1. Introduction

Primary habitat-forming organisms, such as mangroves, bivalves, seagrasses and seaweeds are of fundamental ecological importance and control ecological functions, biogeochemical cycles and biodiversity across a variety of marine ecosystems (Bruno and Bertness, 2001; Stachowicz, 2001; Thomsen et al., 2010). For example, standing seaweed biomass affects biodiversity by providing habitat for epiphytes, invertebrates and fish (Tuya et al., 2009; Thornber et al., 2016; Ramus et al., 2017). Furthermore, seaweeds also affect biogeochemical cycling, for example through photosynthetic carbon fixation, and, following dislodgment and breakages, can subsidise new detrital communities in adjacent habitats such as seagrass beds, salt marshes, sandy beaches and deep off-shore waters (Vanderklift and Wernberg, 2008; Thomsen et al., 2009; De Bettignies et al., 2013; Krause-Jensen and Duarte, 2016; Pedersen et al., 2019). Recently, the habitat cascade concept has highlighted that primary habitat-forming organisms also promote sequential habitat formation that can increase biodiversity through the provision of more or novel niche space and supplies of food (Thomsen et al., 2018; Gribben et al., 2019). Such primary habitat-forming organisms have been decimated in many parts of the world by anthropogenic activities (Halpern et al., 2008) and, occasionally, natural mega-disturbances including earthquakes and volcanic activity (Bodin and Klinger, 1986; Castilla, 1988; Castilla and Oliva, 1990; Castilla et al., 1998; Castilla et al., 2010; Williams et al., 2010; Schiel et al., 2019). However, the implications of the combined loss of both primary and sequential habitat formers following severe disturbances are poorly understood because most studies have only focused on losses of primary habitat formers (Halpern et al., 2008). Here, we address this research gap by quantifying the abundance of primary and secondary habitat-forming organisms and their associated biodiversity before and after a natural mega-disturbance.

Primary marine habitat formers can facilitate secondary habitat formers such as sponges, tunicates and seaweeds (Wahl, 1989; Thomsen et al., 2010; Gribben et al., 2019). These secondary habitat formers, sometimes referred to as secondary structural species (Huston, 1994), keystone structures (Tews et al., 2004), ecosystem engineers (Jones et al., 1994), or foundation species (Angelini et al., 2011; Thomsen et al., 2018), can be found attached to, entangled around, or embedded within stands of primary habitat-forming species (Thomsen et al., 2018).
It is increasingly recognized that secondary habitat-forming species can be important modifiers of ecosystem functioning, biodiversity and biogeochemical fluxes, but only a few studies have detailed their ecology in the context of disturbance (Thomsen et al., 2010; Angelini et al., 2011; Thomsen et al., 2018).

It is important to understand how large-scale destruction events affect aquatic primary producers, biodiversity, and community structure for the purposes of mitigation, amelioration and restoration, especially in instances where areas of high ecological, cultural and commercial value are impacted (Halpern et al., 2007; Bellgrove et al., 2010; Campbell et al., 2014). The impacts of localized disturbances such as wave action (Ebeling et al., 1985; Reed et al., 2011; De Bettignies et al., 2013), smothering by sediment (Airoldi, 1998), and grazing (Valentine and Johnson, 2005; Ling et al., 2015) are well studied and can be important determinants of ecological community structure and function (Dayton, 1971; Short and Wyllie-Echeverria, 1996). By comparison, studying large-scale mega-disturbances such as earthquakes is more difficult because their occurrences are rare, unpredictable and often devastating, preventing time-structured experiments and access to sites and supplies. Building a framework to predict impacts on shallow coastal systems from mega-disturbances is further complicated because underpinning processes operate over very different spatio-temporal scales. For example, following instantaneous uplifts, smaller scale processes like herbivory, competition, light availability and desiccation stress are dramatically altered in concert with larger scale processes like limited propugule pressure and disrupted population connectivity, (Castilla and Oliva, 1990; Waters et al., 2013; Schiel et al., 2019), making it challenging to predict survival and recovery trajectories. Nevertheless, case studies that document ecological impacts from mega-disturbances will increase our collective knowledge about what types of organisms are particularly sensitive (or resilient) and whether micro-habitats can modify effects.

