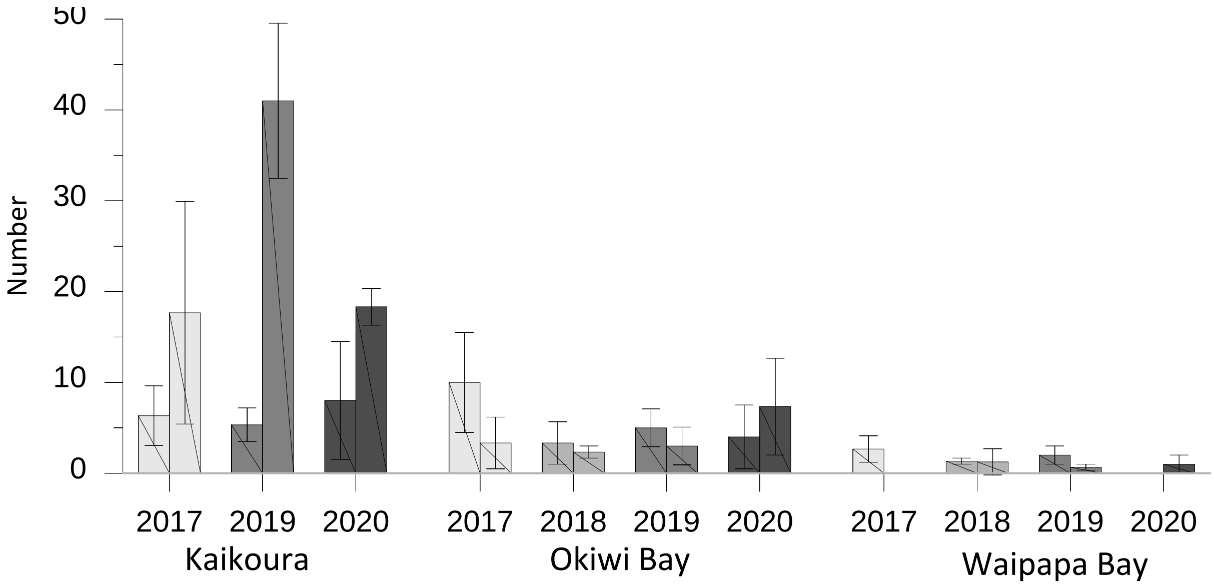


**Figure 27: Average abundances of fish at each site during each survey. In each pair of bars, the left bar refers to the northern site and the right bar to the southern site. N = 3 transects, with the exception of second surveys at Waipapa Bay South, where n = 4. Error bars represent 1 s.e. Transects were 50 m in length, and the area surveyed was 1 m either side of the transect, and 2 m above the transect.**

Most black foot and yellow foot pāua (*Haliotis iris* and *Haliotis australis*) were recorded in about 0.5–3.5 m (Figure 28). Numbers of both species appeared to increase at Okiwi Bay sites from 2017 to 2020. 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, but a small increase in numbers was recorded at Waipapa North (see Figure 25). Several yellow foot pāua were observed in 2020 at Waipapa Bay after being virtually absent between 2017- 2019. Numbers were too low to examine size structure of populations in any detail, but pāua at Waipapa were generally over the legal size limit.

