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Combined impacts of natural and human disturbances on rocky shore communities

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ABSTRACT

Most ecosystems are subject to both natural and human disturbances that can combine to influence populations and assemblages in complex ways. Assessing the relative influences and combined impacts of natural and human disturbance is crucial for managing human uses of ecosystems against the backdrop of their natural variability. We evaluated the separate and combined influences of disturbance from storm waves and disturbance associated with human trampling of rocky shores by conducting an experiment mimicking controlled levels of trampling at sites with different wave exposures, and before and after a major storm event in central California, USA. Results show that trampling and storm waves affected the same taxa and have comparable and additive effects on rocky shore assemblages. Both disturbance types caused significant reduction in percent cover of mussels and erect macroalgae, and resulted in significant re-organization of assemblages associated with these habitat-forming taxa. A single extreme storm event caused similar percent cover losses of mussels and erect macroalgae as did 6–12 months of trampling. Contrary to a predicted synergistic effect of trampling and storm damage, we found that impacts from each disturbance combined additively. Mussel beds in wave-exposed sites are more vulnerable to trampling impacts than algal beds at protected sites. Mussels and erect macroalgae recovered within five years after trampling stopped. These results suggest that impacts from local human use can be reversed in relatively short time frames, and that cumulative impacts can be reduced by setting recreational carrying capacities more conservatively when ecosystems are already exposed to frequent and/or intense natural disturbances.

1. Introduction

Ecosystems may exhibit varying responses to human pressures in part depending on the natural disturbance regimes that shape their structure and dynamics. Ecosystems subject to frequent and/or intense natural disturbance may be less vulnerable to additional human disturbance, as natural disturbance may select for resistant species (Cote and Darling, 2010). However, natural and human disturbances may instead interact synergistically to enhance their individual effects (Breitburg et al., 1998; Folt et al., 1999; Crain et al., 2008). Thus, in contrast with the previous prediction, vulnerability to human impacts may be greater in the presence of intense natural disturbance. Finally, multiple disturbances may add in their impacts on affected ecosystems, resulting in high levels of cumulative impact (Halpern et al., 2008). Understanding how human and

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natural disturbance combine to affect communities and ecosystems is key to devising appropriate management and conservation strategies.

Marine ecosystems are subjected to substantial environmental variation and disturbance over a range of spatial and temporal scales. Among marine ecosystems, intertidal and coastal ecosystems exhibit extreme variation in physical conditions and stressors as they integrate a suite of land and sea-based processes and pressures (Raffaelli and Hawkins, 1996). This is the case for a variety of habitat types, from sandy beaches, to wetlands, macroalgal beds, shallow reefs, tidal flats and rocky shores. Intertidal ecosystems, in particular, are vulnerable to climate change and a variety of anthropogenic disturbances, including pollution, eutrophication, alteration of sedimentation and freshwater input, shoreline modification, introduced species, harvest of organisms, and trampling disturbance (Castilla, 1999, 2000; Crowe et al., 2000; Thompson et al., 2002; Halpern et al., 2007, 2008). These disturbances add to, or combine with natural stressors from exposure to air and high temperatures when the tide is out, and wave disturbance at high tide. Moreover, occasional extreme storms can result in considerable physical disturbance (Denny et al., 2009).

Recreational and educational uses of the shore have been on the rise for the last 50 years due, in part, to improved coastal access and rising coastal populations (Fletcher and Frid, 1996; Thompson et al., 2002) and these can have significant and sometimes lasting effects on populations and communities (e.g. Povey and Keough, 1991; Brosnan and Crumrine, 1994; Fletcher and Frid, 1996; Keough and Quinn, 1998; Schiel and Taylor, 1999). On rocky shores, human visitation and trampling affect species directly by dislodging or crushing individuals or weakening their attachment to the substrate, and indirectly by removing important members of interacting species groups (Brosnan and Crumrine, 1994). Schiel and Taylor (1999) showed experimentally along New Zealand rocky shores that the equivalent of ten people walking over an area of the mid-intertidal in a single event could result in reduction of the dominant alga by 25%; at 200 people passes, less than 10% of the alga's cover remained. When foliose algae canopies vulnerable to trampling are lost, understory algae may suffer subsequent declines due to desiccation and heat exposure and more resistant turf algae can develop in their place (Povey and Keough, 1991; Brosnan and Crumrine, 1994; Fletcher and Frid, 1996; Schiel and Taylor, 1999).

Mobile invertebrates tend to be more resistant to trampling effects, but shifts in abundance are often observed in experimental trampling treatments as some species decline while others, like grazing molluscs, increase in number as they invade new patches of unoccupied space (Povey and Keough, 1991; Keough and Quinn, 1998). Effects of trampling can be detected a year after the disturbance event (Schiel and Taylor, 1999) and recovery has been shown to vary with location, timing and intensity of impact, as well as habitat and species (Povey and Keough, 1991; Brosnan and Crumrine, 1994; Keough and Quinn, 1998; Schiel and Taylor, 1999; Araujo et al., 2012).

Though important insights emerge from prior work, there are many remaining open questions on how impacts from human recreational use of the shore compare, combine and interact with natural disturbances. Moreover, the questions of how natural and human disturbances interact, and how to manage human disturbance under varying regimes of natural disturbance apply to a suite of marine and terrestrial ecosystems.