Here, we assessed the impact of earthquake caused uplift on large canopy-forming intertidal seaweeds and their associated invertebrate communities along a 110 km stretch of the Kaikōura coastline in New Zealand. More specifically, we compared the abundance of four primary habitat-forming seaweed species and a suite of secondary habitat-forming epiphytes as well as their associated invertebrates before and after the earthquake. The primary habitat-forming species were the canopy-forming fucoids *Hormosira banksii*, *Cystophora torulosa*, *C. scalaris* and *C. retroflexa*. *Hormosira banksii* is a desiccation tolerant mid-shore alga of up to 30 cm in length that is composed of simple chains of multiple bead-like vesicles. *Cystophora torulosa* is a low shore species growing to > 50 cm that is morphologically more complex than *Hormosira* in that it has multiple branches that support 4-cm-long branchlets. *Cystophora scalaris* and *C. retroflexa* are typically lower shore – subtidal species that have complex morphologies with many branches and shorter (∼ 1 cm), congested branchlets arising from their main stems (Adams, 1994; Schiel and Hickford, 2001; Schiel, 2006, 2011). The secondary habitat formers quantified in this study were all epiphytes on the fucoid algae and included *Notheia anomala* (an obligate fucoid epiphyte on *H. banksii*), *Ceramium spp.*, *Polysiphonia spp.*, and the articulated coraline, *Jania sphaeraromosa*. These epiphytes have complex, highly branched morphologies and high surface-volume ratios (Adams, 1994; Meltcalf, 2016; Thomsen et al., 2016b). Finally, we quantified the mobile invertebrates that were associated with primary and secondary biogenic habitats and used these data to speculate on earthquake-related cascading ecosystem effects and discuss recovery scenarios, including whether restoration is needed, and whether it should include secondary habitat formers in order to better promote recovery (Bellgrove et al., 2016; Lawler et al., 2006; Halpern et al., 2007; Campbell et al., 2014; Marzinelli et al., 2016).

2. Methods

2.1. Study sites

This study was conducted on four large intertidal flat rocky
platforms at Cape Campbell and Kaikōura peninsula along the east coast of the South Island of New Zealand (Fig. 1). These platforms were intersected by channels and scattered with shallow (< 50 cm) tide pools that were dominated by dense assemblages of canopy-forming seaweeds providing habitat for a variety of other seaweeds and small invertebrates (Lilley and Schiel, 2006; Schiel, 2006, 2011; Schiel et al., 2016; Thomsen et al., 2016b). The tidal range was c. 2 m and the intertidal canopy-forming algae generally occupied a band between 0–1 m above mean low water (mlw). On November 14 2016 the Kaikōura coastal regions experienced a 7.8 Mw earthquake that uplifted much of the 110 km coastline from Goose bay south of Kaikōura to Cape Campbell (Schiel et al., 2018). Most of the coastline experienced an uplift of 1–2 m, with a maximum of almost 6 m at certain locations. The four study platforms were, by comparison, only uplifted 0.5–0.8 m and are still inundated at high tide thereby flushing the tidepools and channels twice a day (Fig. 1) (Hollingsworth et al., 2017; Shi et al., 2017; Schiel et al., 2018).

2.2. Intertidal habitat-forming seaweeds

We quantified the abundance of primary habitat-forming fucoxid seaweed hosts (Hormosira banksii, Cystophora torulosa, C. scalaris, and C. retroroxa) and their smaller, secondary-habitat-forming epiphytes (Notheia anomala and various red algae) on two intertidal reefs at Cape Campbell and two at Kaikōura, before (January–February 2015) and after (February–March 2017) the earthquake. Fucoxid seaweeds included Hormosira banksii in the mid to upper intertidal zone (0.5–1 m above mlw) and C. torulosa and Hormosira in the lower intertidal zone (0–0.5 m above mlw) (Schiel, 2006; Schiel et al., 2016). When Hormosira and C. torulosa were found in the lower zone, they were often inhabited by the obligate epiphyte Notheia anomala (Thomsen et al., 2016b) and epiphytic red algae (e.g., Ceramium spp., Polysiphonia spp. and Jania sphaeraromosa), respectively. The tide pools and channels were often dominated by C. scalaris and C. retroroxa, sometimes inhabited by the same red algal epiphytes.

