Disturbance type and intensity combine to affect resilience of an intertidal community

Henry F. Wootton*, Michael J. Keough

School of BioSciences, University of Melbourne, Victoria 3010, Australia

ABSTRACT: Differing disturbance agents may vary in the local spatial pattern of their effects, which may in turn influence the resilience of communities, particularly if ecologically important species are affected variably. Here, we investigated the effects of disturbance type on the ecologically important intertidal alga *Hormosira banksii* and its understory community at 2 sites in southeastern Australia. Replicate 60 × 40 cm plots containing dense *H. banksii* canopies were disturbed with 11 treatments that varied the severity and type of the disturbance, and included 0 and 100% removal controls, plus a factorial array of 3 disturbance types (cropped, clumped and haphazard removals) crossed with 3 severities of removal (25, 50, and 75% of biomass removed). *H. banksii* cover, sediment loads and understory community were monitored 7 times over 25 mo. *H. banksii* recovery (and thus, resilience) was relatively high and was consistent across sites, but both the type and severity of disturbance had effects. Cropped treatments recovered quickly compared to clumped and haphazard treatments, which took up to 6 mo longer to recover as the severity of disturbance increased. Clumped and haphazard removals also produced varied responses in some understory species. This experiment demonstrates that disturbance type, as well as the more commonly explored disturbance severity, may be an important component of the disturbance–resilience relationship.

KEY WORDS: Recovery · Rocky reefs · Canopy · Intertidal · Ecosystem engineer · *Hormosira banksii*

INTRODUCTION

Natural and anthropogenic disturbance agents both have pervasive effects on marine communities. These effects differ with the agent producing the disturbance (any physical process that causes damage or removes biomass), which can affect the damage caused in areal extent, intensity/severity, and many other ways (Sousa 1984, 1985, 2001, Connell & Keough 1985, Hobbs & Huenneke 1992). This in turn can hamper comparisons between types of disturbance.

Although it is recognized that a range of factors may affect a community's reaction to disturbance (and thus, its resilience, sensu Pimm 1984), most empirical evidence comes from studies that varied a single factor (a pattern first identified by Pickett & White 1985), most often the areal extent or severity.

A more complex view of disturbances has steadily emerged. One important aspect of this complexity has been the acknowledgment that multiple agents of disturbance may be acting, particularly around urbanised coasts. When these agents occur simultaneously, there could be synergies such that each agent magnifies the impact of the other, and there is considerable interest in these synergies (e.g. Hughes et al. 2003, Crain et al. 2008), along with evidence of their ecological complexity and importance (e.g. Falkenberg et al. 2012, 2013, Carnell & Keough 2014).

Even if no synergies occur, or disturbances are not simultaneous, disturbance agents vary in their mode of action, so resilience, in particular recovery rate and

capacity, could depend not only on the extent of damage, but also on the agent producing it. For example, Spear & Storfer (2010) examined forest landscapes disturbed by both harvesting and naturally occurring fires, and found that gene flow in Rocky Mountain tailed frogs was greater in harvested areas, due to higher habitat connectivity. Ruesink et al. (2012) compared the effects of varied types of disturbance on *Zostera marina* seagrass meadows on the US West coast. They found that cutting seagrass areas slowed growth, reduced size and clonal branching while thinning seagrass (by removing whole shoots) increased branching rate of remaining shoots. Whomersley et al. (2010) applied organic enrichment, burial and raking disturbances to intertidal mud flats, and caused varied responses in macrofaunal communities across 2 sites in the United Kingdom.

In many marine environments, habitat-forming species, often labeled ecosystem engineers or foundational species (Dayton 1972, Jones et al. 1994), are important. These species may include reef-building corals, kelps, seagrasses, algae, and mangroves, and where these species are present, overall resilience may well depend on responses of these habitat-formers to disturbance. Disturbance of foundational species may also play a role in transitions to alternative community states, overcoming the resilience results in a transition to a very different, persistent community (Holling 1973, Filbee-Dexter & Scheibling 2014).

Here, we focus on one well-studied habitat-forming species, and ask how its resilience varies with different severities and kinds of disturbance. In south-eastern Australia, the fucalean alga *Hormosira banksii* (hereafter called '*Hormosira*') often forms monotypic stands on mid-tidal rock platforms (Keough & Quinn 1998). Individuals consist of many fronds of fleshy, water-filled receptacles and attach to the substratum via a small, disc-like holdfast (Womersley 1987). Fronds can obtain ca. 40 cm in length and biomass can reach up to 7 kg m^{-2} (Schiel 2006). High densities of *Hormosira* create a canopy that provides physical habitat and protection for many understory species, and canopies have been shown to correlate with higher understory diversity (Schiel 2011) and richness (Schiel 2006). This diversity includes a complex array of ephemeral and longer-lived algae, grazing and carnivorous gastropods, limpets, polychaetes, as well as much smaller and less studied species such as amphipods and isopods. Understory species vary throughout *Hormosira*'s range (e.g. compare Underwood 1998 with Lilley & Schiel 2006), but communities are broadly similar. Severe disturbances are also thought to cause a shift from *Hormosira* habitat to open, bare areas with scarce macroalgae and abundant herbivorous gastropods (Keough & Quinn 1998, Underwood 1998).

Hormosira habitats experience many forms of perturbation, including natural disturbances such as wave or storm damage (Underwood 1998, Schiel 2011), 'burnoff' (Lilley & Schiel 2006), sediment abrasion or burial (Schiel et al. 2006) and anthropogenic changes, which can result from sewage discharge (Brown et al. 1990) and trampling (Povey & Keough 1991, Keough & Quinn 1998, Schiel & Taylor 1999, Minchinton & Fels 2013). Natural rates of disturbance probably vary between regions (see Schiel 2011 for a long-term study showing varied effects, and responses to, storm disturbances), but some dieback from burnoff seems to happen every year (with subsequent regrowth in the cooler months; Keough & Quinn 1998), as well as rarer, larger disturbance events (Underwood 1998, 1999, Schiel 2011). Overall, these disturbances may vary in their effect on *Hormosira* canopies because they manipulate the canopy in different ways. Povey & Keough (1991) showed that increasing intensities of trampling removed increasing percentages of canopy biomass from individual plants, which opened discrete gaps. High UV stress and temperatures are thought to cause burnoff (Lilley & Schiel 2006), which seems to affect the canopy in layers, and storms are capable of inflicting severe damage by removing whole fronds, plants or stands from platforms (Underwood 1998). However, as of yet, little is known about the relative effects of different disturbance types in this system.

In this study, we examined how different types and severities of disturbance affect the recovery of *Hormosira* canopies, their associated understory communities and sediment levels over time. These factors may cause the *Hormosira* canopy to recover at different rates (or not at all), and they could act synergistically. Canopy removal might also affect abundances of understory invertebrates and algae, and one might expect abundances to change as canopy cover recovers, due to a reduction in the protection, or habitat quality, that the canopy affords its understory community.