In this study, we experimentally evaluated the separate and combined influences of physical disturbance from waves and storms, and human disturbance associated with trampling in intertidal temperate rocky reef ecosystems. First, we examine what, if any, are the human-visitation trampling effects on benthic community structure and taxonomic richness. Second, we examine the interaction between wave-related and trampling disturbance, and investigate whether co-occurring disturbances impact intertidal communities additively or multiplicatively – where combined impacts are lower or greater than the sum of individual effects (Breitburg et al., 1998; Folt et al., 1999; Crain et al., 2008; Cote and Darling, 2010). Rocky shore species have many adaptations to withstand natural stresses and disturbance, including an ability to reduce physical dislodgement and injury, which may also provide some inherent resistance to physical disturbances associated with trampling. We hypothesized that trampling effects would be less severe at wave-exposed sites experiencing greater and more frequent physical disturbance from waves than at sheltered sites. Furthermore, we examined whether occasional extreme storm events act independently or synergistically with trampling effects. We hypothesize an interactive effect due to weakening of sessile species' attachment to the rock by trampling, making trampled sites more vulnerable to extreme waves from storms. Finally, to examine management implications of trampling related to human visitation, we examined whether communities in wave-exposed or wave-protected areas recover more quickly from human-visitation trampling effects and asked what are sustainable human visitation levels in rocky intertidal habitats. Thus, we addressed the following questions: 1) Are trampling effects less severe at wave-exposed sites than at wave-protected sites? 2) Do the impacts of extreme waves from storms act independently or synergistically with any trampling impact? 3) What are the timeframes for recovery from trampling disturbance, and do these vary with physical exposure of the shore?

2. Materials and methods

2.1. Study site

The experiment was conducted at Soberanes Point in central California (36° 27′ N 121° 55.7′ W) (Appendix 1 in *Supplementary Materials*) between January 2002 to January 2008. Soberanes Point is open for public access. However, intertidal visitation is difficult due to steep cliffs that protect the area, allowing us to control experimental trampling levels to prescribed amounts. Two wave-exposed headlands and two wave-protected shores were randomly selected along the coastline, 300–500 m apart, with one experimental site (each approx. a 50-m stretch of the coastline) established on each of the exposed headlands and one on each of the protected shores (N = 2 sites per exposure level). Exposed and protected sites were alternated along the coastline (from north to south: protected – exposed – protected - exposed), and separated by 50–100 m stretches of rocky shore. Wave-exposed and wave-protected sites exhibited clear differences in their physical settings and associated benthic communities. Wave-protected shores had offshore rocks that attenuated incoming waves, whereas waves were unobstructed in wave-exposed headlands. Wave-exposed sites were dominated by mussels (the California mussel, *Mytilus californianus*) and articulated and encrusting coralline algae, whereas wave-protected sites were dominated by mixtures of macroalgae – typically the red algae, *Mastocarpus papillatus*, *Endocladia muricata*, and *Mazzaella* spp. Within each site, we haphazardly placed 16 1.0 m^2 permanent plots in the mid-high intertidal zone (1.5–1.8 m above MLLW), for a total of 64 permanent plots across the four sites. Each plot was marked with two screws drilled in the rocky substrate at opposite corners and numbered metal tags.

2.2. Trampling treatments

Plots within study sites were randomly assigned to one of four treatments, with four plots per treatment, simulating a range of human trampling disturbances: 0 (undisturbed control), 20, 100, or 400 steps per plot per month for a period of one year from 30 January 2002 to 30 January 2003. We used Analysis of Variance (ANOVA) to test for differences in the percent cover of dominant taxa (erect algae, algal turfs, encrusting algae, mussels, and anemones; see '*Plot sampling*' below) amongst experimental groups prior to the beginning of trampling treatments and found no significant differences among experimental groups or interactions of treatment groups with either site or exposure, indicating no allocation bias in the selection of plots across treatments (Table 1).

Treatment levels were based on trampling rates observed on nine occasions from July to November 2001 at frequently visited intertidal sites along the Point Pinos shore, Pacific Grove, CA, USA, 30 km north of Soberanes Point (Appendix 1, *Supplementary materials*). We estimated annual visitation rates and visitor step-rates, correcting for the amount of intertidal area accessible for visitation, which varied due to tides and daylight hours, to get an estimate of annual intertidal trampling intensity (steps m^{-2} yr^{-1}). Annual trampling intensity was converted to monthly trampling treatment levels (details in Appendix 2, *Supplementary materials*). We used the median estimated trampling intensity from Point Pinos of 20 steps m^{-2} mo^{-1} (range 4–45 steps m^{-2} mo^{-1}, mean = 17) as a trampling level representative of visitation of easily accessed shores of central California. Additional trampling levels of 100 and 400 steps m^{-2} mo^{-1} were selected to simulate possible future increase in coastal population or locally high visitation rates reported elsewhere and used in published trampling studies (e.g. Oregon, USA: Brosnan and Crumrine, 1994; Northeast England: Fletcher and Frid, 1996; Southern California: USA: Smith and Murray, 2005). Our preliminary observations indicated a lack of clear seasonality in human visitation of the shores in our study area, with visitation being influenced by weather conditions (being greater on sunny days regardless of season) and peaking on holiday weekends throughout the year (personal observations). Based on these observations, we chose to apply the trampling treatment at the same frequency throughout the year, once/month, to mimic the variable (e.g., concentration on sunny weekends) but seasonally homogeneous distribution of shore visitation in central California. Once a month, four of us, ranging 55–65 kg in body weight, visited the site and trampled the experimental plots with 20, 100, or 400 steps. Once assigned to one of these treatment levels, each plot received the same number of steps throughout.

Plots in all four study sites were surveyed once prior to trampling treatment in January 2002, 6- and 12-months after commencement of trampling (August 2002, January 2003), and 14 months after cessation of trampling (March 2004), referred to as "primary sampling dates" from here on. One wave-exposed and one wave-protected site (the two southernmost sites) were also surveyed five years after cessation of trampling, in January 2008 (the other two sites were no longer safe to access at the time of sampling) to test for long-term recovery dynamics.

2.3. Storm event

A major storm event starting on November 8, 2002, nine months after the beginning of trampling treatments, affected the study area. Analysis of hourly wave heights relative to mean sea level (WVHT + MSL, an indicator of the size of waves breaking on the study site) from NOAA National Data Buoy Center Station 46042 – Monterey, 23 nautical miles northwest of the study site, indicated that the November 2002 storm was the largest from January 2000 up to the end of sampling in January 2008, with a maximum WVHT + MSL of 9.4 m. Six other storms had offshore wave heights

Table 1
Analysis of variance testing for differences in percent cover of erect macroalgae, algal turfs, encrusting algae, mussels, and anemones from photographic sampling of permanent plots. Separate analyses were conducted on each of four sampling dates: before the beginning of the experiment, 6 and 12 months from the beginning of experimental trampling, and 14 months after cessation of trampling (short-term recovery). T = Treatment, E = Exposure, S = Site. $n = 4$. *: $P < 0.05$; **$P < 0.01$; ***: $P < 0.001$. F-ratios that are still significant after Bonferroni adjustment for multiple tests are reported in bold.

