



Long-term responses of sandy beach crustaceans to the effects of coastal armouring after the 2010 Maule earthquake in South Central Chile



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ABSTRACT

Earthquakes and tsunamis are large physical disturbances frequently striking the coast of Chile with dramatic effects on intertidal habitats. Armouring structures built as societal responses to beach erosion and shoreline retreat are also responsible of coastal squeeze and habitat loss. The ecological implications of interactions between coastal armouring and earthquakes have recently started to be studied for beach ecosystems. How long interactive impacts persist is still unclear because monitoring after disturbance generally extends for a few months. During five years after the Maule earthquake (South Central Chile, February 27th 2010) we monitored the variability in population abundances of the most common crustacean inhabitants of different beach zones (i.e. upper, medium, and lower intertidal) at two armoured (one concrete seawall and one rocky revetment) and one unarmoured sites along the sandy beach of Llico. Beach morphology changed after the earthquake-mediated uplift, restoring upper- and mid-shore armoured levels that were rapidly colonized by typical crustacean species. However, post-earthquake increasing human activities affected the colonization process of sandy beach crustaceans in front of the seawall. Lower-shore crab *Emerita analoga* was the less affected by armouring structures, and it was the only crustacean species present at the three sites before and after the earthquake. This study shows that field sampling carried out promptly after major disturbances, and monitoring of the affected sites long after the disturbance is gone are effective approaches to increase the knowledge on the interactive effects of large-scale natural phenomena and artificial defences on beach ecology.

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1. Introduction

Sandy beaches are natural dynamic ecosystems that are becoming increasingly disturbed around the world by intensive human direct use, coastal development and erosive evolution (Defeo et al., 2009; Dugan et al., 2010). Beaches are also threatened by intense and transformative major disturbances, such as sea level rise, large storms, beach nourishment (e.g. Hughes et al., 2009; Lucrezi et al., 2010; Peterson et al., 2014; Witmer and Roelke, 2014), and in some regions by mega-earthquakes/tsunamis (e.g. Jaramillo, 2012; Lomovasky et al., 2011; Mascarenhas and Jayakumar, 2008; Seike et al., 2013; Urabe et al., 2013). The most common response to coastal erosion, shoreline retreat, extreme storms and/or tsunamis is to build coastal defences (Nordstrom, 2000). Paradoxically, armouring accelerates beach erosion,

leading to decreases in beach width and intertidal habitat constraining upper-shore communities to such a narrow width that regular inhabitants of these zones are no longer able to establish, resulting in loss of biodiversity (Dugan et al., 2008; Jaramillo et al., 2012a, 2012b; Lucrezi et al., 2010; Rodil et al., 2015).

Sandy beaches located on seismically active areas, such as the coast in South Central Chile, are periodically affected by coseismic coastal deformation and tsunamis, due to large subduction earthquakes (Ruegg et al., 2009). On February 27th 2010, the Maule earthquake (Mw 8.8) hit Chile along the central-southern coast (ca. 33–38°S) resulting in coastal coseismic uplift of up to 2.0 m at several locations in Península de Arauco (ca. 37°S) (Vargas et al., 2011). Coastal ecosystems were strongly affected by the devastating action of the coastal uplift, as well as by the associated tsunami, with consequences for intertidal communities suddenly exposed to drastic changes such as air exposure (Castilla et al., 2010; Jaramillo et al., 2012a, 2012b; Ortega et al., 2014). The coastal uplift associated with the earthquake caused an increase of the total sandy beach width in some locations that resulted in a significant expansion of the upper and mid-intertidal habitats

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potentially available for colonization by macrofauna (Jaramillo et al., 2012a, 2012b).

Physical disturbance is a key factor in structuring infaunal communities and its effect upon beach ecological communities depends on the nature, intensity and frequency of such disturbance (e.g. Defeo et al., 2009; Hughes et al., 2009; Jaramillo et al., 2012a). Previous studies that have focused on the effects of large disturbances have reported a wide range of responses of the resident beach biota (e.g. Jaramillo et al., 2012a, 2012b; Leewis et al., 2012; Lucrezi et al., 2010; Schlacher et al., 2012). This is partly due to the haphazard nature of such events, but mainly because there is often no pre-disturbance community data available, making difficult to assess the effects of such a disturbance (Hughes et al., 2009). Furthermore, the ecological responses of macrofauna to an extreme disturbance event will depend on a suite of factors, including previous conditions of the impacted sites and surrounding areas, features of the biota, seasonality, and the characteristics of the disturbance itself (Hughes et al., 2009; Jaramillo et al., 2012a; Peterson et al., 2014).

The ecological implications of interactions between coastal armouring and major earthquakes have recently started to be studied for beach ecosystems (e.g. Jaramillo et al., 2012a, 2012b; Rodil et al., 2015). For instance, the effects of coastal uplift and armouring in earthquake-affected beaches from Península de Arauco (Chile) included restoration of upper and mid-intertidal habitats seaward of armouring structures followed by rapid colonization of mobile crustaceans typical of these zones, such as talitrid sand hoppers formerly excluded by constraints imposed by the coastal defences (Jaramillo et al., 2012a, 2012b). Simultaneously, the uplift of rocky subtidal substrate generated by the Maule earthquake eliminated low intertidal habitat for ecologically important beach species such as the crustacean anomuran *Emerita analoga* (Jaramillo et al., 2012a, 2012b; Veas et al., 2013). However, monitoring beyond a few months after the disturbance is rarely performed, so little is known of long-term effects (e.g. >3 years) to beach ecosystems (see Leewis et al., 2012; Peterson et al., 2014). Therefore, most of the studies on beach ecological responses to large disturbances show difficulties in separating natural fluctuations in macrofauna diversity from disturbance induced effects. Consequently, there is a little understanding of how beach fauna recovers after an extreme disturbance (Hughes et al., 2009; Peterson et al., 2014).