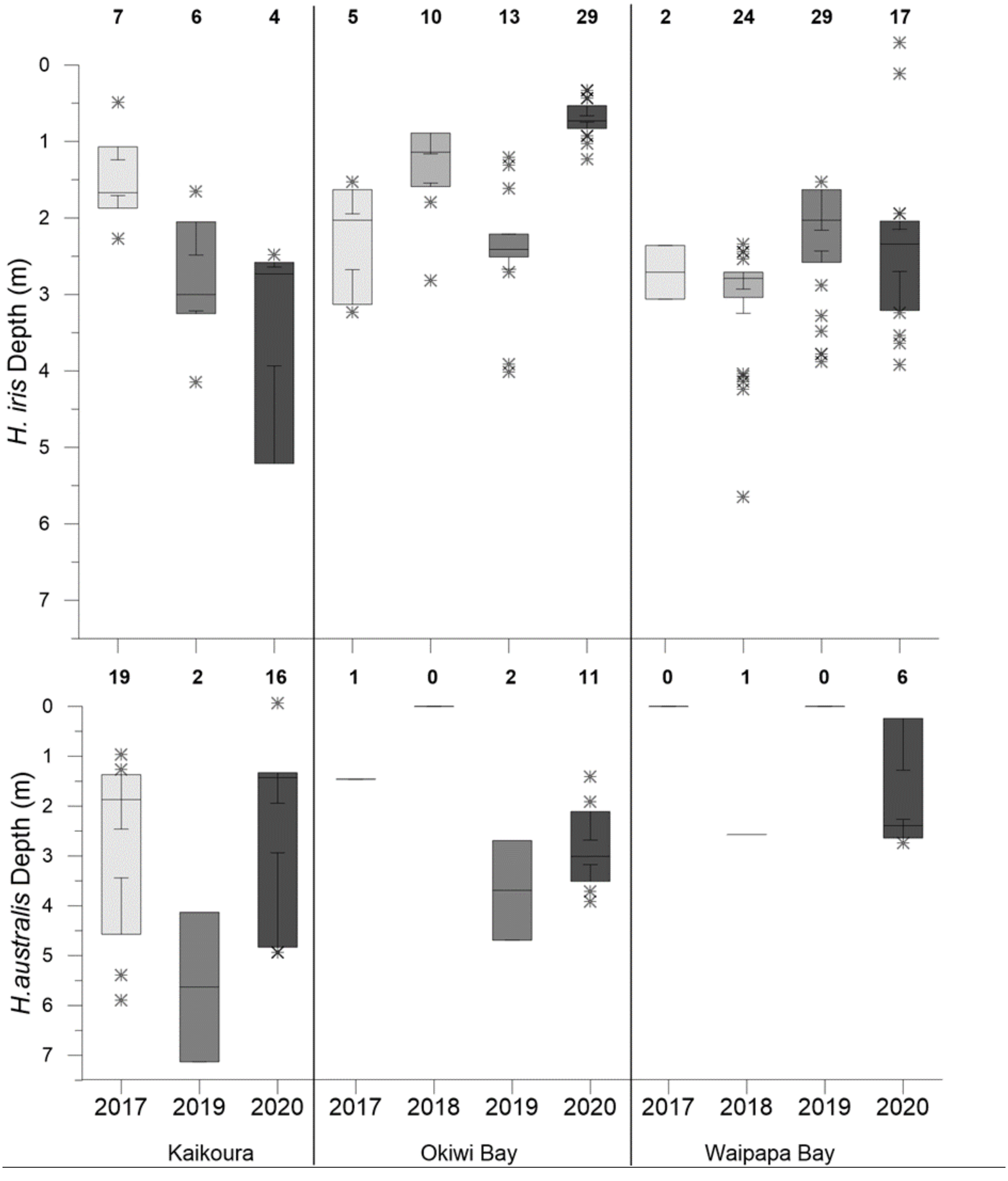


**Figure 28: Box-whisker plots showing *Haliotis iris* (black foot pāua, top) and *Haliotis australis* (yellow foot pāua, bottom) depth distributions at each site through time. Sample counts are at the top of each plot.**