Source	DF	Erect macroalgae		Turf		Encrusting algae		Mussels		Anemones	
		MS	*F*	MS	*F*	MS	*F*	MS	*F*	MS	*F*
Before:											
T	3	38.8	0.4	84.4	0.6	306.4	1.1	205.0	1.1	0.1	0.02
E	1	27851.4	6.6	13645.2	1.8	2933.6	0.8	34894.2	42.8*	376.8	1.7
S(E)	2	4240.3	**19.1*****	7612.0	**49.6*****	3491.8	**30.6*****	815.3	**4.3***	223.7	**9.7*****
E × T	3	55.6	0.5	40.3	0.3	204.1	0.8	135.8	0.7	19.5	2.6
T × S(E)	6	103.1	0.5	144.6	0.9	272.4	2.4	188.5	1.0	7.5	0.3
Residual	48	222.0		153.6		114.1		188.6		23.1	
6 months:											
T	3	1932.3	5.8*	245.5	1.4	275.2	1.2	286.6	4.2	2.7	1.0
E	1	27,859.8	**193.6****	1459.4	3.6	989.5	1.2	30611.9	**99.9****	73.1	0.5
S(E)	2	143.9	0.6	402.3	**4.9***	839.4	**11.1*****	306.5	1.3	162.8	9.0
E × T	3	1324.1	4.0	128.0	0.8	75.1	0.3	69.8	1.0	4.1	1.6
T × S(E)	6	331.9	1.3	170.6	2.1	230.8	**3.1***	68.1	0.3	2.6	0.2
Residual	48	261.4		82.7		75.8		230.3		18.0	
12 months:											
T	3	184.5	8.2*	369.0	2.8	197.8	2.0	436.6	32.8***	2.1	0.4
E	1	3772.1	**213.6****	8625.8	2.5	1310.3	1.0	19,691.1	**131.9****	207.9	1.7
S(E)	2	17.6	0.3	3480.5	**31.4*****	1364.7	**13.8*****	149.3	0.9	125.9	**5.4****
E × T	3	132.0	5.9*	279.9	2.1	58.7	0.6	274.1	**20.6****	9.3	1.7
T × S(E)	6	22.5	0.3	132.4	1.2	98.4	1.0	13.3	0.1	5.5	0.2
Residual	48	68.3		111.0		99.1		157.7		23.5	
Short-term recovery (*14 months*):											
T	3	1065.8	3.6	219.6	1.3	299.4	2.0	350.0	19.0**	1.9	0.3
E	1	13,616.8	**3700.3*****	4455.6	2.2	1515.2	1.7	18,834.1	**150.4****	86.1	1.6
S(E)	2	3.7	0.02	2018.3	**11.1*****	909.0	**6.2****	125.2	0.8	54.6	4.3*
E × T	3	889.6	3.0	534.5	3.2	31.3	0.2	313.9	**17.1****	10.8	1.6
T × S(E)	6	296.2	1.4	165.7	0.9	152.9	1.1	18.4	0.1	6.8	0.5
Residual	48	215.5		181.2		145.7		156.6		12.8	

>8 m during this 8-year period, while in a majority of cases waves were <6 m (Appendix 3 and Suppl. Fig. S1 in *Supplementary Materials*).

We conducted two additional sampling events just prior to (on November 5) and after the extreme storm event (on November 19, approx.1 week after the cessation of the storm) to examine the immediate effects of storm waves on the rocky shore assemblages involved in the trampling experiment. Comparison of short-term impacts of an extreme storm event among different trampling levels provided an opportunity to determine whether dislodgement of algae and/or invertebrates by storm waves differed among plots with varying histories of human disturbance (associated with trampling treatments of 0–400 steps m^{-2} mo^{-1} applied during the 9 months preceding the storm).

2.4. Plot sampling

Plots were sampled using two non-destructive methods: photographic sampling and *in situ* visual surveys. On each of seven sampling dates (the primary sampling dates: prior to trampling, 6- and 12- months of trampling, 14-months of recovery; 5 years post trampling to assess long term recovery; and before and after the November 2002 storm), percent cover of dominant taxonomic groups was assessed through the use of photography. Plots were photographed using a Nikon Coolpix 995 digital camera mounted on a tripod and 1.0 m^2 frame and subsequently analyzed using the image analysis software Vidana v.1 (freely available at http://www.marinespatialecologylab.org/resources/vidana/) to calculate surface area of the following five species or species groups of sessile organisms: mussels (*Mytilus californianus*), anemones (*Anthopleura* spp.), encrusting algae (encrusting coralline and fleshy algae, i.e., the tetrasporophyte or "*Petrocelis*" phase of the red alga *Mastocarpus papillatus),* turfs (articulated coralline algae, and algal turfs, mainly the red alga *Endocladia muricata*), and erect macroalgae (including coarsely-branched algae, e.g., the red algae *Mastocarpus papillatus*, *Mazzaella affinis*, and the brown algae *Fucus* sp. and *Silvetia compressa*, and foliose algae, e.g., the red alga *Mazzaella flaccida*).