At each reef platform, photographs (= samples) were taken within the tidal zones and channels where Hormosira and Cystophora are commonly found. A total of 2486 photos were taken, with a minimum of 162 and maximum of 483 photos per reef before (summer 2015) or after (summer 2017) the earthquake (see Fig. 1 for details). Each photo was taken 90 cm from, and perpendicular to, the substrate with the same camera, covering 0.97 m² of reef (+ 0.06 m² SD, N = 15). Photos were randomly distributed within this tidal zone on the platform and therefore included tidal channels and tide pools. The percent cover of seaweed hosts and their epiphytes (> 1 cm) were estimated from each photo. Previous research has shown that > 80 % of the local epiphyte biomass is attached to the upper part of the host fronds (Meltcafe, 2016; Siciliano, 2018). This implies that the large majority of epiphytes can be detected from photos and that this rapid and spatially extensive sampling methodology only under-estimates epiphyte abundances by an ecologically insignificant fraction. Our objective was to document reef-wide effects of the earthquake on habitat-forming seaweeds, so we did not stratify data according to small variations in elevation or the patchy intersecting channels and tide pools. Percent cover data were non-normal, had many zeros, and high variance heterogeneity and could not be transformed to fulfil parametric statistical assumptions. We therefore pooled data across reefs and regions to compare relative abundances of the six taxa first before and then after the earthquake using Kruskal-Wallis 1-way analysis of variance (ANOVA) on rank tests, followed by post hoc SNK tests on ranked sums. We also calculated the average percent survival for each seaweed taxa using each reef as a replicate population (N = 4).

2.3. Seaweed-associated invertebrates

Before the earthquake, we had collected invertebrates associated with the dominant habitat-forming seaweeds both in the presence and absence of their most common epiphytes (Notheia attached to Hormosira, red algal epiphytes, including Jania sphaeraromosa and Polysiphonia spp., attached to the three Cystophora species). A total of 466 seaweed fronds were collected from the four reefs by cutting 10–15 cm of the apical frond of each plant (either with or without attached epiphytes) and placing it into a zip-lock bag to prevent the loss of mobile invertebrates (Thomsen et al., 2016b). All the Cystophora samples were collected from tide pools during summer 2015 whereas Hormosira samples were collected from both tide pools and the intertidal platforms in 2013, 2014 and 2015 across all seasons. After the earthquake, 111 fronds were collected in fall 2017 and summer 2018 using similar methods and from the same four reefs. Fewer fronds were collected after the earthquake than before to minimize ecological impact on the sparse remnant seaweed populations. Furthermore, after the earthquake very few canopy-forming seaweed hosts had any attached epiphytes and only in small amounts. The ‘after-earthquake-epiphyte' treatment had therefore both low replication levels and low epiphyte biomass (see Fig. 4 legend for details about replication levels and collected seaweed biomass). In the laboratory, samples were rinsed in freshwater onto a 250 μm sieve. Invertebrates were classified as crustaceans, molluscs, polychaetes or ‘others' and counted under a dissecting microscope (40×). The total biomass of the seaweed frond (with epiphytes when present) was weighted after oven-drying at 65 °C. Invertebrate counts were standardized to gram dry weight of seaweed. Data were then pooled across reefs and regions because not all combination of seaweed species and epiphytes could be sampled at all four reefs (e.g., more Hormosira samples were collected from the lower intertidal zone at sites on the Kaikōura peninsula). Three-way permutation analyses of variance (PERMANOVA) were used to test for the effects of the earthquake (2 levels; before and after), canopy-forming host species (four levels; Hormosira, C. torulosa, C. retroroxa and C. scalaris) and epiphytes (2 levels; with and without epiphytes) for each of the four invertebrate taxa. Data transformation did not achieve homogeneous variances and treatments were unbalanced, so results should be interpreted with caution. We adjusted alpha to 0.01 and interpreted mean effects cautiously, acknowledging that significant effects may alternatively have been caused by heterogeneous variances (Underwood, 1997). However, because we were interested in evaluating the Uplift × Host × Epiphyte interactions, and assessing the relative importance of the three test factors (Levine and Hullet, 2002), we used a biased factorial PERMANOVA over non-parametric ranked ANOVA that does not address interaction terms or relative importance of factors. Significant results for the host test factor and the Host × Uplift interaction were followed by post-hoc t-tests.

