Cascading impacts of earthquakes and extreme heatwaves have destroyed populations of an iconic marine foundation species

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Abstract

Aim: Ecologists traditionally study how contemporary local processes, such as biological interactions and physical stressors, affect the distribution and abundance of organisms. By comparison, biogeographers study the distribution of the same organisms, but focus on historic, larger-scale processes that can cause mass mortalities, such as earthquakes. Here we document cascading effects of rare biogeographical (seismic) and more common ecological (temperature-related) processes on the distribution and abundances of coastal foundation species.

Location: Intertidal wave-exposed rocky reefs around Kaikōura, New Zealand, dominated by large, long-lived, and iconic southern bull kelps (Durvillaea antarctica and Durvillaea willana).

Methods: In November 2016, a 7.8 Mw earthquake uplifted the coastline around Kaikōura by up to 2 m, and a year later the region experienced the hottest summer on record. Extensive sampling of intertidal communities over 15 km coastline were done shortly after the earthquake and heatwaves and 4 years after the earthquake.

Results: Durvillaea lost 75% of its canopy to uplift and the heatwaves reduced canopies that had survived the uplift by an additional 35%. The survey done 4 years after the earthquake showed that Durvillaea had not recovered and that the intertidal zone in many places now was dominated by small turfs and foliose seaweed.

Main conclusions: Cascading impacts from seismic uplift and heatwaves have destroyed populations of Durvillaea around Kaikōura. Surviving smaller and sparser Durvillaea patches will likely compromise capacity for self-replacement and lower resilience to future stressors. These results are discussed in a global biogeographical-ecological context of seismic activity and extreme heatwaves and highlight that these events, which are not particularly rare in a geological context, may have common long-lasting ecological legacies.
1 | INTRODUCTION

Ecologists traditionally study how ubiquitous processes such as competition, predation, disturbance and abiotic stress affect the distributions and abundances of populations, species and communities (Begon et al., 1986; Smith & Smith, 2015). These processes typically take place over short temporal (days-decades) and small spatial (cm-km) scales. Similarly, larger-scale events, such as hurricanes, fires, droughts and heatwaves, which are often associated with climate change, can have important effects on ecosystem structure (Buma, 2015; Lugo, 2008; Lundholm, 2009; Sippel et al., 2018). For example, atmospheric heatwaves have altered population demographics and species interactions and caused poleward range movements and localized extinctions of foundation species, which provide critical biogenic habitat for associated species and ecosystem functioning (Chen et al., 2011; Dillon et al., 2010; Ellison, 2019; Thomas et al., 2004). Like ecologists, palaeontologists and biogeographers also study processes that affect distributions and abundances of organisms but focus on rarer events and longer temporal (millennia to millions of years) and larger spatial (km to global) scales, such as stochastic long-range dispersal incidents or cataclysmic tectonic events that can cause extinctions and dispersal barriers (Black & Black, 1988; Brown, 2009; Cox et al., 2016; Crisci, 2001). However, these traditional disciplinary boundaries are human-made constructs, and it is increasingly recognized that studies across spatiotemporal scales are required for better understanding of present-day distributional patterns (Crisci et al., 2006; Wiens & Donoghue, 2004).

In the marine environment, heatwaves have intensified in recent decades, and models project that they will continue to become stronger and more frequent (Frölicher et al., 2018; Hobday et al., 2018; Oliver et al., 2019; Sen Gupta et al., 2020). Over the last few decades, marine heatwaves have caused coral bleaching, localized extinctions, poleward range-shifts of many species of fish and seaweed and altered species interactions (Cheung & Frölicher, 2020; Smale & Wernberg, 2013; Thomsen et al., 2019; Wernberg et al., 2013). At longer time scales, many coastal ecosystems have also experienced extreme disturbances associated with seismic activity such as earthquakes and volcanic eruptions (Castilla & Oliva, 1990; Castilla et al., 2010). However, traditional marine ecology (e.g. textbooks like Castro & Huber, 2019; Kaiser et al., 2011) do not typically discuss large-scale disturbances associated with seismic activity in a context of contemporary species distributions and biodiversity. Nevertheless, rare mega-disturbances do affect local biodiversity with ramifications for many years to come. For example, historic and contemporary earthquakes have affected present-day species distributions (Haven, 1964; Noda et al., 2016; Rodil et al., 2016). Such examples show that the extreme events traditionally studied by biogeographers and palaeontologists can be relevant for ecologists and the study of contemporary ecosystems.

