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

David R. Schiel1 | Tommaso Alestra1 | Shawn Gerrity1 | Shane Orchard1 | Robyn Dunmore2 | John Pirker1 | Stacie Lilley1 | Leigh Tait3 | Michael Hickford1 | Mads Thomsen1

1 School of Biological Sciences, Canterbury University, Christchurch, New Zealand
2 Cawthron Institute, Nelson, New Zealand
3 National Institute of Water and Atmospheric Research, Christchurch, New Zealand

Correspondence
David R. Schiel, School of Biological Sciences, Canterbury University, Private Bag 4800, Christchurch, New Zealand.
Email: david.schiel@canterbury.ac.nz

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

DOI: 10.1002/aqc.3122
wileyonlinelibrary.com/journal/aqc
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 (Hemández-Miranda, Cisterna, Díaz-Cabrera, Véas, & 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, & Camañ, 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 Kaikoura 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 Kaikoura 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 Kaikoura experienced 0–2 m of uplift (Clark et al., 2017; Hamling et al., 2017). The coastal platforms of the Kaikoura peninsula seem to have been uplifted in their entirety, with little evidence of cracking along the coastline. Some sites around Kaikoura, 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 Kaikoura earthquake assessed key algal species, particularly the southern ‘bull kelps’ Durvillaea antarctica and Durvillaea poha (which are actually fucoid algae and not true kelps) and another fucoid, 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 Kaikoura 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...
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 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 Omihi 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.
Earthquake induced geophysical changes
- Uplift degree, topography, geomorphology

Physical stressors
- Increased temperature, turbidity, sedimentation

Management decisions
- Stressor reduction
  - Access, vehicles
- Harvesting controls
  - Cultural, recreational, economic
- Restoration / enhancement
  - Algae, pāua

Human needs / wants / demands
- Mana whenua, coastal communities

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 Carphophyllum spp., Marginerella 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 celiodotus and Notolabrus fucicola), 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), Omihī (~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...
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 zonational 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.

![Figure 3](image-url) 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
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 (Omihí) 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 Kaikoura peninsula, including Wairepo Reef. Arrays of fibrolite (Hardieflex™) settlement plates (known to be good settlement surfaces for fucoid 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 fucoid 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 g/100 cm²; heavy, 7.3 g/100 cm²; 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 cm². 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 fucoid 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 Kaikoura, whereas the intermediate uplift site of Omihi lost ~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 fucoid *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 Kaikoura the dominant fucoids 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 Omihi, *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 m² 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 turbid gastropods *Cookia sulcata* and *Lunella smaragdus*, mostly found in shaded areas of the low zone. Sites around Cape Campbell, Waipapa Bay, and Omihi 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 Kaikoura (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 m², 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
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 fucoid 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 fucoid 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 fucoids 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 fucoids, 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 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
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 case of *Hormosira* and *Cystophora*, plants can be reproductively active all year round, but *Durvillaea* spp. are reproductive 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 5** Sediment and its effects on zygotes and germings 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 germings 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 germings per 5 × 5-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).

**Figure 6** Dispersal curves for *Cystophora torulosa* and *Hormosira banksii* (a) and *Durvillaea poha* (b), showing the number of propagules per cm² with distance from dense, reproductively active stands of adults of each species. Data from Dunmore (2006).
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,
shore algal beds can contribute around 1500 g C m$^{-2}$ mary productivity and detrital material (e.g. Jack & Wing, 2011). Near- 
teintertidal area is reduced to narrow near especially in the high uplift areas in the middle of the earthquake zone, 
zone is greatly reduced from the previous configuration. In these places, 
tere is still an intertidal zone, but in most cases the actual area of this 
tides. Where recovery is possible, habitat 
and the depth of water cover at high tide is less than 1 m at the highest 
the earthquake, but the immersion times have shortened considerably, 
is too harsh for fucoiids 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 as 
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 suit- 
able 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. Sediment- 
tion is a major problem in coastal waters worldwide, affecting settlement and 
the persistence of intertidal and subtidal assemblages on rocky reefs (Airoldi, 1998; Balata, Piazzci, & Bulleri, 2015). Sediment 
is a cumulative stressor and it often favours coralline and turfing algae 
to the exclusion of kelps and fucoiids (Connell, 2003). We have shown 
here that even small volumes of sediment prevent the effective settle- 
ment of habitat-forming species. Moreover, sediments can interact 
with other factors such as elevated temperature and nutrients, affect 
the growth and mortality of algal germings (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, 
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 fucoids 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 fucoids 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 productively 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 Halitotis 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
with the marine environment in the affected area, especially Ngā Tahu, are longstanding and enacted in a variety of ways (Te Korowai ā Tahu, 2013). 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 ā 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.

**ACKNOWLEDGEMENTS**

Many people participated in the work described here or supported it through gaining us access to damaged sites. We particularly thank our funders, especially Rich Ford and the New Zealand Ministry of Primary Industries, for early support and initial funding, the Ministry of Business, Innovation, and Employment for the funding of recovery work, the Cawthron Institute (especially Dr Chris Corneliussen) for in-kind funding, the National Institute of Water and Atmospheric Research for general support, and the University of Canterbury (especially Prof. lan Wright) for funding our initial disaster work. We thank Dr Sharyn Goldstien for her work in gaining initial access to damaged sites and aiding in community liaison.

**ORCID**

David R. Schiel [https://orcid.org/0000-0002-2055-3185](https://orcid.org/0000-0002-2055-3185)

**REFERENCES**


