



# Local Extinction of Bull Kelp (*Durvillaea* spp.) Due to a Marine Heatwave

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Detailed research has documented gradual changes to biological communities attributed to increases in global average temperatures. However, localized and abrupt temperature anomalies associated with heatwaves may cause more rapid biological changes. We analyzed temperature data from the South Island of New Zealand and investigated whether the hot summer of 2017/18 affected species of bull kelp, *Durvillaea antarctica*, *D. poha*, and *D. willana*. *Durvillaea* spp. are large iconic seaweeds that inhabit the low intertidal zone of exposed coastlines, where they underpin biodiversity and ecosystem functioning. Sea surface temperatures (SST) during the summer of 2017/18 included the strongest marine heatwaves recorded in 38 years of existing oceanic satellite data for this region. Air temperatures were also high, and, coupled with small wave heights, resulted in strong desiccation stress during daytime low tides. Before-After analysis of drone images of four reef platforms (42, 42, 44, and 45°S) was used to evaluate changes to bull kelp over the hot summer. Bull kelp loss varied among species and reefs, with the greatest (100%) loss of *D. poha* at Pile Bay in Lyttelton Harbor (44°S). In Pile Bay, SST exceeded 23°C and air temperatures exceeded 30°C, while *Durvillaea* was exposed for up to 3 h per day during low tide. Follow-up surveys showed that all bull kelps were eliminated from Pile Bay, and from all reefs within and immediately outside of Lyttelton Harbor. Following the localized extinction of bull kelp in Pile Bay, the invasive kelp *Undaria pinnatifida* recruited in high densities (average of 120 m<sup>-2</sup>). We conclude that bull kelps are likely to experience additional mortalities in the future because heatwaves are predicted to increase in magnitude and durations. Losses of the endemic *D. poha* are particularly concerning due to its narrow distributional range.

**Keywords:** canopy forming seaweed, temperature anomaly, marine heatwave, extinction, endemic species, foundation species

## INTRODUCTION

Between 1950 and 2009, mean sea surface temperature (SST) of the Atlantic, Indian, and Pacific Oceans increased by 0.41, 0.65, and 0.31°C, respectively (Hoegh-Guldberg et al., 2014). This increase has brought creeping changes to species distributions around the world (Hoegh-Guldberg and Bruno, 2005; Wernberg et al., 2011; Poloczanska et al., 2013). Superimposed on slow and

gradual temperature increases are discrete heating events covering smaller regions (1–1000 km) and occurring over shorter durations (days–months). These events are referred to as “heatwaves” (Perkins and Alexander, 2013; Hobday et al., 2016; Oliver et al., 2018) and can have more instantaneous and conspicuous effects (Wernberg et al., 2016; Le Nohaïc et al., 2017; Hobday et al., 2018; Smale et al., 2019). For example, in 2011 an extensive heat wave in Western Australia caused large scale southward range contraction of the canopy-forming fucoid *Scytothalia dorycarpa* (Smale and Wernberg, 2013) and kelp *Ecklonia radiata* (Wernberg et al., 2016). During the heatwave, temperatures exceeded the physiological tolerance of these species (Wernberg et al., 2010; Smale and Wernberg, 2013). Similarly, in northern Spain, range contractions have been reported for several canopy-forming seaweeds, including *Fucus serratus* and *Himantalia elongata* (Duarte et al., 2013).

New Zealand recently experienced an exceptionally hot summer with unusually high sea water temperatures in coastal regions of the South Island (Megan, 2018). However, nearshore rocky intertidal marine species on the South Island of New Zealand are embedded within a wide temperate biogeographical region, are not near a convergence with warm subtropical waters, and are therefore expected to be relatively robust to short-term temperature anomalies (Schiel, 2004, 2011; Ayers and Waters, 2005; Schiel et al., 2016).

In southern New Zealand waters, the largest seaweeds over most of the coastline are southern bull kelps (*Durvillaea* spp.), the world’s largest fucoid algae. Because of their occurrence at the intertidal-subtidal margin they can experience both elevated air and sea temperatures during periods of emersion and immersion. On the South Island there are three co-occurring bull kelp species with either narrow endemic (*Durvillaea willana*, *Durvillaea poha*) or wide (*Durvillaea antarctica*) latitudinal ranges (Fraser et al., 2009, 2012). Individuals of these species can reach up to 10 m long, weigh up to 70 kg, and live for up to 10 years (Hurd, 2003). *D. poha* and *D. antarctica* are exposed during low-water on spring tides and *D. willana* is mostly subtidal with only some individuals being exposed on the biggest spring tides. Together, they form dense stands with extensive canopy cover. These bull kelps are important foundation species which control local community structure, affect biodiversity and provide food and habitat to culturally and economically important species, including lobsters and abalone (Smith and Simpson, 1995; Taylor and Schiel, 2005; Schiel et al., 2018b).

The objective of this study was to quantify changes in the abundance of *Durvillaea* spp. and associated short-term ecological changes following the hot summer of 2017/18 in New Zealand. To address the objective, we first quantified temperature changes in New Zealand, focusing on 42.5–45.4°S on the east coast of the South Island. Second, we quantified changes in abundances of bull kelp on reefs from the same regions before and after the 2017/18 summer. We hypothesized that bull kelp generally would decrease in abundance and that *D. poha*, with the most southern northern range limit, would be most severely affected (Smale and Wernberg, 2013; Bennett et al., 2015; Thomson et al., 2015; Wernberg et al., 2016; Arias-Ortiz et al., 2018). Finally, we quantified effects of bull kelp loss, by

comparing changes in abundances of key organisms before and after the hot summer in Pile Bay, to changes that followed from a manipulative bull kelp removal experiment. We hypothesized that bull kelp loss would be followed by rapid colonization of weedy macroalgae, irrespective of whether the loss of bull kelp occurred through high temperatures or experimental removals, and that abundances of weedy macroalgae are correlated negatively with abundances of juvenile bull kelp (Wernberg and Connell, 2008; Flukes et al., 2014; Benes and Carpenter, 2015; Wernberg et al., 2016).