On each of the four primary sampling dates (prior to trampling, 6- and 12- months of trampling, 14-months of recovery), taxonomic richness (number of taxa) and community structure (identity and relative abundance of taxa) were also quantified within each permanent plot by subsampling with 3 randomly placed 20 × 20 cm quadrats through *in situ* visual surveys. *In situ* visual surveys were conducted because photographic sampling does not allow for a quantification of diversity, as many organisms are missed if found in crevices or below the algal canopy and several taxa cannot be confidently identified from photographs. Each 20 × 20 cm quadrat was carefully inspected and organisms were identified to the lowest possible taxonomic level (see Appendix 4 in *Supplementary Materials* for a full list). All mobile invertebrates >5 mm were counted, and the percent cover of all identifiable macroalgae and sessile invertebrates was estimated by assigning a score from 0 (absent) to 4 (100% cover) to each taxon within each of 25 sub-quadrats in which each quadrat was divided with a monofilament grid, then summing the scores across the 25 sub-quadrats. These finer scale data from plot subsampling were used in univariate analyses of taxonomic richness (repeated-measure ANOVA, see below) and in multivariate analyses (PERMANOVA and SIMPER analysis, see below) to examine community-level responses to trampling and wave disturbance.

2.5. Statistical analyses

Data were analyzed using ANOVA and multivariate analyses. For all ANOVA models, homogeneity of variances was examined with Cochran's tests and data were transformed when necessary using the arcsin (percent cover data) or square root (taxonomic richness) transformation. Data were fourth-root transformed for multivariate analyses.

ANOVA was used to analyze the combined effects of trampling and wave-exposure levels on variation in percent cover (from photographic sampling) and taxon richness (from *in situ* sampling) of invertebrates and algae over the four primary sampling dates. Response variables analyzed were percent cover of erect macroalgae, algal turfs, encrusting algae, mussels (*M. californianus*), and anemones (*Anthopleura* spp.), and taxonomic richness. Because plots were permanent and resampled photographically or *in situ* on each date, percent cover estimates from different dates are not independent. Temporal trends in percent cover differed among plots, violating the assumption of no Time × Plot interaction for repeated measure ANOVA designs (Underwood, 1997). Thus, time was not included as a factor in ANOVAs on percent cover and separate analyses were conducted for each sampling date (before trampling began, 6 months and 12 months into the experiment, and 14 months after cessation of trampling). ANOVA models included: Exposure (2 levels, exposed and protected shores, fixed), Treatment (4 levels, 0, 20, 100, 400 steps m^{-2} mo^{-1}, fixed, orthogonal to Exposure), and Site (2 levels, random, nested in Exposure), with $n = 4$ replicate plots per combination of factors. Impacts of trampling, physical exposure of the coastline, and their interaction on taxonomic richness were also examined using ANOVA. There were no significant effects of trampling on taxonomic richness and results are not reported here (see Appendix 5 in *Supplementary Materials*).

In order to examine community-level responses to trampling and wave disturbance, considering the full set of invertebrate and algal taxa quantified through *in situ* visual sampling, we employed a distance-based Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson, 2001). PERMANOVA models included: Time (4 levels, the four primary sampling dates, random), Exposure (2 levels, exposed and protected shores, fixed), Treatment (4 levels, 0, 20, 100, 400 steps m^{-2} mo^{-1}, fixed, orthogonal to Exposure), Site (2 levels, nested in Exposure, random), and Plot (4 levels, nested in the Treatment × Site interaction, random), with $n = 3$ replicate quadrats per combination of factors. We used taxon-level percent cover and mobile invertebrate count data from the quadrat subsampling protocol outlined above. Bray-Curtis dissimilarities calculated on fourth-root transformed data were used as the distance information to decrease the contribution of individual taxa to the multivariate patterns. The percent contribution of each taxon to the dissimilarity between undisturbed plots and plots subject to experimental trampling was calculated by SIMPER analysis (Clarke, 1993). All multivariate analyses were performed using the program PRIMER v6 (Clarke and Gorley, 2006), including the add-on package PERMANOVA+ (Anderson and Gorley, 2008).

The effects of the extreme storm of November 2002 on plots that had a different trampling history were addressed using paired sample *t*-tests and ANOVAs. We first assessed whether the storm event had caused a significant decrease in % cover of the dominant taxa quantified from photographs using *t*-tests to compare cover before and after the storm. Separate tests were conducted for data from exposed and protected sites because % cover values varied greatly with exposure of the coastline (i.e. macroalgae dominate protected sites, whereas mussels are dominant space occupiers at exposed sites). We then used ANOVA, for the taxonomic groups where *t*-tests revealed that a significant cover reduction had occurred, to examine whether the impact of the storm, measured as the relative percent change in cover of a taxonomic group within plots (100 * [% cover before − % cover after]/[% cover before]), varied among trampling levels or an interaction between trampling levels and wave exposure. Treatment and Exposure were fixed factors, and Site was random and nested in Exposure.

Time frames for recovery following the cessation of experimental trampling were addressed by examining control and treatment plots 14 months (short-term recovery) and 5 years (long-term recovery) post trampling treatments. To assess whether differences among trampling levels in the percent cover of the dominant functional groups (mussels and erect algae) persisted 14 months after trampling ceased, *post hoc* pair-wise comparisons were conducted between trampling levels (SNK tests comparing, in pairs, mean percent cover for each trampling level after the ANOVA described above). We assessed long-term recovery by examining differences in erect macroalgae and mussel cover across control and trampling treatments at the single protected and exposed sites sampled five years post-trampling. Because no site replication within exposure was available for this sampling date, we conducted ANOVAs with Treatment (4 levels, fixed) and Exposure (2 levels, fixed), separately for percent cover of mussels and erect macroalgae. In this analysis, the factor exposure is unreplicated because only one site was sampled within each exposure level (the second site was no longer accessible). Therefore, while we kept the term exposure for comparability with previous analyses, results are limited to this site and cannot be generalized to the effects of wave exposure on long-term recovery. We chose to assess recovery by comparing percent cover between treatments and controls, rather than relative to pre-trampling conditions, because there is no reason to assume that abundances will recover to initial conditions. Intervening disturbances and other sources of variability, such as variation in recruitment and growth, would likely contribute to change baseline abundances, i.e., abundances in the absence of trampling disturbance. By using controls as baselines for recovery, we accounted for such natural shifts in our assessment of recovery.

