


The Kaikōura earthquake in southern New Zealand: Loss of connectivity of marine communities and the necessity of a cross-ecosystem perspective

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Abstract

1. The Mw 7.8 earthquake that struck the north-east coast of the South Island of New Zealand in November 2016 caused extensive upheaval, of up to 6 m, over 110 km of coastline. Intertidal habitats were greatly affected with extensive die-off of algal communities, high mortalities of benthic invertebrates, and greatly reduced ecosystem functioning, such as primary productivity. Only isolated pockets of key species remained in these areas, many of which were within protected areas around Kaikōura.
2. The loss of key species of algae and invertebrates fragmented marine populations and compromised connectivity and recovery processes because of the large dispersal distances needed to replenish populations. Severe sedimentation from terrestrial slips and erosion of newly exposed sedimentary rock compromised settlement and recruitment processes of marine species at many sites, even if distant propagules should arrive.
3. The combination of habitat disruption, loss of species and their functioning, and impacts on commercial fisheries, especially of abalone (*Haliotis iris*), requires multiple perspectives on recovery dynamics.
4. This paper describes these effects and discusses implications for the recovery of coastal ecosystems that include the essential involvement of mana whenua (indigenous Māori people), fishers, and the wider community, which suffered concomitant economic, recreational, and cultural impacts. These community perspectives will underpin the protection of surviving remnants of intertidal marine populations, the potential use of restoration techniques, and ultimately a successful socio-ecological recovery.

KEYWORDS

coastal, connectivity, earthquake, ecology, impact, kelp, marine

1 | INTRODUCTION

1.1 | The issues

The recent Mw 7.8 earthquake that struck the north-eastern coast of the South Island of New Zealand has presented one of the more compelling examples of compromised connectivity between different ecosystem components and their interactions with human societies. The earthquake was centred on land, about 15 km inland, propagated through many terrestrial rifts and faults, and progressed through the intertidal and shallow subtidal zones of the coastal environment, causing massive upheaval of the nearshore environment. In total, the fault zone was around 110 km on land (Clark et al., 2017) and another 34 km out to sea (Shi et al., 2017). Taken together, this is considered to be one of the most complex and disruptive earthquakes ever recorded in New Zealand (Duputel & Rivera, 2017; Hamling et al., 2017; Kaiser et al., 2017; Shi et al., 2017). In addition to the devastation of parts of the coastal marine environment, there were large social, economic, and cultural impacts affecting those living along the coastline. This included the isolation of coastal towns by massive terrestrial slips that blocked major roads for a year, the closure of commercial fisheries, economic impacts associated with tourism, and reductions in key taonga (treasured) species that contribute to ecosystem health and services.

Degradation of an environment is usually considered to occur incrementally over time as various stressors accumulate. In this instance, however, major disruption occurred within a period of a few minutes on 14 November 2016. Major socio-ecological effects were associated with the recovery processes, such as the repair of roads, railways, bridges, culverts, and tunnels along the coastline, and also with new uses, relationships, and management initiatives relating to the uplifted coastal environment. The human dimensions have multiple interactions with the new configuration of the coastline and influence the rate and degree of recovery of key habitats and the assemblages that formerly occupied them. In many ways, therefore, this situation presents the reverse of modelled simulations of 'tipping points' from a desired state into some alternative undesirable state of the ecosystem (Horan, Fenichel, Drury, & Lodge, 2011; Levin & Möllmann, 2015; Selkoe et al., 2015). The interest here is the recovery of ecosystems from well beyond their tipping points in a context where widespread reconfiguration of coastal biodiversity and spatial distribution is inevitable. This article presents some of the major effects of the earthquakes on coastal habitats and ecosystems, with a focus on the connectivity issues that have arisen and the challenges associated with recovery.

1.2 | Background coastal uplift and ecological effects

It is known from other large earthquakes that the effects of uplift can be devastating and take many years to recover (Hernández-Miranda, Cisterna, Díaz-Cabrera, Veas, & Quiñones, 2014; Kawamura et al., 2014; Noda, Iwasaki, & Fukaya, 2016). For example, in the 2010 Chilean earthquake (Mw 8.8) there was over 3 m of uplift of some

coastal platforms, which caused bleaching, the loss of coralline algae (Ortlieb, Barrientos, & Guzman, 1996), and almost 100% mortality of macroalgae such as large kelps and bull kelps (Castilla, 1988; Castilla, Manríquez, & Camaño, 2010; Castilla & Oliva, 1990; Vargas et al., 2011). The effects were related to the degree of uplift (Jaramillo et al., 2012), and there were severe impacts on edible and commercial species that were important to local communities. Similar effects were seen in the Kaikōura earthquake. The largest coastal upheavals were seen at or near the sites where the inland rupture extended out to sea. For example, around 20 km north of the Kaikōura peninsula (Figure 1), the uplift was around 6 m (Clark et al., 2017; Hamling et al., 2017). Areas around Cape Campbell experienced about 1–2 m of uplift and areas to the south of Kaikōura experienced 0–2 m of uplift (Clark et al., 2017; Hamling et al., 2017). The coastal platforms of the Kaikōura peninsula seem to have been uplifted in their entirety, with little evidence of cracking along the coastline. Some sites around Kaikōura, such as the extensive Wairepo Reef, are very diverse and have been the subject of ecological sampling and experimental studies for over 20 years (e.g. Schiel, 2011), which proved to be useful for the before-and-after comparisons in this study. It is estimated that this site had around 0.8 m of uplift (Clark et al., 2017; Hamling et al., 2017).

It is noteworthy that several post-earthquake studies have used 'biozones' as indicators of uplift of the coastal zone (Bodin & Klinger, 1986; Carver, Jayko, Valentine, & Li, 1994; Castilla et al., 2010; Clark et al., 2017; Melnick, Cisternas, Moreno, & Norambuena, 2012). One study of the Kaikōura earthquake assessed key algal species, particularly the southern 'bull kelps' *Durvillaea antarctica* and *Durvillaea poha* (which are actually furoid algae and not true kelps) and another furoid, *Carpophyllum maschalocarpum*, as indicators of uplift (Clark et al., 2017) because they occur almost exclusively at the low intertidal-subtidal margins of rocky reefs in this area (e.g. Schiel, Wood, Dunmore, & Taylor, 2006). Clark et al. (2017) used LIDAR (light detection and ranging) and Global Positioning System (GPS) techniques to cross-calibrate uplift and found these algae to be reliable indicators of coastal uplift. It should be noted that some subsidence also occurred during the earthquake, but this seemed to be confined mostly to land and coastal streams (Clark et al., 2017).

A tsunami generated by the earthquake produced waves up to 3 m high, which propagated down the east coast of the South Island (Bai, Lay, Cheung, & Ye, 2017; Hamling et al., 2017). It had few discernible effects in the earthquake area because the coastal morphology deflected the waves and the tsunami surge was less than the 3–6 m of uplift in the rift area. Tsunamis from earthquakes can have devastating effects (e.g. Urabe, Suzuki, Nishita, & Makino, 2013), but because no effects were seen in the Kaikōura earthquake these will not be discussed here.