On November 14, 2016, a 7.8 $M_w$ (on the moment magnitude scale) earthquake struck the northeast South Island of New Zealand, with the epicentre located 60 km south-west of the small coastal town of Kaikoura (Clark et al., 2017; Hamling et al., 2017; Kaiser et al., 2017). With a shallow hypocentre of 15 km and many complex inshore and offshore faults, slips, vertical displacements, coastal uplifts of up to 6.5 m, and >2,000 aftershocks in only 3 days, four of which had magnitude >6 $M_w$, these earthquakes directly affected c. 130 km coastline (Clark et al., 2017; Hamling et al., 2017; Xu et al., 2018). Over the next few months, we observed extensive loss of habitat-forming seaweeds and slow-moving benthic invertebrates, with associated losses of primary productivity, biogenic habitat and altered food webs (Gerrity et al., 2020; Schiel et al., 2019; Thomsen et al., 2020). A year later, over the austral summer of 2017/18, New Zealand experienced the strongest marine heatwave on record (Salinger et al., 2019, 2020). This large-scale extreme marine event, coincided with high air temperatures, low tides and calm sea conditions (Salinger et al., 2020; Thomsen et al., 2019), and had widespread effects such as high glacial melting, losses of habitat-forming seaweeds, and movement of fish into warm waters (Salinger et al., 2020; Schiel et al., 2019; Tait et al., 2021; Thomsen et al., 2019; Thomsen & South, 2019). Following Hobday et al. (2018), this large-scale temperature anomaly was named the "Tasman Sea 2017/18 marine heatwave" (Perkins-Kirkpatrick et al., 2019; Salinger et al., 2019). However, analyses of local sea temperature data show that this heatwave was comprised of multiple consecutive events (see Result section), and the term is hereafter pluralized and referred to as "heatwaves."

Some of the major coastal species that appeared to be immediately affected by the earthquakes were the southern bull kelps, Durvillaea spp. (see Figure 1, hereafter just bull kelps). Bull kelps are the world’s largest fucoid algae, with individuals of some species reaching up to 10 m long, weighing up to 70 kg and living up to 10 years (Hay, 1979, Nelson 2013, Hay, 2020). Bull kelps are also iconic, culturally important seaweeds in New Zealand and other many other places in the southern hemisphere where they control local diversity and ecological functioning (Schiel, 2019; Taylor & Schiel, 2005; Thomsen & South, 2019). Southern bull kelps are also iconic, culturally important seaweeds in New Zealand and other parts of the world, such as Chile. For example, there is a long traditional use of Durvillaea spp. as storage bags, known as "pōhā" in New Zealand, and as a source of food in Chile for at least 14,000 years (Dillehay et al., 2008). The iconic nature of bull kelp is reflected in its use in cultural and spiritual symbolism (Pérez-Lloréns et al., 2020) such as being emblematic of the knowledge and status of the people.
We examined changes to the distribution and abundance of bull kelp around Kaikōura, following the 2016 earthquakes and 2017/18 heatwaves and whether they returned or were replaced by alternative foundation species (large canopy-forming seaweed, such as *Lessonia variegata* and *Carpophyllum mashalocarpum*) that were also common in the region (Schiel, 2006; Thomsen & South, 2019). These results are discussed in the context of other large-scale impacts over long time periods.

### METHODS

#### 2.1 Study system and marine heatwaves in the Kaikōura region

The bull kelp species in this study were *Durvillaea antarctica*, which occurs at the lowest tidal zone, and *D. willana*, which occurs slightly deeper in the subtidal zone and is only partially exposed at the lowest tides. A third bull kelp species, *D. poha*, can be morphologically similar to *D. antarctica*, but inhabits slightly less wave-exposed habitats and is absent (or very rare) along the Kaikōura coastline (Fraser et al., 2012; Peters et al., 2020; Vaux et al., 2021; Velásquez et al., 2020). Additionally, there are two recognized clades of *D. antarctica* in New Zealand that are distributed to the north and south of Banks Peninsula, and therefore, most of the *D. antarctica* populations studied here belonged to the *D. antarctica* “NZ north” clade, whereas the Moeraki samples used as controls in survey 1 were of the *D. antarctica* “NZ south” clade (Fraser et al., 2020). Bull kelps have exceptionally strong and large holdfasts and their heavy fronds affect the subcanopy environment and biodiversity through shading and whiplash (Schiel, 2019; Thomsen & South, 2019). The physical attributes of the Tasman Sea 17/18 marine heatwaves, and covarying environmental factors, such as low wind speed, fewer waves and high land temperatures, as well as co-occurring spring tides, have
been analysed and discussed in great detail (Perkins-Kirkpatrick et al., 2019; Salinger et al., 2019, 2020; Thomsen et al., 2019). To highlight that the Kaikōura coastal region was embedded in this heatwave event, we produced a large-scale heat map showing the maximum extent of the Tasman Sea 17/18 MHWs (i.e. for January 27, 2018, Figure 2a). To show that the 17/18 event was extreme compared to past MHWs, we added local-scale temporal analysis of sea surface temperatures describing all MHWs near Oaro and Kaikōura peninsula (grid centred around 173.625, −42.625 and 173.875, −42.375, respectively) between 1/1-1982 and 1/1-2020. The distance from the reef sites to the grid centre was <25 km. For each of the two sites, we identified all MHWs and calculated their maximum intensity (temperature above the 90% threshold in °C), durations (in days) and cumulative intensity (duration × intensity).