## MATERIALS AND METHODS

### Study Sites

This study was done in the rocky intertidal zone on the east coast of the South Island of New Zealand. Surveys were conducted before and after the heatwave on reefs at Oaro (−42.516396, 173.510030), Pile Bay in the semi-protected Lyttelton Harbor (−43.615418, 172.765899) and two reefs in Moeraki (Kaik, −45.356039, 170.861386 and Point, −45.363833, 170.863349). These reefs extend 40–150 m from the upper intertidal to the subtidal zones, are generally protected from severe wave action by offshore reefs, and have a coastal topography that deflects swells. Following this survey (which showed bull kelp elimination from Pile Bay; see Results), other nearby reefs within and outside Lyttelton Harbor were surveyed to identify the wider area of bull kelp loss. Finally, we also used data from a canopy-loss experiment at Oaro and the two Moeraki reefs to estimate wider ecological impacts from the heatwave.

### Changes in Temperature

First we used offshore sea-surface temperature (SST) to characterize heatwaves at the three main study sites using the R marine heatwave package (Smit et al., 2018). A heatwave was defined as a period of 5 or more consecutive days where the SST was greater than the 90th percentile calculated from > 30 years of data (Hobday et al., 2016). This analysis was based on NOAA high resolution blended analysis of daily SST data in 1/4 degree grids derived from satellites and *in situ* data<sup>1</sup> (Reynolds et al., 2007). Data were used from 30 August 1980 to 20 April 2018 from Oaro (grid centered on 42.625°S, 173.625°E), Pile Bay (43.375°S, 173.125°E) and Moeraki (45.375°S, 171.125°E). The distance from the reef sites to the grid center was < 25 km. To compare the summer of 2017/18 with past temperature anomalies we calculated (1) duration (in days), (2) maximum intensity (temperatures above the 90% threshold) and (3) cumulative intensity (duration × intensity) of all heatwaves, as defined by Smit et al. (2018) during the 38 years of available satellite SST. This analysis was based on daily mean temperatures from offshore waters and was carried out for each of the three sites separately. However, Pile Bay is located within the outer reaches of a harbor so this location may experience higher temperature fluctuations.

<sup>1</sup><https://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.highres.html#detail>

We therefore also analyzed hourly SST from 4 nearby inshore buoys within the harbor from August 2016 to April 2018 (all sites were less than 4 km from Pile Bay<sup>2</sup>). The offshore and Lyttelton Harbor temperature data were analyzed graphically. Finally, we provide additional analyses and data in online **Supplementary Material** to better understand the environmental context and impacts of the hot summer. We analyzed the large-scale extent of the temperature anomaly **Supplementary Figure S1**, visualized marine heatwaves at the three main sites with different graphs (**Supplementary Figures S2, S3**) plotted 38 years of maximum air temperature for the same regions (recorded at the nearest airport, **Supplementary Figure S4**) and corresponding atmospheric heatwaves (**Supplementary Figure S5**), measured rocky shore intertidal high-resolution temperature from Hobo-pendant loggers at Oaro over the summer of 17/18 (**Supplementary Figure S6**), and plotted high resolution wave data from January 2014 to July 2018 from an offshore buoy near Lyttelton harbor (**Supplementary Figure S7**).

## Changes in Abundances of Bull Kelp; Regional Survey

Four reef platforms from Oaro to Moeraki were sampled before the summer of 2017/18 with an Advanced Phantom 3 drone equipped with a 12 MP HD camera. Geo-tagged images were taken at low tide 10 m above the reef, with each image covering c. 95 m<sup>2</sup> that was estimated from survey tapes and 1 m<sup>2</sup> fixed quadrats positioned on each reef (Murfit et al., 2017). Drone images were collected in 2017 before the hot summer, with 20 images collected from Oaro (5 April), 20 from Pile Bay (24 August), 20 from Kaik reef (29 April), and 31 from Point reef (29 May). These reefs were re-visited in April 2018, where each entire reef was photographed (“after” data). Note that these surveys of coastal platforms may have underestimated the abundance of *D. willana*, because it occurs mostly in the subtidal zone. In the laboratory, Orthorectified and georeferenced maps of the reefs were created and the exact locations of the 2017 images were identified using a combination of the geotagged coordinates and visual land markers (boulders, channels, etc.). Percent cover of the three bull kelp species was estimated visually for each image (with a super-imposed grid of 100 cells), differentiating among the three species based on color and width of the blades and stipe characteristics (Adams, 1994; Fraser et al., 2009, 2012; Nelson, 2013). Data contained many zeroes and could not be transformed to variance homogeneity. We therefore tested our hypotheses that bull kelp would decrease in abundance and that *D. poha* would be most severely affected by the hot summer, using Wilcoxon Signed Paired Rank Tests for each of the three species (pooling data across reefs). For this analysis we only included paired before-after images where bull kelps were observed in at least one of the two sampling events.