3. Results

3.1. Trampling effects and interactions with wave disturbance

Erect macroalgae and mussels were negatively affected by trampling (Table 1; Fig. 1). Other algal and invertebrate taxa quantified through photographic sampling - encrusting algae, algal turfs, and the anemone *Anthopleura* spp. - did not show significant responses to experimental trampling (Table 1) and are not reported in figures. Both for erect macroalgae and mussels, effects became evident after experimental disturbance was maintained for several months. After 6 months of experimental trampling, there was a trend for reduced macroalgal cover in the trampled plots (effect of treatment: $p < 0.05$), but this trend was not statistically significant after Bonferroni correction for multiple tests (Table 1). After 12 months, trampling had significant effects both on mussels and erect macroalgae, but patterns differed between wave-exposed and wave-protected sites (Table 1 and Fig. 1).

We found evidence that trampling reduced mussel cover at wave-exposed sites even at low intensities (20 steps m^{-2} mo^{-1}), comparable to the current levels of trampling estimated for accessible shores in our study area (Fig. 1a, and SNK post-hoc comparisons). Trampling at medium intensity (100 steps m^{-2} mo^{-1}) caused a similar reduction in mussel cover than the low trampling levels, whereas trampling at the highest intensity (400 steps m^{-2} mo^{-1}) had significantly greater negative impacts compared to the other treatments (SNKs). In contrast, trampling effects on mussels were not significant at the protected sites (SNKs). Erect macroalgae were not significantly affected by low trampling intensities but were significantly reduced at medium and high trampling levels (100 and 400 steps m^{-2} mo^{-1}) (Fig. 1d, and SNKs). Cover reduction of erect macroalgae in trampled plots tended to be greater at protected than exposed sites, but the interaction was not significant after Bonferroni correction for multiple testing (Table 1).

Trampling had no significant effects on taxonomic richness throughout the study (Appendix 5 in *Supplementary Materials*). In contrast, trampling had significant effects on the relative abundance of different taxa. Analysis of community-wide percent cover and count data from the *in situ* subsampling of plots indicates that experimental trampling had a significant effect on the structure of benthic assemblages (significant Time × Treatment interaction; Table 2). Trampling affected community structure similarly across wave-exposure levels. Community structure, in fact, differed between exposed and protected sites (significant exposure effect) but exposure did not interact with any of the factors (Table 2). Post hoc multivariate pair-wise comparisons (permutation tests) amongst trampling levels indicate that effects become evident after 12 months of trampling for the 100 and 400 steps m^{-2} mo^{-1} treatments compared to controls, and that impacts persisted for at least 14 months after trampling stopped.

SIMPER analysis on data from *in situ* subsampling of plots showed that trampling had opposite effects on several algal and invertebrate taxa, with some taxa decreasing in abundance through the experiment and others that increased (Table 3, and Appendix 6 in *Supplementary Materials*). Community differences among treatments were associated with small changes in many taxa rather than major changes in a few dominant taxa (Table 3, and Appendix 6 in *Supplementary Materials*). Corroborating results from photographic sampling of whole plots (see above), medium and high trampling intensity (100 and 400 steps m^{-2} mo^{-1}) tended to decrease percent cover of mussels and erect foliose algae (e.g., *Mazzaella flaccida*). Percent cover of encrusting and articulated corallines was also decreased by 12 months of trampling, and these effects persisted for 14 months after trampling ceased. In contrast, several invertebrate taxa increased in abundance as a result of community reorganization after experimental trampling. The gooseneck barnacle, *Pollicipes polymerus,* was negatively affected by trampling, but 14 months after disturbance ceased its abundance in trampled plots was greater than in controls, possibly through competitive release from mussels. Similarly, percent cover by the acorn barnacle, *Chthamalus* spp., and abundances of limpets (*Lottia* spp.) were greater in trampled plots than control plots 14 months into recovery (Table 3).

3.2. Short-term effects of a large storm event and the interaction between anthropogenic and natural disturbance

The large storm event in November 2002, after nine months of experimental trampling, had significant negative effects on the same dominant taxa sensitive to trampling, mussels at the exposed sites ($t = 2.2$, $df = 31$, $p = 0.03$) and erect macroalgae at the protected sites ($t = 4.0$, $df = 31$, $p = 0.0003$) (Fig. 2). Non significant ($t = 1.9$, $df = 31$, $p = 0.06$ for mussels, $t = 0.3$, $df = 31$, $p = 0.8$ for erect macroalgae) cover reductions occurred at wave exposure levels where these taxa have naturally low abundances (i.e. at protected sites for mussels, and at exposed sites for erect macroalgae; Fig. 2). Taxa that were not affected by trampling (algal turfs, encrusting algae, and anemones) were also not significantly impacted by the storm at both exposed and protected sites (*t*-tests: $p = 0.06–0.4$).

The large storm resulted in a 26% proportional reduction (SE = 2.6%) of mussel cover at exposed sites where mussels are prevalent, and a smaller (12% + 4.2SE) proportional cover loss at protected sites (Fig. 2). A 42% loss (SE = 4.1%) in erect macroalgae cover occurred at protected sites where macroalgae are prevalent.