1.3 | Connectivity issues

An underlying theme of this article is connectivity, which involves physical, biological, ecological, and human dimensions (encapsulated in Figure 2, which forms a summary and template of the issues covered

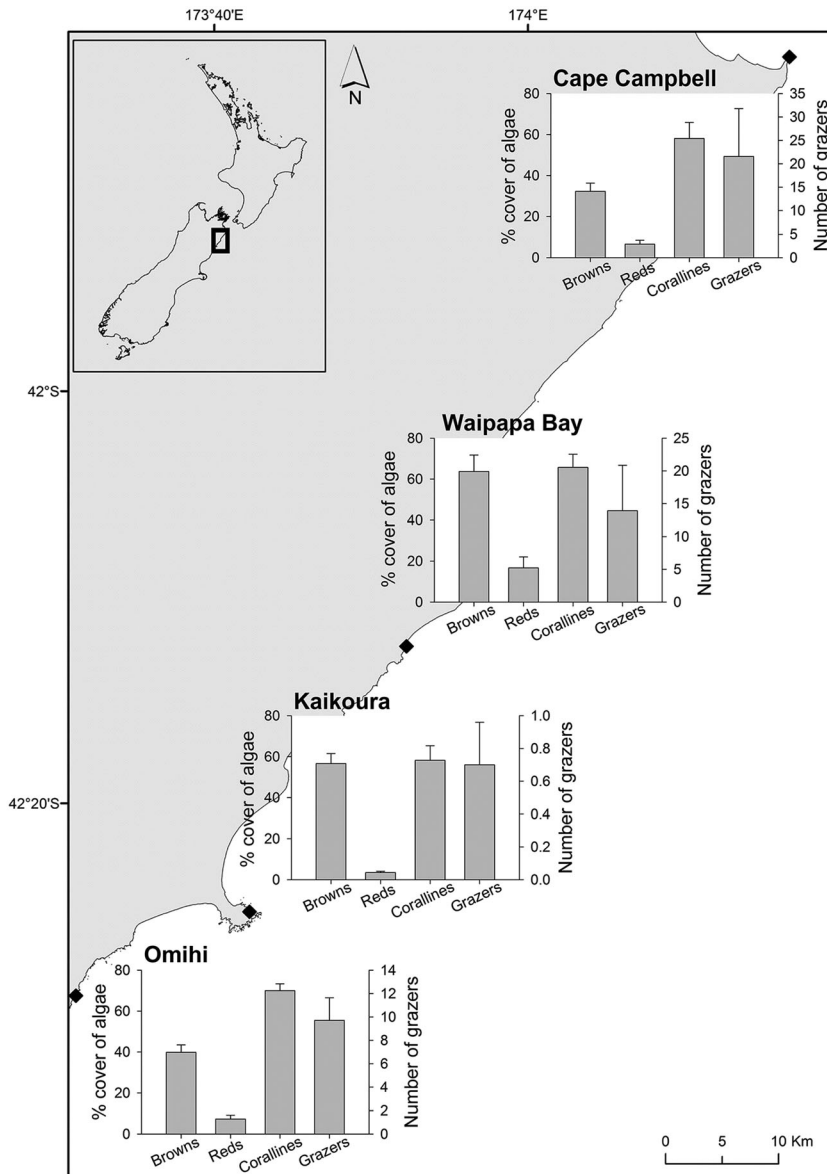


FIGURE 1 Location map of the study sites along the north-east coast of the South Island of New Zealand. Labelled sites represent different degrees of coastal uplift, as documented in this paper. Insert graphs show the percentage cover of dead large brown algae, red algae, turfing coralline algae, and the number of invertebrate grazers per m^2 at Cape Campbell, Waipapa Bay, Kaikōura, and Omihī in November–December 2016, 2–4 weeks after the earthquake. Each graph is a composite of the low and mid-tidal zones at two sites within each of these areas

here). These dimensions are centred around altered ecosystem functions and services and relate to connectivity within and between the marine and human dimensions of earthquake-related events. There were alterations to the topography of the coastline and its geomorphology because of rocky reef areas being pushed into the terrestrial domain, and this caused changes in aspect, temperature, sedimentation, and wave forces to the remaining low intertidal and shallow subtidal areas. These changes also led to a large loss of habitat-forming seaweeds, with potentially wide-ranging effects on the ecological functioning of the nearshore marine zone. It is known that the removal of kelp from coastal habitats by large storms such as hurricanes can have impacts on trophic connectivity between adjacent ecosystems (Filbee-Dexter & Scheibling, 2012). The large brown algae themselves are important sources of carbon upon which much of the nearshore food webs depend (Duggins, Simenstad, & Estes, 1989). Although important, these types of larger scale food-web connections can be difficult to quantify. The local-scale severe loss or extinction of these large algae

within the Kaikōura earthquake zone also affects the connectivity of their populations along the coastline through the fragmentation of populations beyond their capability of dispersing propagules. In these cases, drifting reproductive seaweeds may be the only source of replenishing propagules in the recovery process of fragmented populations, and these depend on coastal flows and the arrival of drifting algae to settlement sites inshore (e.g. Hawes, Taylor, & Schiel, 2017; Hobday, 2000).

Connectivity issues also extend to several aspects of human expectations of usage of the nearshore zone. These include commercial interests such as the abalone (pāua) fishery, recreational uses such as fishing, other economic uses such as increased tourism in the coastal zone, and cultural values, all of which have been affected by the earthquake. The social issues may include reducing ecological stressors through different management initiatives for the coastline. There are also important cultural issues involving *mana whenua* (indigenous Māori), who have a high regard for *taonga* (treasured) species and wider ecosystem health related to the marine environment. This

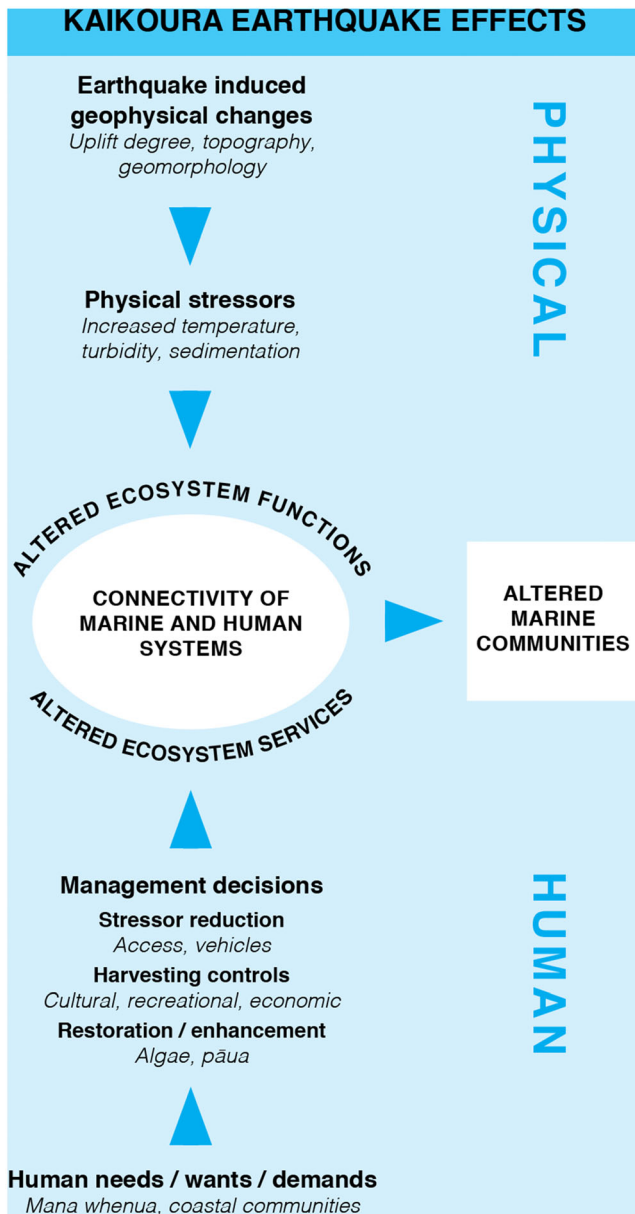


FIGURE 2 A summary and template graphic of the issues centred around altered ecosystem functions and services, related to connectivity within and between the marine and human dimensions of earthquake-related events

is often encapsulated in a holistic view of ecosystems and the recognition of connectivity between land and sea – a concept encapsulated in the Māori philosophy *ki uta ki tai*, ‘from the mountains to the sea’ (e.g. Schiel & Howard-Williams, 2016).