## Changes in Abundances of Bull Kelp; Local Surveys

The regional drone survey showed that *Durvillaea* spp. had become locally extinct at Pile Bay. We therefore visited 19 reefs

in March–May 2018 around Pile Bay, where we had information about the existence of healthy bull kelp in the years prior to the hot summer, based on a combination of geotagged photos and personal observations (by co-authors and locals). At each reef we recorded whether bull kelp blades were present (i.e., *Durvillaea* were alive), only holdfasts remained (“ghost holdfasts,” i.e., *Durvillaea* were dying, see **Figure 1**), or if we could see fresh “rock scars” that are typically visible following the recent detachment of *Durvillaea* holdfasts (i.e., *Durvillaea* have recently died) (Schiel et al., 2018a). We classified each reef as having experienced 100 (not a single blade left), >90 (a few blades were left), 90–30 (patches of blades were left) or <30% (many blades remained, only a few ghost holdfasts were found) loss of bull kelp. In addition to visiting these 19 reefs, we also surveyed the entire Lyttelton Harbor for any traces of surviving bull kelp blades using a boat that was slowly driven along the coastline. These surveys were all done during low tides when emergent bull kelp blades and ghost holdfasts are easy to see. The results from these semi-quantitative surveys were analyzed by visually inspecting maps that showed spatial locations of reefs with surviving bull kelp vs. localized extinctions.

## Effects of Bull Kelp Loss: Changes Following the Hot Summer

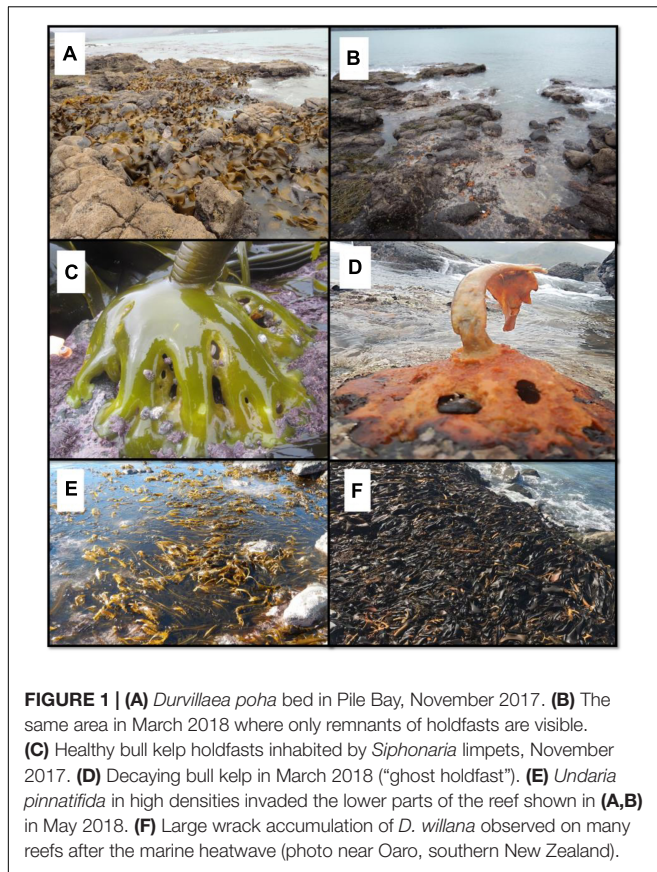
We photographed 10 0.25 m<sup>2</sup> plots with >90% bull kelp cover in Pile Bay (where the canopy was moved to make understory species visible) in August 2017 (“before” data). We then also photographed 13 0.25 m<sup>2</sup> plots at the same sites in March 2018 after bull kelp had been eliminated from the reef (“after” data). From these photos we estimated cover of conspicuous sessile organisms that were easy to identify. Data included many zeros and could not be transformed to variance homogeneity. We therefore used Mann–Whitney ranked *U*-tests on before-after data to test the hypothesis that weedy macroalgae would be more abundant after bull kelp were lost from the reef. We also tested whether mussels changed abundances because mussels were the most common and conspicuous understory species in these plots prior to the hot summer.

## Effects of Bull Kelp Loss: Removal Experiment

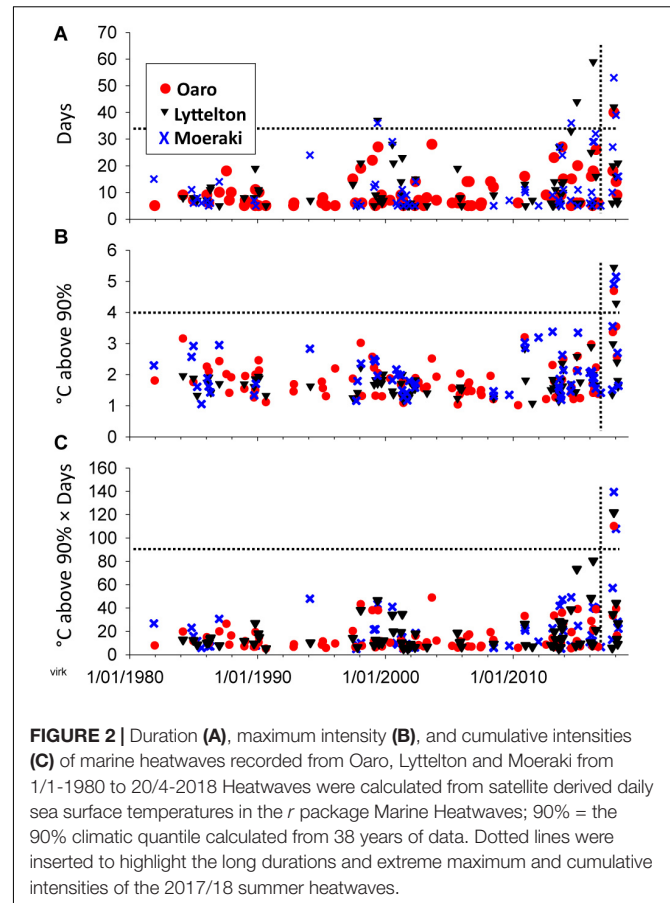
Prior to the summer 2017/18 we had set up a bull kelp removal experiment at Oaro, Kaik and Point reefs, to simulate different intensities of bull kelp loss: no removals (control plots with 100% canopy-cover), removals of blades (cutting blades off 10 cm above the end of the stipe), removals of stipes (cutting the middle of the stipe), and removals of holdfasts (i.e., removing the entire plant, very small holdfasts with diameters less than 2 cm were left undisturbed in all plots). Each plot was 1 m<sup>2</sup> and each treatment was replicated four times. Kaik and Point reef plots were established in May 2017 and Oaro plots in June 2017, just prior to the reproductive period of bull kelp (Taylor and Schiel, 2003, 2005). After 4 months we counted the number of juvenile bull kelps and estimated the percent cover of weedy macroalgae (the green sheet-forming *Ulva* spp. and *U. pinnatifida*), two taxa that were absent in the plots prior to removals. Variances were

