



# Earthquake effects on abalone habitats and populations in southern New Zealand

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**ABSTRACT:** The 2016  $M_w$  7.8 Kaikōura earthquake lifted 140 km of coastline on New Zealand's South Island by up to 6.4 m. This caused extensive mortality and destruction of habitat critical for early life stages of blackfoot abalone *Haliotis iris* (called pāua), a species of cultural and commercial importance. The fishery for pāua was closed, at considerable financial loss to local communities. This study determined the extent to which habitats and populations of pāua survived along the coastline. With aerial imaging, the coast was categorised into broad habitats at a 10 m scale. This was used to select areas for *in situ* assessments of pāua populations and specific habitat features at 26 sites over 1.5 yr. We quantified key habitat features to identify correlates and potential drivers of pāua abundance and distribution. We found that despite extensive habitat degradation from uplift, erosion and sedimentation, abundant pāua in size classes <30 mm shell length indicated that successful settlement and juvenile recruitment had occurred soon after the earthquake. Pāua up to 170 mm shell length also survived in shallow habitats. A generalized linear mixed model showed that pāua were negatively influenced by the degree of uplift, and positively associated with the cover of unconsolidated layered rocks. Juvenile pāua (<85 mm) abundance was greatest at sites with <2.5 m of uplift. There was further recruitment 1.5 yr post-earthquake and evidence of good growth of the previous year's cohort. Despite major disruption to this coastline, there appears to be very good potential for recovery of pāua and the fishery.

**KEY WORDS:** Impact · Pāua · *Haliotis iris* · Abalone · Recruitment · Earthquake · Habitat structure · Recovery

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## 1. INTRODUCTION

Many marine species make use of different habitats over the course of their life histories (Beck et al. 2001, Nagelkerken et al. 2015). For example, settlement and recruitment may occur in highly specific habitats before migration into other areas occupied exclusively by adults (Bayne 1964, Sarver 1979, Goselin 1997, Aguirre & McNaught 2012). Therefore, disturbances to obligate habitats may have severe consequences on other life stages and maintenance of populations (Gibson 1994, Courrat et al. 2009, Aguirre & McNaught 2011). The obligate nature of the shallow, under-rock habitat for juvenile abalone (New Zealand pāua *Haliotis iris*) made them particu-

larly vulnerable to a massive earthquake that lifted around 110 km of coastline by up to 6.4 m (Clark et al. 2017).

The 7.8  $M_w$  Kaikōura earthquake struck the coastal South Island of New Zealand in November 2016 (Hamling et al. 2017). The coastal uplift in this sparsely populated region propagated from its central extreme of >6 m to 0–0.2 m at its northeastern and southwestern ends. This is a high-energy coastline with near-constant oceanic swells, generally turbid inshore waters, and rocky reefs and boulder fields interspersed with sand and gravel. The immediate effect of the earthquake on nearshore marine species was high mortality of algal beds and their resident species (Schiel et al. 2019). There were 3

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potentially negative effects on pāua populations. The most evident was in higher uplift areas, where entire reef complexes were permanently lifted above the high water mark, causing mortality of adult pāua, as tens of thousands were stranded at many sites (Schiel et al. 2019). The second potential impact was failure of post-earthquake recruitment because of reduced adult populations or sublethal effects on surviving pāua. The earthquake occurred when adults were at peak reproductive ripeness (Sainsbury 1982). In one documented case, reproductive adult populations were reduced after a major earthquake in Japan (Takami et al. 2017). The third possible effect was loss of critical habitat for settlement and recruitment. Because the habitat suitable for pāua settlement is confined to very shallow water, even relatively small coastal uplift could have severe impacts on population structure and replenishment of affected populations.

Because of the observed impacts and potential for longer-term effects on populations, the commercial fishery was closed, resulting in considerable financial losses. The recreational fishery and customary fishery, important to New Zealand Māori, were also closed. There was therefore much interest in understanding the likely consequences of earthquake disruptions on pāua populations, particularly on post-earthquake recruitment and the potential for long-term loss of fishable populations.