For brevity, we only show maximum intensity (Figure 2b), whereas duration and accumulated intensity are reported in the Appendix S1. The MHW analyses were done using the R package HEATWAVE version 0.4.5 (Schlegel & Smit, 2018; Smit et al., 2018), which defines a MHW as a period of 5 or more consecutive days where the sea surface temperature is greater than the 90th percentile calculated from a 30 year climatology (period between 1/1-1983 and 31/12-2012). Analyses were based on NOAA high-resolution blended analysis of daily sea surface temperature data in ¼ degree grids derived from satellites and in situ data (oist v2.1, accessed from https://coastwatch.pfeg.noaa.gov/erddap/index.html) (Huang et al., 2021). More details, including codes and outputs, are available at: https://rpubs.com/FranToto/Thomsen2021_MHW and https://github.com/FranToto/Thomsen_etal_2021_MHW_EQ.

**FIGURE 2** (a) Maximal areal extent of the Tasman Sea marine heatwave (January 27, 2018) covering c. 5.4 million km$^2$. (b) Maximum intensity of marine heatwaves recorded offshore of the Kaikōura Peninsula and Oaro between 1982 and 2020 (see Appendix S1 for similar data for other heatwave metrics). (c) Sample sites along the Kaikōura coastline. Oaro is the non-uplifted control reef, and the blue markers show locations of 15 uplifted reefs (0.5–2 m uplift) numbered with distance from Oaro. All reefs were sampled in Survey 1, reefs 1, 2, 4, 6, 7 and 8 were sampled in Survey 2, and reefs 1, 2, 4, 6, 9, and 15 were sampled in Survey 3.
2.2 | Survey 1: Loss of bull kelp within months of the earthquake

The control reef at Oaro was selected due to its proximity to uplifted reefs and because it had similar high cover of bull kelp beds prior to the earthquake (Figure 1a). Oaro and the 15 uplifted reefs (0.5–2 m), were surveyed in February–March 2017 during low spring tides, when access was logistically possible. For this study, the zone that had been inhabited by bull kelp prior to the uplift was divided into three elevation bands. The high band was visibly "white" because all the calcified understory red algae had died and were bleached by the sun (Figure 1b–f). There were also many obvious holdfast scars of dead bull kelp in this zone (Figure 1d,e). The mid band was visibly brown and red or pink because bull kelp canopies were still present, and the understory was still dominated by living encrusting red algae (Figure 1h). Generally, what was previously lower on the intertidal shore became the high band at around >1.75 m above the lowest astronomical tide datum (LAT), the mid band was uplifted from the shallow subtidal zone into the mid-intertidal (~0.75–1.75 m), and the low band (< ~0.75 m above LAT) was uplifted from deeper than around ~0.5 m. At each reef and elevation band, photographs were taken of haphazardly positioned 0.5 × 0.5 m quadrats and we quantified: (1) number of bull kelp stipes with intact blades, (2) number of stipes without blades, (3) percentage cover of intact holdfasts, (4) number of holdfast scars and (5) per cent cover of holdfast scars. Stipes were counted because they represent individuals, whereas holdfasts can consist of several coalesced individuals. Holdfast scars were near-circular, bare reef sections (Schiel, 2019; Thomsen et al., 2019). Data for D. antarctica and D. willana were pooled because these species cannot be separated from observations of scars or holdfasts without stipes. Previous analyses have shown that small-scale, reef-specific degree of uplift did not correlate with any of the five measured responses (Mondardini, 2018) and this aspect was therefore not explored. None of the responses could be transformed to variance homogeneity (Levine’s tests, p < .001), and sampling was unbalanced between elevation bands and uplifted and control reefs. Standard or permutation based ANOVA could therefore not be used (Anderson et al., 2017). Instead, we used pairwise Mann–Whitney tests on relevant data subsets to test for differences between the control site at Oaro versus uplifted reefs (a total of 10 tests for the 5 responses; excluding the high band, which was not present at Oaro) and between the three elevation bands at the uplifted reefs only (a total of 15 tests for the 5 responses). We note that 1 in 20 tests may be inflated based on an a priori significant level of 0.05 when multiple analyses are done (Anderson, 2005). All bull kelp and algae data are reported as means and standard errors (SE).

To relate abundances of bull kelp holdfasts (with or without blades as measured above) to pre-earthquake healthy live bull kelp canopies, percent cover of bull kelp holdfasts was estimated in 40 50 × 50 cm quadrats haphazardly positioned within dense bull kelp beds (i.e. with 100% canopy cover) at Moeraki, a southern site not affected by earthquakes and less affected by the Tasman Sea 17/18 heatwave (Thomsen et al., 2019; Thomsen & South, 2019). The 40 quadrats were collected over a period of 2 years with ten quadrats collected in Autumn and Spring in 2019 and 2020.