<sup>2</sup><http://vmh18812.hosting24.com.au/public/?pid=20>





**FIGURE 1 |** (A) *Durvillaea poha* bed in Pile Bay, November 2017. (B) The same area in March 2018 where only remnants of holdfasts are visible. (C) Healthy bull kelp holdfasts inhabited by *Siphonaria* limpets, November 2017. (D) Decaying bull kelp in March 2018 (“ghost holdfast”). (E) *Undaria pinnatifida* in high densities invaded the lower parts of the reef shown in (A,B) in May 2018. (F) Large wrack accumulation of *D. willana* observed on many reefs after the marine heatwave (photo near Oaro, southern New Zealand).



**FIGURE 2 |** Duration (A), maximum intensity (B), and cumulative intensities (C) of marine heatwaves recorded from Oaro, Lyttelton and Moeraki from 1/1-1980 to 20/4-2018 Heatwaves were calculated from satellite derived daily sea surface temperatures in the *r* package Marine Heatwaves; 90% = the 90% climatic quantile calculated from 38 years of data. Dotted lines were inserted to highlight the long durations and extreme maximum and cumulative intensities of the 2017/18 summer heatwaves.

homogenous after arcsin-square root transformation (Cochran’s  $C$  for the removal treatment and Reef factor;  $p = 0.78$  and  $0.51$ , respectively). Nested Anova (3 reefs nested within 4 removal levels) was therefore used to test the hypothesis that the loss of fronds, stipes or holdfast would result in colonization of weedy macroalgae. A significant effect of removals was followed by SNK *post hoc* tests to identify differences among treatments. Note that the experimental and the before-after impact-analyses supplemented each other; colonization by macroalgae in Pile Bay following the hot summer could be caused by either loss of bull kelp and/or because of high summer temperature, whereas colonization following experimental removals could only be caused by loss of bull kelp. Finally, we were also interested in examining whether weedy macroalgae inhibited bull kelp recovery and vice versa, that is, if bull kelp recruits inhibit weedy macroalgae. These variables were not manipulated in the experiment so that causation cannot be inferred. We therefore tested the hypothesis that the cover of weedy macroalgae correlated negatively with density of juvenile bull kelp across the 48 plots using Spearman’s rank correlation coefficient.

## RESULTS

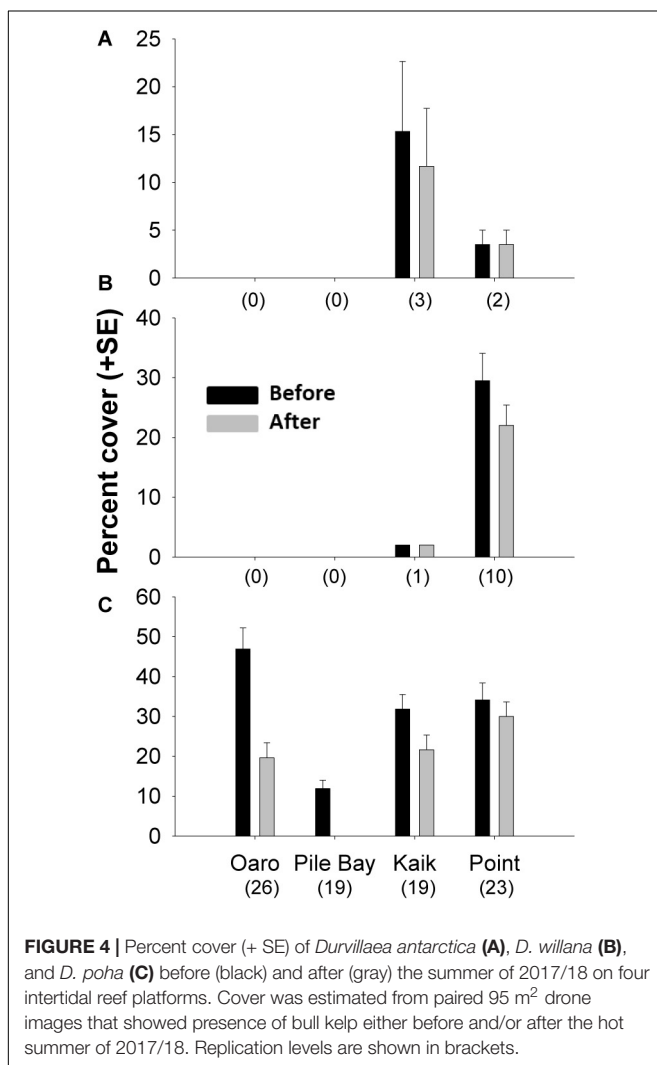
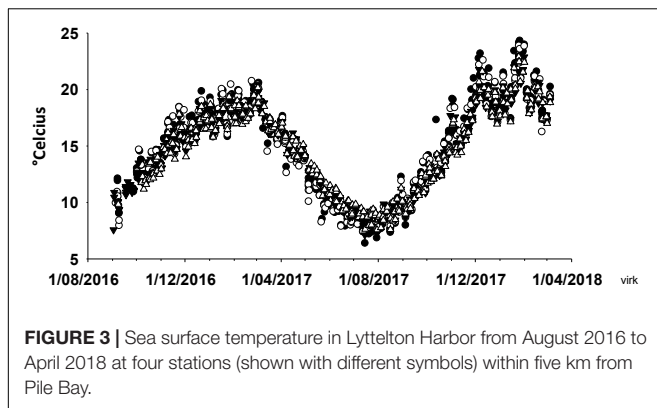
### Changes in Temperature