We tested these ideas by experimentally disturbing *Hormosira* canopies at several intensities (by removing different proportions of the canopy) and 3 patterns (clumped, cropped and haphazard) in a factorial array, and then measuring the responses of *Hormosira* and associated species over 2 yr. We also determined the spatial consistency of our conclusions, by doing the experiment at 2 similar sites ~10 km apart.

MATERIALS AND METHODS

Study sites

All work was done on the ocean coast of central Victoria, in south-eastern Australia. This section of coastline faces S to SW, and is moderately exposed. 13th Beach reef (38.288386° S, 144.476115° E) is a calcarenite platform, ~500 m wide and 100 m from its shoreward edge to the seaward edge. Jan Juc reef (38.356731° S, 144.296493° E) is also a limestone platform, ~300 m wide and 50 m from shoreward edge to subtidal zone. It is ca. 9.5 km due south-west of the 13th Beach site. Both platforms are exposed at midtide, show only small changes in vertical elevation, and are covered in a dense mat of *Hormosira banksii*, whose initial cover ranged from 83 to 100% within experimental plots (usually 95–100%). These sites are typical of *Hormosira*-dominated reefs in south-eastern Australia, but they differ from each other. 13th Beach contains a dense *Hormosira* canopy interspersed with areas of limpet-dominated bare substrate whereas Jan Juc has a more continuous canopy. Understory invertebrate and algal species richness and abundance were lower at Jan Juc than at 13th Beach.

Experimental design

We varied the severity of the disturbance, by removing 0, 25, 50, 75 and 100% of the canopy from 60 × 40 cm plots, and, where there was partial removal of *Hormosira*, we removed biomass in 3 different ways: clumped, haphazard and cropped removals. Cropped removals were designed to mimic a burnoff event, and clumped and haphazard removals were designed to mimic the effects of trampling or storm-disturbance. Severity treatments were designed to assess these 'disturbance types' across a gradient of disturbance. This provided 11 treatments, the 0 and 100% severities (which we define as treatment controls), plus a 3 × 3 factorial array of 3 severities and 3 types of biomass removal.

Individual plants are hard to distinguish due to sediment cover and high density of *Hormosira* (Schiel & Lilley 2007). Therefore, removal of a percentage area of *Hormosira* canopy was chosen as the treatment technique, rather than removal of a percentage of individual plants. The clumped and haphazard removals were completed using a 60 × 40 cm quadrat strung into twenty-four 10 × 10 cm squares. Different removal levels were achieved by removing 6 (25%), 12 (50%) and 18 (75%) squares in a clumped or haphazard manner. Removal of 'squares' from the center of plots created a 'clumped' treatment, and 'squares' were randomly chosen and removed in 'haphazard' plots. Fronds were cut with scissors at their base, while leaving holdfasts intact to minimise collateral damage to the understory and substratum. Cropped treatments were completed by cropping all fronds (again using scissors) within the plots to a percentage of a predetermined average length (10 cm, authors' unpubl. data). For example, all fronds within the plot were reduced to 2.5 cm in the 75% crop treatment. This cropping method ensured a consistent and comparable level of biomass removal between the different treatment types and was designed to represent a disturbance event that only partially removes fronds (as opposed to whole fronds or individual plants) such as a 'burnoff' (Lilley & Schiel 2006) or anthropogenic trampling (Povey & Keough 1991, Schiel & Taylor 1999). The 100% removal treatment involved removing all fronds within the plot (again at their base) and the control plots were left unmanipulated.

At each site, there were 4 replicates of each treatment, arranged in a randomized blocks design, with the blocks separated by >30 m. These blocks ran along platforms parallel to the shoreline, at similar heights to each other, to ensure uniform exposure times. Within each block, plots were marked using plastic wall anchors at the corners, and spaced 1 m apart.

Sites were set up in January 2010 and were sampled a total of 7 times over 25 mo. *Hormosira* cover was surveyed prior to and immediately after disturbance and after 1, 2, 3, 5, 9 and 25 mo, with the final survey designed to assess final recovery. Sediment, rock and algal variables were measured 5 times (at 1, 3, 5, 9 and 25 mo post-manipulation), while mobile animals were sampled 6 times (including pre-treatment, as we believe treatment methods could have impacted abundance, and at 1, 3, 5, 9 and 25 mo post-manipulation). Lilley & Schiel (2006) found that the *Hormosira* canopy took 24 mo to recover from complete removal to control levels at Kaikoura in New Zealand. Another site (Moeraki) only recovered to ~20% cover in this time.

Percentage cover estimates of *Hormosira* were generated from photos (Olympus FE-100 4.0 megapixel camera) and analysed with CPCe (Kohler & Gill 2006), using 100 randomly placed dots on each image.

Subsequent samples involved *Hormosira* canopy cover estimation (from photos), as well as surveys of mobile animals (count data) and other algae, and

sediment variable measurements. Note that *Hormosira* and other algal estimates were analysed independently of each other, and that measurement methods differed due to the *Hormosira* canopy blocking visibility of the understory to aerial photos (photos are a more precise measure). Functional groups were created in order to simplify analyses and deal with statistical problems associated with low-abundance count data. Groups were assigned in accordance to general ecological function, and align with earlier approaches in this system (e.g. Lilley & Schiel 2006). Algal and sediment cover surveys consisted of counting presence under each point using a 15-point grid placed upon the plot to generate an estimate of percentage cover for each variable. Sediment depth estimates were made by averaging 3 randomly chosen point-measurements from the 15 point grid.

Data analysis

Univariate analyses, using linear mixed model ANOVAs, were used to assess responses in *Hormosira* cover, as well as sediment variables and abundance of algal and invertebrate functional groups (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m560p121_supp.pdf for functional group lists). We used 2 analyses. In the first, all treatments were included: site (fixed, 2 levels), removal treatment (fixed, 11 levels), blocks (random, 4 levels, nested within site) and time since disturbance (fixed, 7 [*Hormosira* cover], 5 [sediment, rock and algal variables], and 6 [mobile animal variables] levels). The second analysis was run on the 3 × 3 subset of treatments (3 severities and 3 types of disturbance treatment) where the different factors included severity (or level) of disturbance treatment (fixed effect, with levels of 25, 50 and 75%), type of disturbance treatment (fixed effect; clumped, haphazard and cropped), site (fixed), block(site) (random) and time since disturbance (fixed). Data from control treatments (0% removal and 100% removal) were excluded from this specific analysis to allow us to test for an interaction between effects of type and severity (for full ANOVA tables see Tables S3–S5 and 'Note on interpreting analyses' in the Supplement). Analyses were done using SYSTAT 13 (SYSTAT Software).

We also did a separate analysis on the final survey to explore recovery after 25 mo. This analysis was similar to that described above, but without time (i.e. sites, blocks within sites, and treatments, either as 11 treatments or a 3 × 3 factorial).