Unfortunately, very little quantitative data exist in the study area for pre-earthquake pāua populations, habitat structure and distribution of juvenile habitat. However, at one site with 0.2 m of uplift for which pre- and post-earthquake data were available, an estimated 45 % of juvenile habitat was lost by being pushed upwards into a harsher tidal zone (Schiel et al. 2019) and, across the region, around 21 % of commercially fished reefs were destroyed through uplift or burial by sediment (P. Neubauer unpubl.). However, the life history of pāua and general habitat associations are well-documented. Pāua settle from the plankton onto rocky substrata in the very low intertidal and shallow subtidal zones (McShane & Naylor 1995, Aguirre & McNaught 2011). Once settled, individuals live in cryptic spaces beneath rocks for around 3 yr, become reproductively mature at 70–90 mm shell length (Wilson & Schiel 1995, Naylor et al. 2017), and then migrate to subtidal reef habitats (Poore 1972a, Sainsbury 1982, Schiel 1993), growing about 25–30 mm yr<sup>-1</sup> on average and eventually reaching the minimum legal harvesting size of 125–135 mm shell length, depending on region (Naylor & Fu 2016). In contrast to many other abalone species, juveniles are rarely seen outside of these

shallow rocky habitats or in waters deeper than around 3 m, whereas adults are found predominantly in depths of 3–12 m (Schiel 1990, 1992).

This study concentrated on the inshore rocky habitats where pāua settle and develop for 3 yr. In the earthquake-affected area, rocky intertidal reefs and boulder fields usually end abruptly in sand and gravel. Observations and considerable data collection on intertidal and subtidal rocky reef assemblages immediately after the earthquake showed that habitat for juvenile pāua was largely accessible if sampled at the lowest spring tides. We used field techniques in structured sampling to establish a quantitative baseline against which to gauge the recovery of pāua populations. The study aimed to answer 3 main questions: (1) How extensive were the rocky habitats required by juvenile pāua along the earthquake-affected coastline? We anticipated significant loss and degradation of habitat critical to larval settlement and juvenile survival, especially in areas of greater uplift, but did not know if new habitat had been provided from deeper zones in uplifted areas. (2) Was there evidence of recruitment (i.e. the appearance of small, post-settlement juveniles) to pāua populations following the earthquake, and did this persist over a subsequent reproductive season? (3) With which specific inshore sub-habitats and biota were juvenile and adult pāua associated? Because of limited pre-earthquake knowledge about the structure and habitats of this coastline, identifying key habitat associations could also aid in population enhancement with hatchery-reared pāua, which is of great interest to fishers and the community.

## 2. MATERIALS AND METHODS

The study area encompassed the earthquake-affected northeast coast of the South Island of New Zealand, over a linear distance of ca. 110 km (Fig. 1; Hamling et al. 2017, Schiel et al. 2019). This extended from just south of the township of Kaikōura northeast to Cape Campbell. The structure and functioning of algal-dominated sites around Cape Campbell and Kaikōura have been well-studied (e.g. Lilley & Schiel 2006, Schiel 2011, Schiel & Lilley 2011). The coast is exposed to large oceanic swells, and features rocky platforms, boulder fields, and beaches of gravel and sand. Most of the rocky areas are composed of soft sedimentary rock, which eroded heavily after the earthquake (Schiel et al. 2019).

To address the question of the extent of habitat potentially suitable for juvenile pāua, remote sensing