Oaro, Lyttelton, and Moeraki have experienced many heatwaves since 1980, but with increasing durations and intensities since

2014 (Figure 2). The heatwaves over the 2017/18 summer were particularly strong with maximum and cumulative intensities being approximately two times greater than any recorded event since 1980 (Figures 2B,C). Satellite-derived oceanic SSTs were generally lowest at the most southern site (Moeraki) and highest at the mid-latitude region (Lyttelton) (Supplementary Material), but because data were derived from offshore satellite images they may not have captured temperature extremes at inshore protected bays and inlets or intertidal rocky shores (see discussion in Smale and Wernberg, 2009). Analysis of SST data near Pile Bay within Lyttelton Harbor showed many days with water temperatures exceeding  $23^{\circ}\text{C}$  during the summer of 2017/18 (Figure 3) and intertidal *in situ* loggers at Oaro showed several days where atmospheric temperatures on the reef platforms exceeded  $>45^{\circ}\text{C}$  (when cloudless days co-occurred with big, mid-day low tides, see Supplementary Figure S6).

### Changes in Abundances of Bull Kelp; Regional Survey

Prior to the summer of 2017/18, the four intertidal platforms were dominated by *D. poha*, with smaller patches of *D. willana* and *D. antarctica* at the Point and Kaik reefs (Figure 4). We found a strong reduction in abundances of *D. poha* (Z-Statistic = 7.154,  $p < 0.001$ ,  $n = 87$ ), smaller reductions in *D. willana* (Z-Statistic = 2.032,  $p = 0.042$ ,  $n = 11$ ), and no change in abundance



of *D. antarctica* (Z-Statistic = 1.342,  $p = 0.180$ ,  $n = 5$ ). Importantly, *D. poha* from Pile Bay decreased from 12 to 0 percent cover (Figure 4), suggesting dramatic population-wide effects for this species on this particular reef.

## Changes in Abundances of Bull Kelp; Local Survey

Detailed and targeted follow-up reef-surveys revealed total elimination of bull kelp on 12 out of 19 reefs, including the entire Pile Bay reef (see above, Figure 5). All 12 reefs that experienced total loss of bull kelp were within, or immediately north and south of, Lyttelton Harbor. We were assured that each of these reefs were inhabited by bull kelp before the hot summer of 2017/18 because abundant remnant and decaying ghost holdfasts (Figure 1) attested to very recent living bull kelp populations. It was not possible to distinguish *D. antarctica* and *D. poha* using ghost holdfasts, but our prior qualitative observations and collections from many of these reefs suggested they were mainly *D. poha*. A few surviving blades of *D. poha* were found at one site close to Lyttelton Harbor, and relatively abundant populations were found at reefs > 10 km north and south of the Harbor (Figure 5).

## Effects of Bull Kelp Loss: Changes Following the Hot Summer

There were no *Undaria* under bull kelp canopies in Pile Bay in August 2017. However, in March 2018, after the elimination of bull kelp, densities increased from 0 ( $\pm 0$ ) to 121 m<sup>-2</sup> ( $\pm 20$  SE) juvenile *Undaria* in the area previously occupied by *Durvillaea*, whereas cover increased from 0 ( $\pm 0$ ) to 20.9% ( $\pm 5.6$  SE). Cover of other weedy macroalgae also increased, including *Colpomenia sinuosa* that increased from 0 ( $\pm 0$ ) to 1.6% ( $\pm 0.5$ ) and *Dictyota* sp. that increased from 0.02% ( $\pm 0.01$ ) to 1.6% ( $\pm 0.6$ ). Finally we also found that mussels (mainly *Perna canaliculus*) declined from 7.3% ( $\pm 2.0$ ) to 0.7 ( $\pm 0.1$ )%. These changes in both cover and densities were all significant (all Z-scores > 1.98, all  $p < 0.05$ ).