3. Results

3.1. Intertidal habitat-forming seaweeds

There were significant differences in abundances among seaweed taxa prior to the earthquake (Kruskall-Wallis; χ² = 2407.8, df = 5, p < 0.0001). Across all reefs, Hormosira was most abundant (present in 841 photos with a mean cover of 36 %, Fig. 2A), followed by Cystophora scalaris (315 counts; 9% cover), Cystophora torulosa and N. anomala (ranked together statistically by SNK tests; 231 counts; 4% and 321 counts; 1.4 %, respectively), and finally Cystophora retroroxa and red epiphytes (also ranked together; 63 counts, 0.8 % and 94 counts, 0.7 %, respectively) (Fig. 2A–B). After the earthquake, abundances of seaweed taxa were significantly different (χ² = 1185, df = 5, p < 0.0001) with H. banksii being the most abundant species (379 counts; 0.78 %, Fig. 2C) followed by C. scalaris (167 counts, 4.03 %). Note however that H. banksii actually had lower mean cover than C. scalaris (Underwood, 1997). Finally, the four remaining seaweed taxa
were all statistically similarly ‘rare’ after the earthquake; that is, all taxa were found in very low abundances and only in a few samples (C. torulosa = 26 counts, 0.02 % cover; C. retroflexa = 14 counts, 0.10 %; Notheia = 12 counts, 0.002 %; red filamentous epiphytes = 2 counts, 0.001 %). Analysis of the reef- and population-wide survival rates for the six seaweed taxa indicated that epiphytes were more severely affected than their hosts (Fig. 3). More specifically, only 0.08 % of the Notheia anomala populations attached to Hormosira and 0.05 % of the epiphytic reds attached to Cystophora hosts survived. By comparison, the primary habitat-forming hosts found on the tidal platforms had intermediate survival rates; that is 2.1 % of Hormosira populations and 0.2 % of C. torulosa populations survived. Finally, the primary habitat formers that dominated in the tidal channels and tide pools before the earthquake, had the greatest population survival rates with 20.1 % of C. retroflexa and 14.5 % of C. scalaris surviving.

3.2. Seaweed-associated invertebrates

Seaweed fronds were dominated by crustaceans (57.3 per gDW), followed by molluscs (22.7; primarily gastropods) with fewer polychaetes (1.8) and other invertebrates (0.5; Fig. 4, densities calculated by pooling across all test factors). Statistical analysis of crustacean abundances showed a significant Uplift × Host interaction with more crustaceans inhabiting C. scalaris (278.7 per gDW) and C. retroflexa (219.2) compared to C. torulosa (120.0) and fewer inhabiting Hormosira (19.9) before the uplift (Table 1). By contrast, there were no effects of host species on the abundance of crustaceans after the earthquake. In addition, C. scalaris (279 before vs. 72 after) and C. retroflexa (219 vs. 49) were inhabited by significantly fewer invertebrates per gram of biomass after the uplift. We also found a significant Uplift × Host interaction for molluscs (Table 1). Again, there were no effects of hosts after the uplift, whereas more molluscs inhabited C. retroflexa, C. torulosa and C. scalaris (64.7, 49.4 and 46.1 in. per gDW, respectively) compared to Hormosira (11.5) before the uplift. We also found significantly more molluscs on Hormosira after (23.5) compared to before (11.5), the uplift, but with no before-after differences for the three Cystophora species. In addition, more molluscs inhabited co-occurring hosts and epiphytes (39.9) compared to host species alone (12.9). The analysis of polychaetes also showed a significant Uplift × Host interaction with more polychaetes inhabiting C. retroflexa (18.8 per gDW) than C. torulosa, C. scalaris (7.3 and 5.8, statistically grouped together) and Hormosira (0.16) before the uplift (Table 1). After the uplift fewer polychaetes inhabited Hormosira (0.18) than the three Cystophora species (grouped statistically together, 2.2–4.5 per gDW). Finally, we found no statistical effects on other invertebrates, but these taxa only represented a small fraction of the seaweed-associated invertebrates (Table 1).