2 | METHODS

2.1 | First impressions and basis for sampling and experiments

To understand the sampling design, it is necessary to know the initial observations made in the earthquake zone. First impressions between

mid-November and December 2016 were of widespread mortality to intertidal and shallow subtidal fucoid algae, such as *Carpophyllum* spp., *Margineriella* spp., *Cystophora* spp., and *Durvillaea* spp., which provided the three-dimensional biogenic habitat of the rocky coast. A ‘sea of white’ was visible throughout the newly uplifted rocky areas (Figure 3), which was basal calcareous algae that had bleached from exposure over extensive rocky areas in the former mid-intertidal to shallow subtidal zones. Because of the suddenness of the uplift, some of the more severely affected sites were littered with coastal fishes such as butterfish (*Odax pullus*), labrids (*Notolabrus celidotus* and *Notolabrus fucicola*), juvenile and adult rock lobster (*Jasus edwardsii*), and New Zealand abalone or pāua (*Haliotis* spp.). These were either desiccated or scavenged by birds and mostly disappeared from the reefs over a period of several months. Nearshore water quality was compromised, at least initially, because of the vast die-off of organisms that reduced the dissolved oxygen, often below 5 mg L^{-1} (Tait & Schiel, unpubl. data), which is too low to support coastal organisms. Additionally, there was extensive sedimentation from the drying out and erosion of sedimentary rocks, which often covered the basal substrate.

Black-footed pāua (*Haliotis iris*) were particularly hard hit (Figure 3), as tens or even hundreds of thousands of them, often greater than the minimum legal fishable size of 125 mm shell length, were left exposed on uplifted rocks and boulders. Some of these were returned to the sea, but most died. Many areas of known habitat for juvenile pāua were also uplifted, creating concerns for adequate recruitment in the post-earthquake environment. These ecological impacts had significant economic implications (cf. Potter, Becker, Johnston, & Rossiter, 2015), foremost of which was the closure of the pāua fishery over 110 km of coast, and associated financial losses of millions of dollars to fishers and local communities. The rock lobster fishery was also closed immediately after the earthquake but was reopened within a few months.

2.2 | Sampling design (surveys and experiments)

To illustrate earthquake impacts and connectivity issues in recovery processes, data were used from post-earthquake surveys and from previous unpublished studies in the affected area. Starting within a week of the earthquake, quantitative sampling of uplifted areas was initiated. Surveys were performed where access permitted, as there were large land slips on the escarpments adjacent to the coastal highway that caused road closures in many places for up to a year.

The basic sampling design used stratified random quadrats across newly uplifted intertidal rocky reefs to gauge the extent and types of losses from coastal upheaval. Two or more sites were sampled within areas of different degrees of uplift. Composite data are presented for four areas using combined data for each of these areas (Figure 1): the Kaikōura peninsula (~1 m uplift), Cape Campbell (~1–2 m uplift), Omihi (~2 m uplift), and Waipapa Bay (~6 m uplift; in the vicinity of a major fault that extended into the sea). Sampling was carried out within the pre-earthquake intertidal zone when benthic



FIGURE 3 Upper panel: an extensive area of dead and decaying fucoid algae (mostly *Durvillaea* spp.) at the former intertidal–subtidal margin. White patches on boulders are bleached coralline algae. Lower panel: dead pāua, *Haliotis iris*, that were left high and dry in the intertidal zone along much of the earthquake-affected coastline. Photos were taken near Waipapa Reef, December 2016

organisms were still attached and identifiable, between November 2016 and January 2017. At each site, a survey tape was extended 30–50 m parallel with the shoreline (as local topography allowed) in the upper, mid, and lower portions of a newly exposed reef. These corresponded with the former high, mid, and low intertidal zones, based on clear zonal patterns (cf. Morton & Miller, 1968) and previous experience (Schiel, 2004). The high zone was generally ~1.7–2.0 m above LAT (lowest astronomical tide), the mid zone was at ~0.8–1.4 m, and the low zone was at 0.0–0.4 m. Ten 1-m² (or in some cases 0.25-m²) quadrats were randomly placed along each transect. Within each zone, the percentage cover of all algae (down to ~2 mm in length) and the number of invertebrates of each species were recorded. Most taxa were still identifiable to species level for at least the first month after the earthquake. During this initial period, the air temperature was high (20°C or more), so organisms became desiccated and many were bleached, making the identification of

smaller algae difficult. Because some of the areas of coastline comprised large boulder fields, the tops and sides of boulders were sampled if they fell within quadrats. These data were averaged across four regions of uplift.

There were pre-existing abundance data for algal assemblages at some sites. These were used to illustrate the temporal sequence of change using data collected over 13 years at Wairepo Reef, Kaikōura. This extensive platform has been used both for the long-term monitoring of changes (e.g. Schiel, 2011) and for numerous experiments on ecological processes and functions (with some 50 postgraduate theses and many publications, e.g. Dunmore, 2006; Hawes, 2008; Hawes et al., 2017; Lilley, 2004; Lilley & Schiel, 2006; Schiel, 2011; Schiel & Lilley, 2007; Schiel & Lilley, 2011; Taylor, 2002; Taylor & Schiel, 2003; Walker, 1998). Data presented here were from fixed 1-m² quadrats established in 2004 that were sampled annually. The percentage cover of all algae and the number of mobile invertebrates were recorded.

Particular habitats may be crucial for different life stages of mobile species such as invertebrates. Because of the great concern about the state of pāua populations and their future, we sampled a site for which we had previous information as a gauge of critical habitat loss. This site (Omihī) was known to be good habitat for juvenile pāua (*Haliotis iris*). It had small boulders on top of other small rocks and a cover of coralline algae at the very low intertidal–subtidal margin, a habitat that promotes recruitment and juvenile growth (Aguirre & McNaught, 2011; Schiel, 1992, 1993). This site was mapped using survey tapes and then captured using aerial imagery from a drone to determine the extent of juvenile pāua habitat loss.

The ability to disperse propagules from adult stands is a key feature of connectivity of attached algae. Previous unpublished experiments have tested the dispersal distances of propagules of *Cystophora torulosa*, *Durvillaea* spp., and *Hormosira banksii* (Dunmore, 2006), the most affected taxa of habitat-forming algae. For all species, experiments were performed near dense adult stands on or around the Kaikōura peninsula, including Wairepo Reef. Arrays of fibrolite (Hardieflex™) settlement plates (known to be good settlement surfaces for furoid algae) were put out at various distances from adult stands ($n = 3$, 10×10 -cm plates per each distance). The distances for *Hormosira* and *Cystophora* were 0, 10, 35, 60, 110, and 210 cm from reproductive adults, and the distances for *Durvillaea* were 0.1, 0.35, 0.6, 1, 2, 4, 8, 16, and 32 m from reproductive adults. The number of settled zygotes was recorded daily for 2 weeks during the reproductive season of each species, in summer for *Hormosira* and *Cystophora* and in the late autumn–winter for *Durvillaea*. It was not possible to distinguish the three *Durvillaea* species (*Durvillaea antarctica*, *Durvillaea poha*, and *Durvillaea willana*) from each other using a dissecting microscope in the field.