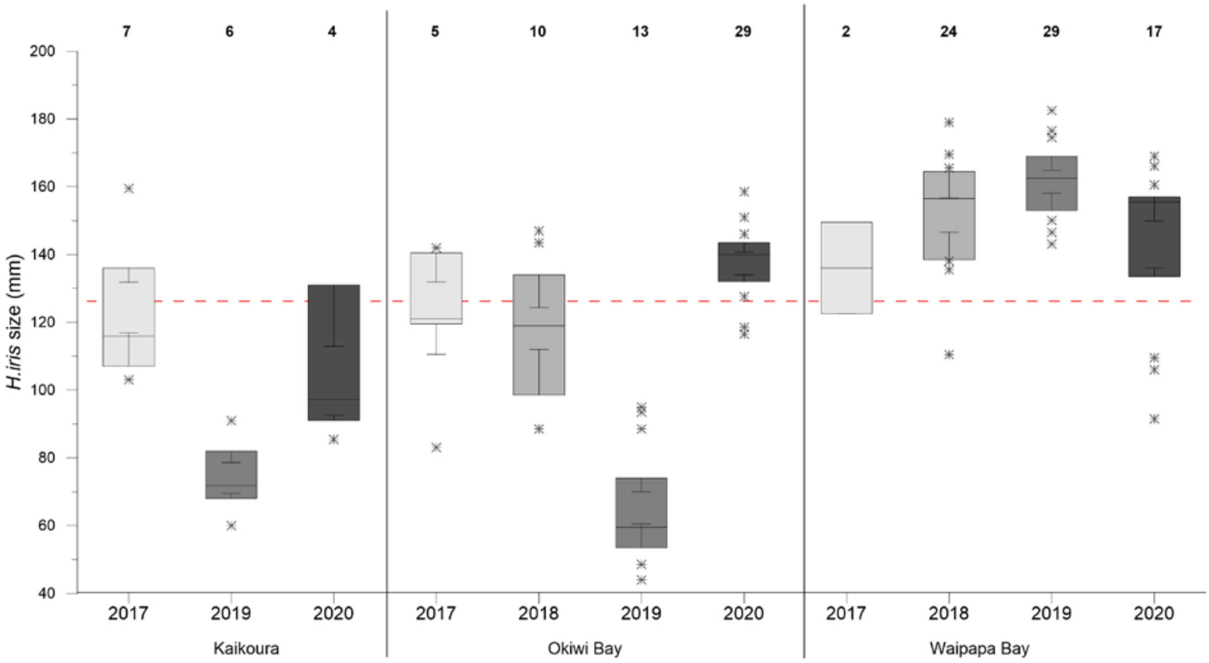


**Figure 29: Box-whisker plot showing *Haliotis iris* (black foot pāua) size distribution at each site through time. Sample counts are at the top of the plot. *Haliotis australis* (yellow foot pāua) sizes are not shown due to their absence or low numbers. The red dashed line represents the legal harvesting size of 125 mm.**

# 4. DISCUSSION

This research extends the previous work done as part of the Kaikōura Earthquake Marine Recovery Package (Alestra et al. 2019) and provides an updated assessment of the state of rocky reef systems that underwent impacts from coastal uplift. Overall, the results of the most recent surveys show that intertidal benthic communities are recovering only in low intertidal zone areas where abundant algal stands have managed to survive or re-establish. However, these low-zone algal communities have undergone significant post-earthquake shifts in species composition and are now dominated by different suites of species compared with the pre-earthquake conditions. Long-lasting impacts on intertidal reefs were still evident three years after the earthquake and varied across uplift levels. Subtidally, there was only minor recovery of seaweeds in de-vegetated areas and previously abundant algal stands appear to have become more sparse and fragmented.

## 4.1 Intertidal rocky reefs

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 the low intertidal. These results confirm that much of the mid-tidal zones, which supported lush and diverse algal communities before the earthquake (Schiel 2004, Schiel 2006), is now unsuitable for colonisation of large algae.

Hot temperatures and high erosion rates are the most likely causes underlying the lack of algal recovery over vast areas of uplifted reefs (Schiel at al. 2018, 2019, Alestra et al. 2019). Temperature data collected from mid-zone areas of uplifted reefs show that, in the absence of algal cover, summer temperatures in proximity to the substratum often exceed 35 °C, with peaks well over 40 °C (Figure 29). Despite the reefs still being submerged at high tide, such extreme low-tide temperatures are lethal to most marine organisms, making any sign of recovery short-lived. For example, sparse recruitment of the habitat-forming fucoid *Hormosira banksii* still occurs in the mid zone at some sites during the cooler months (Figure 29), but the newly settled algae quickly burn off during summer.

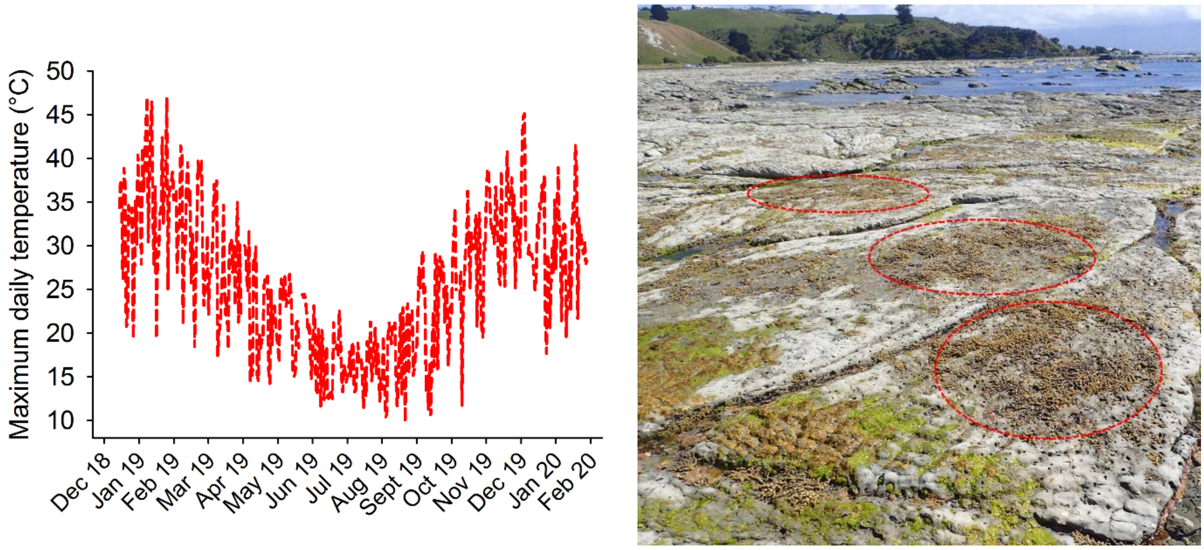


**Figure 29: Summer temperatures in mid-intertidal areas often exceed 35 °C (left) and result in the burn-off of virtually all algae. On the right: patches of *Hormosira banksii* (within the red circles), photographed in spring 2018 did not survive the following summer. Temperature data and photo are from the Kaikōura North 1 site.**