2.3 | Survey 2: Cascading loss of bull kelp after the earthquakes and heatwaves

Six of the uplifted reefs (Figure 2c) were sampled with an Advanced Phantom 3 drone equipped with a 12 MP HD camera, before and after the summer period of the Tasman Sea 2017/18 marine heatwaves. Images were taken 10 m above each reef during low tide, with each image covering c. 95 m², estimated from survey tapes and 1 m² fixed quadrats positioned on each reef (Murfitt et al., 2017; Thomsen et al., 2019). At this height, individual live kelps are easily differentiated from rocks or other seaweeds that have different sizes, shapes and coloration. A total of 161 geotagged drone images (12–35 per reef) were captured between April–July 2017, covering the period from shortly after the earthquakes but before the onset of the heatwaves. Another set of 161 images with similar geocoordinates was collected on these reefs in April 2018 after the heatwaves. In processing images, percent cover of white (calcified dead algae), green (Ulva spp.) and bull kelp areas were estimated visually for each image with a superimposed grid of 100 cells. Based on results from Survey 1, the white and green areas observed in the 2017 drone images on the uplifted reefs were confidently interpreted as representing recently dead bull kelp because there was high percent cover of new reef scars and ghost holdfasts (Figures 1 and 3). Percent loss of bull kelp following the earthquakes was calculated as of cover of (white + green areas)/(white + green + bull − kelp areas) × 100 for each 2017 image. Then, for each image, the of bull kelp lost following the heatwaves was calculated as the area of bull kelp2016/bull kelp2017 × 100. The number of drone images for the heatwave impact was less than for uplift analyses because images with 100% loss of bull kelp from the earthquake were removed from the heatwave analyses. Data had, like for survey 1, strong variance heterogeneity (Levine’s tests, p < .001) and we therefore used three Mann–Whitney tests to investigate whether (a) percent canopy loss from the uplift was greater at the uplifted reefs compared to at Oaro (i.e. an uplift effect due to the earthquake), (b) the loss from the heatwaves was greater at the uplifted reefs compared to Oaro (i.e. if a previous uplift effect modified heatwave effects) and (c) whether the loss reported after the earthquakes was greater than the loss reported from the heatwaves (i.e. the earthquake effects relative to the later heatwave effects, here excluding the Oaro data because this reef did not experience uplift).
2.4 | Survey 3: Recovery or replacement of bull kelp with alternative foundation species after 4 years

Bull kelps are competitively superior foundation species that control biodiversity (Schiel, 2019). However, there are a range of species on the Kaikōura coastline that are also foundation species and, although they are typically subordinate to bull kelps, it is possible that they benefited from large-scale losses of bull kelp to become more dominant. We evaluated whether bull kelp had recovered or been replaced by alternative foundation species such as the barnacle Chthamalus giganteus and the fucoids Petalonia farciminoso and Lessonia variegata. We also evaluated the presence of alternative foundation species in the categories of white/dead encrusting algae, encrusting reds, green and other brown algae. Survey 3 data were only evaluated graphically due to the absence of “before” data and because statistical tests among shore bands were unnecessary due the almost total absence of alternative foundation species in the high and mid bands.

2.5 | Earthquakes and heatwaves in a global context

To consider our results in a global context, rare and potentially cataclysmic events that could have implications for coastal ecosystems were identified by combining the positions of the Kaikōura 2016 earthquake, the Tasman Sea 2017/18 MHW, historically recorded earthquakes and volcanic eruptions, and the 62 most extreme marine heatwaves since 1982 in a single map. Earthquake data were downloaded from the Significant Earthquake Database that contains information on the most destructive earthquakes from 2,150 BCE to the present that had (a) at least moderate damage (≥US $1 million), (b) 10 or more human deaths, (c) Magnitude 7.5 or greater (Modified Mercalli Intensity) and/or (d) generated a tsunami (accessed 1/11-December 2020 at six of the uplifted reefs (Figure 2c). At each reef, between 10 and 15 geotagged digital photographs were taken at random at ca. 1 m from the reef surface in the three elevation bands (high, mid and low) previously dominated by bull kelp. Each of these photos was taken at low spring tide and covered approximately 1 m² reef surface (Thomsen et al., 2020). For each photograph, percent cover was quantified for live D. antarctica and D. willana (Figure 1h), other fucoids and kelp species, and smaller seaweeds grouped into the categories of white/dead encrusting algae, encrusting reds, green and other brown algae. Survey 3 data were only evaluated graphically due to the absence of “before” data and because statistical tests among shore bands were unnecessary due to the almost total absence of alternative foundation species in the high and mid bands.