On a few occasions, a plot could not be located before the tide rose or there was a problem with the photograph, producing missing values. Missing values were replaced with average values from the same treatment (but in other blocks) within the same site, and degrees of freedom were adjusted and significance was modified accordingly (see Table S2 in the Supplement for a full list of missing values).

RESULTS

Hormosira cover varied between 100 and 83% at 13th Beach and 100 and 89.5% at Jan Juc prior to treatment. The cover of *Hormosira* in 0% removal controls never dropped below 57.4% at 13th Beach and 80.6% at Jan Juc and averaged 91.9% across time and sites. The invertebrates and algae associated with *Hormosira* varied between the 2 sites throughout the experiment. 13th Beach generally had higher species richness and density of invertebrates and algae than at Jan Juc.

The most abundant invertebrates were *Lunella* (formerly *Turbo*) *undulata*, *Cominella lineolata* and *Austrocochlea adelaidae*. The limpets *Notoacmea* spp. and *Siphonaria* spp. were common but were generally small individuals (<5 mm). The most common algal species included turfing and encrusting coralline algae and the green algae *Ulva* spp. and *Cladophora* spp.

Hormosira banksii and sediment responses to disturbance

Cover of *Hormosira* was affected by type and severity of disturbance, with interactions between the 2 (Severity × Type × Time interaction, Table 1). Treatment effects and *Hormosira* recovery (defined by the convergence of a disturbance treatment with the undisturbed control) were broadly consistent across sites, except for a difference in recovery profiles between the disturbance type treatments. A reduction of 25% of the *Hormosira* canopy biomass resulted in a recovery period of around 2 mo, regardless of the type of treatment (Fig. 1A,B). Recovery took closer to 5 mo in the 50% removals and 9 mo in the 75% removals for the clumped and haphazard treatments, while recovery in cropped treatments occurred within a few months regardless of treatment severity (except in the 75% reduction at Jan Juc; see Fig. 1B). Recovery had occurred in all treatments after 25 mo, as no effects were seen in the final survey (Table 2).

Table 1. Summary of repeated measures ANOVAs on algal cover and invertebrate abundance (organized into functional groups) as well as rock and sediment cover in the disturbance experiment at *Hormosira*-dominated reef sites on the southeastern Australian coast. (A) Results from an analysis comparing all treatments, (B) results of a further analysis where the effects of severity (0 to 100 % removal of *Hormosira* cover) and type of disturbance (cropped, clumped, haphazard removal; see 'Materials and methods') were separated (see Tables S3 & S4 in the Supplement at www.int-res.com/articles/suppl/ m560p121_supp.pdf for full details). Bold face effect-titles denote effects of interest (discussed in main text). Open square: significant effect (at p ≤ 0.05). Filled square: significant effect of interest (at p ≤ 0.05)

Source	*Hormosira* cover	Sediment depth	Sediment cover	Rock cover	Ephemeral algae	Dead algae	Carnivorous whelks	Grazing snails
(A) All treatments together								
Time-averaged effects								
Site						□	□	□
Block(Site)	□	□	□		□		□	□
Treatment	□	□	□	□	□	□	□	□
Treatment × Site	□	□	□			□		□
Recovery profiles								
Time since disturbance	□			□	□	□	□	□
Site × Time						□		□
Treatment × Time	■		■	■	■	■		
Site-dependent effects of disturbance								
Treatment × Site × Time						□		
Block(Site) × Time	□	□	□	□		□	□	□
(B) Type and severity of disturbance								
Time-averaged effects								
Site						□	□	□
Block(Site)		□	□					□
Type	□		□	□	□	□	□	
Severity	□	□	□	□	□	□		□
Type × Site	□						□	
Severity × Site						□		□
Severity × Type	□		□					
Severity × Type × Site	□	□		□			□	
Type × Block(Site)	□	□	□		□			
Severity × Block(Site)	□		□			□		
Recovery profiles								
Time since disturbance	□			□	□	□	□	□
Site × Time	□					□		□
Type × Time	■	■	■	■	■	■		
Severity × Time	■	■	■	■	■	■		
Severity × Type × Time	■					■		
Site-dependent effects of disturbance								
Type × Site × Time	■							
Severity × Site × Time						■		
Severity × Type × Site × Time								
Block(Site) × Time	□		□	□		□	□	□

