



Kelp DNA records late Holocene paleoseismic uplift of coastline, southeastern New Zealand

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ABSTRACT

Holocene paleoseismic activity on the Akatore Fault zone, southeastern New Zealand, has caused uplift of a 23 km section of coastline by several metres. Prominent relict shoreline terraces are preserved at 6 m and 3 m above the present sea level, and the latter terrace was formed 1000–1400 yrs BP. The main fault strand farther inland has 6 m of late Holocene vertical offset, but the relationships between coastal offsets and fault offsets are not understood. There is no preserved geological evidence on the coastline to distinguish between incremental uplift (e.g., numerous centimetre-scale events) and major, metre-scale, uplift events: a distinction that is important for evaluating regional paleoseismicity. We have used genetic characterisation of populations of live kelp, *Durvillaea antarctica* growing along the shoreline to investigate whether or not there has been a catastrophic uplift event, greater than the two metre tidal range, that was sufficient to extirpate intertidal kelp populations. Our results show that all kelp along the southeastern New Zealand coastline belongs to the same distinctive clade of *D. antarctica*, and inhabits the same ecological niches on exposed rocks and reefs. However, the kelp population on the uplifted coastline is genetically uniform, and clearly distinct from those of flanking shorelines. This regional genetic anomaly is consistent with a major extirpation event, followed by recolonisation from source populations some 30–120 km to the northeast of the uplifted coast. The uplift event caused vertical crustal movement with similar amounts of uplift on the fault plane and the coastline 3 km away. This approach, using genetics of intertidal biota, has potential applications for evaluation of paleoseismicity of other tectonically active shorelines around the world.

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1. Introduction

Sea level is a widely-used datum for quantification of earthquake-related rock uplift or subsidence (Laborel and Laborel-Deguen, 1994; Shaw et al., 2010; Angulo et al., 2013; Mouslopoulou et al., 2015). Depiction by Lyell (1830) of fossil mollusc borings stranded above sea level on 2000 yrs BP Roman pillars was one of the more significant pieces of evidence, in the early days of geological science development, for long-term landscape changes (Ager, 1989). Subsequently, stranded biological remnants such as mollusc shells or associated borings from the intertidal zone have been widely used by paleoseismologists to determine amounts of tectonic uplift relative to sea level in many parts of the world (Laborel and Laborel-Deguen, 1994; Hsieh and Rau, 2009; Shaw et al., 2010; Angulo et al., 2013;

Mouslopoulou et al., 2015). Hence, offsets of intertidal biota on a scale of metres or even tens of metres have been quantified in many tectonically active areas (Laborel and Laborel-Deguen, 1994; Shaw et al., 2010; Hsieh and Rau, 2009; Angulo et al., 2013; Mouslopoulou et al., 2015).

Despite the utility of biological remnants for quantifying amounts of uplift, it is generally not possible to determine if the observed amount of uplifted rock rose in a single large earthquake event, or is a result of a number of incremental offsets from several smaller earthquakes. Direct human observations of land movements made immediately after major events are definitive, and quantification of offsets relative to sea level using biological criteria have been made after such events (Farias et al., 2010; Hamling et al., 2017). However, ancient earthquake events lack this observational support and more indirect criteria are needed, although such criteria are rare or absent from most sites (Hsieh and Rau, 2009).

In this study, we take advantage of the rapid modern advances in genetic science, and use contrasts in genetic signatures of populations of intertidal kelp as an indirect indicator of co-seismic

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coastal uplift in southern New Zealand. This study addresses the origin of a well-defined fossil shore platform that has been uplifted three metres above sea level in the late Holocene, in close proximity to a known active fault. A new rocky shoreline has become established adjacent to the uplifted platform, and that shoreline hosts abundant live kelp of the species that occur widely along the southern New Zealand coastline. The genetic variations of one kelp species can contribute to knowledge of geological evolution of this shoreline and therefore provide useful information on the nature and magnitude of paleoseismic activity for the region. The approach outlined in our study can potentially be extended to use one or more other intertidal species on tectonically active coasts around the world.

In order to determine whether uplift of the shoreline occurred in a single earthquake event, or whether uplift was incremental, we test a specific hypothesis regarding the kelp that is now established in the new intertidal zone. If the tectonic uplift was incremental (e.g., centimetre scale events), some of the established intertidal biota would survive each small increment, and the present kelp will have been derived from the persisting local genetic stock, with no genetic disruption. In contrast, if there was a large uplift event, exceeding the two metre tidal range, the raised intertidal biota would have been completely eliminated (cf. Hsieh and Rau, 2009). Consequently, the new intertidal zone is likely to have been colonised via dispersal from source populations outside the uplifted region, and the new kelp population may thus show genetic signatures of extinction followed by recolonisation. Indeed, under the recently-proposed ‘Founder Takes All’ hypothesis (Waters et al., 2013), dispersing biological lineages expanding into new terrain can leave distinctive genetic signatures. Our results presented herein support the latter scenario.