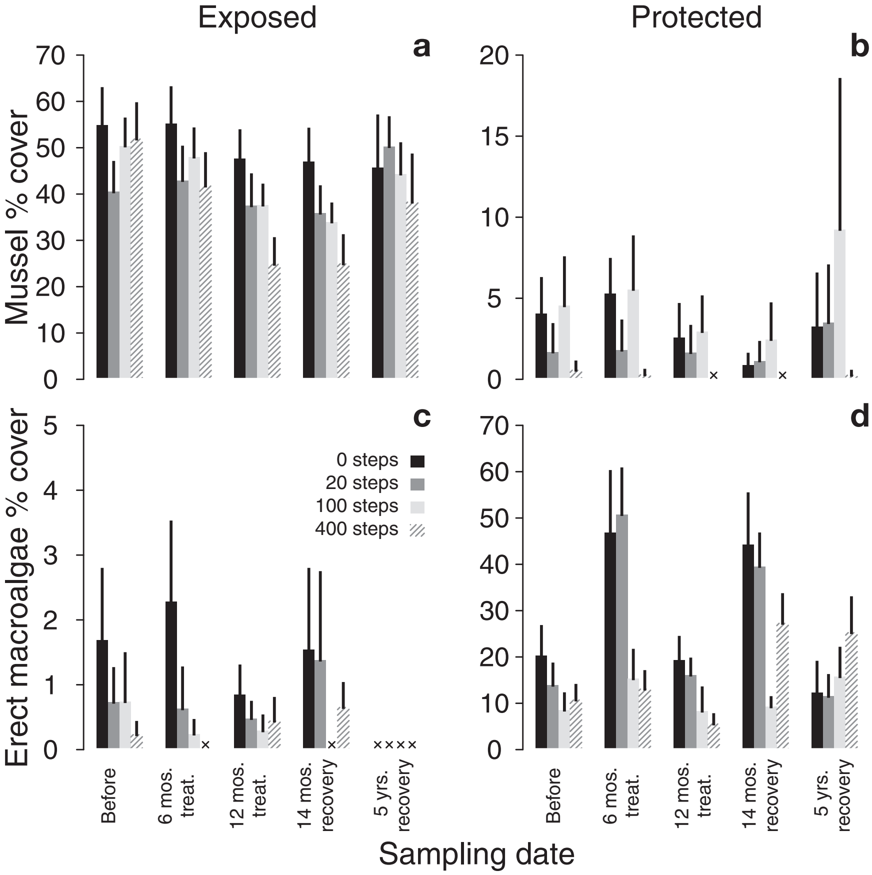

Fig. 1. Temporal trends in mean percent cover (±1 SE) of mussels (a, b) and erect macroalgae (c, d) from experimental plots at wave exposed (a, c) and wave-protected (b, d) sites. Percent cover was quantified before the beginning of trampling, after 6 and 12 months of trampling, and 14 months at 2 exposed and 2 protected sites, and 5 years after cessation of experimental disturbance of plots at one of the exposed and one of the protected sites. $n = 8$ for each exposure-time-treatment combination, except for the five year recovery date where $n = 4$ (only one exposed and one recovery site was sampled). " × " indicates a value < 0.1%.

Table 2
Multivariate analysis (PERMANOVA) based on fourth root transformed Bray-Curtis dissimilarities of individual taxon percent cover (sessile organisms) or counts (mobile invertebrates >5 mm). Tests were performed using 4999 permutations. Tm = Time, T = Treatment, E = Exposure, S = Site, P = Plot. *: $P < 0.05$; **$P < 0.01$; ***: $P < 0.001$.

Source of variation	DF	MS	*F*
Tm	3	19,541	4.7979**
T	3	8992.8	1.5586
E	1	3.1181E5	4.3144*
S(E)	2	72,273	11.978**
Tm × T	9	2319	1.406*
Tm × E	3	7559.7	1.8561
E × T	3	7474.1	1.2954
Tm × S(E)	6	4074	2.7595**
T × S(E)	6	5773	0.9553
Tm × T × E	9	1697.8	1.0294
P (T × S(E))	48	6101.7	7.034**
T × Tm × S(E)	18	1649.5	1.1173
Tm × P (T × S(E))	140	1476.4	1.7019**
Residual	504	867.47	
Total	755		

Proportional cover loss of erect macroalgae at exposed sites was on average 8% (SE = 4.5%) (Fig. 2).

Table 3
Results of SIMPER analyses showing taxa driving dissimilarity (see Table 2) in assemblage structure between undisturbed plots and plots subject to trampling (100 or 400 steps $m^{-2\ -1}$) for 12 months, and 14 months after trampling stopped. Percent contributions to dissimilarity between pairs of treatment levels are reported for each of the taxa. Arrows indicate whether taxa abundances decreased or increased with trampling. Taxa cumulatively accounting for 50% of overall dissimilarity, when ranked from highest to lowest contribution, are reported. Results for the full list of taxa are reported in Appendix 5 in *Supplementary Materials*.

Species	Trampling		Short-term recovery	
	12 mo	12 mo	14 mo	14 mo
	0 vs. 100	0 vs. 400	0 vs. 100	0 vs. 400
Mytilus californianus	5.78↘	6.24↘	6.70↘	6.74↘
Articulated corallines	5.05↘	5.62↘	6.19↘	5.86↘
Lottia scabra	5.10↗	5.40↗	5.83↗	5.54↗
Juvenile limpets	4.97↗	4.35↗	1.90↘	2.00↘
Petrocelis phase	4.95↗	5.76↗	5.11↘	5.27↘
Endocladia muricata	4.79↗	4.14↘	5.67↗	4.38↘
Mazzaella flaccida	4.33↘	4.34↘	4.44↘	4.85↘
Lottia digitalis	4.30↗	4.61↗	4.71↗	4.28↗
Encrusting corallines	3.85↘	3.90↘	4.52↘	4.75↘
Tetraclita rubescens	3.54↘	3.76↗	4.05↗	3.85↗
Pollicipes polymerus	3.18↘	3.36↘	3.57↗	3.41↗
Chtamalus spp.	2.84↗	3.23↗	3.50↗	3.47↗

The extreme storm and trampling had additive effects, not synergistic interactions as we had hypothesized. Storm-related cover losses of erect macroalgae and mussels did not vary significantly amongst plots exposed to different trampling intensities prior to the storm (no effect of trampling, and no trampling × exposure interaction; Table 4). These results suggest that storm impacts acted independently of trampling effects,