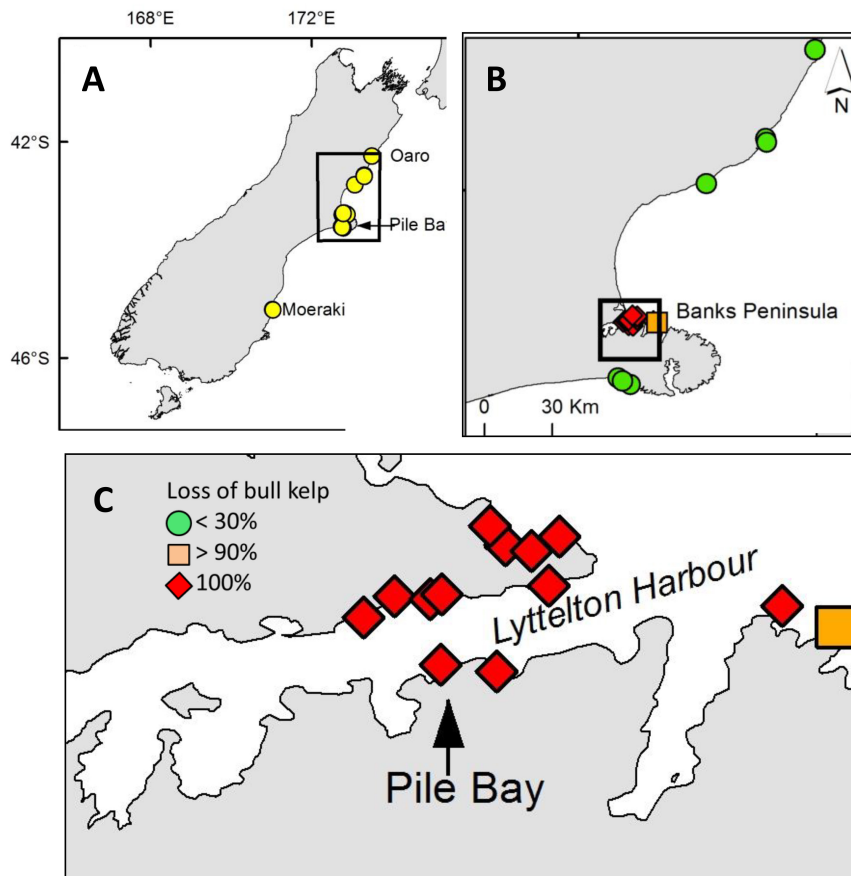
## Effects of Bull Kelp Loss: Removal Experiment

There were no weedy macroalgae (*Undaria* or *Ulva*) under healthy bull kelp canopies in any of the 48 plots prior to removal treatments (data not shown). However, 4 months after the removals we found significant differences in cover of weedy macroalgae ( $F_{\text{removal}} = 8.257$ ,  $p < 0.001$ ) across the three reefs [ $F_{\text{reef}(\text{removal})} = 0.760$ ,  $p = 0.639$ ]. *Post hoc* SNK tests showed significantly more weedy macroalgae in the three removal treatments (which had similar cover) compared to the control plots (Figure 6). *Ulva* generally colonized removal plots at Oaro whereas *Undaria* colonized removal plots at Kaik and Point reefs in Moeraki (Figure 6). We also found a significant negative relationship between cover of weedy macroalgae and density of bull kelp recruits ( $r = -0.414$ ,  $p = 0.003$ , Figure 7).

## DISCUSSION

### Who Died, Where, and Why?

We documented the loss of bull kelp following the unusually hot summer of 2017/18, characterized by high sea and air temperatures, low daytime tides, and reduced wave action (Figures 2,3 and Supplementary Figures S1–S6), so that



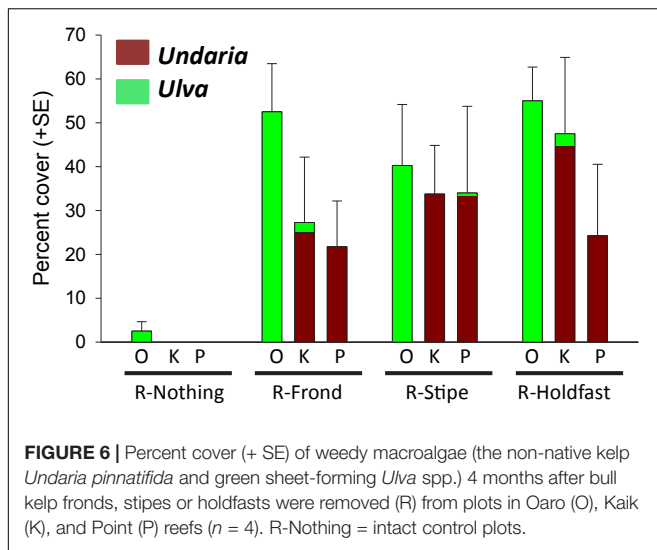
**FIGURE 5 | (A)** Surveyed bull kelp sites on the South Island of New Zealand; drone surveys were done at Oaro, Pile Bay and Point and Kaik reefs in Moeraki. **(B)** Close-up of reefs around Banks Peninsula where detailed searches for live bull kelp blades and dead “ghost holdfasts” were done. **(C)** Close-up of sites with reef-wide extinctions of bull kelp around Pile Bay in Lyttelton Harbor.

*Durvillaea* could have been stressed at both high and low tide. Elevated SST alone can cause similar losses, as has been shown for subtidal kelp and seagrasses around their northern range limits in Western Australia following the Ningaloo 2010/11 marine heatwave (Smale and Wernberg, 2013; Thomson et al., 2015; Wernberg et al., 2016; Arias-Ortiz et al., 2018). However, kelp and seagrasses are typically considered to be more robust to sea temperature anomalies within their range limits (Diaz-Almela et al., 2007; Reed et al., 2016; Wernberg et al., 2016). Our results differ because *D. poha* were eliminated from reefs more than 200 km south of its northern range limit (Fraser et al., 2012). This mid-range local extinction event (Bennett et al., 2015) occurred in inshore bay-waters, which were several degrees warmer than the coastal waters closer to the species northern range limit (Adams, 1994; Fraser et al., 2012). *Durvillaea* species are not tolerant to long periods of desiccation (Hay, 1979; Taylor and Schiel, 2005) and inhabit exposed coasts where wave splash keeps them moist. Typically, individuals have a bleached appearance as they deteriorate, which was observed in earthquake uplifted and exposed *Durvillaea* populations north of Oaro (Schiel et al., 2018a) and also in Lyttelton Harbor (this study). It seems likely that at least *D. poha* was near its ecophysiological limit. Indeed,