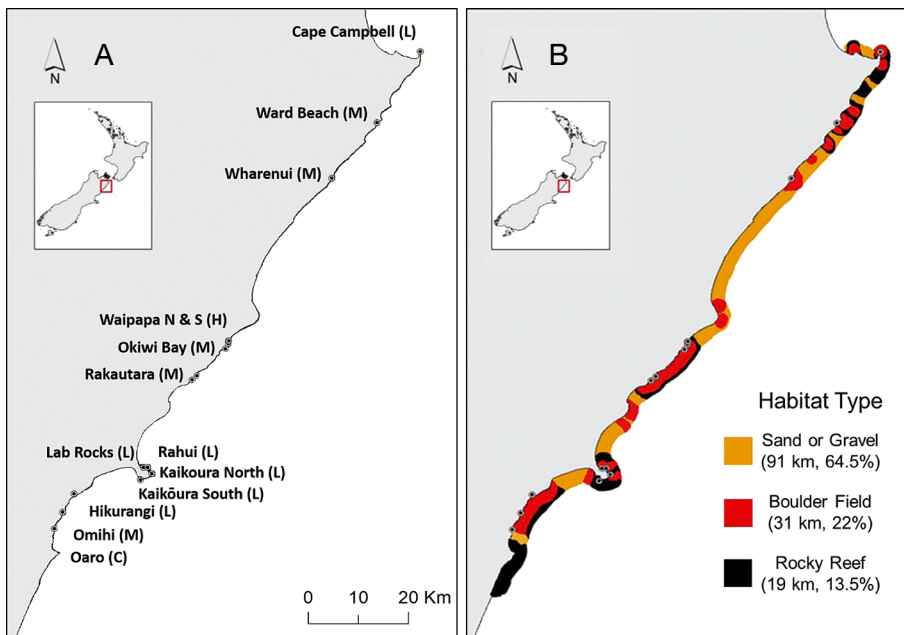


Fig. 1. (A) Coastline of the north-east coast of the South Island of New Zealand, showing the study locations and their degree of uplift. L: low (0.5–1 m); M: medium (1.5–2.5 m); H: high (4.5–6.4 m); C: control (no uplift). There were 2 sites, ca. 250 m apart, within each of the designated locations, except Waipapa and Kaikōura North, which had 3 sites each. (B) Same coastline, showing the main low-intertidal habitat types resulting from the analysis of aerial images collected after the earthquake

techniques were used. High-resolution aerial LiDAR images taken 1 wk after the earthquake during low tide and referenced to pre-earthquake data (Clark et al. 2017; provided to us by Land Information New Zealand) were analysed at a scale of 1:1000 using ArcGIS v. 10.6. This scale allowed analysis of contiguous 100 m<sup>2</sup> segments along the low tide mark. These were categorised into 3 habitat types, which could be readily distinguished: rocky reefs, boulder fields, and gravel or sand. ‘Rocky reef’ was defined as contiguous hard substratum; ‘boulder fields’ were defined as areas with loose rocks and boulders as the dominant substratum; ‘gravel or sand’ was beaches of sand or pea-sized gravel. During subsequent field surveys, we ground-truthed these habitat categories at numerous locations to ensure they accurately described what was present.

Based on information derived from these images, and site accessibility, we conducted *in situ* sampling of 26 field sites for pāua and their habitat associations (Fig. 1). These sites comprised rocky reef and boulder fields that were most likely to support juvenile pāua and encompassed a range of coastal uplift from 0 to 6.4 m, which allowed an assessment of the effects of degree of uplift on pāua. The severely damaged coastal highway was closed for much of this study and there were continuing landslides, so not all areas along the coast were accessible. This sampling addressed the questions of whether young-of-the year pāua recruits were present after the earthquake-disrupted reproductive season of 2016 and,

despite continuing effects of landslides on the coast and adult populations during the 2017 reproductive season, if recruitment continued into 2018. Sampling was done during the lowest tidal series in October–November 2017 and April–May 2018 (ca. 0.2–0.3 Lowest Astronomical Tide). The emphasis of these surveys was on juvenile pāua habitat in the very low intertidal zone, where most juvenile pāua occur, although some individuals can be found to around 2 m below this level if suitable habitat is present. The sampling surveys covered over 15 km (linear measure) of coastline.

At each of the 26 sites, a ca. 600 m long transect parallel to the water’s edge was walked, and 1 m<sup>2</sup> quadrats (n = 20) were sampled along it. Quadrat placement was targeted to potential habitat (i.e. not sand and gravel where no rocks were present, or compacted reefs with no open spaces beneath them). Juvenile pāua cannot be seen without turning over rocks and boulders. In each quadrat, the surfaces of rocks and, where possible, their undersides were examined for pāua, which were reliably found down to around 2 mm shell length. All pāua within each quadrat were measured for maximum shell length using Vernier callipers. This sampling addressed whether young-of-the year pāua recruits were present after the earthquake-disrupted reproductive season of 2016, and whether subsequent recruitment occurred the following year. To address the question of sub-habitat associations and habitat complexity, we carefully deconstructed the habitat within each

quadrat and recorded the substratum type on which pāua were attached (i.e. small, medium, large rocks, gravel, sand, and bedrock). The percent cover of small ( $125\text{--}1000\text{ cm}^3$ ), medium ( $1000\text{--}10000\text{ cm}^3$ ) and large ( $>10000\text{ cm}^3$  but not embedded in the substratum) rocks within each quadrat was recorded, as was cover of sediment and sand, crustose coralline algae (CCA) and articulated coralline algae (coralline turf). Because of habitat layering, the sum of rock cover of the various sizes (total rock cover) and of the corallines could come to  $>100\%$ . We also counted potential competitors and predators of pāua, including snails, stars and crabs (note that no sea urchins were present at any site).

