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Global regime shift dynamics of catastrophic sea urchin overgrazing

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A pronounced, widespread and persistent regime shift among marine ecosystems is observable on temperate rocky reefs as a result of sea urchin overgrazing. Here, we empirically define regime-shift dynamics for this grazing system which transitions between productive macroalgal beds and impoverished urchin barrens. Catastrophic in nature, urchin overgrazing in a well-studied Australian system demonstrates a discontinuous regime shift, which is of particular management concern as recovery of desirable macroalgal beds requires reducing grazers to well below the initial threshold of overgrazing. Generality of this regime-shift dynamic is explored across 13 rocky reef systems (spanning 11 different regions from both hemispheres) by compiling available survey data (totalling 10 901 quadrats surveyed *in situ*) plus experimental regime-shift responses (observed during a total of 57 *in situ* manipulations). The emergent and globally coherent pattern shows urchin grazing to cause a discontinuous 'catastrophic' regime shift, with hysteresis effect of approximately one order of magnitude in urchin biomass between critical thresholds of overgrazing and recovery. Different life-history traits appear to create asymmetry in the pace of overgrazing versus recovery. Once shifted, strong feedback mechanisms provide resilience for each alternative state thus defining the catastrophic nature of this regime shift. Importantly, human-derived stressors can act to erode resilience of desirable macroalgal beds while strengthening resilience of urchin barrens, thus exacerbating the risk, spatial extent and irreversibility of an unwanted regime shift for marine ecosystems.

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1. Introduction

Widespread collapse from kelp beds to sea urchin-dominated barren grounds provides a clear example of an unwanted regime (or phase) shift that has played out many times for temperate reef ecosystems worldwide [1–3]. This transition from luxuriant and productive kelp bed habitats to impoverished and persistent barrens caused by sea urchin overgrazing [4–8] is one of the most distinctive ecosystem-level shifts observable for rocky subtidal seascapes (electronic supplementary material, figure S1). The collapse of kelp beds has been widely publicized, and much research effort has ensued following the realized effect of destructive sea urchin grazing and formation of urchin barren grounds over thousands of kilometres of subtidal rocky reefs worldwide, for example in the NE Pacific in the 1960–1970s, Norwegian coast in the 1970s, NW Atlantic in the 1970–1980s [2], and Tasmania in the 2000s where overgrazing and the threat of widespread kelp collapse has only relatively recently emerged [6,7,9–12].

While urchin barrens are frequently observed and processes underlying fluctuations in sea urchin populations are well known [2,13], as for most instances of marine ecosystem regime shift [14], the general dynamics of collapse and recovery of kelp beds remains poorly defined. Importantly, once sea urchin grazing removes standing macroalgal biomass, the urchin population does not collapse, but rather individual growth rate decreases as urchins switch their feeding to less nutritious encrusting or microalgal and invertebrate biota growing on open rock surfaces [1,4,15,16]. Thus, once formed, urchin barrens can be highly persistent features of rocky reefs, lasting many decades (e.g. in Japan, the barrens or 'isoyake' state has persisted for over 80 years [17]), with individual urchins living up to 50 years on barren grounds [16]. Therefore, the unwanted advent of sea urchin barrens on rocky reefs is dramatic, can be spatially extensive and can persist in the long-term across many generations of urchins.

The need to mitigate the threat of persistently degraded reefs is exemplified in eastern Tasmania where the recent polewards range extension of the sea urchin *Centrostephanus rodgersii*, driven by warming ocean climate, has led to overgrazing of kelp beds [6,7,9,10]. This new manifestation of overgrazing has had clear negative impacts on commercial reef-based fisheries and local biodiversity [6–8,18], motivating the need to understand the dynamics of urchin grazing and the resilience of kelp beds to this threat [9,19,20]. In Australia, no other benthic herbivore has had as large a role as *C. rodgersii* in determining the state of shallow reef communities [12,21], with thousands of kilometres of reef overgrazed within the historical range of the urchin across the New South Wales coast [22]. While widespread urchin barrens (100 000s m²) are evident at several eastern Tasmanian reefs, smaller 'incipient barrens' (10s m²) within otherwise intact kelp beds are common and considered an early warning sign of broader-scale kelp bed collapse along this coast [7,19].