The end point of dispersal is settlement, but this was potentially affected by the great volumes of sediments deposited on rock surfaces at many sites. To test the effects of sediments on the settlement of *Hormosira*, *Cystophora*, and *Durvillaea*, previously published data were re-analysed and augmented with unpublished data. One set of experiments tested the ability of furoid algae to settle and attach using 10×10 -cm settlement plates (Hardieflex™) in a laboratory-based culture unit. Two levels of sediment (light, $1.3 \text{ g}/100 \text{ cm}^2$; heavy, $7.3 \text{ g}/100 \text{ cm}^2$; Schiel et al., 2006) were sprinkled onto the plates, covering 75 and 100% of their surface area, respectively. Known quantities of microscopic algal zygotes (usually around 1 hour old) were poured over them to achieve a density of ~ 100 per cm^2 . Plates with no sediment served as controls, and all replicates ($n = 5$) were mixed haphazardly in one settlement tank. The number of zygotes that successfully attached to each plate was recorded after 1 day (when zygotes are known to be able to attach firmly; Taylor, Delaux, Stevens, Nokes, & Schiel, 2010) after gently washing sediments from treatment plates. To test the effects of smothering by sediments on the early life stages of the three furoid species, another set of experiments was performed post-settlement (data reworked from Alestra & Schiel, 2015). Zygotes of each species were settled onto plates and, after they were attached firmly, a fine layer of sediment was poured over them. Treatments were followed for 2 weeks to gauge survival.

3 | RESULTS

3.1 | Major biological impacts

Sampling along the earthquake coast across degrees of uplift showed the extent of losses of algal beds and associated species (Figure 1). In the region of highest uplift, Waipapa Bay, 63% of large brown algae were lost compared with around 35% at the lower uplift sites at Cape Campbell, and 58% at Kaikōura, whereas the intermediate uplift site of Omihī lost $\sim 40\%$ of large brown algae (Figure 1). The major affected species included *Durvillaea antarctica* and *Durvillaea poha* on the former intertidal–subtidal margin, and *Durvillaea willana*, which normally occurs at 3–4 m depth. Extensive stands of *Carpophyllum maschalocarpum*, *Hormosira banksii*, *Landsburgia quercifolia*, *Lessonia variegata*, and the subtidal furoid *Margineriella boryana* were also exposed. It was clear that the losses did not entirely relate to the degree of uplift, other than the sites of greatest uplift around Waipapa demonstrating the greatest losses (Figure 1). Around Cape Campbell and Kaikōura the dominant furoids were *Hormosira banksii* in the mid zone and *Cystophora torulosa* in the low zone, which together comprised most of the pre-earthquake cover. Around Waipapa and Omihī, *Carpophyllum maschalocarpum* and *Durvillaea poha* dominated the low zone, but few of these survived except at the lowest margins of the reefs. Understorey red algae, including foliose forms of red algae and coralline algae, had extensive cover in the former mid and low zones of all sites, but most of these died (Figure 1).

Grazing invertebrates had been abundant at most sites. There were 10–20 per m^2 of limpets and grazing gastropods (Figure 1). For example, the upper intertidal zone was dominated by *Cellana* limpets (mostly *Cellana denticulata*, *Cellana ornata*, and *Cellana radians*). They suffered nearly 100% mortality, except in a few shaded areas. Surviving grazers included the turbinid gastropods *Cookia sulcata* and *Lunella smaragdus*, mostly found in shaded areas of the low zone. Sites around Cape Campbell, Waipapa Bay, and Omihī had extensive mortality of pāua (mostly *Haliotis iris*). Although hundreds of pāua from these sites were translocated subtidally, it was estimated that thousands of pāua above the minimum legal size for harvest (≥ 125 mm shell length) had died (there are no comprehensive data on actual mortalities).

The time trajectory of losses is illustrated by long-term sampling at Wairepo Reef in Kaikōura (Figure 4). The percentage cover of habitat-forming algae, mostly *Hormosira banksii* and some *Cystophora torulosa*, was between 80 and 90% from at least 2004 until the earthquake, after which it quickly declined to near zero. Similarly, grazing gastropods varied between ~ 5 –15 per m^2 , but also suffered virtually 100% mortality. Species richness was generally between 15 and 20 species, but this declined to around three after the earthquake (Figure 4).

3.2 | Physical environment effects

One of the remarkable features of the uplifted reefs was the deterioration of boulders and reef surfaces as they dried out and were no longer tidally inundated or were denuded of stabilizing algae. These rocky

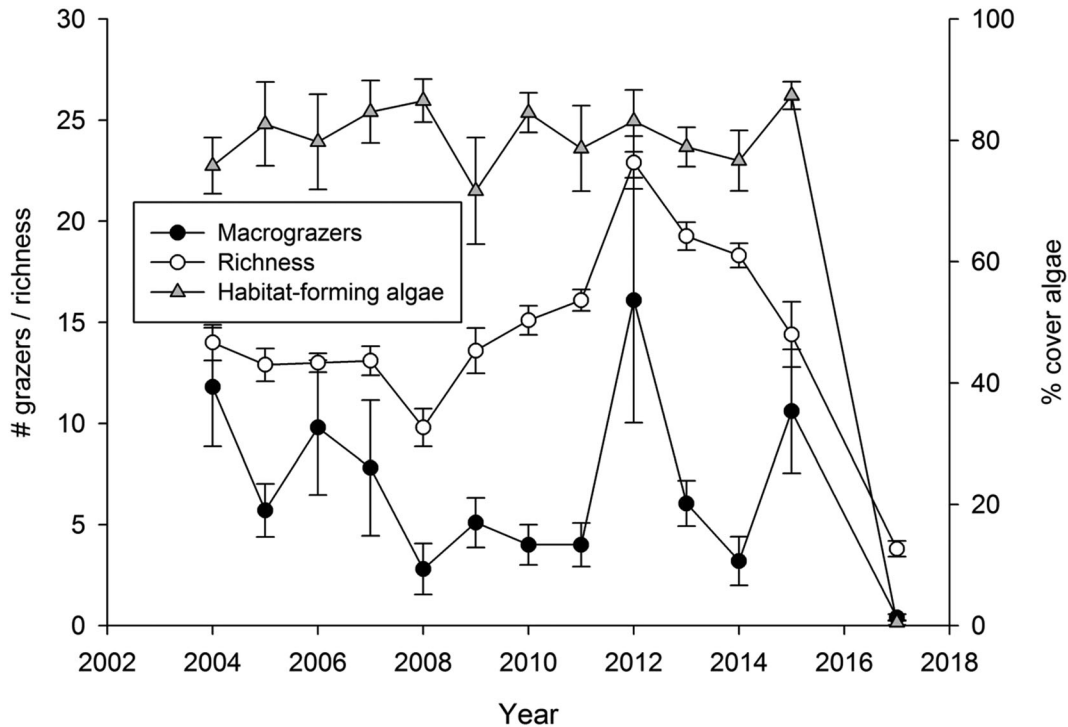


FIGURE 4 Temporal variation in the percentage cover of habitat-forming algae (mostly *Cystophora torulosa* and *Hormosira banksii*), the abundance of grazing invertebrates (limpets, trochids, and turbinid gastropods), and species richness per m² in the mid intertidal zone at Wairepo Reef, Kaikōura. Means ± SEs are shown