Data from the ArcGIS yielded a map of habitat categories and are presented in coloured contours of the coastline. Pāua shell length data are presented as size-frequencies across all sites for each of the 2 sampling periods, which allowed assessment of recruitment and progression of size classes over time. A Kolmogorov-Smirnov test was done to test for significant changes in population structure between sampling events. To determine which habitat features most affected abundance of juvenile pāua, we compared generalized linear mixed models (GLMMs). The terms uplift, total rock cover, CCA, sand and silt cover, gravel cover, and number of other invertebrates were included in a 0-inflated negative binomial GLMM using the R package 'glmmTMB' (Brooks et al. 2017). We systematically removed habitat metrics until the lowest Akaike's information criterion (AIC) score was achieved. In this model, continuous values for uplift from the LiDAR data (i.e. site-specific) were used to account for the possibility that small differences in uplift may have large impacts on pāua counts. Sampling event was included as a random variable in all models to account for random variation over time. A zero-inflated model was selected because data were over-dispersed relative to a zero-inflated Poisson model, many quadrats did not contain pāua, and field observations indicated that empty quadrats commonly occurred in plots with high uplift, high sand or gravel cover, low rock cover or low CCA cover.

We evaluated within-habitat associations of pāua using a chi-squared test comparing the proportions at which different habitats occurred with the proportions of the total number of pāua

found on each substratum. This analysis excluded sand habitat on which there were no pāua. Size-frequency distributions of pāua within each habitat type allowed an assessment of habitat use by different life stages of pāua.

### 3. RESULTS

The ArcGIS analysis of aerial images showed broad-scale heterogeneity of habitats along the coastline, with varying interspersed stretches of sand or gravel, rocky reef and boulder fields (Fig. 1B). At the scale in this analysis, the coastline was 140 km long. Sand and unstable gravel occupied 65% (91 km, measured at a 1:1000 scale) of the coastline. These areas did not support any pāua populations. Rocky reefs, which support pāua, comprised 14% (19 km) of the coastline. Boulder fields, the most likely habitat for juvenile pāua, occupied 22% (31 km) of coastline. These boulder areas ranged a horizontal distance of up to 10 m from their lower to upper margins. Altogether, around 36% of the uplifted coastline (ca. 50 km) contained hard substrata potentially suitable for pāua populations.

The surveys 1 yr after the earthquake (October–November 2017) showed 3 distinct modes in size frequency (Fig. 2). It was clear that some recruitment had occurred post-earthquake because there was a distinct mode in the 3 smallest size classes. Juveniles grow around  $25\text{ mm yr}^{-1}$  in shell length (Poore 1972b),

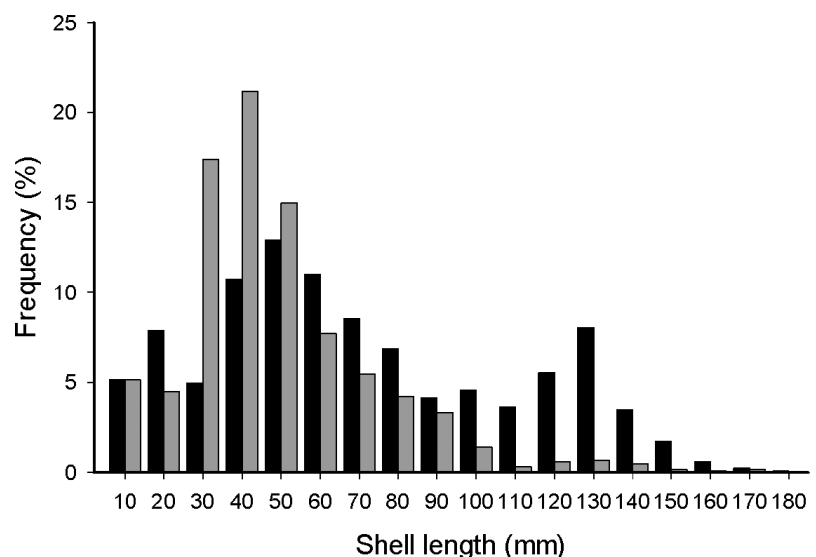


Fig. 2. Length-frequency distribution for all pāua measured 1 yr (dark bars) and 1.5 yr (lighter bars) after the earthquake ( $n = 1208$  and  $1000$ , respectively). The numbers on the x-axis indicate the upper limit of each size class