Recent synthesis by Ling *et al.* [9] defined the transition from kelp beds to *C. rodgersii* barrens in eastern Australia as a nonlinear regime shift, whereby a critical threshold in sea urchin abundance triggers overgrazing of kelp beds. This threshold behaviour typifies the 'sudden' nature of collapse documented for many ecosystems [23,24]. More importantly, the threshold of urchin abundance triggering destructive overgrazing of kelp beds (forward shift, *F*) is markedly greater than the threshold in urchin abundance at which kelp beds can begin to recover (reverse shift, *R*), demonstrating discontinuous regime-shift dynamics with hysteresis (figure 1a). Given that some kelp beds have locally collapsed and small incipient-barrens patches formed by *C. rodgersii* are common along the eastern Tasmanian coast (figure 1b), the widespread collapse to barrens, as in New South Wales (figure 1c), is currently of major socioecological concern [6,7].

While significant advances have been made in understanding regime shifts driven by sea urchin grazing in Australian [9,20] and Nova Scotian kelp-bed systems [3,25,26], the threshold dynamics (for both forward and reverse shifts) have not been well characterized for urchin-grazing systems generally. Here, we ask whether available evidence indicates a globally coherent pattern of discontinuous regime-shift dynamics for urchin overgrazing.

To explore global dynamics, we compile available empirical data for a wide range of rocky reef systems prone to high sea urchin abundances and overgrazing impacts. Importantly, while sea urchin grazing can occur at broad coastal scales, it is interactions between grazing sea urchins and their macroalgal food at local scales (10^0–10^1 m²) that leads to the emergent and widespread collapse of standing algal beds [26–28]. Thus, to understand regime-shift dynamics at this scale, for each discrete rocky reef system, we examine (i) frequency distributions of reef state (i.e. percentage macroalgal cover) across a range of reef conditions (i.e. urchin biomass) where both macroalgal cover and sea urchin abundance has been co-recorded *in situ* in the same quadrat spaces, and (ii) responses of macroalgal beds to natural or manipulated changes in urchin abundance. Finally, we examine the existence of state-dependent feedbacks and stressors implicated in triggering and maintaining regime shifts between macroalgal beds and urchin barrens.