reefs were mostly soft sedimentary rock. Datum marks (steel bolts that had been screwed down to the reef surface prior to the earthquake) showed how extensive the erosion was in the months following the earthquake (Figure 5a). Within 2 months of the earthquake, the erosion at a 0.8-m uplift site (Wairepo Reef, Kaikōura) was 3.5 cm (averaged over five embedded bolts). The resulting sediments were very fine grained, and often washed down into the new tidal zone, covering most surfaces. Experiments showed that these types of sediments can both reduce settlement of furoid zygotes and smother established germlings, thereby preventing populations from being replenished after disturbances (Schiel et al., 2006; Taylor & Schiel, 2003). For example, even a fine cover of sediments reduces the attachment of furoid zygotes to between 26% (*Durvillaea*) and 60% (*Hormosira*) of settlers, with effects on *Cystophora* being intermediate at 33% (Figure 5b). When a heavy sediment load (a few mm thick) was present on settlement surfaces, no *Durvillaea* and few of the other species managed to attach. It was interesting to note that the stickiest zygotes, those of *Durvillaea*, attached to sediment grains and simply washed away when sediments were removed (Schiel et al., 2006). The least sticky zygotes, those of *Hormosira*, rolled between sediment grains and some of them attached to plates. When *Hormosira*, *Durvillaea*, and *Cystophora* germlings were established on plates and then covered with sediment for 2 weeks, there were significant differences in survival among species (Figure 5c). *Durvillaea* and *Cystophora* showed no differences in survival between treatments, whereas *Hormosira* zygotes with sediments had only 35% survival relative to controls. These experiments show, therefore, that the survival of early life stages of key furoids is possible if they are already

established on rock surfaces and only covered with sediments for short periods, but that increasing sediment volumes have a great effect on the ability of these species to survive.

Prior to settlement, however, propagules must arrive from source populations. For habitat-forming furoids, the dispersal distances of propagules tend to be small, with most landing very close to reproductive adults (Figure 6). Zygotes of both *Cystophora torulosa* and *Hormosira banksii* generally drop immediately beneath the adults or just outside their canopies, with relatively few making it beyond 2 m (Figure 6a). Propagules of *Durvillaea* spp. settle further from adults, but few make it more than 30 m (Figure 6b). Other (unpublished) experiments showed there are density-dependent effects between settlement (when propagules arrive) and recruitment (their visible stages when they are juvenile plants), with mortality usually well beyond 90% between these stages (Schiel & Foster, 2006). Moreover, isolated plants or those that grow in low densities beyond the juvenile stages are often stunted in their adult stage (cf. Schiel, 1985). From this earlier work, it is estimated that it takes around 250 settlers per cm² of *Hormosira*, 100 per cm² of *Cystophora*, and 20–50 per cm² of *Durvillaea* to produce sufficient juveniles and adults to form a closed-canopy stand. These numbers can accumulate over a reproductive season, as there can be daily settlement over a season by each species. There is also a large difference in maximum sizes of each species and the number of individuals that form a closed canopy at 1 year of age. The demographics of the early life stages therefore have a great effect on the recovery of populations. Of course, there is wide variation in the survival of the early life stages onwards, but the figures here give an indication of the orders

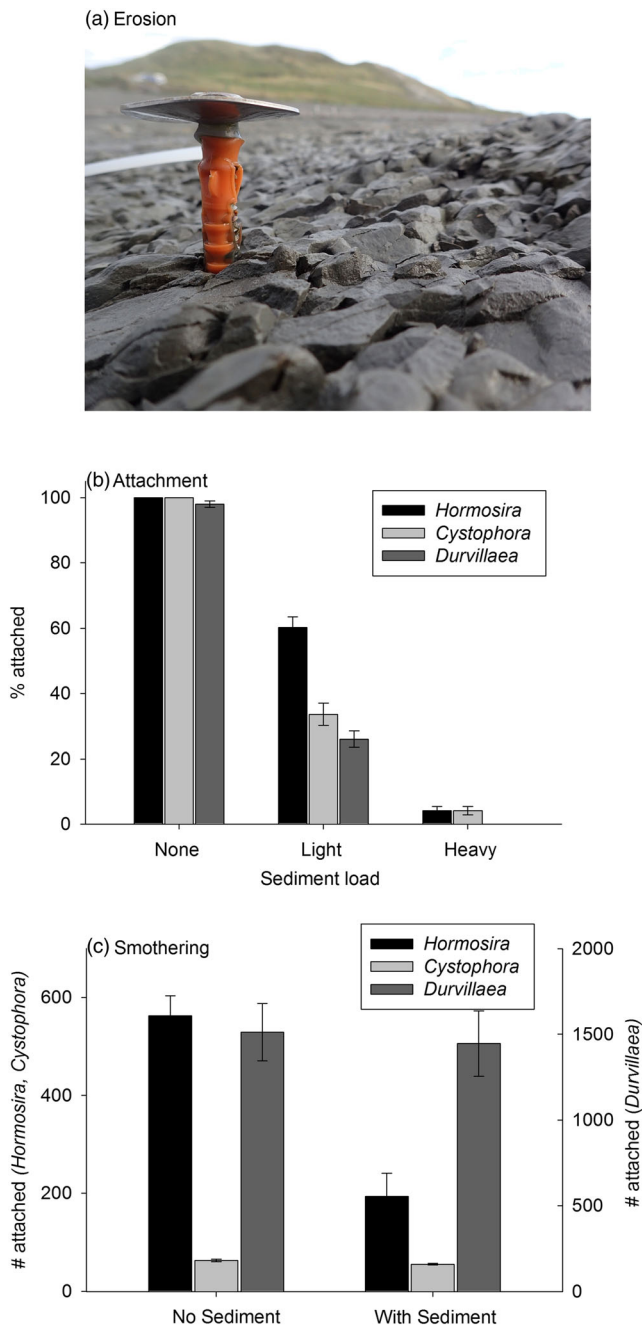


FIGURE 5 Sediment and its effects on zygotes and germlings of large brown algal species. (a) Erosion of the mudstone substrate in the intertidal zone of Cape Campbell. This bolt was embedded in the reef prior to the earthquake. The photo was taken in June 2017, 6 months after the earthquake, and the erosion distance is 35 mm. (b) Percentage cover of attached germlings of three habitat-forming species (*Cystophora torulosa*, *Durvillaea poha*, and *Hormosira banksii*) on substrate without sediment, with light (67 DWg m^{-2} , 50% covering) and heavy (382.2 DWg m^{-2} , 100%) cover. (c) Number of attached germlings per $5 \times 5\text{-cm}$ plate with (400 DWg m^{-2}) and without sediment. Data for (b) amended from Hurley (2009) and Schiel et al. (2006); data for (c) reworked from Alestra and Schiel (2015)

of magnitude in which propagules must arrive and attach for the recovery of populations to occur. The provision of potential settlers is also affected by the reproductive season of each species. In the