The use of armoured defences in coastal areas is expected to increase in the near future in response to a combination of expanding human populations, increasing subsidence and beach erosion, periodical occurrence of catastrophic events and global sea level rise (e.g. Dugan et al., 2008; Nordstrom, 2014; Ruegg et al., 2009). The Chilean coast experiences recurrent large subduction earthquakes (Moreno et al., 2010; Vargas et al., 2011) and major coastal development with accompanying armouring structures (Jaramillo, 2012). Since armoured beaches are thought to be more vulnerable to disturbances than natural unarmoured beaches (Castelle et al., 2008; Dugan et al., 2008; Lucrezi et al., 2010) the potential exists for stronger negative ecological effects of coastal armouring and earthquakes. In this research, we examined the long-term responses of beach crustaceans (representing the highest percentage of beach macrofauna) to the combined effects of armouring and the emergence of a new upper-shore habitat following the Maule earthquake at the sandy beach of Llico (Península de Arauco, Chile). The typical beach macroinfaunal zones were sampled a few weeks prior to the earthquake in front of two armouring sites and one adjacent unarmoured site. After the earthquake, we surveyed repeatedly, from 2010 to 2015, the crustacean community at the same sites to measure changes in beach habitat (i.e. beach face slope and intertidal width) and biota caused by the earthquake-mediated coastal uplift. Specifically, we wanted to examine the direct effect of the coseismic uplift on the population abundances of the main beach macrofaunal species, and whether shore-armouring influence the long-term responses of those species to a large earthquake event.

2. Material and methods

2.1. Location, sites and sampling design

This study was conducted at the sandy beach of Llico (37°11'38" S, 73°33'44" W), on the northern coast of Península de Arauco in South Central Chile (Fig. 1). Tidal range was close to 1.0 m (i.e. microtidal). Continental uplift at this location during the Maule earthquake was approximately 2.0 m (Moreno et al., 2010; Vargas et al., 2011). The coastal uplift associated with the earthquake at Llico caused a large increase of the total beach width up to 12.5 times (Jaramillo et al., 2012b). The study area included two sites located in front of armoured sections of the beach located on the western and eastern sides of a jetty (Figs. 1–2). The site located west of the jetty is in front of a concrete seawall while that located on the eastern side is in front of a rocky revetment (Figs. 1–2). The armouring structures were located low enough on the beach profile to interact with waves during high tides (Fig. 2). The third study site was an unarmoured section of the beach located nearly 350 m east of the armoured sites (Figs. 1–2). In terms of the morphodynamic beach state (sensu Short and Wright, 1983), before the earthquake, the sites in front of the revetment and the seawall were close to a reflective state (i.e. narrow beaches having coarse sands and steep slopes), while the beach site was close to an intermediate state (i.e. wider beaches having fine to medium sand with gentle slopes). After the earthquake, the three sites were close to an intermediate state.

We started surveying the intertidal zones at the three beach sites in late January 2010. We sampled invertebrate crustaceans (i.e. the most abundant macrofauna in this beach) retained on a 1 mm sieve (Schlacher et al., 2008) setting up four replicated shore-normal transects 5 m apart from each other, extending from the upper intertidal to the low tide level of sites located in front of the seawall, the rocky revetment and in the unarmoured beach site. Along these transects we sampled each of the three typical beach faunal zones dominated by crustaceans along sandy beaches of South Central Chile (McLachlan and Jaramillo, 1995): i) the upper zone occupied primarily by the talitrid amphipod *Orchestoidea tuberculata* Nicolet, 1849, usually extending from the toe of the dunes to a limit located around the drift line or high tide level, ii) the mid zone occupied by two cirrolanid isopod species, *Excirrolana braziliensis* Richardson 1912 and *Excirrolana hirsuticauda* Menzies, 1962, extending from the drift line to the effluent line, and iii) the lower zone occupied primarily by the anomuran crab *E. analoga* (Stimpson, 1857), extending from the effluent line to the lowest tide level. Five core samples of sediments were collected at each of the three faunal zones with a metal cylinder (10 cm in diameter) to a depth of 30 cm at equally spaced levels across the zone, for a total sampling area of 0.04 m² per zone on each transect. The five core samples from each zone and transect were pooled and sieved through a 1 mm sieve and the collected organisms were stored in 10% formalin in sea water until laboratory sorting. Following the Maule earthquake on the 27th of February 2010, intertidal surveys as described above were repeated at each of the three sites during seventeen more sampling dates in 2010 (April, July and September), 2011 (January, March, August and November), 2012 (February, May, August and October), 2013 (February, July and December), 2014 (July and November), and 2015 (January). To ensure temporal independence of samples, the position of the first transect was randomly determined within each site on each sampling date, with the other three transects laid out at fixed five m distances away.

Beach width was measured as the distance in metres, between the landward boundary of the beach defined by the toe of foredune or armouring structures and the low tide level during spring tides. The beach face slope was measured at each of the four transects of each site using the method of Emery (Emery, 1961). Beach face slope was expressed as 1/x, where x was the distance in metres at which a height difference of 1 m between two consecutive intertidal levels is reached.