3 | RESULTS

3.1 | Marine heatwaves in the Kaikōura region

The Kaikōura peninsula and Oaro have experienced 105 and 119 marine heatwaves, respectively, since 1982 (Figure 2b). At Kaikōura and Oaro, the three (4.4°C, 40 days, 3.5°C, 37 days and 3.2°C, 20 days) and two (4.7°C, 40 days, 3.6°C, 20 days) strongest events on record occurred, respectively over the summer of 2017/18.

3.2 | Survey 1: Loss of bull kelp after the earthquakes

There were significant differences in the low band between the uplifted reefs and the Oaro control reef, for all response variables (p < .001), except “stipe with blades” (p = .50, Figure 3). However, in the mid band only “stipes without blades” (p = .001) and “holdfast percentage cover” (p = .027) were significantly different between Oaro and the uplifted reefs. Densities of stipes without blades were greater at uplifted reefs compared to Oaro in the low (0.12 ± 0.07 SE vs. 0.07 ± 0.04 SE) and mid (0.12 ± 0.12 SE vs. 0.07 ± 0.04 SE) bands. The percentage cover of holdfasts was greater at uplifted reefs compared to Oaro, for the mid (13.3 ± 0.42 vs. 4.25 ± 2.89) and low (18.3 ± 0.91 vs. 11.96 ± 0.65) bands. Densities (0.49 ± 0.07 vs. 0.20 ± 0.04) and per cent cover (2.97 ± 0.47 vs. 1.05 ± 0.25) of holdfast scars in the low band were greater at the uplifted reefs compared to Oaro.

For the uplifted reefs only, most responses were significantly different between elevation bands (p < .001). There were significant increases in percentage cover and density of holdfast scars from low, to mid, to high bands and significant decreases in the percentage cover of holdfasts (Figure 3a,b,e). Per cent cover of holdfast scars increased from to 2.97 (±0.47) to 9.38 (±0.49), density of holdfast scars increased from 0.49 (±0.07) to 2.08 (±0.11) whereas per cent cover of remaining holdfasts decreased from 18.33 (±0.92) to 7.77 (±0.51), from the low data from 1982 to 2017). First, shape-polygons were extracted from Figure 5 in Sen Gupta et al. (2020). These were overlaid onto a map of the world’s coastline, converted to raster-format and the distance of coastline affected by each extreme marine heatwave was calculated. The same methodology described in Sen Gupta et al. (2020) was used to quantify the attributes of the Tasman Sea 2017/18 heatwaves and calculate the length of affected coastline to allow for direct comparisons with the 62 other extreme events. Coastlines have fractal properties, so calculating absolute coastline distance depend on the scale of observation. We therefore used the same scale to calculate the global coastline as well as MHW-impacted coastlines (1:10,000,000), to provide a robust measure of the percentage of coastline affected. More details, including R- codes related to calculating coastal distances for earthquakes, volcanic eruptions and extreme MHWs, are at https://github.com/FranToto/Thomsen_etal_2021_MHW_EQ and https://rpubs.com/FranToto/Thomsen2021_MHW.
to high bands. For stipes without blades, the greatest densities were in the mid band (2.17 ± 0.07; Figure 3c) with similar lower densities between the low and high bands (1.29 ± 0.12). By comparison, densities of stipes with blades were greater in the low compared to the mid and high bands (Figure 3d, 4.41 ± 0.34 vs. 0.25 ± 0.05). Finally, the holdfast-canopy survey from Moeraki, showed that lower elevation bands within extensive closed bull kelp canopies had, on average, 8 ± 1.4% cover of holdfasts (n = 40). This result suggests that the low and mid bands at the uplifted reefs, prior to the earthquakes likely had closed bull kelp canopies (Figure 3e). The quadrats at Moeraki also had 56.7 ± 3.7% cover of encrusting coralline algae showing that healthy bull kelp beds have high abundances of encrusting coralline beneath their canopies (see Appendix S1).

3.3 | Survey 2: Cascading loss of bull kelp after the earthquakes and heatwaves

Loss of bull kelp after the earthquake was significantly greater at the uplifted reefs compared to Oaro across all bands (35.3 ± 3.2 vs. 61.2 ± 6.6%, p < .001; U-Statistics = −3.53, N = 239). Finally, on the uplifted reefs only, the loss from the earthquakes was significantly greater than the subsequent loss following the heatwaves (75.5 ± 2.3 vs. 35.3 ± 3.2%, p < .001; U-Statistics = −8.27, N = 336).