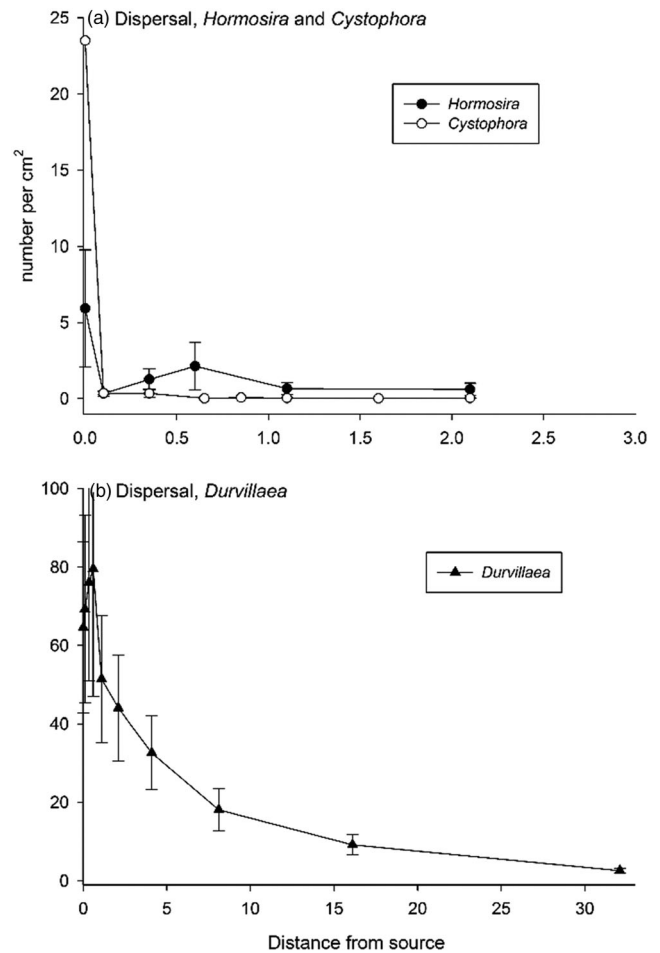


FIGURE 6 Dispersal curves for *Cystophora torulosa* and *Hormosira banksii* (a) and *Durvillaea poha* (b), showing the number of propagules per cm^2 with distance from dense, reproductively active stands of adults of each species. Data from Dunmore (2006)

case of *Hormosira* and *Cystophora*, plants can be reproductively active all year round, but *Durvillaea* spp. are reproductively active only during winter.

The loss of physical habitat is of concern for recovery. One perspective is that species will simply redistribute themselves downwards as they adjust to new tidal zones. This can only be the case, however, if there is comparable and adequate rocky shore habitat for colonization in the newly configured intertidal and subtidal zones. The extent of this habitat remains to be determined and will depend on the extent of newly uplifted subtidal habitat. In the low intertidal to subtidal margin it is known that at least some key habitat for juvenile pāua (*Haliotis iris*) has been lost. Pāua settle primarily on thin algal films on small boulders generally situated on smaller rocks and gravel (Morse, Froyd, & Morse, 1984; Morse & Morse, 1984; Moss, 1999). At Omihi, south of Kaikōura, around 48% of this habitat was lost through uplift (Figure 7). It is a continuing process to determine how much of such habitat remains over the 110 km of coastline and the extent to which pāua are recruiting. In the meantime, the commercial and recreational fisheries remain closed (as of December 2018).

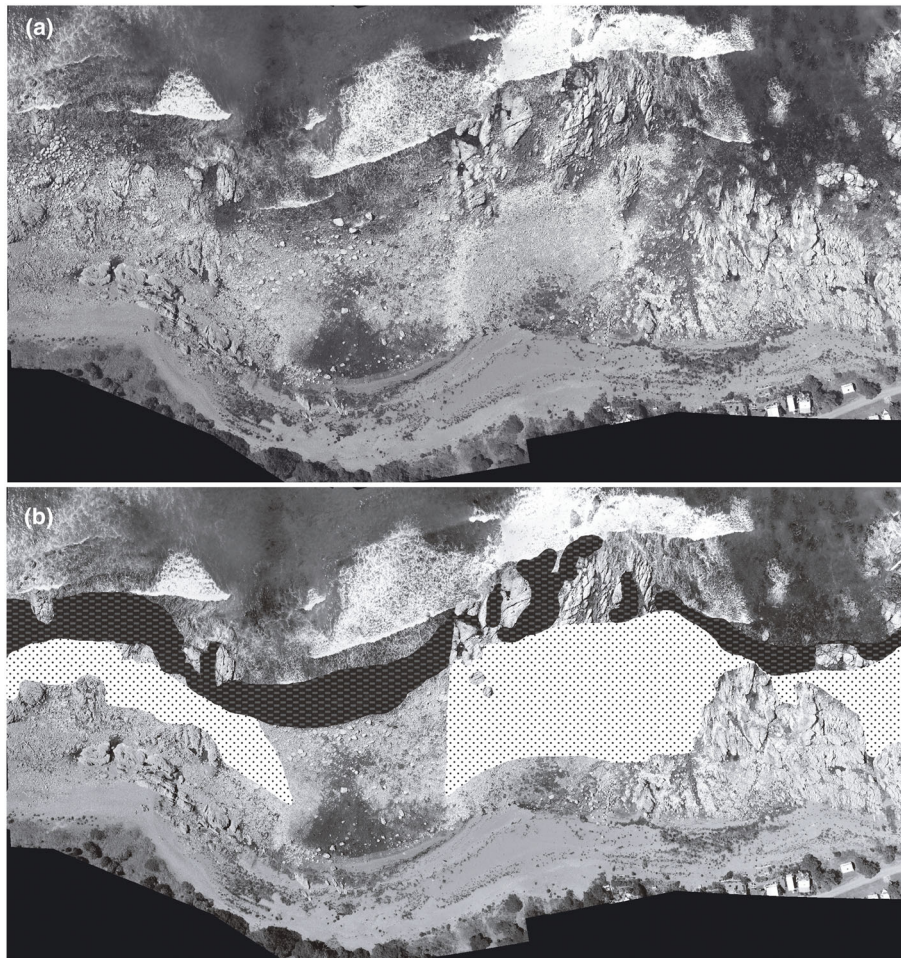


FIGURE 7 Post-earthquake, drone-acquired image of a reef near Omihi, south of Kaikōura. (a) Low-tide image; (b) juvenile pāua habitat that was lost with uplift in the earthquake (light stippled area in the centre of the image) and the remaining juvenile habitat on the lower shore after the earthquake (dark stippled shading). These changes represented a 48% decrease in pāua juvenile habitat at this site after the earthquake. The length of the reef in the images is 358 m

The issues relating to social and cultural perspectives are layered and unfolding. Headlands, small bays, and reefs isolated by high tides before the earthquake are now accessible at all tides. Recreational vehicles ply these new areas, often related to fishing. Adventure tourism has expanded into these new areas. For example, around 40 km of gravel beaches that were previously isolated by tides can now be navigated around Cape Campbell. Each of these usages reflects values to some sector of society, but also has potential consequences for the environment. These include the disruption of nesting birds and hauled-out seals, trampling and vehicle disturbance of rocky platforms that previously supported diverse intertidal communities, increased access to places for pāua and lobster fishing, and potentially increased illegal fishing. Many of these social and cultural effects may be in conflict. In general, they are in the early stages of being resolved in the post-quake landscape and management implications are in the early stages of development. Interconnections with many other aspects of socio-ecological recovery, including those illustrated above, will be important to the identification of opportunities and resolution of competing demands.