and pāua with smaller shell lengths comprised approximately 15% of the sampled population. Another size mode occurred at ca. 50 mm. These were immature pāua that were large enough that they would have recruited prior to the earthquake and survived the uplift. There was also a mode around the minimum legal fishing size of 125 mm, again showing that a proportion of large mature individuals survived the earthquake. The majority of these intertidal adults were found at uplifted sites and were likely brought up by the earthquake from the subtidal to the intertidal zone, where they are not normally found because of their easy access to fishers.

After 1.5 yr, the size distribution was skewed right. Another year class of small individuals had recruited, and the previous year's cohort had progressed to size classes beyond ca. 30 mm. The mode of large adults (>120 mm) had largely disappeared by the second sampling period, decreasing from 25 to just 3.1% of the population between sampling events. This equated to a reduction in the average density of adult pāua in intertidal habitats from  $0.72 \pm 0.16$  to  $0.21 \pm 0.05 \text{ m}^{-2}$  (mean  $\pm$  SE) between censuses and was most likely due either to illegal fishing of readily accessible pāua or migration to deeper water. A Kolmogorov-Smirnov test comparing size-frequency data from each sampling period showed a significant difference ( $D = 0.293$ ,  $p < 0.001$ ), confirming that the population structure significantly shifted between surveys.

The GLMMs were run with all measured variables, and the final model used was chosen on the basis of the lowest AIC score. The abundance of other invertebrates added almost nothing to the model, and silt and sand made only a modest, non-significant contribution. The final model showed that total rock cover made the greatest contribution to juvenile pāua abundances, followed by degree of uplift and CCA cover (Table 1). The total variation accounted for by the model was moderate; the conditional  $R^2$ , taking account of fixed and random effects (Nakagawa &

Schielzeth 2013), was 0.318. There was high variation in pāua abundances across these factors. To illustrate this variation, individual quadrat data are plotted across each factor (Fig. 3A–D).

About half of the quadrats sampled had no pāua in them (Fig. 3E). The greatest concentrations of pāua were at sites with less than 2.5 m of uplift (Fig. 3a). Pāua density ranged up to  $83 \text{ m}^{-2}$  at these sites, whereas at the higher uplift sites, pāua numbers were rarely greater than  $18 \text{ m}^{-2}$ . The cover of layered rocks had a nearly parabolic relationship to pāua numbers (Fig. 3B). Relatively few pāua occurred where rock cover was below about 20% or above 140%. The habitats with this very high cover of rock often featured bedrock or very large boulders embedded in sand or gravel, with smaller rocks on top. The areas with intermediate cover, where unconsolidated rocks sat atop smaller rocks of many sizes, creating maximum cryptic space, supported the most pāua. Coralline algae up to ca. 90% cover (approximately half of the available surface covered in CCA due to rock layering) supported the largest numbers of pāua (Fig. 3C). Where this cover was extensive and covered all available rock, however, there were fewer pāua. Silt and sand cover did not