3.4 | Survey 3: Replacement of bull kelp with alternative foundation species

There were no bull kelps in the high band, a few scattered individuals in the mid band, and low cover in the low band (Figure 5, 1.5% D. antarctica, 7% D. willana). By contrast, small foliose, filamentous, and turf seaweeds, typically between 3 and 30 cm long, dominated the low and mid-elevation bands. Encrusting algae were found in all bands but were less common in the low band (4% cover) compared to healthy bull kelp beds (typically c. 60% cover, see supporting data). Six alternative foundation species were found in the mid (with low cover values) and low elevation bands (with low to mid-cover values) including Carpophyllum maschalocarpum (most common), followed by Lessonia variegata, Cystophora scalaris, C. torulosa, Landsburgia quercifolia, Marginariella spp. and Hormosira banksii.
3.5 | The Kaikōura earthquakes and marine heatwaves in a global context

The Significant Earthquake Database showed that >6,200 large and destructive earthquakes occurred over the last 4,150 years (Figure 6), of which 453 were of similar or of larger magnitude than the Kaikōura 7.8 Mw event. Furthermore, a minimum of 9,908 volcanic eruptions have been confirmed over the same time period, with a mean Volcanic Explosivity Index (VEI) of 1.9 and where 529 events had a VEI 4 or more. From these data, it was calculated that 4,186, 2,749, 2,565, 2,606 and 4,002 events occurred 0–10, 11–25, 26–50, 51–100 or more than 100 km from the coastline, respectively. In other words, 75% (12,106) of the recorded seismic events occurred with 100 km of a coastline (Figure 6) and may therefore have affected coastal organisms.

Around 175,597 km of the world’s coastline has been affected by the 62 most extreme marine heatwaves recorded between 1982 and 2017. Using Sen Gupta et al. (2020) methodology to identify areas with “Max intensity, with severity >2,” the maximum areal extent of the Tasman Sea 2017/18 was estimated to cover 5.4 million km$^2$ on the 27/01/2018 (Figure 2a), with a maximum intensity of 15.8°C M km$^2$ (on 28/01/2018), based on a core date range of 15/11/17-14/04/18. These data, when sorted by Maximum Intensity $S \geq 2$, make the Tasman Sea 2017/18 event the 5th most extreme event recorded worldwide since 1982. From these data, we calculated (as for the 62 previously recorded extreme events) that an additional 6,703 km coastline was affected, adding the total amount of coastline affected by extreme marine heatwaves since 1982 to 182,300 km (Figure 6), representing about 15% of global coastline.

4 | DISCUSSION

4.1 | Loss of bull kelp

The earthquakes in November 2016 uplifted ca. 50 km of wave-exposed rocky substrate between 0.5 and 6 m (31 km of boulder reefs and 16 km of consolidated reef) (Gerrity et al., 2020). This uplift caused a 75% canopy loss of bull kelp in the southern Kaikōura region. Furthermore, we found an additional 35% canopy loss of the surviving bull kelp populations following consecutive heatwaves over the summer of 2017/18.

Dramatic uplift-associated loss has also been observed on wave-protected reef-platforms for smaller intertidal habitat-forming fucoids, such as Hormosira banksii and Cystophora spp., following the same earthquakes (Schiel et al., 2019; Thomsen et al., 2020). It is likely that the 75% loss of bull kelp encapsulates a disproportional amount of the intertidal D. antarctica compared to the shallow subtidal D. willana (Figures 1h and 5) because D. antarctica was instantly lifted to a very high elevation characterized by extreme emersion and desiccation stress (Morton & Miller, 1973). By comparison, D. willana...
inhabits depths of 0–5 m, and therefore, many individuals have remained within the vertical range of the species after the 0.5–2 m uplift at the study sites (Hay, 1979; 2020; Vaux et al., 2021). Greater rates of heatwave-associated loss of bull kelp were also proportionally less on the uplifted reefs compared to Oaro (Figure 4), perhaps because the uplift had already selected harder individuals (Bennett et al., 2015; Coleman & Wernberg, 2020; Gurgel et al., 2020; King et al., 2018) or possibly because the bull kelp beds contained D. poha, a species of bull kelp with a typically southern distribution and likely less tolerant to temperature stress (Thomsen et al., 2019; Vaux et al., 2021; Velásquez et al., 2020). Together, the earthquakes and heatwaves have massively reduced the abundance of bull kelp along the Kaikōura coastline, ranging from heatwave only induced losses at non-uplifted sites (>60% at Oaro) to beyond the extent quantified in this study (north of Kaikoura peninsula to Cape Campbell) where reefs were uplifted up to 6 m and almost all bull kelp were destroyed (Gerrity et al., 2020; Schiel et al., 2019; Thomsen et al., 2020).

To date, most research on impacts from marine heatwaves has focused on the effects of temperature on subtidal algal forests in isolation (Smale et al., 2019; Straub et al., 2019). However, grazing, wave exposure, turbidity or nutrient levels can modify temperature-induced losses of kelp (Butler et al., 2020; Ling et al., 2009; Tait et al., 2021; Zimmerman & Robertson, 1985). Multiple co-occurring and cascading ecological stressors and disturbances often have complex interactions and it is therefore important to quantify impacts from marine heatwaves in concert with other stressors (Crain et al., 2008; Harvey et al., 2013; Hawkins et al., 2008). Here, bull kelp losses from heatwaves were smaller on reefs that had already experienced losses due to seismic uplift, but these results could have been modified by other covarying stressors such as high summer air temperatures, high irradiance, lower-than-usual tides and low wave energy events (Salinger et al., 2019, 2020; Thomsen et al., 2019). In other words, impacts from marine heatwaves may often be modified by a complex set of covarying factors, and therefore, they should be studied as a multi-factorial stressor.