2. General setting

2.1. Regional geology and landscape

The South Island of New Zealand lies on a major tectonic plate boundary and is seismically active with major earthquakes affecting coastal communities (Christchurch, Kaikoura; Fig. 1a) within the last decade. This study was carried out on the southeastern coast of the South Island (Fig. 1b) where the coastline is largely controlled by the active Akatore Fault zone (Litchfield and Norris, 2000). The main strand of the Akatore Fault is partly submerged offshore and strikes towards the city of Dunedin, prompting detailed paleoseismological investigations along the fault (Litchfield and Norris, 2000; Gorman et al., 2013; Taylor-Silva, 2017).

The Mesozoic Otago Schist forms the relatively hard crystalline basement rocks of the area, and dissected schist landscape dominates the area (Fig. 1b; Bishop and Turnbull, 1996). The schist this is unconformably overlain by erosional remnants of Cretaceous-Cenozoic sedimentary rocks and these rocks, combined with partially oxidised clay-altered schist immediately underlying the unconformity, are relatively soft and more readily eroded than fresh schist. These softer rocks dominate much of the coastline on the northwestern (downthrown) side of the Akatore Fault (Figs. 1b; 2a-c). Fresh basaltic cliffs occur around a Miocene volcano on which the city of Dunedin is built, near the northern limit of the Akatore Fault (Fig. 1a; Bishop and Turnbull, 1996). Soft altered schist and sediments along the coast are being actively eroded by the sea, leaving a broad (up to 100 m wide) wave-cut platform in the intertidal zone (Fig. 2a-c). The eroding coastline on the downthrown side of the fault has remnants of a Late Pleistocene sea level highstand terrace 5–10 m above present sea level (Bishop and Turnbull, 1996; Litchfield and Norris, 2000). This highstand terrace is typically covered in 1–3 m of glacially-derived aeolian silt (loess; Fig. 2c).

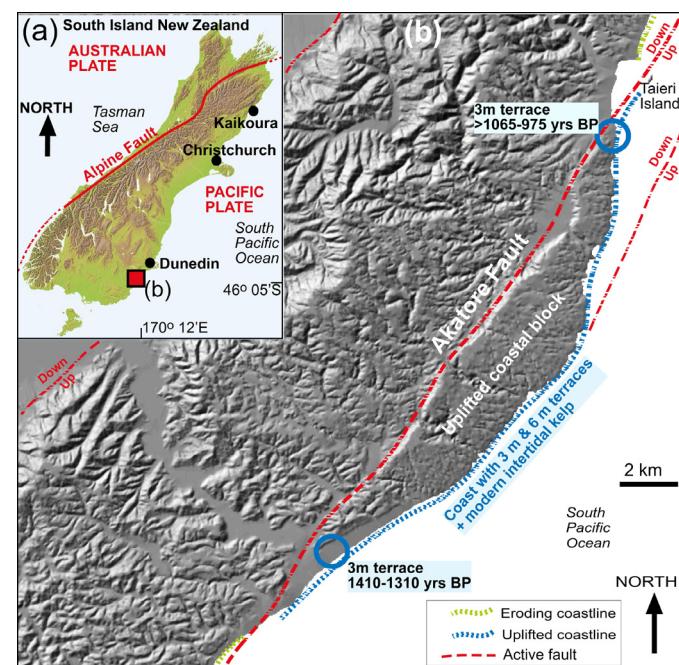


Fig. 1. Geological and topographic setting for this study. (a) South Island lies on tectonic plate boundary, and the Akatore Fault (red square; b) is a distal active fault as part of plate boundary deformation. (b) Hillshade digital image of the Akatore Fault zone and adjacent areas (details from Bishop and Turnbull, 1996; Litchfield and Norris, 2000; Gorman et al., 2013). (For interpretation of the colours in the figure(s), the reader is referred to the web version of this article.)

2.2. Akatore Fault and uplifted coastal block

The upthrown southeastern side of the onshore Akatore Fault consists of erosion-resistant fresh schist basement that has been uplifted from below the regional unconformity. This uplifted schist forms a well-defined coastal block that protrudes into the ocean with ~23 km of steep rocky coastline (Figs. 1b; 2b). The uplifted coastal block is bounded inland by the prominent scarp, ~60 m high, of the Akatore Fault (Figs. 1b; 2b; 3a-c). The fault scarp was formed by accumulation of Late Pleistocene-Holocene vertical fault motion (Bishop and Turnbull, 1996; Litchfield and Norris, 2000; Taylor-Silva, 2017). Of particular significance for paleoseismology of the fault, and for the present study, is the strong evidence for up to three late Holocene earthquakes (last 1400 yrs), each with vertical offsets of ~2–3 m on the fault scarp (Litchfield and Norris, 2000; Taylor-Silva, 2017).

The Akatore Fault passes offshore at the northeastern and southwestern ends of the uplifted coastal block, and the amounts of late Holocene offsets decrease offshore. The northeastern end of the coastal block tapers where the fault passes offshore to form a set of fault-parallel intertidal reefs and the emergent Taieri Island (Figs. 1b; 2a; Gorman et al., 2013). The southwestern end of the fault disappears offshore with only minor intertidal reefs in abundant longshore-drifting sand.