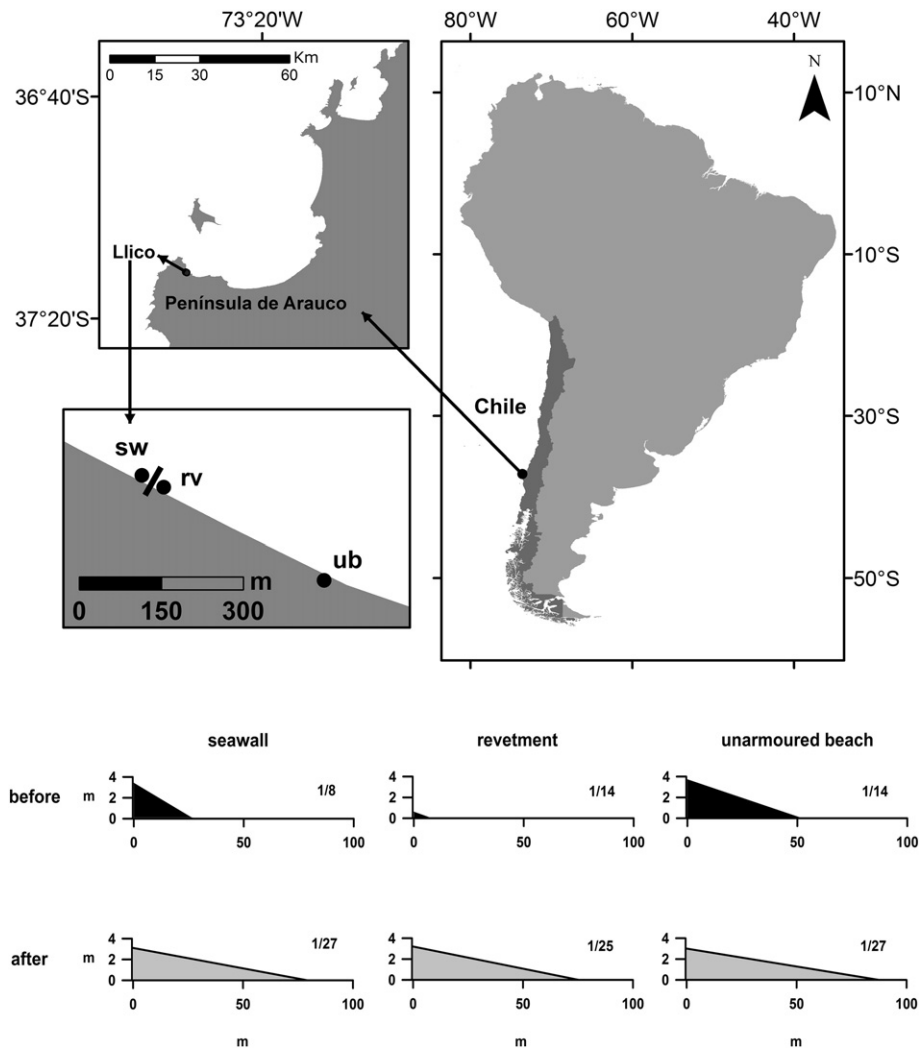


Fig. 1. Location of the study sites at the beach of Llico (Península de Arauco, South Central Chile), and the approximate locations (black dots) of sandy sites in front of the seawall (sw), the rocky revetment (rv), and the unarmoured beach (ub). The black solid line between the sw and rv dots represents the jetty that separates both beach sites. The bottom panels show the difference in beach width (metres) and beach face slope ($1/x$) before (January 2010) and after earthquake condition (an average over 17 sampling dates, see Table 1).

2.2. Statistical analyses

Data was first assessed with boxplots and Cleveland dotplots to identify patterns and outliers. Invertebrate abundances (measured as counts) were presented as individuals m^{-1} to accommodate beach width changes (Jaramillo et al., 2012a). Comparisons of the abundance of each invertebrate species among sites over time were analysed separately through generalized linear models (GZLM). Site (three levels: seawall, revetment and unarmoured beach) was considered a fixed factor, time (18 dates) a continuous co-variable in the model, and transects were considered replicates ($n = 4$). We assumed the dependent variable to be Poisson distributed with a log-link structure. When overdispersion was detected, the standard errors were corrected using a quasi-GZLM model (Zuur et al., 2009). Model fit was evaluated through Akaike's Information Criterion (AIC). Model assumptions were checked: (i) plots of residuals versus fitted values to verify homogeneity, (ii) quantile–quantile plots or histograms of the residuals for the assessment of normality, and (iii) residuals versus each explanatory variable to check for data independence. Analyses were fitted in R 3.2.0 (R Development Core Team, 2014).

3. Results

After the earthquake (February 27th, 2010), the coastal coseismic uplift modified the beach intertidal width and changed dramatically the beach face slope at Llico (Figs. 1–2; Table 1). All sampling sites became wider and flatter by April 2010, and remained so until the end of the study (Figs. 1–2; Table 1). Post-earthquake changes in beach width and slope were more apparent in front of the seawall and the revetment (Fig. 2; Table 1).

The earthquake coseismic uplift promoted significant changes in the population abundances of the most common species of mobile crustacean macrofauna in all typical beach intertidal zones. The response and direction of change in the abundance of the macroinvertebrate species varied with both, the extreme disturbance event and coastal armoring. Before the earthquake (January 2010), the abundance of *O. tuberculata* in the upper intertidal was low at the seawall and unarmoured sites (<30 and 400 ind m^{-1} , respectively), and inexistent at the revetment site (Fig. 3). After the earthquake (February 27th, 2010), the abundance of *O. tuberculata* increased significantly over time ($p < 0.001$, Table 2) for the three sites (Fig. 3). However, this increase in the abundance pattern was not consistent among