Ongoing reef erosion, especially of large mudstone platforms, are also contributing to poor widespread algal recovery. Hot, dry conditions (Stephenson & Kirk 1998) and absence of algal cover (Bosence 1983, Steneck 1986) are critical factors driving high erosion rates. Erosion data collected as part of our MBIE research between 2018 and 2020 showed lower erosion rates (2.6 mm per year) in areas experimentally maintained as shaded and moist at low tide, compared with areas lacking shade and water at low tide (7.7 mm per year). This confirms that heat and desiccation can greatly affect the physical structure of the uplifted reefs, in addition to the intertidal biota.

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 (around 1 m) at Cape Campbell and around the Kaikōura Peninsula. The latest surveys showed a steady increase in the abundance of large brown algae at most low- and medium-uplift sites, but a lack of recovery at the Waipapa Bay sites, in the area of highest uplift. Between November 2018 and November 2019, the abundance of large brown algae also continued to increase at the control sites in the Oaro area, where they experienced high mortality during the 2017–2018 hot summer (Alestra et al. 2019, Thomsen et al. 2019).

Despite increasing abundances at many sites, comparisons with pre-earthquake data show that post-earthquake assemblages of large brown algae are no longer dominated by bull kelp (*Durvillaea* spp.), but with other species of fucoids (primarily *Carpophyllum maschalocarpum*) representing the vast majority of large brown algae cover three years after the earthquake. Since 2017, no site showed increasing abundances of bull kelp and there was no sign of recovery at the Waipapa Bay sites, where bull kelp was completely extirpated. The post-earthquake distribution of bull kelp is highly patchy, with dense stands surviving in pockets of favourable habitat, such as headlands, reef fringes, and offshore rocks. More target aerial drone surveys are required to capture this variability and assess the state of bull kelp forests more accurately, but the data clearly show a decline in bull kelp cover at most sites along the transect lines. At the same time, the cover of *Carpophyllum maschalocarpum* and other smaller fucoids increased almost everywhere, particularly where there was low uplift. The implications of changing patterns of abundance of dominant canopy-formers in the low intertidal are difficult to predict but may be profound. There are obvious morphological differences between bull kelp and other smaller fucoids, which may not exert the same strong control on the associated communities of algae (Taylor & Schiel 2005) and invertebrates (Smith & Simpson 1995), and may not play the same role in nearshore food webs because they are less palatable to herbivorous fish (Taylor & Schiel 2010).

The abundance of fleshy red algae, a speciose group which accounts for the majority of the diversity in low zone algal communities, increased in areas where large brown canopies decreased. As in previous surveys, three 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. Pre-earthquake data show that algal communities at medium- and high-uplift sites were not dominated by fleshy red algae before the earthquake. Fleshy reds most likely benefitted from the high earthquake mortality of large browns and their widespread expansion reshaped low zone communities in areas with uplift greater than 1.5 m (Figure 30).

**Figure 30: Widespread loss of fucoid canopies (left) was associated with the expansions of turfs of red algae (right) where the uplift exceeded 1.5 m. This may result in reduced productivity and preclude the return to the original state.**

Shifts from fucoid canopies to turfs of red algae are usually associated with reduced community complexity and lower productivity (Schiel & Lilley 2011, Tait & Schiel 2011, Alestra et al. 2014). Even more importantly, the recovery of large canopy-forming algae following disturbances can be inhibited by the proliferation of low-lying algal turfs (O'Brien & Scheibling 2018). Our regression analyses confirmed that this may be occurring along the earthquake-affected coastline, with denser fucoid canopies being found in the presence of sparser turfs or red algae and vice versa. Turf domination of benthic communities adds to the impact of poor connectivity among fragmented stands of surviving brown algae. The majority of the gametes of large fucoids disperse only a few metres away from the source plants (Dunmore 2006) and the combination of limited propagule supply and competitive exclusion by fleshy red algae makes the re-establishment of canopies of large brown algae unlikely without interventions of restoration or rehabilitation. As part of the MBIE research, we are currently attempting to re-establish populations of *Durvillaea poha* (the bull kelp species most affected by the earthquake) using zygote seeding and transplants in areas of reef from which low-laying red and brown algae were cleared.

Encrusting and turf-forming coralline algae were abundant in the low zone at most sites independently of the degree of uplift, 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 also unrelated to the degree of uplift and highly variable across sites. Despite limpets experiencing high mortality in the immediate aftermath of the coastal uplift, the earthquake does not seem to have left a long-lasting legacy on their abundances. Unlike large habitat-forming brown algae, connectivity among surviving limpet populations was likely maintained because they are broadcast spawners with considerable larval dispersal, which facilitates faster recovery.