Along the coastline of the uplifted coastal block the loess-covered Late Pleistocene highstand terrace feature is largely absent. Instead, there are two uplifted Holocene coastal platforms that now form terraces at 3 m and 6 m above present high tide level (Bishop and Turnbull, 1996; Litchfield and Norris, 2000). Taieri Island has an uplifted schist rocky shore, but no well-defined uplifted terraces, and presumed remnants of the Late Pleistocene highstand terrace are still preserved locally (Fig. 3a). The onshore 3 m terrace has been dated from uplifted marine mollusc shells at ~1400 yrs BP, with post-uplift nonmarine debris dated at ~1000 yrs BP (Fig. 1b; Litchfield and Norris, 2000). The relationships between these uplifted coastal terraces and the late Holocene earth-



Fig. 2. Typical erosional coastal topography to the northeast and southwest of the onshore segment of the Akatore Fault. (a) Eroded flat shore platform with kelp-encrusted schist reefs to northeast of the upfaulted coastal block, with view offshore to the northeastern portion of the fault near Taieri Island. (b) Hillshade digital image of the Akatore Fault zone and adjacent coast (from [Geographx.co.nz](#)) showing locations of eroded coastlines in a & c (black arrows show photo directions). (c) Eroding Cretaceous sedimentary rocks on the coast to southwest of uplifted block, with flat intertidal platform and residual boulders encrusted with kelp.

quakes that uplifted the basement along the Akatore Fault scarp farther inland is not known (Litchfield and Norris, 2000). The uplift of the shoreline to give the 3 m terrace along the uplifted coastal block is the subject of this study.

3. Approach and methods

3.1. Kelp ecology and genetics in paleoseismology

A key question that arises from established geological observations on the geometry of the Akatore Fault is whether the uplifted coastal block moved essentially vertically during earthquakes so that metre-scale uplift at the coast was the same as metre-scale uplift at the fault. Alternatively, the coastal block may have rotated and tilted downwards to the southeast so that uplift at the coast was less than that at the fault. Related to this general question is the interrelated question to be specifically addressed in this study: was the 3 m coastal terrace uplifted in a single large earthquake event, and did that uplift leave an enduring genetic signature of extinction-recolonisation; or was it raised incrementally by a number of smaller earthquake events that did not leave a biological signature? To address these questions, we genetically analysed southern bull-kelp, *Durvillaea antarctica*, from around the southern New Zealand coastline, and contrasted these results to the same species on the Akatore uplifted coastal block.

This bull-kelp species is a keystone intertidal seaweed that occurs abundantly throughout mid-high latitude rocky coasts of the

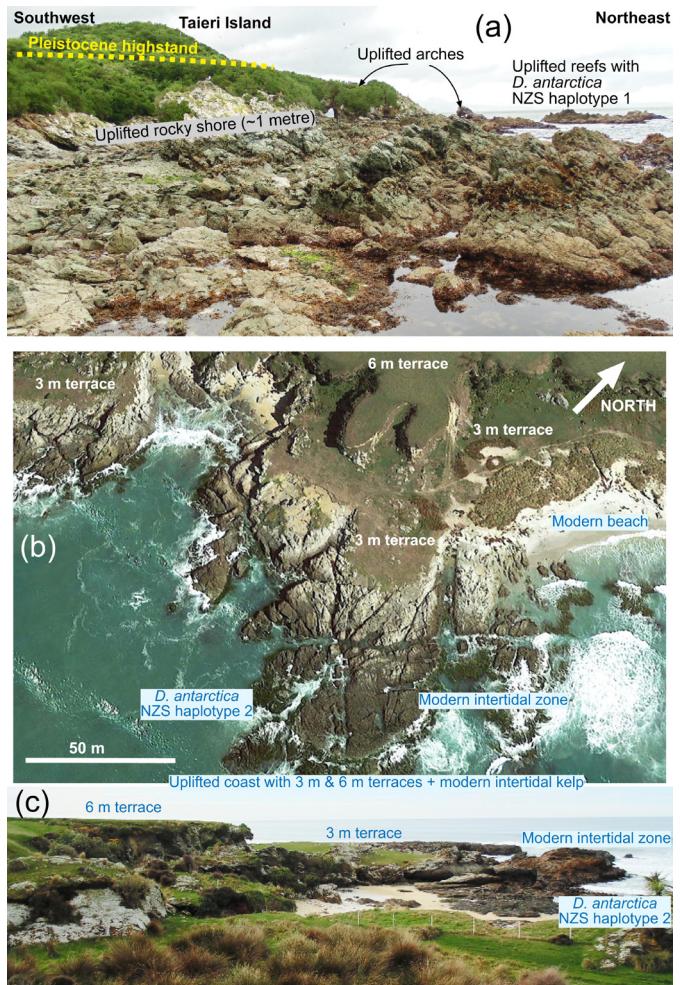


Fig. 3. Coastal landforms of fresh schist rocky shores in the uplifted coastal block of the Akatore Fault. (a) Shoreline with minor uplift at Taieri Island. (b) Vertical aerial view (from Google Earth) of the rocky coast and 3 m and 6 m terraces at Watsons Beach (Fig. 2b). (c) Oblique photograph of the rocky shore and uplifted terraces at same locality as b.