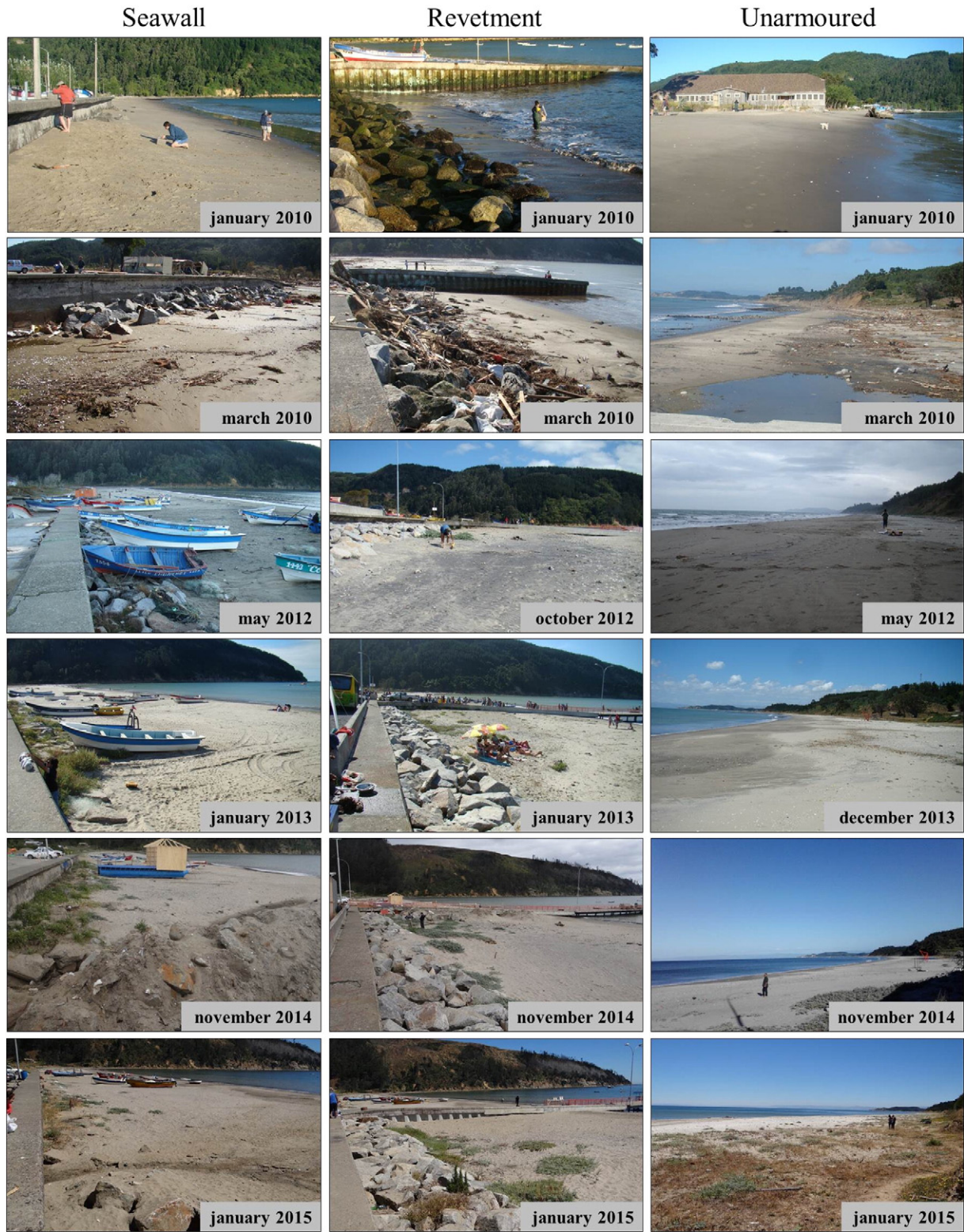


Fig. 2. Before/after Maule earthquake (February 27th, 2010) pictures of the armoured sandy beach sites located in front of a concrete seawall and a rocky revetment, and those of the unarmoured site at the beach of Llico. Note the vast mechanical disturbance usually observed at the site located in front of the seawall.

sites (i.e. significant site:time interaction, $p < 0.01$; Table 2). Thus, the increase in the abundance of this talitrid species was significantly higher ($p < 0.001$; Table 2) at the revetment than at the seawall site (Fig. 3). For instance, the mean population abundance of *O. tuberculata* in front of the revetment was 1995 ± 524 ind m^{-1} (mean \pm SE), and the highest numbers (>5000 ind m^{-1}) were collected in November 2011,

July 2013 and July 2014 (Fig. 3). In front of the seawall, the mean abundance of *O. tuberculata* was 552 ± 103 ind m^{-1} , and peak numbers (~ 2000 ind m^{-1}) were recorded in August 2011 and February 2012 (Fig. 3). Extensive repair work on the concrete seawall during November 2014 disrupted the upper intertidal zone (Fig. 2) affecting the presence of talitrids, thus low numbers

Table 1
Mean beach width (metres) and mean (\pm SD) beach face slope (1/slope, see Material and methods) of the three sites sampled ($n = 4$ transects per site) before and after the Maule earthquake (February 27th 2010) at the sandy beach of Llico (Península de Arauco, South Central Chile). Beach width was homogeneous at each transect (SD = 0).

| | Date | Seawall | | Revetment | | Unarmoured beach | | |
|------------|----------------------|---------|-----------|-----------|-----------|------------------|-----------|----------|
| | | Width | Slope | Width | Slope | Width | Slope | |
| Before 27F | January 2010 | 27 | 8 (0.4) | 8 | 14 (1.3) | 52 | 14 (0.6) | |
| After 27F | April 2010 | 80 | 35 (1.7) | 70 | 32 (0.4) | 80 | 24 (0.9) | |
| | July 2010 | 78 | 30 (1.5) | 84 | 37 (1.5) | 80 | 26 (0.5) | |
| | September 2010 | 138 | 43 (1.9) | 100 | 33 (0.3) | 130 | 42 (1.2) | |
| | January 2011 | 82 | 22 (0.9) | 81 | 24 (0.4) | 52 | 22 (0.5) | |
| | March 2011 | 100 | 28 (0.5) | 89 | 29 (0.9) | 98 | 28 (0.6) | |
| | August 2011 | 100 | 35 (1.5) | 103 | 28 (0.6) | 117 | 49 (1.9) | |
| | November 2011 | 83 | 22 (0.3) | 87 | 21 (0.4) | 130 | 30 (0.8) | |
| | February 2012 | 80 | 27 (1.7) | 83 | 27 (1.2) | 100 | 28 (0.3) | |
| | May 2012 | 72 | 21 (0.3) | 61 | 23 (2.2) | 86 | 26 (1.5) | |
| | August 2012 | 65 | 22 (0.5) | 86 | 26 (0.6) | 90 | 27 (1.6) | |
| | October 2012 | 93 | 29 (1.3) | 93 | 25 (0.6) | 107 | 34 (1.9) | |
| | February 2013 | 74 | 26 (1.2) | 66 | 21 (1.0) | 112 | 30 (2.0) | |
| | July 2013 | 54 | 45 (1.0) | 54 | 16 (0.1) | 78 | 26 (0.5) | |
| | December 2013 | 61 | 21 (1.4) | 59 | 19 (1.4) | 98 | 34 (1.5) | |
| | July 2014 | 74 | 24 (0.6) | 74 | 20 (1.0) | – | – | |
| | November 2014 | 87 | 16 (0.6) | 91 | 28 (4.9) | – | – | |
| | January 2015 | 65 | 20 (1.1) | 55 | 16 (1.6) | 50 | 24 (2.2) | |
| | Total mean after 27F | | 82 (19.3) | 27 (8.1) | 79 (15.4) | 25 (5.9) | 94 (24.1) | 30 (7.3) |

(76 ± 76 ind m^{-1}) were recorded in January 2015 (Fig. 3). No significant differences were found between the unarmoured and the seawall or between the unarmoured and the revetment sites (Table 2, Fig. 3). Thus, the post-earthquake mean population abundance of *O. tuberculata* at the unarmoured site was 870 ± 125 ind m^{-1} , with peak numbers (>1500 ind m^{-1}) collected at several different dates (November 2011, February, May and October 2012, and December 2013) (Fig. 3).