4. Discussion

The uplift of reefs along the Kaikōura coastline in New Zealand had a devastating impact on intertidal primary and secondary habitat-forming seaweeds and on the mobile invertebrates that depend on these biogenic habitats. We expect there will be wider implications associated with this loss such as reduced primary production, habitat for juveniles of coastal species, organic cross-system subsidies and lost secondary production with potential ramifications for rock lobsters and fish of...
This possibly explains why losses of marine epiphytes have not been commercial, cultural and customary value (Choat, 1982; Edgar, 1990b; Schiel, 2006; Wernberg et al., 2006; Schiel and Lilley, 2007; Thomsen et al., 2010; Tuya et al., 2010; Schiel et al., 2018).

4.1. Loss of primary habitat-forming hosts

The reefs at Cape Campbell and Kaikōura experienced a dramatic loss of primary habitat-forming seaweeds on large intertidal reefs following the c. 0.5-0.8 m uplift. This result was not surprising; intertidal seaweeds are marine organisms that typically are limited upwards by desiccation stress (Hatton, 1932; Schonbeck and Norton, 1979; Dromgoole, 1980; Brown, 1987). The hypothesis that increased desiccation stress caused the loss of canopy-forming seaweeds was supported by our population-survival results; species dominating the tide pools and channels (Hormosira, C. torulosa) had lower survival than species inhabiting tide pools and channels (C. scalaris, C. retroflexa) (Morton and Miller, 1973; Schiel, 2006; Schiel and Lilley, 2007; Schiel, 2011), some of which were still filled with water, after the uplift.

*Cystophora scalaris* and *C. retroflexa* are common canopy-forming species in the shallow subtidal zone (Schiel and Hickford, 2001; Shears and Babcock, 2004) and the higher survival in tide pools suggests that subtidal populations could have also survived the uplift. However, because *Hormosira* and *C. torulosa* were rare in the former subtidal zone, these species have likely experienced more dramatic region-wide losses, and, depending on the extent and configuration of the new uplifted intertidal zone, may have slow recovery and only establish much smaller populations that therefore could be more susceptible to future stressors and local extinctions (Shaffer, 1981; Frankham, 1996).

4.2. Loss of secondary habitat-forming epiphytes

Dramatic losses of primary habitat-forming species are visually striking and have been documented following large disturbances in previous studies (Castilla, 1988; Castilla and Oliva, 1990). However, it is more difficult to document the loss of less common and inconspicuous species such as epiphytes that can play an important ecological role through secondary habitat formation (Thomsen et al., 2018). This possibly explains why losses of marine epiphytes have not been

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**Table 1**

Three-factorial PERMANOVA testing for effects of earthquake associated uplift, canopy-forming fucoid seaweed host (*Hormosira banksii, Cystophora torulosa, C. scalaris, C. retroflexa*) and epiphytic seaweed (Epi: present-absent) on the abundance of mobile invertebrates (> 250 μm) per gram of seaweed. Transformation did not achieve homogeneity of variances therefore significance results should be interpreted with caution. Alpha value for assessing significance was 0.01.

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**Fig. 4.** Densities of invertebrates associated with canopy-forming seaweed hosts (+ SE; A, B) and their epiphytes (C, D) before (A, C) and after (B, D) the Kaikōura earthquake, standardized to number per gram dry weight of seaweed biomass. Horm = *Hormosira banksii*, C. tor = *Cystophora torulosa*, C. sca = *C. scalaris*, C. ret = *C. retroflexa*. N from left to right = 235, 13, 14, 9 (A), 30, 19, 31, 16 (B), 139, 20, 30, 6 (C) and 6, 3, 4, 3 (D). Densities were calculated from seaweed samples weighing, on average (from left to right) 5.4, 3.2, 2.5, 2.8 (A), 5.5, 3.2, 3.7, 2.8 (B), 5.8, 6.8, 3.2, 2.6 (C) and 2.4, 2.9, 2.5, 3.3 g dry weight of the primary habitat-forming host and 0.00 (A, B, samples collected without epiphytes), 1.61, 1.81, 0.79, 0.61 (C) and 0.20, 0.03, 0.31 and 0.02 (D) g dry weight of secondary habitat-forming epiphyte.
documented following large scale disturbances – in contrast to recognized importance of terrestrial epiphytes in conservation ecology (Lõhmus and Lõhmus, 2010; Ellis et al., 2011).