Areas dominated by *Hormosira* often trap substantial quantities of sediment under the canopy. In our study, sediment levels tended to follow changes in *Hormosira* cover throughout the experiment. Intact controls contained high sediment loads at the start of the experiment, with a depth of 1.3 cm and 69 % cover (Fig. 1C,D). Over the following months, sediment load decreased to ~1 cm depth and 35 % cover. Complete removal of *Hormosira* caused substantial reductions in both sediment depth (Fig. 1C) and cover (Fig. 1D). Both treatment type and severity affected the amount of sediment retained in plots (Table 1). A 25 % reduction in *Hormosira* canopy had little effect, but larger canopy reductions produced larger responses. For example, 50 and 75 % reduction treatments had half the sediment depth of 25 % reductions after 5 mo (Fig. 1C). Cropped plots also retained more sediment than those disturbed by clumped and haphazard removals (Fig. 1C,D), with a ca. 30 % increase in sediment depth (Fig. 1C) and ~10 % increase in canopy cover (relative to other treatment types, Fig. 1D), for up to 9 mo following disturbance. After 25 mo, sediment cover and depth did not differ between treatments (Table 2).
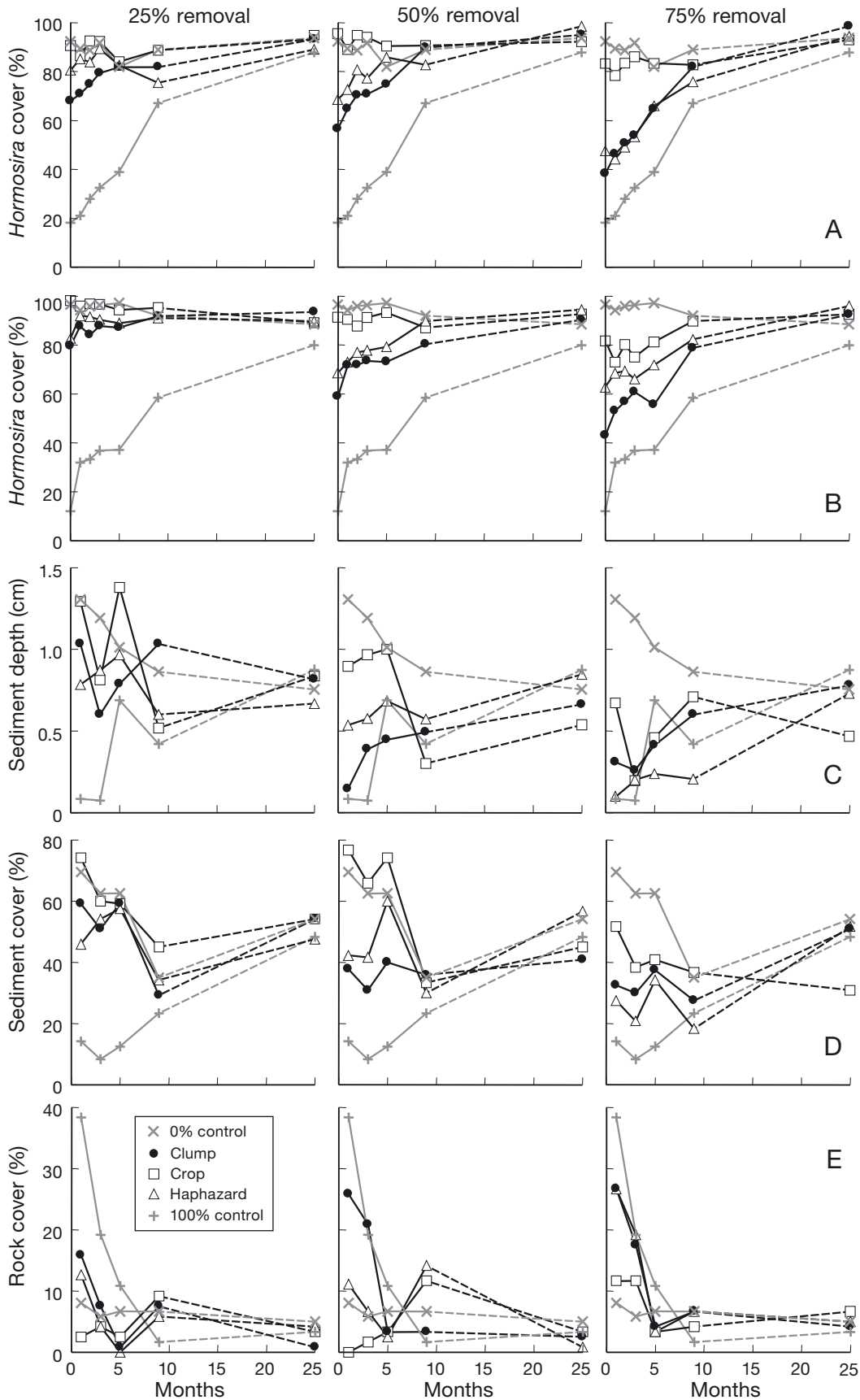
Fig. 1. Temporal variation in *Hormosira banksii* cover at (A) 13th Beach and (B) Jan Juc, as well as (C) sediment depth, (D) sediment cover and (E) rock cover throughout the experiment at the oceanic coast of central Victoria, south-eastern Australia. Values are mean percent-cover estimates within plots averaged across blocks. All variables except *Hormosira* cover are also averaged across sites, because there were no relevant interactions with site. Each panel shows changes for 3 disturbance types (cropped, clumped and haphazard treatments; see 'Materials and methods' for details). Controls (0 and 100% canopy removal) are shown (in grey) on all panels for reference. Error bars are not shown, to preserve the clarity of the figures, and relevant measures of variation (treatment × time residuals) can be found in Tables S3 & S4 in the Supplement at www.int-res.com/articles/suppl/m560p121_supp.pdf

Table 2. Summary of ANOVAs on the final survey (2 yr after disturbance) of the experiment at *Hormosira*-dominated reef sites on the south-eastern Australian coast. Algal cover and invertebrate abundance, as well as rock and sediment cover analyses are presented. (A) Results from an analysis comparing all 11 treatments, (B) results of a further analysis where the effects of severity (0–100% removal of *Hormosira* cover) and type of disturbance (cropped, clumped, haphazard removal; see 'Materials and methods') were separated (see Table S5 in the Supplement at www.int-res.com/articles/suppl/m560p121_supp.pdf for full details). Open square: significant at $p \leq 0.05$

Source	*Hormosira* cover	Sediment depth	Sediment cover	Rock cover	Ephemeral algae	Dead algae	Carnivorous whelks	Grazing snails
(A) All treatments together								
Site		□				□		□
Block(Site)	□	□	□				□	□
Treatment						□		□
Treatment × Site						□		
Residual								
(B) Type and severity of disturbance								
Site						□		□
Block(Site)	□	□	□					□
Type						□		□
Severity								
Type × Site						□		□
Severity × Site								
Severity × Type						□		
Severity × Type × Site						□		
Type × Block(Site)						□		

Disturbance opened up bare space (rock cover), which was gradually occupied by more ephemeral algae and eventually by *Hormosira*. The amount of bare space varied with disturbance type and severity (Table 1). Low severity disturbance produced only a slight, brief increase in the amount of bare space, while removing 75% of *Hormosira* tripled the amount of bare space (Fig. 1E). Cropped treatments also had less bare space than either clumped or haphazard treatments (Fig. 1E). Again, these differences were greatest directly after treatment and recovery occurred throughout the experiment, presumably as other algal species started to grow back and/or recruit (Table 1, Fig. 1E). Once again, recovery was evident after 25 mo (Table 2).

Responses of other taxa to *Hormosira* removal

Overall, the severity of disturbance produced larger responses than the type of disturbance treatment. The carnivorous whelks functional group, dominated by the scavenger *Cominella lineolata*, showed an effect of disturbance type (Table 1). Cropped plots retained higher numbers than other treatments and this stayed consistent across severity and time (Table 1, Fig. 2). On average throughout the experiment, cropped treatments contained 1.2 whelks, clumped treatments contained 0.9 whelks and haphazard

treatments had 0.7 whelks (Fig. 2). There was no interaction between type and level of disturbance (Table 1). Interestingly, whelk abundance in control plots switched after 9 mo, but there were generally more individuals in 0% controls (0.9 whelks) compared to 100% controls (0.6 whelks) on average over time (Fig. 2). Two years after disturbance, carnivore numbers (whelks) did not differ between treatments (Table 2).

Grazer abundance was generally low at Jan Juc, and results were driven by effects at 13th Beach, where grazing snails were present in higher numbers in lower severity disturbance plots (Table 1, Fig. 3). At 13th Beach, a 75% reduction in *Hormosira* cover resulted in an overall drop of between 1 and 2 snails per plot compared to the other severities of disturbance. Undisturbed controls contained an average of over 10 snails per plot, much higher than all other treatments (4.6 on average) (Fig. 3). No treatment by time interactions occurred (Table 1) and after 25 mo, recovery was incomplete as treatment and treatment type effects still existed (Table 2).