Southern Hemisphere (Fig. 4a-c; Fraser et al., 2009a). *D. antarctica* is commonly accompanied along the southern New Zealand coasts by a related species, *D. poha* (Fig. 4a, c; Fraser et al., 2012). However, *D. antarctica* has an ecological preference for the most exposed parts of the low intertidal zones, whereas *D. poha* has a preference for marginally more sheltered settings (Fig. 4c; Fraser et al., 2009b, 2012).

The intertidal range of coastal Otago is approximately 2 m. *Durvillaea antarctica* inhabits the lower intertidal zone and subtidal fringe (Morton, 2004), and its vertical distribution and subsequent survival on the shore varies depending on exposure to surf, and also to water temperature (Thomsen et al., 2019). Effects of the Kaikoura earthquake of November 2016 (Fig. 1a; Clark et al., 2017; Hamling et al., 2017; Waters and Fraser, unpublished data) have facilitated quantification of the amount of uplift required to extirpate the kelp on exposed coasts with active surf splashing. Uplift exceeding 2 m is apparently required to completely extirpate populations of this kelp species (e.g., Clark et al., 2017, their Fig. 2d), whereas uplift of <2 m may not fully extirpate the kelp populations (e.g., Clark et al., 2017, their Fig. 2c). These observations indicate that the crucial factors determining whether kelp specimens die soon after uplift are the degree of exposure above the surf splash zone, and associated desiccation and solar radiation effects.

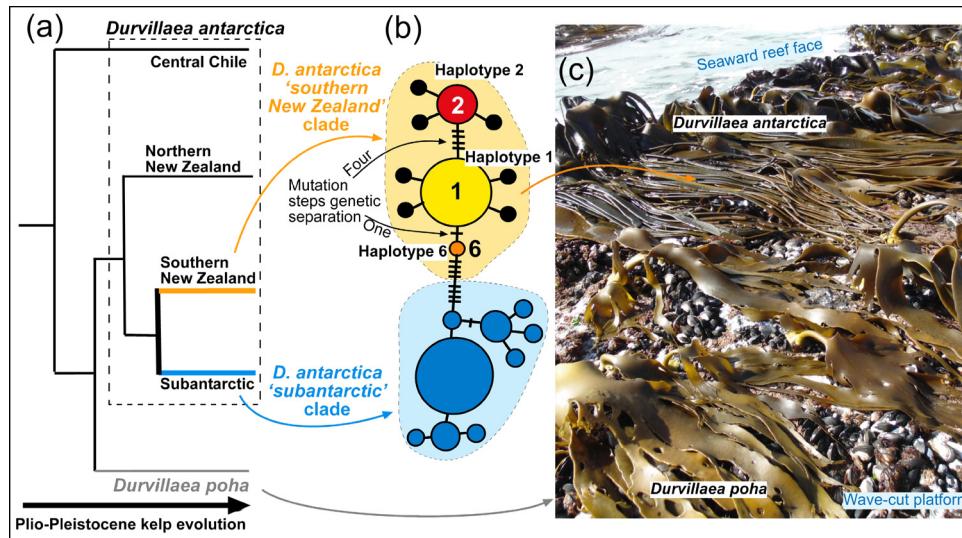


Fig. 4. Relationships among buoyant *Durvillaea* spp. in the Southern Hemisphere, with emphasis on southern New Zealand (after Fraser et al., 2010; Waters et al., 2018). (a) Generalised phylogenetic tree showing relationships between species *D. poha* and *D. antarctica*, and principal clades within *D. antarctica*. (b) Phylogenetic networks for southern New Zealand *D. antarctica*, with circle size scaled to haplotype frequency, showing the small genetic distinctions between widespread Southern New Zealand haplotypes NZS1 (yellow), NZS2 (red) and NZS6 (orange) (this study) relative to the sister clade ('subantarctic', blue). (c) Photograph of coexisting *D. antarctica* (long thin fronds; genetically NZS6) and *D. poha* (wide, flattened fronds) on intertidal reefs near Kuri Bush (Fig. 5b).

The species *D. antarctica* includes genetically-defined clades that are found in different geographical areas within the overall range (Fig. 4a; Fraser et al., 2009a, 2009b). These clades can be further subdivided genetically into different haplotypes that also typically have some geographical restrictions (Fig. 4b; Fraser et al., 2009a, 2009b, 2010). The clade of interest in this study is characteristic of southern New Zealand, and includes several distinct haplotypes (Fig. 4a, b) which were the targets of our genetic analyses.

Mitochondrial DNA cytochrome oxidase I (COI) is a commonly-employed DNA 'barcoding' marker for resolving distinct genetic lineages within and among closely related species. Both global and local population-genetic baselines have previously been determined for *D. antarctica* COI (Fraser et al., 2009a, 2009b; Bussolini and Waters, 2015). Notably, southern New Zealand populations of this species are dominated by two common COI haplotypes NZS1 and NZS2 (Fig. 4a-c), which have broadly non-overlapping distributions. Specifically, NZS1 dominates the coast to the south of Dunedin, and NZS2 dominates the east Otago coast north of Dunedin (Fig. 5a; Collins et al., 2010; Bussolini and Waters, 2015). These two common, closely-related haplotypes are distinguished from each other by just 4 mutational changes (Fig. 4b). Additionally, NZS6 is the third most common haplotype (Fig. 4b) that occurs infrequently to the south of Dunedin (Fig. 5a). The three NZS haplotypes used in this study fall within the distinctive southern New Zealand clade (NZ-South), which is substantially divergent from other regional genetic units within this species (Chile, NZ North, Subantarctic; Fig. 4a, b).