In this study, finely branched epiphytes with high surface-volume ratios provided important habitat for invertebrates, despite their low biomass (Fig. 4). This result was most striking for the morphologically simple Hormosira and relatively coarsely branched C. torulosa (with lowest surface-volume ratios) that provide poorer biogenic habitat compared to the more complex C. scalaris and C. retroflexa (with intermediate surface-volume ratios). In other words, finely branched epiphytes enhanced the capacity of coarsely branched intertidal seaweeds to provide habitat for small invertebrates. However, the finely branched structure of the epiphytes is likely also responsible for their poor resilience to uplift, because high surface-volume ratios cause high desiccation rates (Dromgoole, 1980; Thomsen et al., 2016b). At our study sites, the common red algae, Jania sphaeroramosa, Polysiphonia spp., Ceramium spp. and Lophothamnion hirtum, are facultative epiphytes that can attach to a wide variety of hosts and rocky substrates (Adams, 1994). Therefore, there should be greater potential for red algal epiphytes to be resilient over large scales, because populations are likely to have survived in the subtidal zone. By contrast, Notheia is an obligate epiphyte that only attaches to Hormosira (Parrish, 1977; Thomsen et al., 2016b).

The near extinction of Notheia on uplifted intertidal reefs suggests a long-term threat for this species; First, Notheia was disproportionately affected with only a few individuals surviving on the reefs. Second, Notheia is confined to a narrow elevation band and is susceptible to desiccation (Meltcalfe, 2016; Thomsen et al., 2016b). Third, the host Hormosira (and therefore also Notheia) is rare in the subtidal zone providing limited source populations to support recolonization. Finally, Notheia appears to be disproportionately more abundant on reefs with large Hormosira populations (Thomsen, pers. obs) and the new topography along uplifted coastline may not be suitable for the establishment of large Hormosira populations (Schiel et al., 2018). Taken in concert, this secondary habitat-forming species will likely occur in much lower abundances in the future (indeed, recent visits to the same impacted reefs in November 2018 suggest even smaller populations of Notheia on surviving Hormosira hosts).

4.3. Loss of seaweed-associated invertebrates

The seaweeds sampled provided habitat for small mobile invertebrates, predominantly crustaceans and molluscs, as shown in other studies (Taylor and Cole, 1994; Taylor, 1997). More invertebrates generally inhabited the finer branched C. retroflexa and C. scalaris than the coarser branched Hormosira and C. torulosa (Russo, 1990; Taylor and Cole, 1994; Siciliano, 2018). This result could also reflect differences in micro-habitats between the primary habitat formers because fine-branched seaweeds were more common in the tide-pools and channels that might have been favourable to greater invertebrate survival. By comparison, the coarsely branched species were more common on the intertidal platforms where desiccation stress can be strong (Lilley and Schiel, 2006; Meltcalfe, 2016; Thomsen et al., 2016b). Epiphytic facilitation of invertebrates was strongest for molluscs, a group that was dominated by herbivorous gastropods, when the epiphytes were attached to coarsely branched hosts, supporting data from many other studies (Norton and Benson, 1983; Edgar and Robertson, 1992; Martin-Smith, 1993; Gartner et al., 2013; Thomsen et al., 2016b). Increased numbers of molluscs on epiphytes supports the ‘affinity-distinctiveness’ hypothesis that predicts that habitat cascades should be strongest when inhabitants have affinity for secondary habitat formers that are form-functionally distinct from primary habitat formers (Thomsen et al., 2016a). In other words, grazing snails are particularly facilitated by finely branched palatable epiphytes attached to coarsely branched less palatable hosts. By contrast epiphytes attached to the morphologically more complex C. scalaris and C. retroflexa, only facilitated invertebrates by providing additional but functionally similar habitat space.