Before the earthquake, the mid-intertidal isopod *E. braziliensis* was a common inhabitant at the unarmoured (703 ± 262 ind m^{-1}) and seawall (802 ± 658 ind m^{-1}) sites (mean \pm SE), and no individuals

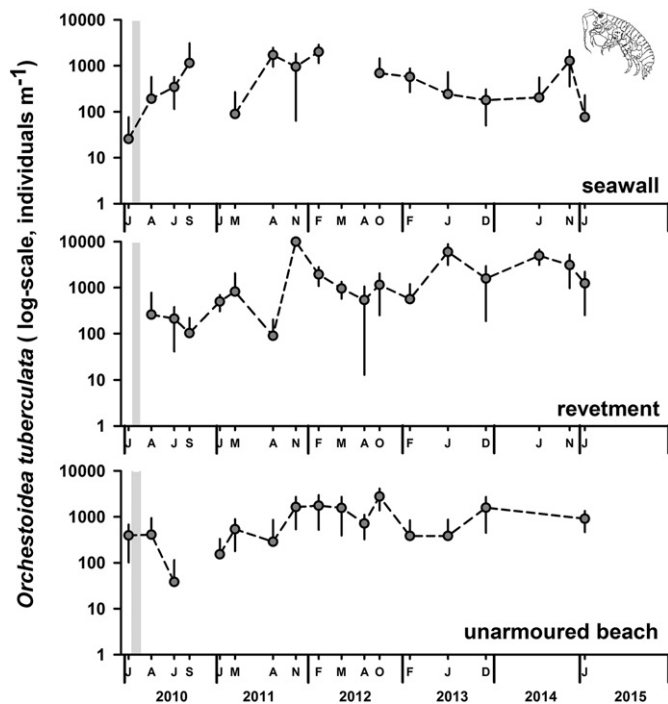


Fig. 3. Mean (\pm SD, log-scale) abundance (ind m^{-1}) of *Orchestoidea tuberculata* at the three sandy beach sites sampled at Llico. The light grey column is used to separate the sampling carried out before the earthquake (late January 2010) from that carried out after February 27th, 2010.

were collected in front of the revetment (Fig. 4). After the earthquake, the abundance of this cirrolanid species increased over time ($p < 0.001$; Table 2), but this pattern was not consistent among sites (i.e. significant site:time interaction, $p < 0.001$; Table 2). Thus, the increasing abundance of *E. braziliensis* was significantly higher at the unarmoured site compared to both, the seawall ($p < 0.001$) and revetment ($p < 0.01$) sites (Table 2, Fig. 4). For instance, the average abundance (mean \pm SE) of *E. braziliensis* at the unarmoured site was 1334 ± 429 ind m^{-1} , high numbers (>1000 ind m^{-1}) were recorded in March 2011 and December 2013, and $>10,000$ ind m^{-1} were collected in January 2015 (Fig. 4). No significant differences were found between the revetment and seawall sites (Table 2). The post-earthquake mean abundances of *E. braziliensis* at the seawall and revetment sites were 389 ± 85 and 453 ± 82 ind m^{-1} , respectively (mean \pm SE). The maximum abundances collected at the armoured sites were recorded in January 2015 (>2000 ind m^{-1}) in front of the seawall, and in February 2013 (>2000 ind m^{-1}) in front of the revetment (Fig. 4).

Before the earthquake, the mid-intertidal isopod *E. hirsuticauda* was abundant at the unarmoured (764 ± 385 ind m^{-1}) and seawall (3680 ± 411 ind m^{-1}) sites (mean \pm SE), and no individuals were collected in front of the revetment (Fig. 5). After the earthquake, the abundance of *E. hirsuticauda* showed a significant and consistent increase over time for all the three sites ($p < 0.001$; Table 2). The post-earthquake mean abundances (\pm SE) were 6340 ± 1213 (unarmoured), 4551 ± 762 (seawall), and 5441 ± 840 (revetment) ind m^{-1} , reaching maximum abundances of $>30,000$ (February 2013), $>20,000$ (January 2015), and $>22,000$ (January 2015) ind m^{-1} at the unarmoured, seawall and revetment sites, respectively (Fig. 5).

The low intertidal crab *E. analoga* was very abundant, and the only one crustacean species present in all the three sites before the earthquake (mean \pm SE; unarmoured: 4393 ± 847 , seawall: $21,594 \pm 3302$, revetment: 4431 ± 1677 ind m^{-1}) (January 2010). After the earthquake, we recorded mean abundances of *E. analoga* of 5309 ± 662 for the unarmoured, 3302 ± 449 for the seawall and 4658 ± 628 ind m^{-1} for the revetment sites. Thus, the abundance of *E. analoga* showed no significant differences among sites (Table 2). However, the abundance of this anomuran crab decreased significantly over time at the three sites ($p < 0.001$; Table 2, Fig. 6). For instance, the abundance of *E. analoga* at the end of the study (January 2015) was 1337 ± 481 , 891 ± 309 , and 1019 ± 424 ind m^{-1} for the unarmoured, seawall and revetment sites, respectively, as compared to the mean values recorded during January 2010 (Fig. 6).