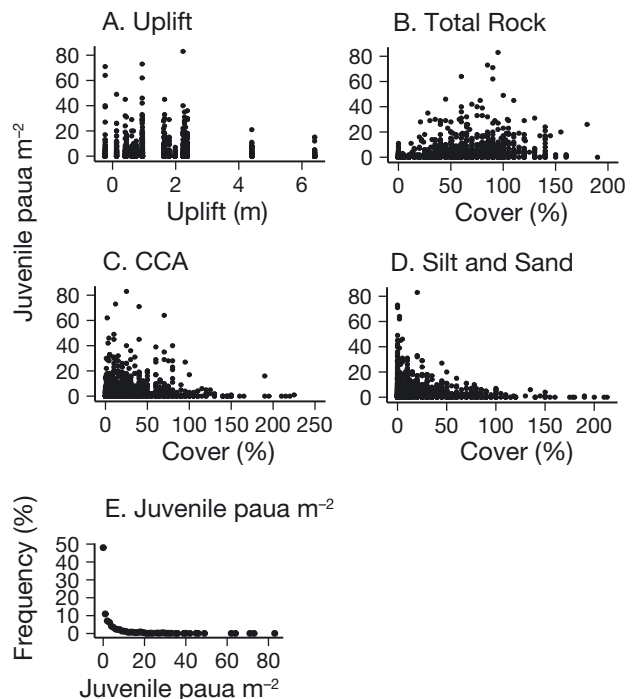


Table 1. Results of a generalized linear mixed model on the abundance of juvenile pāua (<85 mm shell length) with respect to the factors uplift, total rock cover and crustose coralline algae (CCA) cover. The number of observations = 1360. Silt and sand cover, and counts of invertebrates were removed on the basis of their Akaike's information criterion scores

Factor	Estimate	SE	Z	p
Uplift (m)	-0.2083	0.0351	-5.94	<0.001
Total rock cover (%)	0.5929	0.0589	10.06	<0.001
CCA cover (%)	0.1211	0.0563	2.15	0.032

Fig. 3. Relationship between the mean number of juvenile pāua (<85 mm shell length) per  $\text{m}^2$  and: (A) site uplift in m; (B) total rock % cover; (C) crustose coralline algae % cover; (D) silt and sand cover; (E) frequency distribution of number of juvenile pāua in each quadrat ( $n = 1360$  quadrats). Each dot is an individual quadrat

contribute significantly to the overall model, but this factor clearly has some effect on pāua (Fig. 3D). Where silt and sand covered layered rocks or where it comprised the dominant substratum, there were few, if any, pāua. Another measure of variation is the distribution of pāua numbers across quadrats (Fig. 3E). Over half (53%) of the quadrats contained pāua, and most of these had 20 or fewer individuals.

Pāua across all size classes showed strong associations with sub-habitats, particularly on large and medium sized rocks ( $\chi^2_5 = 491$ ,  $p < 0.001$ , Table 2). Although large ( $>10000 \text{ cm}^3$ ) and medium rocks ( $1000\text{--}10000 \text{ cm}^3$ ) comprised 51 % of the surveyed area, 75 % of the pāua encountered were found on them. Only 13% of pāua were found attached to unstable small rocks ( $125\text{--}1000 \text{ cm}^3$ ), and very few were found on gravel. Most size classes of pāua were represented in each of the 4 main categories of rocky substrata (Fig. 4). Sub-adult pāua ( $<85 \text{ mm}$  shell length) were well-represented on medium and large rocks, where they occurred mostly on the undersides, and relatively few were found on small rocks and bedrock. Although relatively few pāua  $>100 \text{ mm}$  shell length were encountered (as adults are primarily subtidal; Schiel 1992), these larger pāua were also most common on medium and large rocks. Very few pāua of all size classes, but particularly adults, were found on small rocks, which tended to be unstable, especially in more exposed sites.

#### 4. DISCUSSION

Extreme events can have long-lasting effects on marine ecosystems, affecting both habitats and a wide range of species. Several studies bear similarities to the effects seen in New Zealand, and illustrate damage to marine communities and recovery times. Studies in Chile, for example, a country prone to earthquakes (Hamling et al. 2017, Jaramillo et al. 2017), showed that effects and recovery times depended on the degree of uplift (Jara-

millo et al. 2012). For example, Castilla et al. (2010) found that over 3 m of coastal uplift from a massive earthquake in 2010 caused widespread destruction of invertebrate and algal habitats, with recovery taking many years. Tidal zones had been altered and recovery depended on species colonising the new rocky reef configurations that had been subtidal before the earthquake (Castilla & Oliva 1990, Castilla

Table 2. Observed versus expected counts of pāua across large rock, medium rock, small rock, gravel and bedrock collected from surveys done 1 and 1.5 yr after the earthquake. Percent cover of each type of substratum is compiled across all data. The proportion of pāua is calculated across substrata on which they were found (sand was omitted). The size classes of rock on which pāua were found were defined as: small ( $125\text{--}1000 \text{ cm}^3$ ), medium ( $1000\text{--}10000 \text{ cm}^3$ ) and large ( $>10000 \text{ cm}^3$ ). Observed pāua counts are numbers actually recorded on each type of rock, and expected pāua counts are based on proportions of each substratum type and total number of pāua.  $\chi^2_5 = 491$ ,  $p < 0.001$