Despite some consistency between the most recent results and those of previous surveys, the long-term future of these intertidal communities remains problematic because of ongoing changes in the physical environment, which is contributing to delays in the recovery process. In particular, over the last 24 months, significant changes in patterns of gravel accumulation were seen in the Waipapa Bay and Ward areas, with gravel building up in the low intertidal zone, the area of greatest post-earthquake diversity, and even inundating entire sites (Figure 31). It remains to be seen whether these physical processes of erosion and sedimentation will settle down and allow greater recovery of reef biota.

**Figure 31: Widespread gravel inundation was observed in some areas with medium and high uplift (on the left, Waipapa Bay). The low intertidal zone is often the first area to infill with gravel, threatening the persistence of post-earthquake algal communities. For example, bull kelp plants smothered by gravel are a common occurrence at Ward (right).**

## 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 and Okiwi Bay). The most obvious effects were on the abundances of understorey 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 and 2020 surveys, 2.5 and 3.5 years after the earthquake respectively, 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. The most striking difference compared with previous surveys was the decrease in large brown algae at some Kaikōura Peninsula and Okiwi Bay sites. This decline has also been observed at other sites included in the original Kaikōura Earthquake Marine Recovery Package (Alestra et al. 2019), which were recently re-sampled as part of the MBIE research. Reasons for this decline are unclear, but it may be due to a combination of altered wave dynamics because of the uplift, extreme wave events, marine heatwaves, 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. Recruits of large brown algae have been recorded, 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. As part of the MBIE research, large brown algae collected from unaffected locations are being transplanted to facilitate the recovery of large brown algae at Waipapa Bay.

## 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. Extended post-earthquake monitoring of rocky reef habitats is extremely valuable given that the uplifted coastline is still in a transient state of recovery, in 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 will be helpful to characterise the impacts of other local (e.g., floods, sedimentation, and pedestrian and vehicle traffic) and global stressors (e.g., heatwaves) on the recovery of some equilibrium of the post-earthquake ecosystem. Finally, this work provides an important spatial and temporal context for experimental studies and for important management decisions, particularly regarding a range of human uses and the re-opening of the pāua fishery.

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# 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.; Tait, L.W.; Schiel, D.R. (2014). Effects of algal turfs and sediment accumulation on replenishment and primary productivity of fucoid assemblages. *Marine Ecology Progress Series 511*: 59–70.

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

Barrientos, S.E.; Ward, S.N. (1990). The 1960 Chile earthquake: inversion for slip distribution from surface deformation. *Geophysics Journal International 103*: 589–598.

Bosence, D.W.J. (1983). Coralline algal reef frameworks. *Journal of the Geological Society 140*: 365–376.

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

Dunmore, R.A. (2006). Demography of early life stages of habitat-forming intertidal fucoid algae. PhD dissertation, University of Canterbury, New Zealand.

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

Hamling, I.J.; Hreinsdóttir, S.; Clark, K.; Elliott, J.; Liang, C.; Fielding, E.; Wright, T.J. (2017). Complex multifault rupture during the 2016 Mw7.8 Kaikōura earthquake, New Zealand. *Science 356*: eaam7194.

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.

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.

Morse, A.N.; Morse, D.E. (1984). Recruitment and metamorphosis of *Haliotis* larvae induced by molecules uniquely available at the surfaces of crustose red algae. *Journal of Experimental Marine Biology and Ecology* 75: 191–215.

O'Brien, J.M.; Scheibling, R.E. (2018). Turf wars: competition between foundation and turf-forming species on temperate and tropical reefs and its role in regime shifts. *Marine Ecology Progress Series 590*: 1–17.

Robinson, L.J. (1992). Population and reproductive ecology of *Turbo smaragdus* in the Kaikōura region. MSc dissertation, University of Canterbury, New Zealand.

Schiel, D.R. (2004). The structure and replenishment of rocky shore intertidal communities and biogeographic comparisons. *Journal of Experimental Marine Biology and Ecology 300*: 309–342.

Schiel, D.R. (2006). Rivets or bolts? When single species count in the function of temperate rocky reef communities. *Journal of Experimental Marine Biology and Ecology 338*: 233–252.

Schiel, D.R.; Alestra, T.; Gerrity, S.; Orchard, S.; Dunmore, R.A.; Pirke–r, 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.

Schiel, D.R.; Lilley, S.A.; South, P.M. (2018). Ecological tipping points for an invasive kelp in rocky reef algal communities. *Marine Ecology Progress Series 587*: 93–104.