The severity and type of disturbance had independent effects on ephemeral algae (Table 1). Ephemerals became more abundant as the severity of disturbance treatment increased but were also more common in the clumped and haphazard treatments than in cropped plots (Fig. 4A). Cover increased from initial low values in clumped and hap-
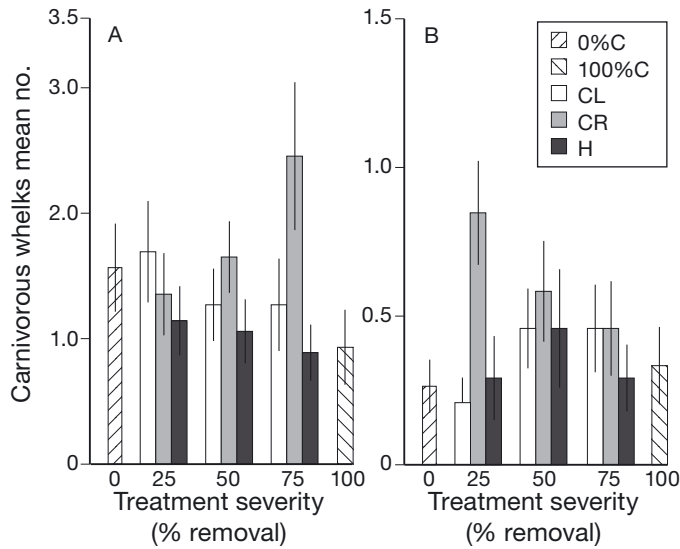
Fig. 2. Abundances of the carnivorous whelk functional group in a *Hormosira*-dominated reef at (A) 13th Beach and (B) Jan Juc, south-eastern Australia. Values are mean number estimates (±SEM) within plots averaged across blocks and time. Bars show abundance of clumped (CL, open bars), cropped (CR, light grey bars) and haphazard (H, dark grey bars) treatments at different levels of severity of *Hormosira* removal. Hatched bars: controls, 0 and 100% removal
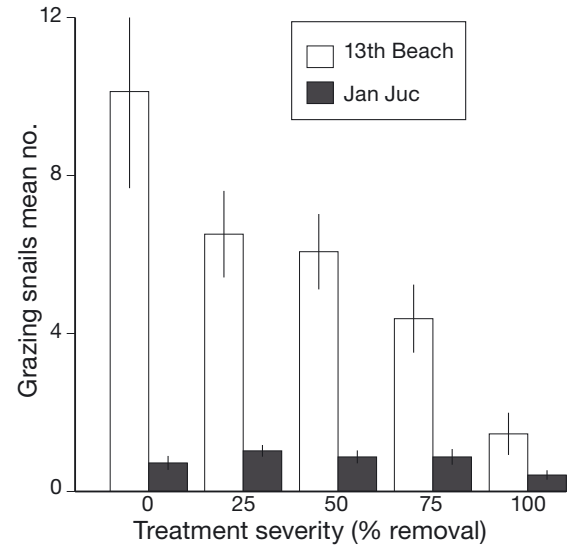
Fig. 3. Abundances of the grazing snail functional group across treatment severities at 2 *Hormosira*-dominated reef sites at the south-eastern Australian coast; 13th Beach (open bars) and Jan Juc (grey bars). Values are mean number estimates (±SEM) within plots averaged across blocks as well as sites, treatment types and time. Treament severity: percentage of removal of *Hormosira* cover, 0 and 100% removal served as control
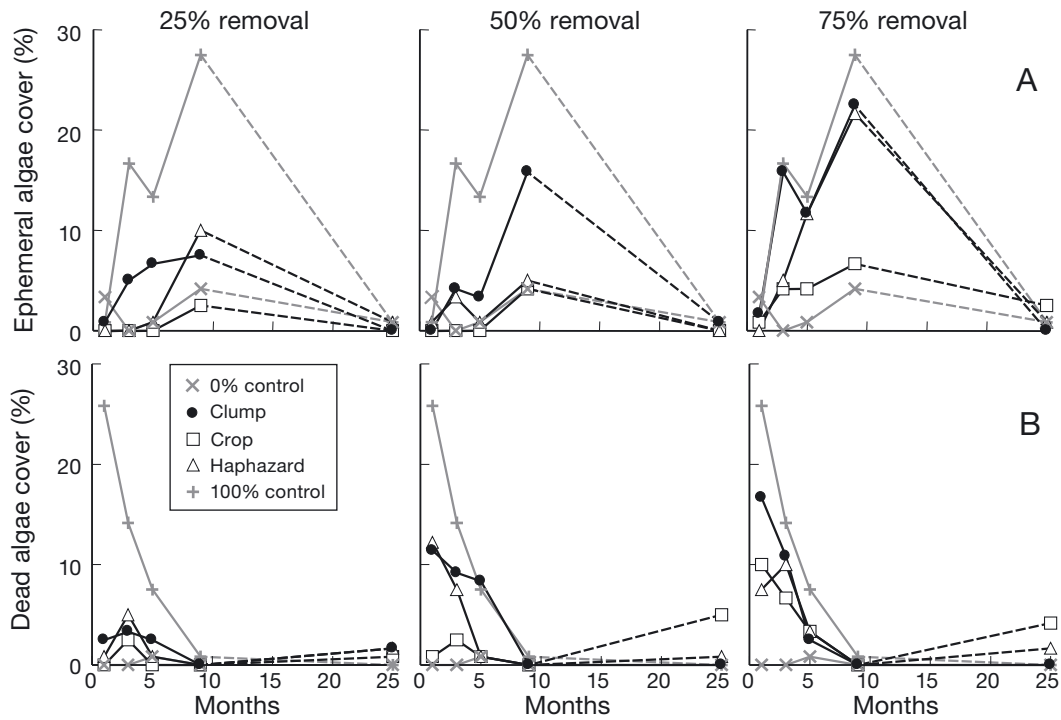

Fig. 4. Temporal variation in (A) ephemeral algae and (B) dead algae abundances (as percent cover) at varying severities of disturbance (25, 50 and 75% *Hormosira* removal) throughout the experiment at *Hormosira*-dominated reef sites in south-eastern Australia. Values are mean percent-cover estimates within plots averaged across blocks as well as sites (error bars omitted for clarity of presentation, but see Tables S3 & S4 in the Supplement for relevant measures of variation). Control treatments of 0 and 100% *Hormosira* removal are shown for reference in all plots along with the 3 disturbance types: cropped, clumped and haphazard removal (see 'Materials and methods' for details)

hazard treatments to an average of 15.2% and 12.2% respectively (pooled across treatment severities), after 9 mo (Fig. 4A). Similarly, abundance was >2 times higher in 75% removal plots than in 25 or 50% removal treatments (pooled across treatment types) at the same time point (Fig. 4A). Ephemerals peaked at 9 mo with 27.5% abundance in 100% removal treatments, in contrast to 4.2% cover in 0% removal controls (Fig. 4A). Abundance dropped away after 9 mo to show no difference between any treatments at the end of the experiment (Table 2, Fig. 4A).