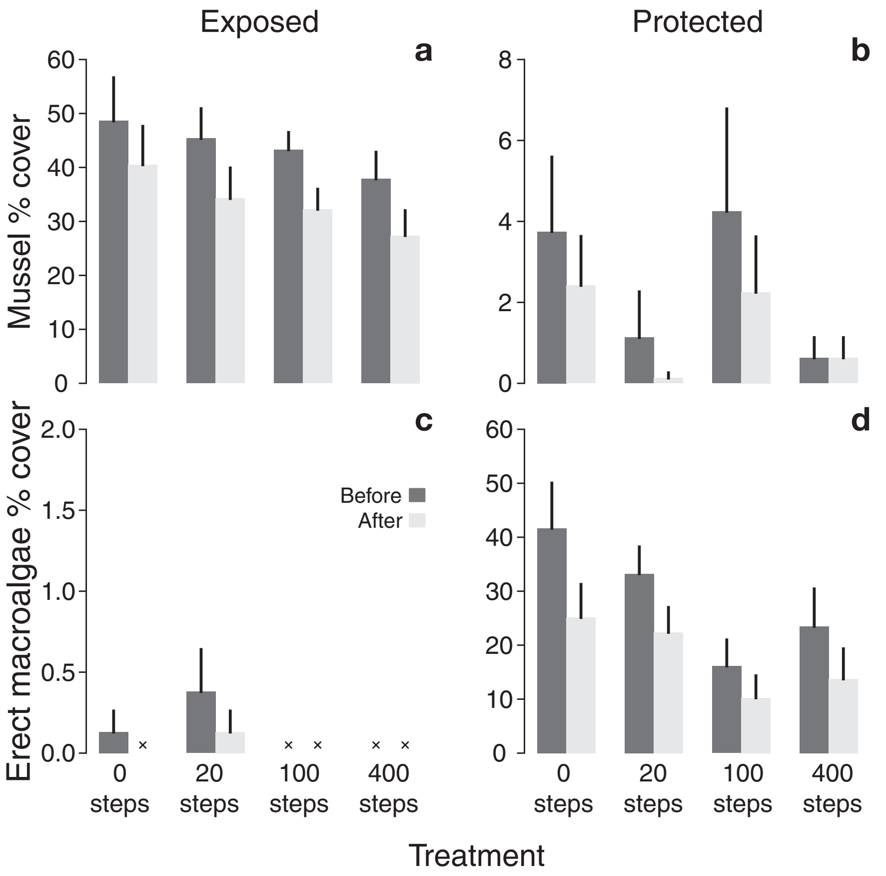

Fig. 2. Mean percent cover (±1 SE) of mussels (a,b) and erect macroalgae (c,d) from experimental plots at wave-exposed (a,c) and wave-protected (b,d) sites before and after an extreme storm event 9 months into trampling treatments. $n = 8$ for each exposure-time-treatment combination. " × " indicates a value < 0.1%.

Table 4
Analysis of variance testing for differences in relative cover loss {[(% cover before − % cover after)/% cover before] × 100} of mussels and erect macroalgae after a storm event. T = treatment, E = exposure, S = Site. $n = 4$. $^*P < 0.05$; $^{**}P < 0.01$.

Source	DF	Mussels		Erect macroalgae	
		MS	*F*	MS	*F*
T	3	178.7	0.8	381.9	0.7
E	1	5000.4	16.3	18,632.3	52.3*
S(E)	2	307.0	1.1	356.6	0.6
E × T	3	552.1	2.6	917.4	1.6
T × S(E)	6	211.6	2.6	583.4	1.0
Residual	48	283.1		617.3	

causing similar damage across control plots and plots under varying degrees of trampling.

3.3. *Recovery after trampling*

Plots showed little recovery 14 months after trampling ceased (Table 1 and Fig. 1). At this stage, mussel cover showed no trends towards recovery (Table 1 and Fig. 1), and percent cover of erect macroalgae in medium and high intensity trampling treatments was also still low, though statistically indistinguishable from undisturbed controls (SNK tests). Differences in community structure between control and trampled plots that were revealed after 12 months of trampling through SIMPER analysis (Table 3) persisted 14 months after trampling ceased. Thus, there is no evidence for recovery in community structure for at least 14 months post-trampling.

Five years after cessation of trampling, in Jan-2008, percent cover of both mussels (Treatment: $F_{3,24} = 0.5$, p = 0.70; Exposure × Treatment: $F_{3,24} = 0.25$, $p = 0.85$) and erect macroalgae (Treatment: $F_{3,24} = 1.0$, p = 0.41; Exposure × Treatment: $F_{3,24} = 1.0$, $p = 0.40$) were statistically indistinguishable amongst treatment and control plots at both the single exposed and protected monitored sites, suggesting full recovery of these dominant taxa (Fig. 1).

4. Discussion

Our evaluation of the separate and combined influences of natural disturbance from waves and human disturbance associated with trampling on rocky-shore assemblages yielded several new insights. First, both types of disturbance caused significant reduction in abundances of the same intertidal habitat–forming taxa (mussels and erect macroalgae), indicating the same types of organisms are vulnerable to both trampling and wave-related physical disturbances. In contrast, other intertidal invertebrates (e.g. anemones) were not affected significantly by these disturbances, and some taxa even increased following experimental trampling (e.g. barnacles and limpets), possibly through competitive release from negatively affected groups (e.g. Povey and Keough, 1991; Keough and Quinn, 1998). In general, some taxa appear to be vulnerable to multiple disturbances, and thus be reduced or removed from high cumulative impact. Moreover, disturbances had direct and indirect effects, causing both a reduction of vulnerable taxa and a shift in the structure of the whole assemblages. Second, disturbance from storm waves and human trampling have comparable and additive effects on rocky intertidal communities. A single extreme storm event caused reduction of mussel and erect macroalgal cover (10–42% cover loss, on average, for different taxa and wave exposure) comparable to the disturbances associated with 6–12 months of repeated trampling (between 7 and 33% cover loss in medium to high intensity trampling treatments relative to control plots). Third, trampling impacts on sensitive taxa persisted more than a year after the cessation of treatments, but full recovery occurred over relatively short time frames, within five years.