Substratum	Proportion of substratum	Proportion observed pāua	Expected pāua counts	Observed pāua counts
Large rock	0.326	0.520	605	966
Medium rock	0.189	0.231	351	428
Small rock	0.204	0.127	378	236
Gravel	0.098	0.006	182	12
Bedrock	0.184	0.115	340	214

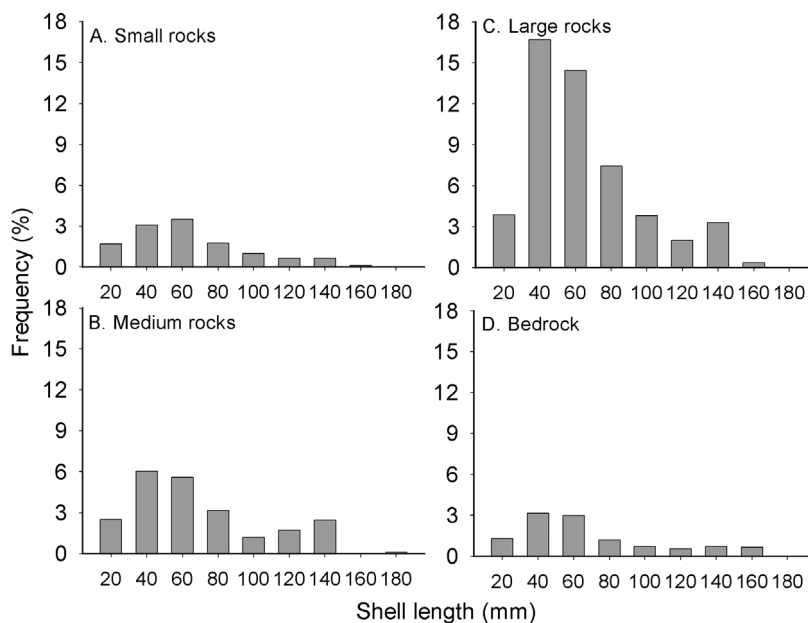


Fig. 4. Length-frequency distributions for all pāua measured on: (A) small rocks ( $125\text{--}1000 \text{ cm}^3$ ); (B) medium rocks ( $1000\text{--}10000 \text{ cm}^3$ ); (C) large rocks ( $>10000 \text{ cm}^3$ ); (D) bedrock. Length-frequency distributions were calculated by combining data for all pāua measured in post-earthquake surveys (the numbers of pāua across all size classes and substratum types sum to 100%). The numbers on the x-axis indicate the upper limit of each size class. Gravel substratum was not included due to negligible usage by pāua. The numbers on the x-axis indicate the upper limit of each size class. Gravel substratum was not included due to negligible usage by pāua.  $N = 1844$

et al. 2010). In Japan, Sato & Chiba (2016) found a persistent decrease in intertidal molluscan species after a large earthquake, and Takami et al. (2017) reported that abalone recruitment was affected by an earthquake-generated tsunami, apparently because sea urchins were removed from abalone settlement areas dominated by CCA, which then became dominated by other macroalgae. These studies illustrate effects of large disturbances on molluscan species and their habitats, and how the inter-dependence of new habitat configurations and recruitment events may influence recovery trajectories.

Our study illustrates some of the complexities involved in recovery of an important molluscan species, the abalone *Haliotis iris*. Well over 100 km of productive coastline were affected by varying coastal uplift. Because recruitment habitat for this species is in the low intertidal and shallow subtidal zones, it was not clear that suitable habitat would exist after severe uplift. Initial observations (Schiel et al. 2019) were that there was high mortality of pāua, and much of their habitat was likely to have been lost and may not have been replaced from uplifted subtidal areas. There was also heavy sedimentation of the coast in the months following the earthquake, which could have affected pāua populations by burial of habitats and reduced juvenile recruitment. The scale of the physical effects across the coastline and the types of habitats that existed post-earthquake were therefore areas of focus.