Table 2

Results of the generalized linear models (GZLM; Poisson distributed with a log-link structure) containing pair-wise contrasts for the main invertebrates (response variables: *Orchestoidea tuberculata*, *Excirolana braziliensis*, *Excirolana hirsuticauda* and *Emerita analoga*) of the typical beach zones at Llico.

| Response variable | Source | Anova output | | | Model summary | | | | | |
|-----------------------|------------------------|------------------------|----------|--------|---------------|-------------|-------------|---------|--------|--------|
| | | df | χ^2 | p | Contrasts | Estimate | SE | t value | p | |
| <i>O. tuberculata</i> | Site | 2 | 23.6 | <0.001 | Ub-Rv | -0.38 | 0.53 | -0.72 | 0.471 | |
| | | 1 | 33.3 | <0.001 | Ub-Sw | 0.42 | 0.55 | 0.76 | 0.448 | |
| | Time | 1 | 12.9 | <0.01 | Sw-Rv | -0.80 | 0.53 | -1.5 | 0.135 | |
| | | 2 | 12.9 | <0.01 | Time (Ti) | 0.08 | 0.03 | 2.55 | <0.05 | |
| | <i>E. braziliensis</i> | Site | 2 | 36.8 | <0.001 | Ub:Ti-Rv:Ti | 0.07 | 0.04 | 1.59 | 0.114 |
| | | | 1 | 81.9 | <0.001 | Ub:Ti-Sw:Ti | -0.10 | 0.05 | -1.88 | 0.06 |
| | | Time | 1 | 20.8 | <0.001 | Sw:Ti-Rv:Ti | 0.16 | 0.05 | 3.55 | <0.001 |
| | | | 2 | 20.8 | <0.001 | Ub-Rv | 1.65 | 0.97 | 1.71 | 0.09 |
| | | <i>E. hirsuticauda</i> | Site | 2 | 2.3 | 0.319 | Ub-Sw | 2.36 | 0.89 | 2.64 |
| 1 | | | | 68.8 | <0.001 | Sw-Rv | -0.71 | 0.92 | -0.78 | 0.439 |
| Time | | | 1 | 0.67 | 0.717 | Time (Ti) | 0.34 | 0.04 | 7.92 | <0.001 |
| | | | 1 | 24.5 | <0.001 | Ub:Ti-Rv:Ti | -0.21 | 0.07 | -3.2 | <0.01 |
| <i>E. analoga</i> | | | Site | 2 | 0.67 | 0.717 | Ub:Ti-Sw:Ti | -0.28 | 0.07 | -4.26 |
| | 1 | | | 24.5 | <0.001 | Sw:Ti-Rv:Ti | 0.06 | 0.07 | 0.88 | 0.379 |
| | Time | | 1 | 0.67 | 0.717 | Ub-Rv | -0.15 | 0.18 | -0.85 | 0.399 |
| | | | 1 | 24.5 | <0.001 | Ub-Sw | -0.29 | 0.19 | -1.51 | 0.131 |
| | <i>O. tuberculata</i> | | Site | 2 | 0.67 | 0.717 | Sw-Rv | 0.13 | 0.18 | 0.72 |
| | | 1 | | 24.5 | <0.001 | Time (Ti) | 0.13 | 0.02 | 7.88 | <0.001 |
| | | Time | 1 | 0.67 | 0.717 | Ub-Rv | -0.07 | 0.17 | -0.4 | 0.685 |
| | | | 1 | 24.5 | <0.001 | Ub-Sw | -0.14 | 0.18 | -0.8 | 0.416 |
| | | Time | 1 | 0.67 | 0.717 | Sw-Rv | 0.07 | 0.17 | 0.4 | 0.678 |
| 1 | | | 24.5 | <0.001 | Time (Ti) | -0.07 | 0.01 | -4.8 | <0.001 | |

Models included site (Ub: unarmoured beach, Rv: revetment and Sw: seawall) as a fixed factor and time (Ti: 18 dates) as a continuous co-variable. SE: standard error. Significant effects appear in *italics*.

4. Discussion

The Maule earthquake severely struck the southern-central coast of Chile on February 27th, 2010. The epicentre and subsequent land-level changes affected primarily the coast along Península de Arauco, including the coastline of Llico (Moreno et al., 2010; Vargas et al., 2011). Previous studies showed that the coseismic uplift around this region was approximately up to 2.0 m, causing a dramatic change on the

littoral biota of this shoreline (Castilla et al., 2010; Jaramillo et al., 2012a, 2012b; Vargas et al., 2011).

Post-earthquake changes in beach morphology were notorious in the coast of Llico, and the strongest changes occurred in front of the artificial coastal defences. Before the earthquake, the intertidal width and the beach face slope were totally different at the three sites at Llico. Thus, the unarmoured beach site was wider and flatter than both, the seawall and revetment sites. Also, the revetment site showed the

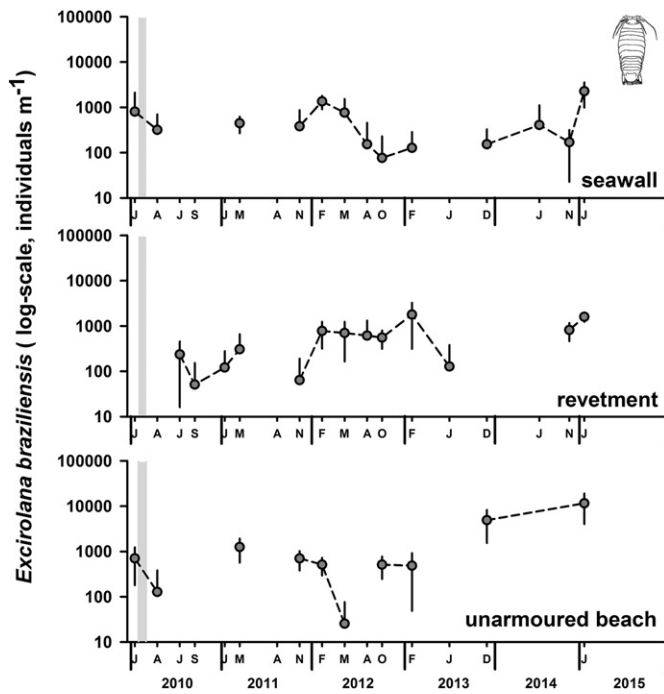


Fig. 4. Mean (\pm SD, log-scale) abundance (ind m^{-1}) of *Excirolana braziliensis* at the three sandy beach sites sampled at Llico. The light grey column is used to separate the sampling carried out before the earthquake (late January 2010) from that carried out after February 27th, 2010.