3.2. Sampling, genetic analysis and data repository

Our sampling strategy (Table 1) focused intensively on accessible rocky coastline within the uplifted coastal block of the Akatore Fault zone (6 localities), and on the flanking coastline immediately to the northeast and southwest (12 localities). This more intense sampling was conducted specifically for this study, and results can be compared to previously-collected samples from farther afield on the same coastlines (Table 1; Fig. 5a).

Kelp frond tissue was collected from 3–20 (typically >10) *Durvillaea antarctica* specimens per sampling locality (Table 1). Samples were preserved in ethanol, and subsequently air-dried and stored in silica gel. Total DNA was extracted from preserved kelp

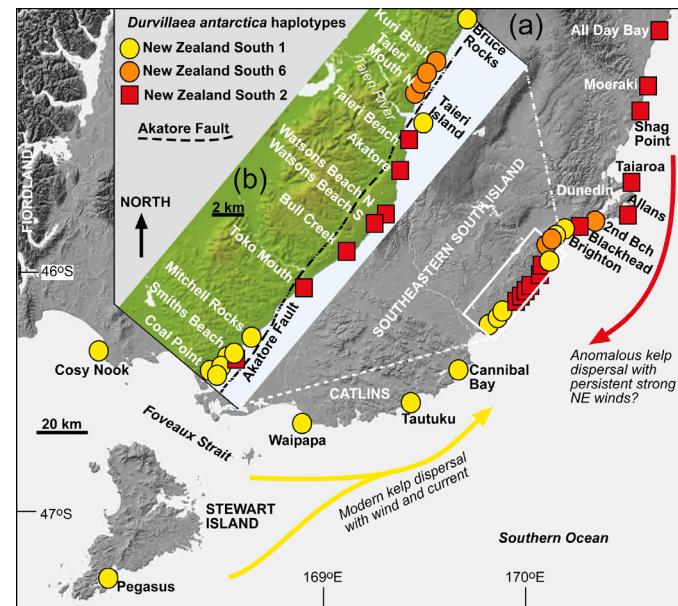


Fig. 5. Sample sites (Table 1) and distribution maps of the principal southern New Zealand haplotypes of *D. antarctica*. (a) Southeastern South Island. (b) Enlarged map of the haplotype distribution in relation to the Akatore Fault uplifted coastal block.

tissue using chelex, and mtDNA COI was amplified and sequenced, following the methods of Fraser et al. (2009a, 2009b). These new DNA sequences were edited using Geneious R11 (<https://www.geneious.com>).

Five distinct COI sequences (= haplotypes; Table 1) within the New Zealand South (NZS) clade of *D. antarctica* were identified using Basic Local Alignment Search Tool (BLAST) searches to compare new sequences against previously published data compiled from Collins et al. (2010) and Bussolini and Waters (2015). These data represented a total of 229 COI sequences sourced from 31 sampling localities (Table 1). A phylogenetic network of aligned COI sequences was constructed using PopArt 1.7 (Leigh and Bryant, 2015; <http://popart.otago.ac.nz>), with the areas of haplotype 'circles' scaled to their frequencies, and mutations among haplotypes indicated with transverse lines (Fig. 4). In this study, we focus

Table 1

Geographic and genetic details of *Durvillaea antarctica* samples from southern New Zealand (Fig. 4a, b). Collections new to this study are indicated by asterisks; previous data are compiled from Collins et al. (2010), Bussolini and Waters (2015) and Fraser et al. (2018).