These results contribute to the existing body of literature on how physical disturbance shapes marine populations and communities (Levin and Paine, 1974; Denny, 1987) and to our still limited understanding of the combined impacts and interactions of multiple stressors (Folt et al., 1999; Crain et al., 2008). Local management of human disturbance can reduce cumulative impacts on natural ecosystems (Halpern et al., 2007), and knowledge of what types of human uses and associated stressors interact synergistically with other anthropogenic or natural disturbances can direct to the most effective actions (Strain et al., 2014). Thus, understanding how different sources of disturbance may combine and interact has both basic and applied relevance. In practice, our results help set a recreational carrying capacity for shore visitation, and suggest that different visitation levels might be set depending on the characteristics of natural assemblages present, as influenced by physical exposure of the coastline.

Our hypotheses that wave-exposed assemblages would be more resistant to human trampling, but that extreme storm waves would act synergistically with trampling to dislodge sessile organisms were not supported. Contrary to our expectation that organisms on exposed shores subject to frequent wave disturbance should be more resistant to additional mechanical disturbance, mussels on exposed headlands exhibited the greatest vulnerability to trampling disturbance among all taxa we monitored, with significant reduction of percent cover even at the lowest trampling levels applied during the experiment. Proportional cover loss of mussels caused by trampling was also greater at wave-exposed than wave-protected shores. The high vulnerability to trampling in organisms already subject to high levels of physical disturbance from waves may be explained by the different characteristics of the two disturbances. Waves pull on organisms attached to rocky shores, exerting lift forces that organisms differentially withstand depending on their morphological and material property characteristics (Denny, 1987; Denny et al., 2009). In contrast, trampling results in direct pressure being exerted on the organisms. Thus, the thickness and strength of mussel shells may determine their susceptibility to being crushed as people step on them. More generally, disturbances affecting individuals and populations through different mechanisms, as may be the case here, may result in additive effects. In contrast, non-additive (e.g. synergistic) effects may more commonly occur when disturbances share a common ‘mode of action’ (Breitburg et al., 1998).

Previous authors hypothesized synergism between wave disturbance and trampling of rocky shore assemblages, whereby trampling may damage macroalgal thalli and mussel byssal threads rendering them more susceptible to breakage during storms (e.g. Brosnan and Crumrine, 1994). Our results instead show that extreme storm waves caused similar reduction of macroalgal and mussel cover in plots that were subjected to different trampling levels during the nine months preceding the storm. Sustained trampling did not increase vulnerability of these taxa to storm impacts: both trampling and waves impacted the same taxa and reduced their abundance through their combined effects, but impacts were additive not interactive, i.e. the presence of one disturbance did not enhance the impact of the other.

The identity and functional role of affected taxa is crucial in determining whether impacts remain limited to those taxa or have cascading effects on other taxa. Both mussels and erect macroalgae can be considered habitat-forming or foundation species in that they create three-dimensional space and microhabitats and alter physical conditions for a suite of other species. Natural and human impacts on foundation species have the potential to affect whole communities and species interactions (Underwood, 1999; Schiel, 2006; Micheli et al., 2008a). Loss of foundation species is expected to result in decreased diversity and changes in community structure. Our results support this hypothesis in rocky shore communities: we documented significant differences in assemblage structure, though not in taxonomic richness, following 12 months of experimental trampling and up to 14 months after its cessation. Depending on the taxa, we found both negative and positive responses to experimental disturbance, indicating that community level responses are complex and likely result from both direct and indirect effects of disturbance (e.g., Povey and Keough, 1991; Brosnan and Crumrine, 1994; Fletcher and Frid, 1996; Castilla, 1999, 2000; Schiel and Taylor, 1999; Schiel and Lilley, 2011).

Recovery of mussels and macroalgae from sustained trampling, in the absence of additional human disturbance, occurred over time scales of a few years (>1 and < 5 years). Previous studies addressing longterm recovery from disturbance also documented full recovery of canopy algae within similar time frames, although alteration of community composition persisted up to eight years (Schiel and Lilley, 2011). Rates of recovery of populations and assemblages following disturbance depend on the life history characteristics of species, e.g. reproductive output, age at maturity, and life span; however, other factors and processes, including persistent disturbance regimes, altered species interactions, decreased genetic diversity and increased susceptibility to disease may slow down or prevent recovery (Hutchings and Reynolds, 2004; Micheli et al., 2008b). The short time frame (<5 years) for recovery indicates that impacts of trampling on rocky intertidal assemblages may be reversed relatively quickly through protection.

To our knowledge, this is the first study to examine how the impacts of trampling may vary with physical exposure of the shore. On wave-exposed rocky points or headlands, even the relatively low current levels of recreational use we documented in our study area (20 steps m^{-2} per month, or 1–40 visitors per day within ~100-m stretches of the coastline) can, over 6–12 months, cause mussel cover reductions comparable to those of an extreme storm event. Extreme storm events have been increasing in the past 40 years (Wang and Swail, 2001; Menéndez et al., 2008), and such trends may increase in the next decades under climate change scenarios (IPCC, 2007). Because storm wave impacts and human trampling add up in their impacts on mussel beds, which also appear to be negatively affected by lower levels of trampling than erect macroalgae and exhibit slow recovery, setting a precautionarily low recreational carrying capacity (e.g. Dixon et al., 1993) is recommended to reduce cumulative impacts to wave-exposed shores. This could be achieved by establishing no-access reserves on exposed rocky points and/or by directing people away from these sites, e.g., via marked ‘itineraries’ or trails.

Increasing pressure on natural ecosystems from human use makes it imperative that impacts are understood and managed accounting for the natural disturbances that simultaneously shape ecosystems. Investigations of how human impacts combine and interact with co-occurring disturbances and natural variation in environmental conditions contribute to our understanding of the multiple processes that shape ecosystems and to the practical management of coastal areas in the face of increasing pressure from multiple uses.

Author contributions

FM, KH, CK, SS and GO conceived and designed the experiments. All authors conducted fieldwork. FM, SF, JT, SS and GO analyzed the data. FM wrote a majority of the manuscript; all other authors contributed to the discussion of results and to the writing of the manuscript.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.ocecoaman.2016.03.014.

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