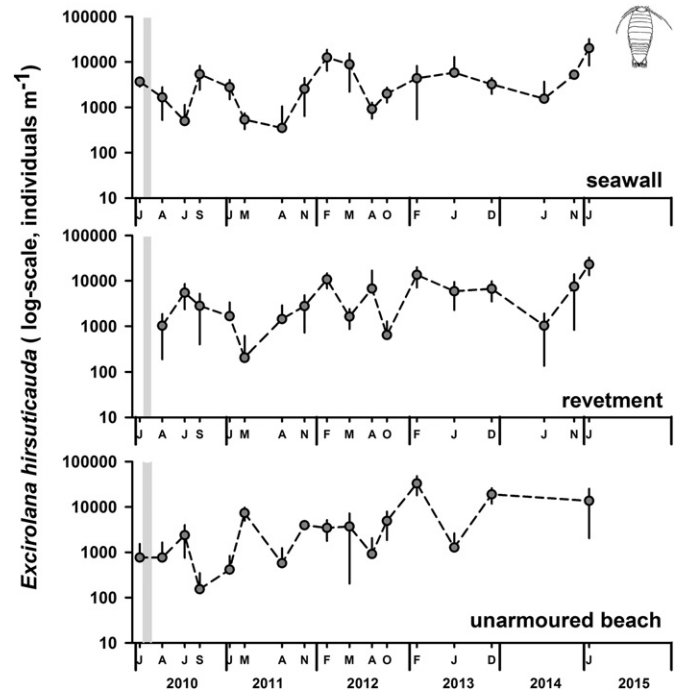


Fig. 5. Mean (\pm SD, log-scale) abundance (ind m^{-1}) of *Excirolana hirsuticauda* at the three sandy beach sites sampled at Llico. The light grey column is used to separate the sampling carried out before the earthquake (late January 2010) from that carried out after February 27th, 2010.

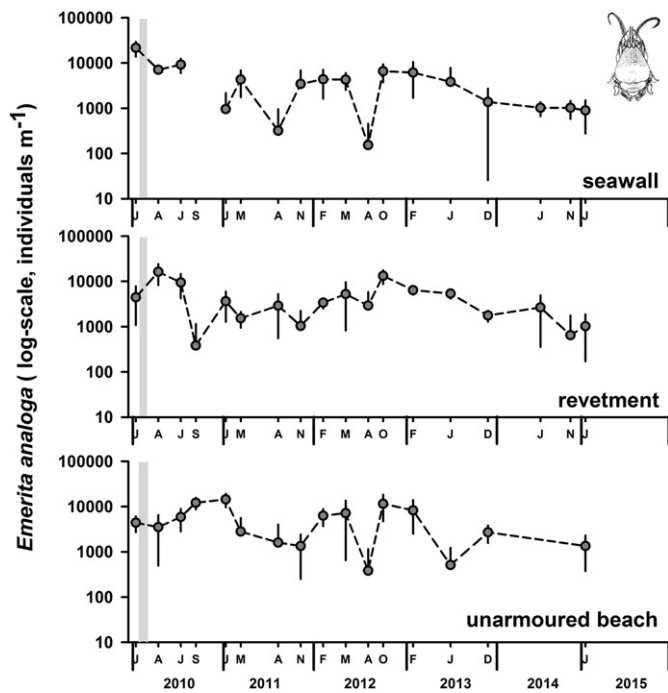


Fig. 6. Mean (\pm SD, log-scale) abundance (ind m^{-1}) of *Emerita analoga* at the three sandy beach sites sampled at Llico. The light grey column is used to separate the sampling carried out before the earthquake (late January 2010) from that carried out after February 27th, 2010.

shortest intertidal width when compared to the unarmoured and the seawall sites. After the earthquake, part of the intertidal that before the earthquake was absent was restored in both armoured sites. The mean intertidal width and slope became similar among the three sites, and the extent of those changes still remains after five years of the earthquake.

Human induced disturbances on beaches, such as coastal armoring, occur in the form of gradual disturbance, while large perturbations are occasional and may exceed the capacity of beach macrofauna to cope with such drastic changes (Witmer and Roelke, 2014). While these two types of disturbances have differing effects on beach communities because they operate over varied time scales, their interaction can produce unexpected ecological outcomes (Jaramillo et al., 2012a). Therefore, the long-term data obtained at Llico beach for five years after the Maule earthquake provides a valuable insight into potential interactive effects between two different major physical disturbances on beach habitats and biota. The armoring structures at Llico were built low enough in the intertidal to constantly interact with waves and tides, preventing any upper and mid-intertidal community of invertebrate species to thrive in front of the armoring structures before the earthquake, as shown elsewhere where artificial defences are a common feature of the littoral landscape (Dugan et al., 2008; Walker et al., 2008; Lucrezi et al., 2010; Jaramillo et al., 2012a, 2012b).

The coseismic uplift had a significant and positive effect on *O. tuberculata*, *E. braziliensis* and *E. hirsuticauda*, especially in front of the armoring structures. Thus, where coastal armoring constrained landward extent of the beach, increases in the intertidal width created a new upper-shore habitat that was rapidly colonized by mobile upper-intertidal and mid-shore macroinvertebrate species, most likely via migration from the adjacent unarmoured site (Jaramillo et al., 2012a, 2012b). Before the earthquake, the talitrid sandhopper *O. tuberculata* was the common invertebrate species at the unarmoured site and in front of the seawall, but it was absent in front of the revetment. After the earthquake, numbers of *O. tuberculata* increased over time at the three sites. Talitrids have short-timing positive responses

to large perturbations due to their reproductive ability, strong plasticity and also to the accumulation of wrack along beaches, which provides food and habitat (e.g. Fanini et al., 2005; Ishida et al., 2015; Jaramillo et al., 2012a). Interestingly, the increase in abundance of this species was higher at the revetment site compared to the seawall site, probably related to increasing post-earthquake human activities in front of the seawall (see below). The emergence of a new post-earthquake beach area was also of benefit to the mid-intertidal species *E. braziliensis* at the three sampling sites. However, this species showed a larger increase at the unarmoured site compared to the armoured sites. The other mid-intertidal species, *E. hirsuticauda* increased constantly over time at the three sites. After the earthquake, upper and middle-shore invertebrate species emerged and thrived within a relatively short period of time. For instance, before the earthquake, there was no upper and middle-shore invertebrate species in front of the revetment. *O. tuberculata* and *E. hirsuticauda* appeared for the first time in less than two months after the Maule earthquake, while *E. braziliensis* recolonized the area in front of the revetment after five months. However, the largest numbers of the three species at the two armoured sites were collected approximately after a year of the earthquake. The earthquake and following tsunami dragged and deposited enormous quantities of debris covering some of the newly emerged habitat suitable for beach invertebrates, a fact that probably slowed down the colonization process in front of the two armoured sites until it was totally removed during late 2011.