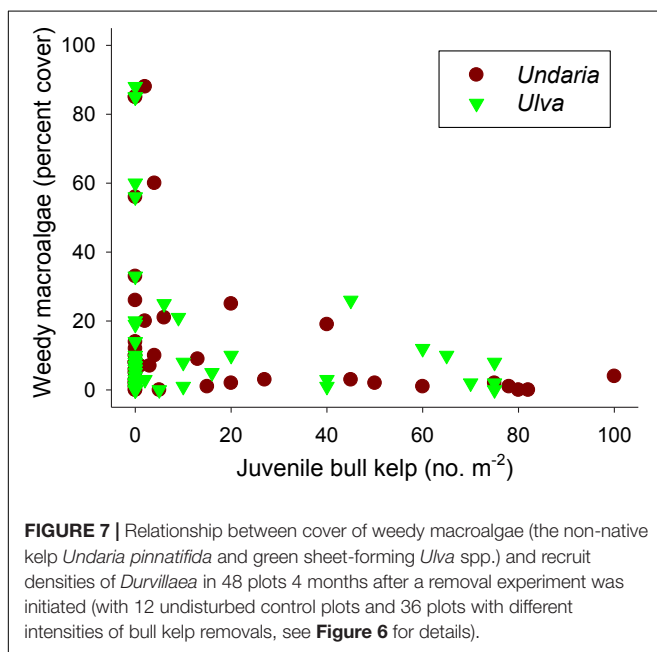
there appeared to be a relationship between maximum observed temperature and bull kelp loss (Pile Bay > Oaro > Moeraki), as seen for *Ecklonia radiata* in Western Australia following the Ningaloo 2010/11 heatwave (Wernberg et al., 2016).

The three *Durvillaea* species typically occupy the intertidal-subtidal fringe with their down-shore distributions shifting from *D. poha* that is exposed on all spring tides, to *D. antarctica* and then *D. willana* which is normally subtidal and exposed only on the largest spring tides (Adams, 1994; Fraser et al., 2012). The ocean temperatures analyzed in this study do not account for air-temperature stress occurring during emersion that can correlate with furoid canopy-cover (Schiel et al., 2016). Coastal air and water temperature typically co-vary over larger and longer time-scales (Rayner et al., 2003; Schiel et al., 2016) and air temperature was also high during the 2017/18 summer (**Supplementary Figures S4–S6**). This almost certainly contributed to the die-off of *D. poha*, which is typically exposed to the air for longer than other species of *Durvillaea* (Fraser et al., 2012). It is likely that the die-off of bull kelp therefore reflects the net effects of duration and intensity of extreme water and air temperatures, their timing relative to diurnal and lunar cycles, but also the configuration of the landscape (e.g., slope, aspect). Finally, after





**FIGURE 6** | Percent cover (+ SE) of weedy macroalgae (the non-native kelp *Undaria pinnatifida* and green sheet-forming *Ulva* spp.) 4 months after bull kelp fronds, stipes or holdfasts were removed (R) from plots in Oaro (O), Kaik (K), and Point (P) reefs ( $n = 4$ ). R-Nothing = intact control plots.



**FIGURE 7** | Relationship between cover of weedy macroalgae (the non-native kelp *Undaria pinnatifida* and green sheet-forming *Ulva* spp.) and recruit densities of *Durvillaea* in 48 plots 4 months after a removal experiment was initiated (with 12 undisturbed control plots and 36 plots with different intensities of bull kelp removals, see **Figure 6** for details).

being exposed to desiccation and high air temperatures at low tides (exceeding  $45^{\circ}\text{C}$ , see **Supplementary Figure S6**), the elevated seawater temperature increased stress and offered little opportunity for recovery.

Our results suggest that *D. poha* was more affected than *D. willana* that again was more affected than *D. antarctica*, a pattern that co-varies with their northern range limits. *D. poha* inhabits only the South Island of New Zealand, *D. willana* is found on the South Island and in the southern North Island, whereas *D. antarctica* is common around the coast of New Zealand as well as in temperate Australia and Chile (Adams, 1994; Fraser et al., 2009, 2012). Similar relationships between poleward range limits and resistance to temperature stress have been shown for both terrestrial and aquatic organisms (Hickling et al., 2006; Wernberg et al., 2011; Poloczanska et al., 2013;

Smale et al., 2019). As previously noted, our drone survey prior to the heatwave was not designed to sample the more wave-exposed *D. antarctica* and more subtidal *D. willana* so their losses were calculated from fewer drone images and require further studies. However, qualitative observations support our quantitative analyses showing some loss of both species at Moeraki, and we observed unusually large wrack accumulations, particularly of *D. willana*, at many sites from Oaro to Moeraki (cf. **Figure 1**).