### 4.2 Dominant intertidal seaweeds 4 years after the earthquakes

No alternative foundation species (sensu Thomsen & South, 2019)—large perennial habitat-forming fucoids or laminarians—colonized the high and mid bands of the uplifted coastline previously inhabited by bull kelp. The high band of the former bull kelp habitat turned white because the substrate had high cover of encrusting calcareous red algae that were bleached by the sun following the uplift (Figure 1) (Schiel et al., 2019). This band became inhabited by typical upper-shore species such as limpets, barnacles and small seaweeds (Figure 5). The mid band of green ephemeral turf algae was initially short-lived (Schiel et al., 2019), but 4 years after the earthquakes it returned in late spring and summer (Figure 5). Ephemeral turf algae are often the first colonizers after disturbances in this region and around the world (Connell et al., 2014; Filbee-Dexter & Wernberg, 2018; Lilley & Schiel, 2006). Finally, the low intertidal to shallow subtidal band became dominated by a mixture of foliose, bladed, filamentous and turf algae (e.g. *Polysiphonia* spp., *Sarcophalia* spp.), patches of surviving bull kelp (mainly *D. willana*) and scattered alternative foundation species, such as the kelp *Lessonia variegata*.
and the fucoids *Carpophyllum maschalocarpum* and *Marginariella boryana* (Figure 5).

### 4.3 Wider ecological consequences

While it is challenging to determine the exact areal extent of bull kelp loss following the earthquakes, preliminary estimates suggest that around 125,000 m² bull kelp forest could have been lost to the uplift (if 25% of the rocky coastline was dominated by bull kelp and that the combined mid and high bull kelp band on average was ca. 10 m wide). The wider cascading impact from the uplift and heatwaves have resulted in the loss of millions of bull kelp individuals and likely an ongoing reduction in bull kelp cover on the Kaikōura coast (Figure 7). Surviving smaller and more patchy populations can have lower genetic diversity and may be less resilient to recover from future disturbances (Buma, 2015; Elmqvist et al., 2003; Frankham, 2005). Furthermore, new ecological states can arise when severe or cumulative disturbances serve as tipping points from one state to another and alter patterns of recruitment, habitat dominance and networks of interactions within an ecosystem (Benedetti-Ceccchi et al., 2015; Dai et al., 2012; Hawkins et al., 2015; Moore, 2018). It is likely that the positive feedbacks (propagule pressure, habitat maintenance) that maintained bull kelp forests have been lost and it is possible that a new stable state dominated by small turf and foliose algae is in development (Figure 7), as has been seen in many other parts of the world (Filbee-Dexter et al., 2016; O’Brien & Scheibling, 2018). Such turf assemblages are typically limited by large canopy-forming algae, but once established can prohibit colonization by canopy-formers through habitat modification, competition for primary space and the resulting reductions in propagule pressure (Jenkins et al., 2004; Kennelly, 1987; Petraitis & Dudgeon, 2004; Smale, 2020). If such an alternative state persists, it will likely result in long-term reductions of bull kelp-associated species and ecosystem services such as carbon-storage and the dampening of wave action (Filbee-Dexter & Wernberg, 2018; Smale, 2020).

### 4.4 Caveats and limitations of the study

The inherent unpredictability of cataclysmic events such as earthquakes often necessitates ad hoc research designs such as the one presented here. In this instance, we had very few data for the most impacted zones prior to the earthquake, which would have allowed for direct before/after contrasts. Instead, we developed a method based on robust ecological criteria (presence of dead, decaying and living bull kelp holdfasts) to estimate the extent of bull kelp cover prior to the earthquakes and heatwaves at our study sites. The tenacity of the bull kelp holdfasts, contrasts to an unimpacted control site, ancillary data from a southern reference site, and our extensive experience working on the Kaikōura coastline (Schiel et al., 2019; Schiel et al., 2016; Thomsen et al., 2020) contributed to this being a robust, if not ideal method. For example, it was impossible to determine whether decayed holdfasts were *D. antarctica* preventing us from assessing the pre- and post-earthquake relative abundance of these species at our study sites. Another limitation of this study was the lack of multiple control sites to incorporate site-site variability into our contrasts between uplifted and non-impacted reefs. However, our control reef at Oaro was the only unimpacted reef along ~100 km of coastline, and the only accessible bull kelp reef for hundreds of kilometres and is typical of bull kelp reefs elsewhere (Schiel, 2019; Schiel et al., 2018; Thomsen et al., 2019).