Smith, S.D.A; Simpson, R.D. (1995). Effects of the 'Nella Dan'oil spill on the fauna of *Durvillaea antarctica* holdfasts. *Marine Ecology Progress Series 121*: 73–89.

Steneck, R.S. (1986). The ecology of coralline algal crusts: convergent patterns and adaptive strategies. *Annual Review of Ecology and Systematics 17*: 273–303.

Stephenson, W.J.; Kirk, R.M. (1998). Rates and patterns of erosion on inter-tidal shore platforms, Kaikōura Peninsula, South Island, New Zealand. *Earth Surface Processes and Landforms: The Journal of the British Geomorphological Group* 23: 1071–1085.

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

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.

Taylor, D.I.; Schiel, D.R. (2010). Algal populations controlled by fish herbivory across a wave exposure gradient on southern temperate shores. *Ecology 91*: 201–211

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.W.; 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*:84.

# 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 | 2020 |
| **Kaikōura North Rahui** | T1 | L | -42.4155 | 173.7089 | -42.4153 | 173.7093 | 7.0 | 5.3 | 5 | | 15 | | 14 | 19 |
| | T2 | L | -42.413 | 173.7073 | -42.4134 | 173.7072 | 7.0 | 4.5 | 5 | | 20 | | 20 | 20 |
| | T3 | L | -42.4135 | 173.7063 | -42.4132 | 173.7065 | 5.7 | 2.0 | 5 | | 20 | | 20 | 20 |
| **Kaikōura South S2** | T1 | L | -42.4355 | 173.6921 | -42.4356 | 173.6926 | 4.6 | 2.6 | 5 | | 20 | | 20 | 20 |
| | T2 | L | -42.4352 | 173.6929 | -42.4351 | 173.6926 | 6.8 | 4.1 | 5 | | 20 | | 20 | 20 |
| | T3 | L | -42.4347 | 173.6926 | -42.435 | 173.6931 | 7.3 | 5.6 | 5 | | 19 | | 20 | 20 |
| **Okiwi Bay North** | T1 | M | -42.2171 | 173.8726 | -42.5209 | 173.509 | 5.5 | 3.9 | 1-2 | 1.5 | 20 | 20 | 20 | 20 |
| | T2 | M | -42.2178 | 173.8717 | -42.218 | 173.872 | 4.2 | 2.4 | 4 | 2 | 20 | 20 | 20 | 20 |
| | T3 | M | -42.2181 | 173.8716 | -42.2183 | 173.872 | 5.4 | 2.9 | 4 | 2 | 20 | 20 | 20 | 20 |
| **Okiwi Bay South** | T1 | M | -42.2189 | 173.8665 | -42.2194 | 173.8665 | 4.1 | 2.1 | 1 | | 18 | 20 | 20 | 20 |
| | T2 | M | -42.2189 | 173.869 | -42.219 | 173.8696 | 3.8 | 2.2 | 1 | 2 | 12 | 19 | 17 | 20 |
| | T3 | M | -42.2191 | 173.8697 | -42.2194 | 173.8701 | 5.4 | 3.3 | 5 | 2.5 | 19 | 20 | 20 | 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 | 19 |
| | T2 | H | -42.205 | 173.8798 | -42.205 | 173.8803 | 5.5 | 4.4 | 1.5 | 2.5 | 18 | 20 | 18 | 13 |
| | T3 | H | -42.2056 | 173.8796 | -42.2057 | 173.8802 | 6.1 | 5.3 | 1.5-2.5 | 2.5 | 17 | 12 | 18 | 20 |
| **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 | 20 |
| | T3 | H | -42.2096 | 173.8774 | -42.21 | 173.8778 | 4.9 | 3.6 | 2 | 1.5 | 11 | 14 | 7 | 20 |
| | T1b | H | | | | | | | | | | 20 | 19 | 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) 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**

| | Control vs Medium uplift - Average dissimilarity = 91.98 | | | | |
|---|---|---|---|---|---|
| Taxa | Average abundance Control | Average abundance Low-uplift | Average dissimilarity | Contribution % | Cumulative contribution % |
| *Ulva* spp. | 25.06 | 0.13 | 37.22 | 40.47 | 40.47 |
| *Chamaesipho columna* | 2.12 | 0.07 | 13.99 | 15.21 | 55.68 |
| *Pyropia* spp. | 1.85 | 0.3 | 12.49 | 13.58 | 69.25 |
| *Enteromorpha* spp. | 3.27 | 0.04 | 5.73 | 6.23 | 75.48 |
| Coralline turf | 0.51 | 0 | 4.28 | 4.65 | 80.13 |
| *Limnoperna pulex* | 0.25 | 0.11 | 3.49 | 3.79 | 83.93 |
| Tube-forming polychaetes | 0.11 | 0 | 3.12 | 3.4 | 87.32 |
| Encrusting algae | 0.12 | 0.02 | 2.36 | 2.56 | 89.88 |
| *Mytilus galloprovincialis* | 0.3 | 0.04 | 2.01 | 2.18 | 92.07 |