The cover of dead algae was positively related to *Hormosira* canopy. Early in the experiment, 0% removal controls contained almost no dead algae while 100% removal controls contained much higher amounts (26% cover after 1 mo; Table 1, Fig. 4B). Dead algae in 100% removals were more than double that seen in the 50 and 75% removal plots, as high *Hormosira* canopy removal drove higher amounts of dead algae (Table 1, Fig. 4B). Dead algae were also prevalent in haphazard and clumped plots in contrast to cropped plots (Table 1, Fig. 4B). Dead algae then declined through time in all treatments to very low values at 9 mo (Table 1, Fig. 4B). A small peak appeared in cropped treatments at the 50 and 75% severities of removal at the end of the experiment (Table 2, Fig. 4B).

DISCUSSION

We found that the severity of a disturbance can affect the resilience of an ecosystem, as can the type of disturbance, but type effects were less common than severity effects. The *Hormosira* canopy recovered, except when it was removed completely, at both sites over a 25 mo period, and most of the recovery occurred within 9 mo of disturbance. *Hormosira* removal had varying effects on its associated understory community, and recovery also occurred in these taxa, but was generally slower.

Hormosira, which is described as an important autogenic engineer (Keough & Quinn 1998), showed broadly consistent patterns of recovery across sites, and the patterns depended on the severity and type of disturbance. Recovery time increased incrementally with increasing severity of disturbance treatment when disturbances were applied as haphazard or clumped removal, but the cropped treatments recovered quickly, regardless of severity. At the end of the experiment, all treatments had recovered to abundances not significantly different from those in unmanipulated controls.

Recovery rates of *Hormosira* can vary substantially (Keough & Quinn 1998, Lilley & Schiel 2006, 2011), but probably largely depend on the extent of holdfast damage (Underwood 1998) and other spatial or temporal factors. Underwood (1998) studied a canopy before and after a natural storm and demonstrated that recovery rate largely depends on the severity of damage received. Recovery was slower as the severity of disturbance increased, and full recovery took up to 5 yr. Recovery in our study was likely to be from regeneration from holdfasts, rather than recruitment, because recovery was relatively quick, and did not coincide with the peak reproductive season in spring/early summer (Lilley & Schiel 2006).

Disturbance also affected sediment loads on the substratum. Increasing severity of disturbance reduced sediment load at both sites. Sediment load generally decreased over winter, especially in low severity treatments, but recovered by the end of the experiment, when no differences between treatments existed. High severity treatments had lower sediment loads in general, and were more consistent throughout the experiment. These results suggest that the *Hormosira* canopy has a positive influence on understory sediment loads. This is important due to a potential smothering of growth and recruitment of algae (Schiel et al. 2006, Alestra & Schiel 2015), and cascading or other effects on invertebrates (Littler et al. 1983, Balata et al. 2007, Walker 2007). High sediment loads can even be agents of disturbance themselves. For example, Balata et al. (2007) experimentally increased sediment loads on subtidal assemblages of invertebrates and algae in the northwest Mediterranean, which led to loss of beta diversity on vertical and horizontal plots.

Rock or bare space increased, unsurprisingly, as more *Hormosira* cover was removed. Bare space was also greater in clumped and haphazard treatments than in cropped plots. These differences were most pronounced soon after disturbance. *Hormosira* quickly regrew from holdfasts, apart from small pulses of ephemeral algae in winter to spring. *Hormosira*'s regrowth to dominance is usually observed in this system, even when the canopy is damaged further, and no functional replacement of *Hormosira* has been observed (Povey & Keough 1991, Keough & Quinn 1998, Underwood 1998, Schiel & Taylor 1999, Lilley & Schiel 2006, Schiel 2006, 2011, Schiel & Lilley 2007).

A result of particular interest was seen in the group of carnivorous snails, where cropping of the *Hormosira* canopy increased their abundance regardless of treatment severity. Cropped canopies may have

affected abundances due to, for example, a facilitation of movement, enhanced feeding opportunity and/or ability or enhanced protection from higher predators (or combinations of these factors). Previously, Underwood (1999) demonstrated a facilitation of whelks by the *Hormosira* canopy, where feeding on prey species was enhanced. Here, we present the first evidence of a particular disturbance type heightening abundances of this group which consists of scavenging feeders and active predators, who can sometimes be influential (Menge 2000).

Grazing snails are known to correlate with the *Hormosira* canopy after disturbance events (Povey & Keough 1991). The findings of this study are somewhat consistent with this, as snails were affected by the severity of treatment at 13th Beach alone. Abundance was generally very low at Jan Juc, and treatment effects were not seen in this group. Grazer abundance is likely to be biologically significant as they influence algal composition (e.g. Scott & Russ 1987) and reduce microalgal films (e.g. Keough et al. 1997). Grazers are thought to be unable to feed upon mature *Hormosira* plants but are believed to reduce growth and impede recruitment of younger recruits (Underwood & Jernakoff 1984). Underwood (1998) experimentally manipulated grazer abundance (crossed with disturbance treatments) and found a trend that growth and recruitment of *Hormosira* was slower when grazer abundance was high, but eventually regrew to control levels. Recovery in grazing snails did not occur by the end of Underwood's (1998) experiment, but their abundance can sometimes lag behind changes in the *Hormosira* canopy (Keough & Quinn 1998). Similarly, treatment effects were still present in the final survey of our experiment, but overall, there was little evidence of a reduction in *Hormosira* recovery by grazers in our study. We believe this was caused by a combination of gastropod community structure at our sites, as well as fast *Hormosira* canopy recovery. True limpets, considered the most important grazers in this system (Povey & Keough 1991), were uncommon at these sites and, in previous studies, took up to 12 mo to recruit into disturbed plots on other platforms (Povey & Keough 1991, Keough & Quinn 1998). *Hormosira* holdfasts were also left intact in our treatments, which has led to fast canopy recovery in previous experiments (Povey & Keough 1991). Ultimately, the effects of grazers on *Hormosira* recovery may be greater when disturbances remove holdfasts or on shores where limpets are more abundant.

There was recruitment of ephemeral algae at 13th Beach after severe disturbance, and abundance was

higher after clumped and haphazard disturbances than after cropping. The appearance of these early successional species after a disturbance event is common in this system (Lilley & Schiel 2006, Schiel & Lilley 2007) and also in similar systems (Connell 1972, Sousa 1979, Benedetti-Cecchi & Cinelli 1992). Following a peak at 9 mo, the abundance of ephemeral algae fell by the final survey, which was conducted in February–March, coinciding with high UV stress and peak burnoff at this time of year. This is in accordance with Bellgrove et al. (2004), who found that *Ulva rigida* cover declined between December and February on rock platforms only about 20 km away from the sites of the present study. Differences in the abundance of ephemeral algae among our treatments decreased over time and no effect of treatment was observed at our final survey. These findings suggest that growth of ephemeral algae is modulated by provision of free space and access to light for growth, as well as physical conditions in the summer months.

Dead algae (i.e. burnt or bleached algae from all algal taxa) increased in high severity treatments and in clumped and haphazard plots soon after disturbance. This period coincides with a peak in temperature stress, UV radiation and long intertidal exposure times, as very low tides often occur around midday at this time of year. Occurrence of dead algae then declined over time as weather became milder and/or *Hormosira* recovered.