After the earthquake, the increase in the abundance of *O. tuberculata*, *E. braziliensis* and *E. hirsuticauda* was evident at the three sites studied at Llico. However, there was some variability in the increasing numbers of these three species over time, most likely related to natural seasonal fluctuations, but also to post-earthquake human activities. Coastal defences are built to protect coastal sites from erosion and retreat, but also to facilitate human activities, such as fishing and tourism (Nordstrom, 2000). The Maule earthquake promoted a significant increase in the intertidal beach width, allowing large numbers of invertebrates to colonize intensively their natural beach zones in front of the armoring structures. At the same time, the level of human activities in front of the armoring structures increased after the earthquake due to the availability of a new upper-shore area for recreational and labour use, such as landing and boat docking (as illustrated in Fig. 2), which resulted in constant habitat disturbances within the new habitat. These activities probably affected the colonization process of *O. tuberculata*, mainly in front of the seawall where most of those human activities occurred. Indeed, previous studies have found a negative correlation between numbers of talitrids and human uses of beaches (e.g. Bessa et al., 2014; Fanini et al., 2005; Veloso et al., 2008). Also, human activities were common at the unarmoured site of Llico before and after the earthquake (Rodil et al., 2015), probably interfering with the invertebrate dynamics at this site. Nonetheless, the unarmoured site supported populations of *O. tuberculata*, *E. braziliensis* and *E. hirsuticauda* before and also after the earthquake. This is probably linked to the type of human activities performed at the armoured sites, (e.g. boat docking and use of tractors to pull out boats from the water) as compared to the unarmoured beach site where human activities were limited to light leisure activities, such as sun-bathing or trampling.

Repair work on the concrete seawall affected the newly created upper-shore habitat at this site during November 2014. This major human intervention was probably responsible for the dramatic decrease in the numbers of *O. tuberculata* at that time, and probably for the low numbers collected in the following sampling date. Construction strongly alters beach environments, where seawalls encourage continued erosion of the beach face, thus loss of intertidal organisms (Dugan et al., 2008; Griggs, 2005). Although we do not have data to check the long-term responses of *O. tuberculata* after the wall reparations, this species is known to have short-timing positive responses to large perturbations (Jaramillo et al., 2012a). Thus, less than two months after

the repair work numbers of *O. tuberculata* were collected again in front of the seawall.

The sand crab *E. analoga* was the only species present simultaneously at the three sites before and after the earthquake. This anomuran species was less affected by armouring since inhabits the lower-shore beach habitat away from the defence structures (Jaramillo et al., 2012a, 2012b). Large numbers of *E. analoga* were found before the earthquake at the armoured and unarmoured beach sites, but the abundance of this species declined significantly after the earthquake. Previous studies have related high-mortality rates of subtidal soft-bottom species, including *E. analoga*, with mega-earthquakes and large tsunami heights (e.g. Jaramillo et al., 2012a; Lomovasky et al., 2011; Seike et al., 2013; Urabe et al., 2013). In Lebu, a beach located nearly 40 km south of Llico, a decrease in the density of *E. analoga* was also observed after the earthquake, a fact probably related to a massive adult mortality due to wash-over by the tsunami to beach levels located above the drift line (see Jaramillo et al., 2012a; Veas et al., 2013). Hence, the extension of the ecological changes at Llico after the earthquake will depend on the species affected and the proximity of source populations, as well as shoreline evolution and human responses to the disaster (Jaramillo et al., 2012a; Liew et al., 2010; Wong, 2009).

We want to stress the fact that only one sampling event before the earthquake might influence the information regarding the crustacean community fluctuations, and that more samplings before the earthquake would give a more complete picture of the crustacean community. However, we know that the artificial defences at Llico were built long before the earthquake event, and low enough in the intertidal to constantly interact with waves and tides affecting the crustacean community. Therefore, we are certain that the low abundance or even the absence of any upper and mid-intertidal community of crustacean species before the earthquake was caused by the constant presence of seawater in front of the armouring defences rather than by a temporal variation in the abundance of the crustaceans.

Traditionally, the ecological effects of large physical disturbances on beach invertebrates are challenging to isolate from natural benthic patterns due to a lack of information regarding natural fluctuations in the community structure at the specific study site (Hughes et al., 2009). Nearly all previous studies on beach community impacts of large disturbances continued monitoring for less than a year following the disturbance event (but see Hughes et al., 2009; Peterson et al., 2014 for longer-term inferences). Consequently, we have learned little about the recovery of the beach ecosystem following a large physical disturbance, and how this varies according to the presence and type of coastal defence. Long-term monitoring is essential to examine community-level recovery processes, and thus to understand implications of disturbances on coastal ecosystems (Seike et al., 2013; Urabe et al., 2013). Our study at the sandy beach of Llico monitored combined impacts of an earthquake-mediated uplift and the presence of armouring for up to five years. Field sampling carried out promptly after major disturbances, and constant monitoring of the affected sites long after the disturbance is gone are fundamental to increase the knowledge on the joint effects of large-scale natural phenomena and artificial defences on beach ecology. This knowledge is useful for implementing thorough coastal plans in a shoreline where armouring is expected to increase in the near future to cope with recurrent mega-earthquakes/tsunamis (Moreno et al., 2010; Ruegg et al., 2009; Vargas et al., 2011), and the exponential growth of human populations in coastal areas (Nordstrom, 2014).

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