## Possible Co-occurring Stressors

Our study was, in essence, a natural experiment (Hargrove and Pickering, 1992) like other marine heatwave impact studies (Garrabou et al., 2009; Short et al., 2015; Wernberg et al., 2016; Smale et al., 2019). Other factors could have contributed to the loss of bull kelp, but we argue that temperature effects were the most significant region-wide stressor. First, bull kelp are long-lived plants with relatively low seasonal variation in the cover of adult canopies that maintain consistent beds for long time periods (Hay, 1979; Santelices et al., 1980; Westermeier et al., 1994; Hurd, 2003; Taylor and Schiel, 2005). This implies that large scale die-offs are unusual events that previously only have been reported following dramatic seismic uplifts (Castilla, 1988; Schiel et al., 2018a). Second, there were no unusually large storms during the 2017/18 summer (**Supplementary Figure S7**). Given that storms rarely cover 600 km coastline and that bull kelp are adapted to high wave action and can survive massive storms, it seems unlikely to have caused the extensive large-scale mortalities recorded in this study (Taylor and Schiel, 2003, 2005; Thomsen and Wernberg, 2005; Taylor et al., 2010). Third, we did not observe any unusual turbidity or sedimentation events at any of our regular sampling sites during the summer of 2017/18. Fourth, bull kelps are typically not limited by grazers along the east coast of New Zealand, even though the odacid fish *Odadax pullus* can affect juvenile recruitment at some sites and have characteristic bite marks (Taylor et al., 2010). Finally, we are not aware of any bull kelp pathogens, except for gall-forming parasites, which are relatively harmless and clearly visible and were not observed to occur (Goetze et al., 2012; Murúa et al., 2017). Nevertheless, it is plausible that temperature stressed bull kelp became more susceptible to infectious diseases and thereby accelerated the decay (Campbell et al., 2011, 2014; Case et al., 2011; Marzinelli et al., 2015). Similarly, temperature stressed and bacteria-coated bull kelp may also have experienced increased grazing from limpet, snails and herbivorous fish (Kristensen et al., 1992; Taylor et al., 2010; Campbell et al., 2014). However, these indirect effects are proximate stressors that would only effectuate after bull kelp were stressed by high temperatures.

## Ecological Implications of Die-Off

The loss of an algal canopy can have positive and negative effects on sub-canopy species (Lilley and Schiel, 2006; Schiel, 2006; Wernberg and Connell, 2008; Wernberg et al., 2013; Flukes et al., 2014). At Pile Bay the dominant understory taxa, encrusting coralline algae, did not appear to be immediately affected but weedy macroalgae, including ephemeral (*Ulva*, *Colpomenia*), opportunistic (*Undaria*) or low-lying (*Dictyota*) species increased, probably due to competitive release from

*Durvillaea* (Taylor and Schiel, 2005; Arkema et al., 2009; Benes and Carpenter, 2015; Schiel et al., 2018b). Colonization by *Undaria pinnatifida* was also seen in the removal plots in Moeraki, supporting past studies done within stands of *Durvillaea* spp. and other canopy-forming algae in New Zealand (Thompson and Schiel, 2012; South et al., 2016; South and Thomsen, 2016; Schiel et al., 2018b), Australia (Valentine and Johnson, 2003, 2004), and the United Kingdom (De Leij et al., 2017). In places where *Undaria* was not present, other opportunistic fast-growing seaweeds, especially *Ulva*, colonized disturbed plots. This was also seen after the extensive canopy loss of *Durvillaea* and other furoid algae after seismic uplift along 100 km of coastline (Schiel et al., 2018b). We also found that mussels decreased dramatically following bull kelp loss, possibly due to increased predation from shore birds, fish and crabs (Rilov and Schiel, 2006), or increased exposure to light and decreased humidity – stress-factors exaggerated by the high summer temperatures. It is likely that more complex effects will follow over time. For example, calcareous encrusting algae may be outcompeted by turf-forming taxa (Wernberg et al., 2013; Connell et al., 2014; Filbee-Dexter and Wernberg, 2018) with cascading negative effects on species that depend on these algae, such as abalone (*Haliotis* spp.) that cue in on this substrate for larval settlement (Morse and Morse, 1984; Daume et al., 1999; Roberts et al., 2004). It is also possible that expansion of weedy macroalgae creates an unfavorable habitat for *Durvillaea* to recolonize, should it be dispersed into the harbor by drifting individuals (Taylor and Schiel, 2003; Taylor et al., 2010; Fraser et al., 2011). Indeed, past studies, and our new correlation analysis, suggests that weedy macroalgae can inhibit recruitment of large and long-lived macroalgae, that instead require rocky substratum to attach firmly to – and thereby withstand years of strong hydrodynamic wave-forces (Taylor and Schiel, 2003; Taylor et al., 2010; Wernberg et al., 2013; Connell et al., 2014; Filbee-Dexter and Wernberg, 2018).

## CONCLUSION

Extensive losses of bull kelp were recorded at many reefs along three degrees of latitude following an unusually warm summer with *Durvillaea* being eliminated from the warmest areas. Following the die-off, weedy macroalgae, especially the non-native kelp *Undaria pinnatifida* and sheet-forming *Ulva* spp. rapidly colonized empty spaces. The long-term implications are not yet clear, but if the trend of warming seas and increased intensities of marine heatwaves continues (Oliver et al., 2018), especially when coincident with hot air temperatures, there may be “press” effects that habitat-forming species such as *Durvillaea* cannot overcome (Martínez et al., 2018). Where

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appropriate micro-habitats still exist, there may be a need to enhance connectivity between remaining populations by the use of novel techniques, such as transplantations, restoration, and strain selection, to ensure the long-term survival of these iconic foundation species in affected areas.

## DATA AVAILABILITY

The datasets generated for this study are available on request to the corresponding author.

## ETHICS STATEMENT

Drone surveys were done with high sensitivity to wildlife. In particular, sites and timing of surveys were chosen to avoid potential effects on seals and seabirds. If these species were present, flights were postponed to another day.

## AUTHOR CONTRIBUTIONS

MT conceived the idea for the manuscript, collected some of the data, analyzed most of the data, and wrote the manuscript. LM, TA, SG, LT, and PS collected some of the data and commented on the manuscript. SL analyzed some data and commented on the manuscript. DS commented on the manuscript.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2019.00084/full#supplementary-material>



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**Conflict of Interest Statement:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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