Results seen in ephemeral and dead algal groups suggest temporal variation in relationships between the *Hormosira* canopy and understory algal species (and possibly invertebrate community, but this was harder to quantify as the low numbers we found for these groups may have hidden effects). For example, access to light and provisioning of bare space for growth is important at milder times of the year (see Reed & Foster 1984 for a subtidal example), while protection from UV radiation and temperature stress is important in the summer months, to prevent desiccation and burnoff. Martone et al. (2010) found that desiccation, rather than temperature or light was the driver of 'bleaching' in an intertidal coralline alga. We noticed higher moisture retention under the *Hormosira* canopy compared to bare areas throughout the experiment (authors' pers. obs.). These relationships with canopy are perhaps unsurprising in short lived, blooming species such as those seen in ephemeral algae, as life-history strategies have evolved to deal with high rates of turnover (Sousa 1980). Ephemeral algal blooms may also affect attractiveness of plots to other species, as for example, they

are a source of food for invertebrate grazers (Wilhelmsen & Reise 1994). Therefore, there were likely to be indirect effects on trophic relationships. These blooms can also hinder other macroalgal recruitment by the pre-emption of space (e.g. Foster et al. 2003). Whether this happened here is hard to determine, as most *Hormosira* recovery is likely to have resulted from holdfast regeneration, rather than recruitment, of which we saw little evidence.

Responses to the severity of disturbance were common in this study. Almost all measured variables, apart from the abundance of carnivorous whelks, were affected by more severe perturbation levels. Unsurprisingly, effects generally increased incrementally with increases in *Hormosira* canopy removal, where stronger disturbance caused more damage, and led to longer recovery times. Interestingly, all effects disappeared by the end of the experiment, tracking *Hormosira* cover, which suggests high resilience in this system. We also saw no evidence of a shift to any alternate states (Holling 1973, Filbee-Dexter & Scheibling 2014), where grazers may dominate and hold down algal abundances, as proposed in the literature (Underwood & Jernakoff 1984) and supported by some empirical evidence (Underwood 1998, Keough & Quinn 1998, Lilley & Schiel 2006). However, this may have occurred if *Hormosira* holdfasts were removed, but *Hormosira* recovery was fast in our study and probably suppressed grazer recruitment. As such, the preservation of holdfasts following disturbance may be an important threshold of resilience to disturbance in this system, and warrants further investigation. There may also be spatial variation in *Hormosira* resilience, as Keough & Quinn (1998) only saw a shift to bare areas and limpets at 1 of 3 rock platforms.

We also found complex effects (Type × Severity interactions) on species other than *Hormosira*, as the effect of a disturbance of a given severity depended on the kind of agent that produced the disturbance. In our experiment, this was seen consistently when disturbance occurred by removing algal tissue while leaving the holdfast intact. In this case, increasingly severe disturbances had little additional effect. Abundance in the carnivorous whelk functional group increased when *Hormosira* canopy was cropped. This cropping treatment was designed to mimic the effects of a burnoff event, which can occur across whole platforms or even regions (authors' pers. obs.), and can disturb up to 70% of the local *Hormosira* canopy (King 1992). Therefore, responses to burnoff may be occurring at broad scales and this is likely to have strong implications for resilience. For example, facili-

tation of predators may reduce abundances of grazers across sites or regions. This could indirectly increase resilience, as grazers are thought to be able to suppress *Hormosira* recruitment (Underwood & Jernakoff 1984). *Hormosira* also recovered much faster from cropped plots than clumped or haphazard ones, as cropped fronds do not have to fully regrow from holdfasts. High resilience to burnoff is also unsurprising, as it occurs at least to some extent, in most summers (Keough & Quinn 1998). Conversely, clumped and haphazard treatments, as well as full removal controls, opened up free space in the *Hormosira* canopy. This allowed for recruitment of ephemeral algae in the cooler months, but also resulted in higher burnoff of these species at warmer times. Clearly, disturbance types are imposing variable and important effects, and similar examples in the literature suggest these effects extend across many ecosystems (Spear & Storfer 2010, O'Connor & Anderson 2010, Whomersley et al. 2010, Ruesink et al. 2012).

Recovery of the *Hormosira* canopy was effected by both the type and severity of disturbance in this study. This recovery was relatively fast, and likely due to quick growth from intact holdfasts. Obligate understory species responded to the type of disturbance applied, as well as the severity of disturbance treatments. Generally, resilience of these species followed that of the *Hormosira* canopy closely. These findings suggest a high level of resilience. Currently, our knowledge of resilience is built upon studies of strong perturbations, but our findings suggest that disturbance types are an important part of responses to disturbance. Further exploration of these relationships seems particularly important, as the very nature of disturbance is likely to change over time, along with climate. A full array of disturbance types must therefore be understood in this system and others, if we are to build robust models of resilience.

LITERATURE CITED

Alestra T, Schiel DR (2015) Impacts of local and global stressors in intertidal habitats: influence of altered nutrient, sediment and temperature levels on the early life history of three habitat-forming macroalgae. J Exp Mar Biol Ecol 468:29–36

Balata D, Piazzi L, Benedetti-Cecchi L (2007) Sediment disturbance and loss of beta diversity on subtidal rocky reefs. Ecology 88:2455–2461

Bellgrove A, Clayton MN, Quinn GP (2004) An integrated study of the temporal and spatial variation in the supply of propagules, recruitment and assemblages of intertidal macroalgae on a wave-exposed rocky coast, Victoria, Australia. J Exp Mar Biol Ecol 310:207–225

Benedetti-Cecchi L, Cinelli F (1992) Effects of canopy cover, herbivores and substratum type on patterns of *Cystoseria* spp. settlement and recruitment in littoral rockpools. Mar Ecol Prog Ser 90:183–191

Brown VB, Davies SA, Synnot RN (1990) Long-term monitoring of the effects of treated sewage on the intertidal macroalgal community near Cape Schanck, Victoria, Australia. Bot Mar 33:85–98

Carnell PE, Keough MJ (2014) Spatially variable synergistic effects of disturbance and additional nutrients on kelp recruitment and recovery. Oecologia 175:409–416

Connell JH (1972) Community interactions on marine rocky intertidal shores. Annu Rev Ecol Syst 3:169–192

Connell JH, Keough MJ (1985) Disturbance and patch dynamics of subtidal marine animals on hard substrate. In: Pickett STA, White PS (eds) The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, FL, p 125–151

Crain CM, Kroeker K, Halpern BS (2008) Interactive and cumulative effects of multiple human stressors in marine systems. Ecol Lett 11:1304–1315

Dayton PK (1972) Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. In: Parker BC (ed) Proceedings of the colloquium on conservation problems in Antarctica. Allen Press, Lawrence, KS, p 81–96