| | Low uplift vs Medium uplift - Average dissimilarity = 96.31 | | | | |
|---|---|---|---|---|---|
| Taxa | Average abundance Control | Average abundance Medium-uplift | Average dissimilarity | Contribution % | Cumulative contribution % |
| *Pyropia* spp. | 7.55 | 0.3 | 44.07 | 45.76 | 45.76 |
| *Limnoperna pulex* | 0.01 | 0.11 | 10.58 | 10.98 | 56.74 |
| *Ulva* spp. | 0.29 | 0.13 | 7.98 | 8.29 | 65.03 |
| *Chamaesipho columna* | 0.05 | 0.07 | 6.93 | 7.2 | 72.23 |
| Encrusting algae | 0.21 | 0.02 | 4.9 | 5.09 | 77.31 |
| *Mytilus galloprovincialis* | 0 | 0.04 | 3.92 | 4.07 | 81.38 |
| *Scytosiphon lomentaria* | 0.22 | 0 | 3.25 | 3.38 | 84.76 |
| *Enteromorpha* spp. | 0.59 | 0.04 | 3.15 | 3.27 | 88.02 |
| *Aulacomya maoriana* | 0 | 0.03 | 2.1 | 2.18 | 90.21 |

**B) Post-earthquake mid zone**

| Taxa | Control vs Low uplift - Average dissimilarity = 96.05 | | | | |
|---|---|---|---|---|---|
| | Average abundance Control | Average abundance Low-uplift | Average dissimilarity | Contribution % | Cumulative contribution % |
| *Gelidium caulacantheum* | 0.05 | 16.15 | 12.77 | 13.29 | 52.61 |
| *Hormosira banksii* | 0.28 | 14.06 | 10.24 | 10.66 | 63.27 |
| *Ulva* spp. | 1.44 | 10.8 | 8.36 | 8.7 | 71.97 |
| Encrusting coralline algae | 2.17 | 6.92 | 5.89 | 6.13 | 78.1 |
| Encrusting algae | 5.5 | 0.1 | 3.59 | 3.73 | 81.84 |
| *Cystophora scalaris* | 0 | 1.61 | 1.6 | 1.66 | 83.5 |
| *Echinothamnion hystrix* | 0 | 1.96 | 1.53 | 1.59 | 85.09 |
| *Sarcothalia lanceata* | 0 | 2.44 | 1.49 | 1.55 | 86.65 |
| *Champia novae-zelandiae* | 0 | 1.7 | 1.2 | 1.25 | 87.9 |
| *Pyropia* spp. | 1.41 | 0 | 1.08 | 1.12 | 89.02 |
| *Enteromorpha* spp. | 1.19 | 0.01 | 0.88 | 0.92 | 89.94 |
| *Colpomenia bullosa* | 0.18 | 0.93 | 0.8 | 0.83 | 90.76 |

| Taxa | Control vs Medium uplift - Average dissimilarity = 91.05 | | | | |
|---|---|---|---|---|---|
| | Average abundance Control | Average abundance Medium-uplift | Average dissimilarity | Contribution % | Cumulative contribution % |
| Articulated coralline algae | 49.8 | 0.82 | 37.02 | 40.66 | 40.66 |
| *Gelidium caulacantheum* | 16.15 | 1.82 | 12.05 | 13.24 | 53.9 |
| *Ulva* spp. | 10.8 | 9.08 | 10.38 | 11.4 | 65.3 |
| *Hormosira banksii* | 14.06 | 0 | 10.31 | 11.32 | 76.63 |
| Encrusting coralline algae | 6.92 | 1.04 | 5.18 | 5.68 | 82.31 |
| *Cystophora scalaris* | 1.61 | 0 | 1.58 | 1.73 | 84.05 |
| *Echinothamnion hystrix* | 1.96 | 0.22 | 1.54 | 1.69 | 85.73 |
| *Sarcothalia lanceata* | 2.44 | 0 | 1.48 | 1.62 | 87.36 |
| *Champia novae-zelandiae* | 1.7 | 0 | 1.19 | 1.31 | 88.67 |
| *Polysiphonia* spp. | 0.81 | 0.55 | 0.88 | 0.97 | 89.64 |
| *Colpomenia bullosa* | 0.93 | 0 | 0.78 | 0.86 | 90.49 |