Site	Latitude	Longitude	NZS1	NZS6	NZS2	NZS3	NZS13
All Day Bay	45°10'58.38"S	170°54'28.47"E			11		
Moeraki	45°21'21.37"S	170°51'31.96"E			4		
Shag Pt	45°28'3.47"S	170°49'42.82"E			11		
Taiaroa Head	45°46'19.15"S	170°43'41.36"E			7	1	
Allans Beach	45°48'53.29"S	170°44'46.41"E	2	2	8		
Second Beach	45°54'59.94"S	170°29'8.02"E	3	5			
Blackhead	45°55'43.65"S	170°25'38.06"E			10		
Brighton	45°56'54.91"S	170°20'12.72"E	5				
Bruce Rocks	45°58'55.63"S	170°16'30.18"E	10				
Kuri Bush Nth*	46°1'28.58"S	170°13'56.80"E		4			
Kuri Bush Sth*	46°1'39.98"S	170°13'42.85"E		3		1	
Taiheri Mouth Nth 1*	46°2'5.86"S	170°13'19.14"E	2	3			
Taiheri Mouth Nth 2*	46°2'17.98"S	170°13'6.91"E		5			
Taiheri Island*	46°3'23.22"S	170°13'7.81"E	5				
Taiheri Beach*	46°4'15.49"S	170°12'8.24"E	1	1	5		
Akatore	46°6'46.05"S	170°11'35.94"E			9		
Watsons Beach 1*	46°9'37.07"S	170°9'20.57"E			5		
Watsons Beach 2*	46°9'49.85"S	170°9'4.16"E			7		
Bull Creek*	46°10'45.12"S	170°7'53.04"E			10		
Toko Mouth*	46°13'29.22"S	170°2'35.05"E			9		
Mitchells Rocks*	46°16'19.24"S	169°58'24.93"E	10				
Smiths Beach*	46°17'30.26"S	169°55'37.47"E	5		5		
Smiths Beach Sth*	46°17'57.39"S	169°55'29.62"E	5				
Coal Point 1*	46°18'9.55"S	169°54'48.30"E	2		1		
Coal Point 2*	46°18'16.41"S	169°54'36.65"E	4				
Coal Point 3*	46°18'23.86"S	169°54'31.57"E	5				
Cannibal Bay	46°28'4.89"S	169°45'37.41"E	3				
Tautuku	46°36'27.28"S	169°25'39.12"E	16				
Waipapa	46°39'43.47"S	168°50'47.49"E	11				
Cosy Nook	46°19'56.36"S	167°42'2.14"E	8				
Port Pegasus	47°12'4"S	167°40'58"E	5				
(Total)			(102)	(23)	(102)	(1)	(1)

particularly on three common southeastern New Zealand haplotypes NZS1, NZS2 and NZS6, as defined by Bussolini and Waters (2015). The New Zealand South clade of *D. antarctica* is genetically most closely related to the sub-Antarctic clade (Fraser et al., 2009a, 2009b), with only eight mutations separating these haplotype groupings (Fig. 4a, b).

All genetic data have been formally deposited in the international data repository GenBank (<https://www.ncbi.nlm.nih.gov>). GenBank accession details for COI haplotypes are: NZS1 (FJ550089), NZS2 (FJ550106), NZS3 (FJ550109), NZS6 (FJ550108). Haplotype NZS13 (new to this study) has been deposited as GenBank MK875764.

4. Results

DNA sequencing of our *D. antarctica* collection revealed a sharp genetic discontinuity between samples from within the 23 km uplifted zone relative to samples from flanking populations immediately to the northeast and southwest. Specifically, all localities within the zone (6 sites, $n = 48$; Table 1) were dominated by a distinctive kelp haplotype NZS2 (GenBank accession FJ550106), a lineage which is otherwise largely restricted to coastlines 30–120 km north of the uplifted zone (Fig. 5a, b). Samples from localities immediately to the northeast and southwest of the uplifted zone (12 localities, $n = 70$), by contrast, were dominated by the widespread South Island haplotype NZS1 (FJ550089) and NZS6 (FJ550108) (Table 1). Hence, our data show a signature of phylogeographic disruption mediated by coastal uplift that apparently occurred 1000–1400 yrs BP (Fig. 1b; 5b). The apparently anomalous presence of a few specimens yielding NZS2 immediately south of the uplift zone (e.g. Smiths Beach; Fig. 5b; Table 1) likely represents localised southward spread of this recolonised haplotype into an unstable boulder habitat (Fig. 2c).

The 23 km regional genetic anomaly is thus tightly correlated to the coastal boundaries of the uplifted coastal block of the onshore Akatore Fault (Fig. 5a, b). The kelp genetic data show that there has been a major coastal uplift event such that the kelp in the intertidal zone was all extirpated, followed by recolonisation by the same species, *D. antarctica* Southern New Zealand clade, with different genetic haplotypes (Fig. 5a, b; Table 1). These results imply that the coastal block was uplifted vertically during a major earthquake along the Akatore Fault farther inland, with similar amounts of vertical offset (2–3 m) at the coast and along the fault (Fig. 6a, b). The amount of vertical motion apparently decreased offshore to the southeast (Fig. 6b).

The amount of rock uplift decreased to the northeast and southwest where the Akatore Fault passes offshore, and both ends of the uplifted coastal block coincide with the kelp genetic discontinuities (Fig. 5a, b). The northeastward taper of the uplift of the northeastern end is particularly well constrained by our data (Figs. 5a, b; 6a, b). The last onshore outcrops of the 3 m terrace at Taiheri Beach (Fig. 5b) have haplotype NZS2 in the intertidal zone, as do some nearshore reefs that were uplifted from beneath a sandy cover. In contrast, the nearby Taiheri Island has undergone distinctly less uplift and has haplotype NZS1 in the intertidal zone (Figs. 2a; 3a; 5a, b; 6a, b).