In addition to the loss of animals, there are likely also cascading loss of secondary production and trophic provisioning along the uplifted coastline. We showed that more than 300 invertebrates inhabit each gram of seaweed (dry weight) on semi-protected intertidal reefs dominated by canopy-forming seaweeds. Scaling these results up to entire reefs suggest that billions of invertebrates were lost very quickly. However, these small mobile invertebrates typically have low habitat-affinities (Bell, 1991; Duffy and Hay, 1991; Taylor and Cole, 1994; Taylor, 1998) and conspecific taxa are likely to have survived the earthquake by inhabiting subtidal seaweeds, providing source populations for recolonization. Unfortunately, little is known about the taxonomic identities, host affinities and niche breadth of small seaweed-associated invertebrates. It is possible that a few species have high host-specificity (e.g., for Hormosira or Notheia) and may therefore have been detrimentally affected by the loss of their hosts. Finally, we note that these animals provide a key trophic link to higher trophic levels, as an abundant food source for predatory fish, crabs, and rock lobster (Pinkerton et al., 2008; Feary et al., 2009).

4.4. Data limitations

Analyses of impacts following unpredictable disasters are typically limited by the availability of pre-disaster data as well as difficulties associated with reaching impacted sites and finding surviving organisms. Ideally, impact analyses are based on well-planned Beyond-BACI designs (Benedetti-Cecchi, 2001), but it was clearly impossible to anticipate this earthquake and uplift (Castilla, 1988; Castilla et al., 2010). Therefore, we had not collated data to fit the requirements of the Beyond-BACI analytical approach and we only have spatially extensive seaweed cover data for entire reefs from one survey prior to the earthquake. However, these intertidal Hormosira-Cystophora seaweed communities have been present for at least 30 years when seaweed research was initiated along this coastline (Schiel, 2011; Schiel et al., 2016). Furthermore, our results are not representative of more exposed coastlines because Hormosira is not biomechanically adapted to strong wave action (Thomsen and Wernberg, 2005; McKenzie and Bellgrove, 2009). We also lacked an un-impacted ‘control’ site, but research from nearby regions (Banks Peninsula, Moeraki peninsula) has shown no major changes to intertidal seaweed populations or seaweed-associated animals. A final discussion point is that seaweed cover was quantified from geo-tagged photos, a method that provides spatial references, allows suspicious data points to be revisited and corrected, and can be used to collect large amounts of data points in a short time frame (Foster et al., 1991; Dethier et al., 1993; Drummond and Connell, 2005; Abdo et al., 2006). In this study, data collection efficiency was of highest priority because the intertidal study sites were semi-remote reefs where seismic aftershocks and breakdown of infrastructure posed a significant threat (Hollingsworth et al., 2017; Shi et al., 2017; Schiel et al., 2018). It is well established that cover estimations from photos are accurate for large conspicuous and distinct species, such as the four canopy-forming hosts studied here (Foster et al., 1991; Dethier et al., 1993; Drummond and Connell, 2005; Abdo et al., 2006). Photos can also be used to quantify marine epiphytes, although abundances can be slightly under-estimated if microscopic fragments and epiphytes attached to below-canopy stems are overlooked (Miller-Myers and Virlstein, 1999; Virlstein, 1999; Borg et al., 2006). However, for our study species, most of the epiphytic biomass are found on upper parts of the host fronds and are visible from the photographs (Meltcalfe, 2016; Siciliano, 2018). Thus, pre-earthquake epiphyte abundances may be slightly under-estimated. However, after the earthquake only small and scattered host individuals survived, thereby eliminating ‘hidden’ subcanopy epiphyte components. This implies that we may have slightly over-estimated epiphyte survival rates, but this bias only strengthens our conclusion that epiphytes were most severely affected. In other
words, despite any of the discussed data limitations, our results clearly documented dramatic short-term losses of seaweed hosts and seaweed-associated invertebrates with particularly severe losses of epiphytes.