**C) Post-earthquake low zone**

| Taxa | Low uplift vs Medium uplift - Average dissimilarity = 66.89 | | | | |
|---|---|---|---|---|---|
| | Average abundance Control | Average abundance Low-uplift | Average dissimilarity | Contribution % | Cumulative contribution % |
| *Carpophyllum maschalocarpum* | 38.43 | 14.79 | 10.33 | 15.44 | 15.44 |
| Encrusting coralline algae | 33.53 | 40.12 | 9.22 | 13.78 | 29.22 |
| Articulated coralline algae | 12.97 | 10.75 | 4.48 | 6.7 | 35.93 |
| Encrusting algae | 11.88 | 4.13 | 4.07 | 6.08 | 42.01 |
| *Echinothamnion hystrix* | 3.22 | 8.43 | 3.26 | 4.88 | 46.89 |
| *Marginariella boryana* | 3.73 | 7.2 | 2.94 | 4.4 | 51.29 |
| *Durvillaea willana* | 3.75 | 5.03 | 2.6 | 3.89 | 55.18 |
| *Streblocladia muelleriana* | 0.34 | 8.13 | 2.52 | 3.76 | 58.94 |
| *Durvillaea poha* | 3.93 | 3.56 | 2.36 | 3.53 | 62.47 |
| *Ulva* spp. | 3.03 | 5.43 | 2.15 | 3.22 | 65.69 |
| *Pterocladia lucida* | 0.68 | 6.84 | 2.13 | 3.19 | 68.88 |
| *Cystophora scalaris* | 4.68 | 1.09 | 2 | 3 | 71.87 |
| *Ectocarpus* spp. | 1.18 | 4.27 | 1.8 | 2.69 | 74.56 |
| *Lessonia variegata* | 2.08 | 3.75 | 1.63 | 2.43 | 76.99 |
| *Gelidium microphyllum* | 3.73 | 1.48 | 1.49 | 2.23 | 79.22 |
| *Chondria macrocarpa* | 1.25 | 3.95 | 1.42 | 2.13 | 81.35 |
| Filamentous red algae | 1.31 | 3.7 | 1.41 | 2.1 | 83.46 |
| *Polysiphonia* spp. | 2.64 | 1.11 | 1.15 | 1.72 | 85.18 |
| *Halopteris* sp. | 2.98 | 1.36 | 1.11 | 1.67 | 86.85 |
| *Dictyota* spp. | 2.29 | 0.64 | 0.83 | 1.24 | 88.09 |
| *Sarcothalia lanceata* | 0.07 | 2.65 | 0.82 | 1.22 | 89.31 |
| *Glossophora kunthii* | 1.73 | 0.69 | 0.67 | 0.99 | 90.31 |

| Taxa | Low-uplift vs High-uplift - Average dissimilarity = 81.9 | | | | |
|---|---|---|---|---|---|
| | Average abundance - Low-uplift | Average abundance - High-uplift | Average dissimilarity | Contribution % | Cumulative contribution % |
| *Carpophyllum maschalocarpum* | 38.43 | 6.51 | 15.76 | 19.24 | 19.24 |
| Encrustng coralline algae | 33.53 | 21.67 | 12.92 | 15.78 | 35.02 |
| *Streblocladia muelleriana* | 0.34 | 18.47 | 6.54 | 7.99 | 43.01 |
| Articulated coralline algae | 12.97 | 0 | 6.03 | 7.37 | 50.37 |
| Encrusting algae | 11.88 | 1.44 | 5.55 | 6.77 | 57.14 |
| *Echinothamnion hystrix* | 3.22 | 11.7 | 4.79 | 5.84 | 62.99 |
| *Chondria macrocarpa* | 1.25 | 9.73 | 3.74 | 4.56 | 67.55 |
| *Cystophora scalaris* | 4.68 | 0 | 2.7 | 3.29 | 70.84 |
| *Ulva* spp. | 3.03 | 3.87 | 2.36 | 2.89 | 73.73 |
| Filamentous red algae | 1.31 | 4.9 | 2.06 | 2.52 | 76.25 |
| *Durvillaea willana* | 3.75 | 0 | 1.69 | 2.06 | 78.31 |
| *Marginariella boryana* | 3.73 | 0 | 1.68 | 2.05 | 80.35 |
| *Gelidium microphyllum* | 3.73 | 0 | 1.65 | 2.02 | 82.37 |
| *Durvillaea poha* | 3.93 | 0 | 1.55 | 1.9 | 84.27 |
| *Halopteris* sp. | 2.98 | 0.31 | 1.53 | 1.87 | 86.13 |
| *Polysiphonia* spp. | 2.64 | 0 | 1.28 | 1.57 | 87.7 |
| *Glossophora kunthii* | 1.73 | 1.95 | 1.21 | 1.48 | 89.18 |
| *Dictyota* spp. | 2.29 | 0.25 | 1.09 | 1.33 | 90.52 |