4 | DISCUSSION

The coastal effects of the Kaikōura earthquake share many features with large-magnitude earthquakes elsewhere. At the same time, there is a high degree of novelty in the scale of effects and the context dependency of recovery processes. This context involves differential impacts to the physical habitats along the coastline, the biogenic habitat in the assemblage of species present, the alteration of many ecological functions, and the social and cultural interactions that have come into play. Complex physical alterations of the coastal topography underpin many of these effects. Here, we discuss these issues as they relate to natural and human-assisted recovery processes, focusing on connectivity issues.

4.1 | Marine ecosystem recovery

Ecological science is often based on small-scale, tractable experimentation as tools to provide insights and inference (Underwood, 1996,

2000). In a sense, the Kaikōura earthquake provided a massive clearance experiment that allows a test of how informative small-scale experiments are in forecasting recovery from large-scale impacts (akin to oil spills, see Hawkins et al., 2017). There have been numerous experiments over many years on the effects of stressors on key algal species (Alestra & Schiel, 2014, 2015; Alestra, Tait, & Schiel, 2014; Taylor & Schiel, 2003, 2010), grazer dynamics (Dunmore, 2006; Schiel et al., 2006; Walker, 1998), the role of diversity in resilience and recovery after disturbances (Lilley & Schiel, 2006; Schiel & Lilley, 2007, 2011), and the early life-stage demographics of habitat-forming macroalgae (Alestra et al., 2014; Alestra & Schiel, 2014; Dunmore, 2006; Taylor & Schiel, 2010). The Kaikōura earthquake will be a test of how well the knowledge and understanding gained from these studies may scale up from essentially patch dynamics to entire seascapes.

The recovery of intertidal and shallow subtidal communities will depend on their degree of uplift and a set of coinciding conditions. These include the physical presence of suitable habitat, such as rocky substrata onto which organisms can colonize, the effects of rock weathering and suspended sediments, the proximity of sources of propagules for key algae that form biogenic habitat, and the development of sufficient numbers and sizes of new populations to support diverse and resilient communities. There will be a relationship between recovery and the pre- and post-earthquake configuration of reefs. At all locations there is still an intertidal zone, but in most cases the actual area of this zone is greatly reduced from the previous configuration. In these places, especially in the high uplift areas in the middle of the earthquake zone, the intertidal area is reduced to narrow near-vertical surfaces in many places. Many of the pre-quake areas have permanently changed from large intertidal or even subtidal reefs into terrestrial habitats that are being colonized by grasses and trees. Other locations, such as Wairepo Reef on the Kaikōura peninsula and the platforms around Cape Campbell, still have similar areas of intertidal inundation as before the earthquake, but the immersion times have shortened considerably, and the depth of water cover at high tide is less than 1 m at the highest tides. Where recovery is possible, habitat-forming algae, the fucoids and kelps, will be the focal points of recovery of the nearshore ecosystem because most other species depend on them for habitat, shelter, and food (Lilley & Schiel, 2006). Their large-scale loss has numerous potential flow-on effects to the wider ecosystem because of lost primary productivity and detrital material (e.g. Jack & Wing, 2011). Near-shore algal beds can contribute around 1500 g C m^{-2} (kelps) and 900 g C m^{-2} (fucoids) annually (Mann, 1972, 1973; Vadas, Robert, Wright, & Beal, 2004), and the loss of production and biomass over the earthquake-affected coastline is immense.

Studies from Chile, where there have been several large-magnitude earthquakes over the past several decades, have shown large impacts on species similar to those in New Zealand. Castilla et al. (2010) showed, for example, that an Mw 8.8 earthquake caused coastal uplift of >8 m, which led to bleaching, the loss of coralline algae (Vargas et al., 2011), and almost 100% mortality of belt-forming algae such as the bull kelp *Durvillaea* (Castilla et al., 2010). These took many years to recover. Similarly, in Japan the minor subsidence of some coastal areas (<1 m) has resulted in the poor recovery of coastal

assemblages, with mortalities occurring up to 1 year after the earthquake (Noda et al., 2016). As observed in our case, the severity of earthquake impacts depended to a large extent on the degree of uplift. Also, in Chile there were severe effects on edible and commercial species that were associated with habitat loss, which had substantial repercussions for the well-being of coastal communities (Jaramillo et al., 2012). Together, these studies point to the prospect of many years for recovery to occur from the Kaikōura earthquake.

In any case, the prime requisite for recovery is the presence of rocky reef. At this stage, it is unknown how much rock is available in the shallow coastal zone. It is clear in most places, however, that the new intertidal zone is generally steeper and with less overall area than before the earthquake. These steeper shores are likely to have greater direct wave action and tend to favour animals rather than large algae (Hawkins & Hartnoll, 1983), although *Durvillaea poha* can occur on very steep shores (Taylor & Schiel, 2010). At Wairepo Reef and around Cape Campbell, summer seawater temperatures can now reach >25°C and air temperatures can reach >40°C in the intertidal zone at high tide (Schiel, unpublished data), which, if experienced over long periods, is too harsh for fucoids to survive. Many other areas have an intertidal zone of steep boulders that descend to gravel. It is likely, therefore, that the formerly extensive beds of common intertidal species such as *Cystophora torulosa* and *Hormosira banksii* will be far less extensive than they were prior to the earthquake. So far, there is little evidence that these formerly abundant species will be able to simply move lower down on the shore, because of the general unavailability of suitable rocky reef.

4.2 | Continuing land–sea connections

Increased sediment loads and their transport throughout the near-shore system have not dissipated in all areas, particularly those with reduced wave exposure or situated near eroding coastal cliffs. Sedimentation is a major problem in coastal waters worldwide, affecting settlement and the persistence of intertidal and subtidal assemblages on rocky reefs (Airoldi, 1998; Balata, Piazzi, & Bulleri, 2015). Sediment is a cumulative stressor and it often favours coralline and turfing algae to the exclusion of kelps and fucoids (Connell, 2003). We have shown here that even small volumes of sediment prevent the effective settlement of habitat-forming species. Moreover, sediments can interact with other factors such as elevated temperature and nutrients, affect the growth and mortality of algal germlings (Alestra et al., 2014; Alestra & Schiel, 2014), and may also alter grazer dynamics through differential effects on some species such as limpets (Airoldi & Hawkins, 2007). Sediments in the water column reduce the level and spectral quality of penetrating light and can lead to the shallowing of algal habitats (Connell et al., 2008; Kautsky, Kautsky, Kautsky, & Waern, 1986; Tait, Hawes, & Schiel, 2014).

Sediment run-off will no doubt be a continuing process along many parts of the earthquake coast. Stephenson and Kirk (2000) compared the effects of waves and weathering on the erosion of reefs around Kaikōura. They found that breaking waves and associated hydraulic

forces do not play a large role in platform development. Instead, the weathering reduces rock strength by as much as 50%. This is especially so in summer, when immersion, exposure, and drying are important processes in erosion (Stephenson & Kirk, 2001). Over 30 years, Stephenson, Kirk, Hemmingsen, & Hemmingsen, 2010 found the mean surface lowering of reefs to be 1.09 mm per year. This is a small fraction of what we saw from our markers, which showed erosion of around 35 mm over several months. Interestingly, Stephenson and Kirk (2001) found that encrusting coralline algae can help to protect rocks in the wetting and drying process. Their conclusion that weathering is the only process responsible for breaking down the sedimentary rock, to be transported away by waves, is highly relevant to post-earthquake coastal studies. In many areas, these weathered sediments accumulate in the low intertidal and shallow subtidal zone. For much of 2017, they were covered by green algae (mostly sea lettuce, *Ulva* spp.) and effectively prevented the recruitment of most other species. The connectivity of the remaining seaweed populations may well be further impeded by sediment loads in some areas.