4.5. Seaweed recovery and mitigation

The most important factor to determine the future distribution of seaweed and associated invertebrates along the uplifted coastline is the new configuration of rocky reefs; specifically, whether there are now more or less intertidal and subtidal rocky reef space than before the earthquake. Our observations suggest that the Kaikoura coastline today has fewer, smaller and steeper wave protected intertidal reefs than before the earthquake (Schiel et al., 2018). As a result, this region will likely support fewer and smaller populations of Hormosira, Notheia and C. torulosa in the future. Another issue facing the Kaikoura coastline is accelerated erosion of newly uplifted rock, and the subsequent enhanced sediment deposition in the intertidal zone (Schiel et al., 2018, 2019), resulting in either bare (and continually eroding) rock or gravel substrates at possible colonisation sites. Elsewhere along the uplifted coast, small green ephemeral seaweeds (Ulva spp.) have become abundant in lower to mid zones (Schiel et al., 2018, 2019) and these seaweeds may compete for space with recolonizing primary habitat formers, at least in the short term (Sousa, 1979).

Reductions in the quantity of subtidal reef could alter biotic forces (predation, grazing) that can be important in structuring intertidal communities, especially in the lower shore (Ríov and Schiel, 2006). To be successful, colonizers of the new intertidal zones of the uplifted reef must be able to tolerate the modified desiccation, light, temperature, sediment and hydrodynamics regimes. Furthermore, colonization is likely to be limited by propagule supply (Verling et al., 2005), genetic bottlenecks (Peery et al., 2012), allee-effects (Levitan and McGovern, 2005), competitors (Worm and Chapman, 1998) and grazers (Jenkins et al., 1999). For example, propagule pressure is now dramatically reduced. In addition, isolated and patchy new recruits of canopy-forming seaweed may be selectively targeted by grazers (Choat, 1982; Taylor and Schiel, 2010) or outcompeted by early colonizing opportunistic algae (Taylor and Schiel, 2003; Taylor et al., 2010; Alestra and Schiel, 2014; Alestra et al., 2014). It is therefore possible that reductions in suitable reef area and negative biotic feedback mechanisms could prevent colonization by canopy-forming fucoid seaweed over greater time scales. Indeed, in both eastern and Western Australia, canopy-forming seaweeds and their associated biodiversity have not recovered following large scale regional losses (Wernberg et al., 2013; Marzinelli et al., 2014, 2016; Wernberg et al., 2016).

If natural recolonization does not occur over the next few years, perhaps lost seaweed could be rehabilitated to protect local biodiversity, food networks and recreational and commercial fisheries – as has been achieved in Australia (Bellgrove et al., 2010; Marzinelli et al., 2014). For example, seaweeds have been transplanted to suitable reef areas by seeding zygotes onto plates, ropes or the reef itself and by transplanting fertile individuals from other locations to facilitate “natural” recruitment (Taylor and Schiel, 2003; Schiel et al., 2006; Bellgrove et al., 2010; Marzinelli et al., 2014). We suggest that it would also be beneficial to incorporate epiphytes in possible restoration projects. For example, transplanting Hormosira with attached epiphytic Notheia could better facilitate the recovery of this obligate epiphyte and its habitat cascade (Thomsen et al., 2016b). Similarly, opportunistic green algae (Ulva spp.) that now occupy much of the uplifted coastline (Schiel et al., 2018) may prevent colonization of the larger canopy-forming seaweed by pre-emption of space and sediment accumulation feedback mechanisms (Hay, 1981; Schiel et al., 2006; Alestra and Schiel, 2014; Alestra et al., 2014; Connell et al., 2014). Such enemy interactions could be reduced by removing competitors to maximize the survival of transplants and new propagules thereby speeding up the recovery of seaweeds. Using a combination of restoration methods may thereby support populations to exceed minimal viable population size thresholds and facilitate self-sustaining populations. Finally, we also suggest that restoration efforts are carried out in a population genetic context to preserve the original genetic diversity of surviving populations as much as possible (Lande, 1988; Fraser et al., 2009; Coleman et al., 2011; Bellgrove et al., 2016).

Author contributions

Mads S. Thomsen conceptualized the paper, collected many data, analysed the data and wrote the paper. Paul M. South, Isis Metcalfe, Alfonso Siciliano, Shawn Gerrity, Tommaso Alestra, and David R. Schiel collected some of the data and commented on the various manuscripts draft versions.

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