Our first question in this study was how much rocky habitat suitable for pāua existed along the post-earthquake coastline. Our analysis of aerial images showed that around 14 % of the coastline had rocky reefs, and another 22 % had boulder fields potentially suitable for juvenile pāua. This enabled us to target sites within the different degrees of uplift for intensive sampling of pāua. Our second question addressed the concern that juvenile settlement and subsequent recruitment may have been compromised by the earthquake. The earthquake occurred in mid-November, a time when adult pāua have ripe gonads and spawn (Wilson & Schiel 1995, Naylor et al. 2017). The surveys done 1 yr after the earthquake revealed recruitment along the coastline, as evidenced by size classes less than the annual growth rate of pāua (ca. 25–30 mm yr<sup>-1</sup>). Pāua with shell lengths as small as 2 mm were seen at many sites. These size classes would have resulted from pāua reproduction around the time of the earthquake. Given our observations of high adult mortality in the month following the earthquake, it was somewhat surprising to see the full representation of pāua sizes (up to 170 mm shell length) at the sampling sites

(Fig. 2). Under normal circumstances, this shoreline is heavily fished commercially and recreationally, and it is unusual to see large pāua in the intertidal zone. These large pāua may have been resident on subtidal reefs pushed upwards by the earthquake, or they may have moved upwards and remained there due to greatly reduced fishing pressure.

Sampling at 1.5 yr showed another likely mode of recruitment, again with pāua in the smallest size classes. There was a very large mode in the range of 30–60 mm shell length, which likely represented growth of the previous year's recruitment, although exact growth rates need to be confirmed by tagging studies, which are currently underway. If these growth rates are representative, however, and persist through time with adequate survival, these post-earthquake recruits could reach the minimum legal harvesting size of 125–130 mm shell length in 5–6 yr. It was also noteworthy that the large pāua (>120 mm shell length) seen at 1 yr had mostly disappeared. This may have been due to illegal fishing, which was known to have occurred along the coastline as the coastal highway opened, or from the pāua moving into subtidal habitats.

Our third question was to determine associations of pāua with specific features of habitats across sites. It was no surprise that the layering of rocks within sites was the most important habitat feature relating to juvenile pāua abundance. Small pāua require under-boulder habitat for shelter, which occurs almost exclusively where large rocks sit on top of smaller rocks, forming complex layered sub-habitats. Water flows freely around and through these types of sub-habitat, keeps them largely free of fine sediments, and helps trap algal detrital food on which pāua feed (Cornwall et al. 2009). Where these finely scaled habitats occur, juvenile pāua are plentiful and per-area densities are high (see also Aguirre & McNaught 2011). As in other abalone species, the presence and abundance of CCA greatly facilitate recruitment (e.g. Morse & Morse 1984, Rogers-Bennett et al. 2011), and these corallines are abundant on the medium–large rocks where juvenile pāua occur.

The relationship between pāua abundances and silt, sand and gravel is interesting. Although silt, sand and gravel did not have a large effect in the GLMM, few or no pāua were found where their cover was high. The abundance of these mobile materials is the result of dynamic processes at many sites along the coast. For example, shifting gravel from storm waves and mud from occasional severe rain have buried some areas near survey sites in which large numbers of pāua were previously found (Fig. 5).



Fig. 5. Immediately post-earthquake, large numbers of dead and dying pāua were seen along the coastline, scattered among newly uplifted boulders and rocks (left panel); many inshore sites were inundated with gravel and sand in large storm events in the 2 yr after the earthquake, covering much juvenile pāua habitat (right panel)

These events are exacerbated by the severe, post-earthquake erosion of sedimentary rocks, which are fragmenting and becoming highly mobile. In many areas, damaged and eroding coastal cliffs yield huge loads of sediment during rain events, which flow over intertidal areas into nearshore waters, often burying juvenile habitat. It remains to be seen, therefore, how well the good juvenile habitat we have identified will persist over time along this coastline.

Pāua are known as 'taonga' (treasured) species by New Zealand Māori and are of special cultural importance, in addition to being of great recreational and economic value. Understanding the status and recovery of pāua populations along the earthquake-affected coastline was therefore considered a top priority. The results of this study, plus ongoing subtidal surveys of adult populations by commercial fishing divers (McCowan & Neubauer 2018), have produced recruitment and population data that will underpin decisions on opening the fishery, most likely in a cautionary way over time. It is noteworthy that based partially on habitat requirements we identified, over 167 000 hatchery-reared pāua were placed into selected sites by the pāua industry and Kaikōura community. It is hoped that a combination of natural recovery and intervention with seeded pāua will enable this fishery to re-open and be sustainable. The long-term prognosis will greatly depend on the stability of the low intertidal rocky habitats studied here and subsequent adaptive management of the fishery.

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