4.3 | Connectivity of populations

Effective settlement and subsequent recruitment of algae to form biogenic habitat is essentially a numbers game. It is clear that large numbers of viable propagules must arrive at particular patches for recruitment to occur (reviewed by Schiel & Foster, 2006). Reed (1990), for example, showed that male and female kelp spores must be at a minimum of 1 per mm² for fertilization and sporophyte formation to occur. Early life stages of furoids have such high mortality that very large numbers of propagules, often hundreds per square cm, are needed to establish populations. Because effective dispersal distances tend to be small from attached reproductive furoids and kelps (Figure 6; Gaylord, Reed, Raimondi, Washburn, & McLean, 2002; Schiel, 2011), populations may leap-frog along a coast from pockets of remaining plants. More likely, however, is the haphazard seeding of populations from drifting reproductive plants (Hawes et al., 2017; Hobday, 2000), which potentially improves the dispersal distances greatly (Schiel, 2011). *Hormosira* and *Durvillaea* remain reproductively active while drifting at sea (Hawes, 2008). To be effective in providing settlers to intertidal and shallow rocky reef habitats, these plants must get back to shore in sufficient numbers to seed populations. Hawes et al. (2017) showed that the inshore transport of reproductive drifting algae occurred only occasionally, when onshore winds and incoming tides coincided. This process may be aided by the presence of largely intact low intertidal and subtidal algal beds in Customary Protected Areas around Kaikōura, which may potentially act, somewhat fortuitously because of little damage, as safe-haven reservoirs of source populations.

The interaction of compromised connectivity, sediments, and habitat loss may be particularly crucial for the important invertebrate *Haliotis iris*. Recruitment of this species occurs in very shallow water, of usually no more than several metres in depth, on rocks covered by encrusting coralline algae (McShane & Naylor, 1995a; Tong, Moss, & Illingworth, 1987); the extent to which this particular habitat

remains along the uplifted coast is yet to be determined. Small juveniles that would have resulted from spawning around the time of the earthquake were seen in remaining habitats in mid to late 2017; however, the extent of remaining juvenile habitat remains to be determined, as does how recruitment in this new configuration of coastline will feed back into a sustainable fishery. The minimum legal fishing size of 125 mm shell length takes at least 6 years to be reached (McShane & Naylor, 1995b). Because pāua and most other herbivorous gastropods have planktonic larvae, it seems likely that their populations will recover more quickly than those of large perennial algae, if suitable juvenile habitat is present.

4.4 | Connectivity with communities

Hughes, Carpenter, Rockström, Scheffer, and Walker (2013) argue that when a regime shift occurs past a tipping point, we must get back to safe levels of anthropogenic drivers. Resilience is based, to a great extent, on connectivity as a buffer for unpredicted external shocks and ameliorating effects of local populations through inputs from the broader system (Hughes et al., 2013; Scheffer et al., 2012). In the case of earthquake-affected reefs this may involve managing anthropogenic stressors such as vehicular and human traffic over reefs and increased access to fishing.

There are several opportunities for the design of interventions to assist the re-establishment of self-maintaining marine communities in the short to medium term. An essential step is to assess the vulnerabilities of remaining populations, such as in areas where increased anthropogenic stressors persist. A risk assessment is important to inform both ecological recovery strategies and the management of sustainable uses, such as tourism and fisheries. It is also important that both short- and long-term threats to recovery are considered, such as continuing disturbance in the proximity of road construction sites, and altered vulnerability to climatic events, such as increased wave forces (cf. Schiel, Lilley, South, & Coggins, 2016). Both categories are amenable to avoidance or mitigation in the design of earthquake recovery responses. For example, road construction phase timing can be used to reduce the impacts of short-term disturbance on key ecological events, and the design of permanent structures can contribute to the long-term resilience of the coastal zone (Temmerman et al., 2013). These examples illustrate the potential depth of connections between societal aspects of recovery and the natural environments concerned.

There are also societal connectivity issues of increased access between land and sea that has occurred in many formerly isolated areas of coastline, which were relatively pristine and difficult to access, but now seem to be focal points of human activities. The conservation implications of these losses are great and potentially increasing. Not only have key features of the nearshore ecosystem been lost or compromised, but areas for bird nesting and seal haul-out are now fully accessible because they are no longer isolated by headlands and high tides. In the earthquake zone, therefore, the former topography of the coastline that afforded protection through the isolation of many areas has essentially been reversed by rendering many areas fully

accessible at all stages of the tide along the coast. The time scales of recovery from these sorts of events are likely to be well over a decade, if at all. This assessment is based on our small-scale studies, repeated over many parts of the coastline, which show that even local-scale disturbances to algal canopies can take up to 8 years to recover, even when surrounded by reproductively active adults (Schiel & Lilley, 2011). The re-establishment of the associated diverse community and restoration of pre-disturbance primary productivity can also take over 8 years (Schiel & Lilley, 2011; Tait & Schiel, 2011). With such a massive reduction of algae on the earthquake coast, coupled with the loss of rocky reefs, increased sedimentation, and increased stressors in many areas, it seems highly unlikely that recovery would take any less time than the small-scale experiments.

Attention to the connectivity aspects of ecological recovery can include opportunities to improve outcomes through targeted investments in spatial planning and good design (Duarte et al., 2015). These might involve overcoming algal connectivity barriers by transplants of key species to accelerate recruitment into areas isolated from source populations. Earlier small-scale studies suggest that transplant technologies such as the use of settlement plates and direct algal transfers may offer useful intervention tools to address connectivity effects (Taylor & Schiel, 2003). There may also be value in re-seeding pāua populations from hatchery-reared juveniles, a process that is already being undertaken by the commercial industry.

The perspectives of indigenous people are crucial to the social context of the earthquake and the recovery. Māori cultural connections with the marine environment in the affected area, especially Ngāi Tahu, are longstanding and enacted in a variety of ways (Te Korowai o Te Tai o Marokura 2012). Legal recognition of Māori ancestral connections was provided in the Te Runanga O Ngai Tahu Act 1996, in accordance with genealogy and the continuity of occupation of the land (Tau, Goodall, Palmer, & Tau, 1990). Ngāi Tahu aspirations and governance roles in the affected area are recognized in legislation (e.g. New Zealand Government, 1996), with a wide spectrum of policies and plans through the implementation of the Kaikōura Marine Strategy (Te Korowai o Te Tai o Marokura, 2012) and through cultural values, advice, and impact assessments informing the day-to-day governance of the statutory authorities involved.

Two years after the earthquake, few of these issues have been resolved and there has been little recovery of the algal beds along the earthquake-affected coastline. Coastal usage is increasing and it appears that management intervention will be required to reduce anthropogenic stressors. It appears that the most likely strategies will involve natural recovery processes combined with interventions that reduce stressors as much as possible. The maintenance of local resources and their continued resilience is also recognized as an important component of dealing with change (Hinkel, Bots, & Schlüter, 2014). Although the current understanding of these changed land-use patterns is at an early stage, they will be important aspects of the earthquake recovery process.

The role of restoration, such as improvements to pāua recruitment through hatchery-reared juveniles, will play a role in some aspects of commercial recovery. Overall, however, anthropogenic stressor

reduction is crucial to the recovery of these reefs, which will occur through natural processes and over many years.

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