Falkenberg LJ, Russell BD, Connell SD (2012) Stability of strong species interactions resist the synergistic effects of local and global pollution in kelp forests. PLOS ONE 7: e33841

Falkenberg LJ, Connell SD, Russell BD (2013) Disrupting the effects of synergies between stressors: improved water quality dampens the effects of future CO_2 on a marine habitat. J Appl Ecol 50:51–58

Filbee-Dexter K, Scheibling RE (2014) Sea urchin barrens as alternative stable states of collapsed kelp ecosystems. Mar Ecol Prog Ser 495:1–25

Foster MS, Nigg EW, Kiguchi LM, Hardin DR, Pearse JS (2003) Temporal variation in an algal-dominated high intertidal assemblage. J Exp Mar Biol Ecol 289:15–39

Hobbs RJ, Huenneke LF (1992) Disturbance, diversity, and invasion: implications for conservation. Conserv Biol 6: 324–337

Holling CS (1973) Resilience and stability of ecological systems. Annu Rev Ecol Syst 4:1–23

Hughes TP, Baird AH, Bellwood DR, Card M and others (2003) Climate change, human impacts, and the resilience of coral reefs. Science 301:929–933

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373–386

Keough MJ, Quinn GP (1998) Effects of periodic disturbances from trampling on rocky intertidal algal beds. Ecol Appl 8:141–161

Keough MJ, Quinn GP, Bathgate R (1997) Geographic variation in interactions between size classes of the limpet *Cellana tramoserica*. J Exp Mar Biol Ecol 215:19–34

King A (1992) Monitoring and management of human activity on rocky shores. PhD thesis, University of Melbourne

Kohler KE, Gill SM (2006) Coral Point Count with Excel extensions (CPCe): a visual basic program for the determination of coral and substrate coverage using random point count methodology. Comput Geosci 32:1259–1269

Lilley SA, Schiel DR (2006) Community effects following the deletion of a habitat-forming alga from rocky marine shores. Oecologia 148:672–681

Littler MM, Martz DR, Littler DS (1983) Effects of recurrent sand deposition on rocky intertidal organisms: importance of substrate heterogeneity in a fluctuating environment. Mar Ecol Prog Ser 11:129–139

Martone PT, Alyono M, Stites S (2010) Bleaching of an intertidal coralline alga: untangling the effects of light, temperature, and desiccation. Mar Ecol Prog Ser 416:57–67

Menge BA (2000) Top-down and bottom-up community regulation in marine rocky intertidal habitats. J Exp Mar Biol Ecol 250:257–289

Minchinton TE, Fels KJ (2013) Sediment disturbance associated with trampling by humans alters species assemblages on a rocky intertidal seashore. Mar Ecol Prog Ser 472:129–140

O'Connor KC, Anderson TW (2010) Consequences of habitat disturbance and recovery to recruitment and the abundance of kelp forest fishes. J Exp Mar Biol Ecol 386: 1–10

Pickett STA, White PS (1985) The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, FL

Pimm SL (1984) The complexity and stability of ecosystems. Nature 307:321–326

Povey A, Keough MJ (1991) Effects of trampling on plant and animal populations on rocky shores. Oikos 61: 355–368

Reed DC, Foster MS (1984) The effects of canopy shading on algal recruitment and growth in giant kelp forests. Ecology 65:937–948

Ruesink JL, Fitzpatrick JP, Dumbauld BR, Hacker SD, Trimble AC, Wagner EL, Wisehart LM (2012) Life history and morphological shifts in an intertidal seagrass following multiple disturbances. J Exp Mar Biol Ecol 424–425: 25–31

Schiel DR (2006) Rivets or bolts? When single species count in the function of temperate rocky reef communities. J Exp Mar Biol Ecol 338:233–252

Schiel DR (2011) Biogeographic patterns and long-term changes on New Zealand coastal reefs: non-trophic cascades from diffuse and local impacts. J Exp Mar Biol Ecol 400:33–51

Schiel DR, Lilley SA (2007) Gradients of disturbance to an algal canopy and the modification of an intertidal community. Mar Ecol Prog Ser 339:1–11

Schiel DR, Taylor DI (1999) Effects of trampling on a rocky intertidal algal assemblage in southern New Zealand. J Exp Mar Biol Ecol 235:213–235

Schiel DR, Wood SA, Dunmore RA, Taylor DI (2006) Sediment on rocky intertidal reefs: effects on early post-settlement stages of habitat-forming seaweeds. J Exp Mar Biol Ecol 331:158–172

Scott FJ, Russ GR (1987) Effects of grazing on species composition of the epilithic algal community on coral reefs of the central Great Barrier Reef. Mar Ecol Prog Ser 39:293–304

Sousa WP (1979) Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. Ecology 60:1225–1239

Sousa WP (1980) The responses of a community to disturbance: the importance of successional age and species' life histories. Oecologia 45:72−81

Sousa WP (1984) The role of disturbance in natural communities. Annu Rev Ecol Syst 15:353−391

Sousa WP (1985) Disturbance and patch dynamics on rocky intertidal shores. In: Pickett STA, White PS (eds) The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, FL, p 101−124

Sousa WP (2001) Natural disturbance and the dynamics of marine benthic communities. In: Bertness MD, Gaines S, Hay ME (eds) Marine community ecology. Sinauer Associates, Sunderland, MA, p 85−130

Spear SF, Storfer A (2010) Anthropogenic and natural disturbance lead to differing patterns of gene flow in the Rocky Mountain tailed frog, *Ascaphus montanus*. Biol Conserv 143:778−786

Underwood AJ (1998) Grazing and disturbance: an experimental analysis of patchiness in recovery from a severe storm by the intertidal alga *Hormosira banksii* on rocky shores in New South Wales. J Exp Mar Biol Ecol 231: 291−306

Underwood AJ (1999) Physical disturbances and their direct effect on an indirect effect: responses of an intertidal assemblage to a severe storm. J Exp Mar Biol Ecol 232: 125−140

Underwood AJ, Jernakoff P (1984) The effects of tidal height, wave-exposure, seasonality and rockpools on grazing and the distribution of intertidal macroalgae in New South Wales. J Exp Mar Biol Ecol 75:71−96

Walker JW (2007) Effects of fine sediments on the settlement and survival of the sea urchin *Evechinus chloroticus* in northeastern New Zealand. Mar Ecol Prog Ser 331: 109−118

Whomersley P, Huxham M, Bolam S, Schratzberger M, Augley J, Ridland D (2010) Response of intertidal macrofauna to multiple disturbance types and intensities—an experimental approach. Mar Environ Res 69:297−308

Wilhelmsen U, Reise K (1994) Grazing on green algae by the periwinkle *Littorina littorea* in the Wadden Sea. Helgol Meersunters 48:233−242

Womersley HBS (1987) The marine benthic flora of Southern Australia. Part II. Board of the Botanic Gardens and State Herbarium, Government of South Australia, Adelaide