5. Discussion

5.1. Kelp dispersal and recolonisation

While the fertilised eggs of *Durvillaea* disperse for only a few metres in the intertidal zone before they settle (Dunmore, 2006), detached adult specimens of buoyant *D. antarctica* can potentially raft for substantial distances at sea. Additionally, whereas the vast majority (>90%) of bull-kelp (*D. antarctica*) rafts typically disperse

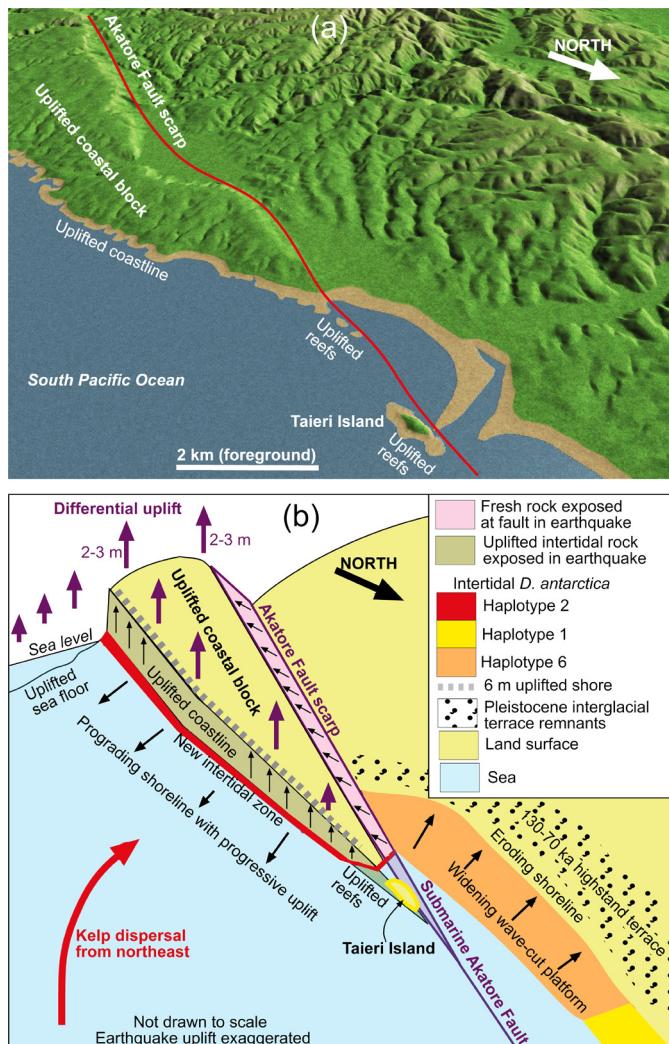


Fig. 6. Geology, topography, and kelp distribution at the northeastern end of the uplifted coastal block of the Akatore Fault. (a) Oblique view of hillshade landscape looking southwest (constructed by [Geographx.co.nz](#)). (b) Cartoon sketch of the view in a, with scales exaggerated to show principal features in this study. Amount of fault uplift tapers towards the northeast so that Taieri Island underwent insufficient uplift to fully extirpate intertidal biota, and some pre-existing kelp (NZS haplotype 1) survived the event.

over relatively small spatial scales (e.g. 0–10 km; Garden et al., 2011), extensive evidence also exists for their long-distance dispersal over hundreds or thousands of kilometres (Smith, 2002; Garden et al., 2011; Waters et al., 2018). Recolonised regions can be characterised by ‘sectors’ of relative genetic homogeneity (e.g. Hewitt, 2000; Fraser et al., 2009a, 2009b). Notably, the uplifted Akatore coast has substantially lower regional kelp haplotype diversity relative to the non-uplifted coastal populations immediately to the northeast and southwest.

New Zealand’s uplifted Akatore coastline was apparently recolonised by rafting kelp sourced from coastal populations some 30–120 km to the north (Fig. 5a). This dispersal runs counter to prevailing oceanographic patterns that favour dispersal from the south or southwest with prevailing currents and winds (Fig. 3a; Chiswell, 2009; Collins et al., 2010). However, recent studies highlight that strong-wind events can disrupt prevailing oceanographic connectivity patterns, and drive anomalous long-distance dispersal of buoyant material across oceanographic barriers (Fraser et al., 2011; Monzón-Argüello et al., 2012; Garden et al., 2014; Waters et al., 2018; Fraser et al., 2018). Short-lived weather events such as tropical cyclones typically induce strong northeast winds

in this area for only hours, or days at most (Waters et al., 2018). These events are unlikely to have driven the kelp colonisation of the Akatore area from the northeast, although our recent observations have detected kelp with Dunedin-sourced basalt at least 7 km southwest of their potential sources after a weeklong period of strong northeast winds in late 2018. Similarly, *D. antarctica* kelp from the New Zealand ‘north’ clade (Fig. 4a) has been found beachcast in eastern South Island, more than 100 km southwest of the closest source population (Bussolini and Waters, 2015).

Perhaps more likely, annual (e.g., La Niña) or decadal variations in Pacific Ocean meteorology that periodically cause persistent northeast winds in the New Zealand region (Folland et al., 2002) may have coincided with the large Akatore earthquake-driven shoreline uplift. Decadal variations in prevailing winds have been identified as likely facilitators of Polynesian migrations across the Pacific Ocean in the last 1200 yrs, and these included periods of prevailing northeast winds that may have allowed the original colonisation of New Zealand (Goodwin et al., 2014).