### 4.5 The Kaikōura earthquakes and heatwaves in a global context

Earthquakes and extreme heatwaves are often considered unique and rare disturbances that have little relevance for traditional and contemporary ecology (e.g. textbooks such as Begon et al., 1986; Castro & Huber, 2019; Kaiser et al., 2011; Nybakken, 1993; Smith & Smith, 2015). However, on a global scale almost 15,000 high-impact
earthquakes and volcanic eruptions have been recorded over the last 4 millennia, of which 75% were within 100 km of the coastline, providing circumstantial evidence that seismic activity may have common legacy effects. While the individual traits (e.g. uplift, subsidence or horizontal displacement) of these 15,000 earthquakes have not been studied, it is likely that their impacts varied depending on their traits and magnitudes, and the physical and biological characteristics of the affected shoreline. For example, earthquakes can directly affect organisms by altering their elevation on a shore, through indirect effects such as increased sedimentation, but also through the destruction and creation of new habitat, as occurs when boulders are deposited in the marine environment (Bodin & Klinger, 1986; Castilla et al., 2010; Schiel et al., 2019; Thomsen et al., 2020; Vaux et al., 2021). The Kaikōura earthquake provided evidence to support recent research that has implicated historic seismic events in the contemporary distribution of bull kelps in New Zealand (Craw et al., 2020; Hay, 2020; Parvizi et al., 2020; Vaux et al., 2021). It is likely that strong seismic events have been important structural forces that underly present-day coastal ecology in many parts of the world.

Superimposed on dramatic geological events are an increasing number of unusually hot oceanic conditions that are caused by heatwaves (Oliver et al., 2019; Sen Gupta et al., 2020). Temperature affects all aspects of biology, from biochemical rates at subcellular levels, reproduction rates, control over species ranges and ultimately the distribution of world’s major biomes (Bartsch et al., 2012; Lüning, 1990; Spalding et al., 2007). It is therefore not surprising that strong heatwaves have altered the ecology of impacted regions (Rogers-Bennett & Catton, 2019; Smale et al., 2019; Straub et al., 2019). Globally, we estimated that the most extreme of these events have caused elevated temperatures across ca. 182,300 km of coastline (ca. 15% of global coastline see Results) since 1982. A few of these events have been studied in detail, demonstrating significant, and often detrimental, impacts on local marine biota (Jones et al., 2018; Montie et al., 2020; Rogers-Bennett & Catton, 2019; Smale et al., 2019; Thomsen et al., 2019; Wernberg et al., 2016), but most events have simply not been studied.

Many types of large-scale extreme disturbances can create similar ecological legacy effects and are likely important drivers of contemporary species-distribution patterns. For example, extreme 1000-year floods, fires and hurricanes can devastate coastal communities through extreme run-off, water turbidity, enhanced sedimentation, lowered salinity, wave action, altered biogeochemistry and through ash-deposits (Dunbar & McCullough, 2012; Ely et al., 1993; Flannigan et al., 2006; Kunkel et al., 2013). Furthermore, some of these events are more important on coastlines that have low seismic activity (i.e. coastlines that appear less affected in Figure 6). The possibility that many of these events will become stronger and more frequent in the future, highlights their importance in both ecology and biogeography and calls for greater inter-disciplinary cross-scale approaches (Alfieri et al., 2017; Ely et al., 1993; Flannigan et al., 2006; Walsh & Pittock, 1998).

5 CONCLUSION

This study demonstrated that cumulative effects from seismic uplift and a subsequent heatwave caused great mortality of a marine foundation species. The uplift first caused 75% canopy loss of bull kelp, and then, the heatwaves killed an additional 35% of those remaining, resulting in cascading losses of likely millions of individuals on the Kaikōura coast. Four years after the uplift, bull kelp had not recovered and the low zone was instead inhabited by a mixture of patchy bull kelp beds (dominated by D. willana), a few other perennial habitat-forming species such as Carpophyllum maschalocarpum, and small ephemeral turf and foliose algae. This represented a different ecological system maintained by new feedback loops that likely slow down or hinder recovery of bull kelp beds and lower their resilience to future stressors. Cataclysmic events may be relatively common on global historical scales because more than 12,000 major events have been recorded within 100 km of the coastline over the last four millennia, and because relatively recent extreme marine heatwaves have occurred along more than 180,000 km coastline or about 15% of global coastline around the world. Thus, the ecological legacy effects of large-scale disturbances, such as earthquakes, heatwaves and other extreme events, may be relatively common. It is worthwhile viewing local-scale short-term ecological research in this wider historical context. Models that incorporate appropriate legacy effects will likely yield better interpretation of contemporary local-scale processes.

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

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DATA AVAILABILITY STATEMENT

The data presented in this study are openly available in DRYAD at https://doi.org/10.5061/dryad.v6wwpzgwq.

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**BIOSKETCH**

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

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