5.2. Biological indicators of earthquake uplift events

Genetic data from the current study reveal the lasting biological legacy of tectonically-mediated disruption of coastline topography and biota ~1000 yrs BP in coastal New Zealand. The persistence of genetic signatures of past upheaval likely reflects the role of “density blocking” (Ibrahim et al., 1996; Waters et al., 2013), whereby early-arriving recolonising lineages can dominate and exclude subsequent dispersers. Such patterns are particularly likely to persist in species that form dense populations and typically disperse only small distances, but are also capable of long-distance dispersal (Ibrahim et al., 1996).

These dramatic biotic effects of earthquake uplift imply that genetic analysis can potentially be used to reconstruct the geological and biotic details of prehistoric earthquakes elsewhere in the world. While previous DNA studies have shown that genetic data can be used to reconstruct the impacts of major earth-history events over vast (e.g. continental and circumpolar) scales (Hewitt, 2000; Riddle et al., 2000; Fraser et al., 2009a, 2009b, 2011), the current study reveals the persisting genetic legacy of sudden tectonic upheaval over relatively tight spatial scales (tens of kilometres). These new data thus highlight the key role of ongoing geological processes in rapidly generating (Beheregaray et al., 2003) and reshaping finescale biodiversity patterns.

The approach we have defined for using genetics to characterise tectonically uplifted shorelines is likely to be most useful on exposed coasts where there is most potential for receiving far-travelled biota. For example, the Pacific coast of Chile is highly tectonically active (Farias et al., 2010; Jararmillo et al., 2012; Melnick, 2016) and is also, fortuitously, host to the same kelp species that we have used in our New Zealand study, albeit a different clade (Fig. 4a; Fraser et al., 2010). Island environments such as the Pacific coast of Taiwan or the Atlantic Ocean are also plausible places to undertake studies such as ours to identify genetically-defined tectonic uplift zones (cf. Hsieh and Rau, 2009; Angulo et al., 2013) as these settings can receive dispersing biota most readily.

Molluscs such as *Lithophaga* and *Dendropoma*, and the rock borings that they produce, have been used extensively as indicators of coastal uplift in the Mediterranean Sea (Lyell, 1830; Laborel and Laborel-Deguen, 1994; Sivan et al., 2010; Shaw et al., 2010; Evelpidou et al., 2012). While such molluscs may have generally low intrinsic dispersal ability, and thus exhibit strong regional genetic structure, they are potentially capable of long distance dispersal and colonisation (e.g. via rafting; Calvo et al., 2009). Our genetic approach may therefore be of use in resolving questions relating to slow incremental uplift versus large catastrophic up-

lift steps in numerous tectonically active shorelines around the Mediterranean Sea. In particular, our genetic approach may be usefully applied to *Lithophaga* in the vicinity of the famous Roman pillars first described by Lyell (1830) as indicators of long-term uplift and reinterpreted by Ager (1989) as indicators of a single major uplift event. This unresolved question relating to one of the best-known examples of coastal uplift is precisely the same as the question we have addressed in this study in southern New Zealand.

6. Conclusions

Offsets of coastlines are useful indicators of tectonic uplift and are directly relevant to paleoseismological studies of earthquake magnitudes and frequencies. However, topographic offsets can be produced by either single large earthquake events, or by incremental accumulation of several small offsets, and it is difficult to resolve the difference between these scenarios from the geological record. We have addressed this problem in a coastal fault zone, along the active Akatore Fault, in southern New Zealand by using genetics of the kelp species *Durvillaea antarctica* that inhabits the uplifted shoreline and adjacent coasts.

Genetic analysis of mitochondrial DNA allows detailed comparisons to be made between different populations of this same kelp species. Our study examined DNA sequence analyses of approximately 200 kelp specimens from around 30 southern New Zealand localities. The kelp from the studied area is all genetically part of a Southern New Zealand clade of the species *D. antarctica*, with differences only at the level of genetic haplotypes within this clade (Fig. 4a-c). Importantly, the uplifted coastline hosts *D. antarctica* kelp from only one haplotype, and this haplotype is distinctly different from those found on the immediately adjacent coastlines (Fig. 4a-c; 5a, b).

Our results show that there was a single event in the late Holocene that caused sufficient coastal uplift (>2 m) to completely extirpate the intertidal biota over 23 km of coastline, and allow recolonisation of kelp from external sources (Fig. 6a, b). The recolonising kelp had distinct genetic differences from its neighbouring populations, and those genetic differences have persisted on the uplifted coastline for more than 1000 yrs. Colonisation of the uplifted coastline involved a *D. antarctica* haplotype that only occurs 30–120 km to the northeast. The only exception in our results occurs where the amount of fault-related uplift tapered to the northeast to an offshore island, with only minor vertical uplift (<1 m) that allowed kelp with the pre-existing genetic haplotype to survive (Fig. 6a, b).

Our results highlight the lasting coastal biological effects of earthquake uplift and suggest that biological data can provide key evidence for reconstructing major prehistoric earthquake events elsewhere in the world. We suggest that future studies will detect earthquake-mediated biological disruption in numerous tectonically active coastal regions of the globe. Additionally, application of the latest genomic research tools presents unique opportunities to detect fine-scale signatures of coastal upheaval and biological recolonization in many of the world's most geologically dynamic regions.

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