2. Methods

(a) Frequency distributions of reef state across changing reef conditions

To inform regime-shift dynamics between beds of canopy-forming macroalgae and sea urchin barrens within particular reef systems, we acquired data within the depth range of occurrence of both reef states—i.e. from the shallow wave-determined limit of urchin grazing on algal beds to the deep light-limited margin of these beds, excluding reef areas heavily laden with sand. We adopted a landscape ecology approach to determine whether reefs exist as a vegetated, unvegetated or some mosaic between alternative macroalgal and urchin barren states. To enable direct comparison of systems supporting different sizes of canopy-forming seaweeds, reef state was described by the planar percentage cover of macroalgae. While algal cover can exceed 100% for multi-layered kelp beds, planar cover is capped at 100%. This allows comparison of habitat-forming seaweeds of varying morphology, ranging from laminarian kelp forests to low-lying algal canopies of the Canary Islands and the Mediterranean (electronic supplementary material, figure S1). Percentage cover is the most frequently reported metric of macroalgal abundance across rocky reef systems; where it was not measured directly conversion factors were used to generate cover estimates from counts of individual macroalgae within quadrats. Conversions to percentage cover were performed using (i) previously defined species-specific relationships between individual counts and percentage cover; (ii) morphometric scaling, in
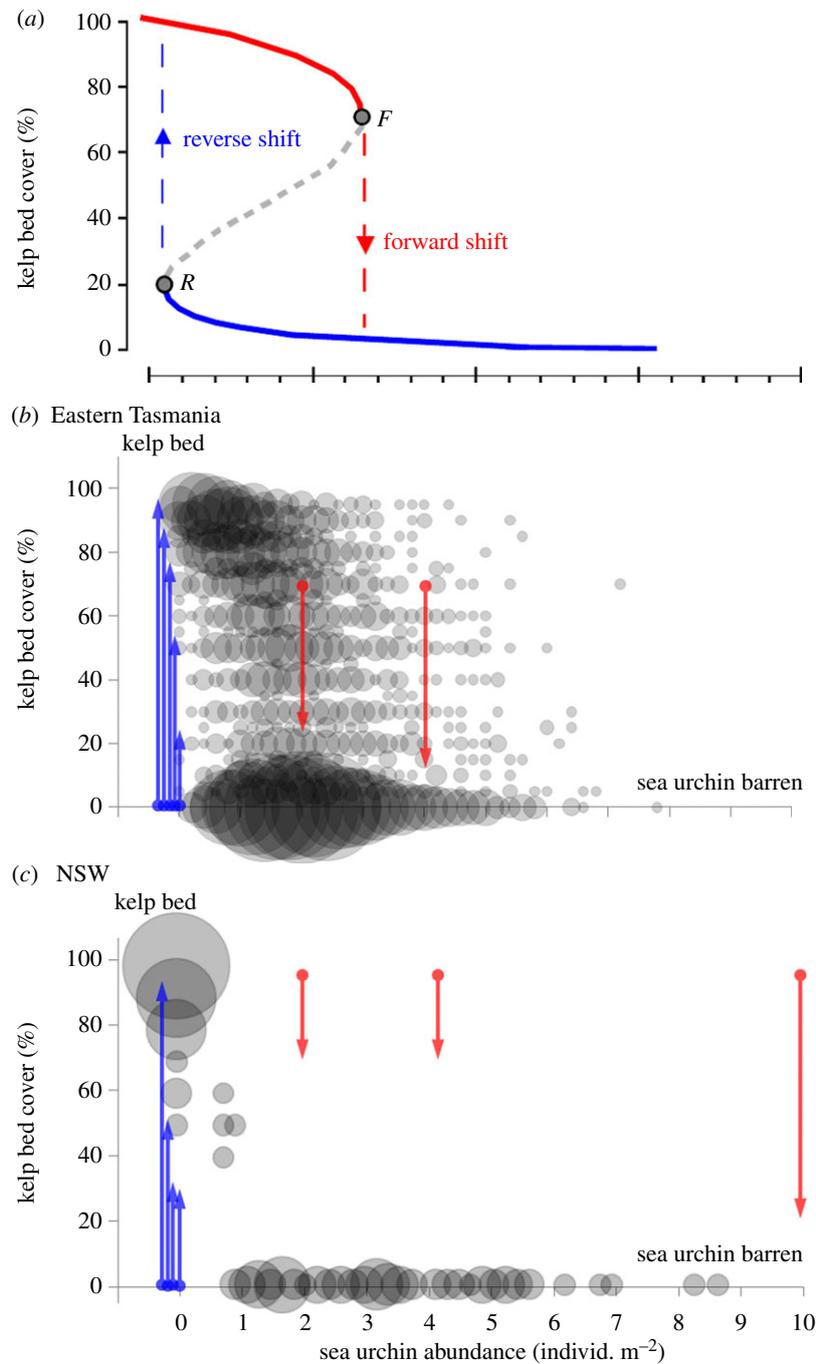
Figure 1. Catastrophic regime shift between kelp beds and sea urchin barrens. (a) Conceptual schematic of catastrophic 'discontinuous' regime-shift dynamic (redrawn from Ling et al. [9], after Scheffer et al. [24]). If the reef system occurs in the kelp state on the upper path (red) but close to the threshold F, a slight increase in sea urchin density may induce a catastrophic forward shift to the alternative and stable sea urchin barrens state. Once barrens have formed, reverting back to the kelp state is difficult, because the system demonstrates hysteresis, and the reverse shift (blue path) occurs only if sea urchin density is reduced below the return threshold at R. The broken grey line indicates an unstable equilibrium between the alternative stable states. (b,c) Scatter plots of kelp bed cover (%) across a range of sea urchin density (individuals m^{-2}) for (b) recently established *Centrostephanus rodgersii* in eastern Tasmania (n = 5135; 5 × 1 m quadrats sampled in 2001–2002 and 2008) and (c) historical range of grazing impacts in New South Wales (NSW; n = 129, 5 × 1 m quadrats sampled in 2004–2006). Scatter plots are defined by semi-transparent bubbles, where increasing bubble size indicates increasing frequency of particular combinations of urchin density and macroalgal cover: darker shading indicates increased overlap between neighbouring bubbles. Overlaid arrows indicate magnitude and direction of ecosystem response to removals and additions of *C. rodgersii* in respective systems (after electronic supplementary material, table S2).

which average planar canopy area of individual adult stages was determined (see electronic supplementary material, table S1).

Rocky reef 'condition' was defined as sea urchin biomass (wet weight, g m^{-2}) because numerical density alone does not allow standardization across reef systems supporting urchins of different individual size and mass. Even within species, density-dependent processes can result in areas of few large or many small sea urchins, with similar biomass per unit area [16]. Because sea urchin biomass was rarely measured directly within individual quadrats,

it was estimated using two approaches: (i) where test diameter (TD) was recorded for individuals, wet weight was estimated by allometric conversion and summed across individuals in a quadrat (electronic supplementary material, table S1), and (ii) where individual TD was not recorded, mean wet weight per individual sea urchin was estimated from species-specific allometric conversion of the average TD from a sample of the population, which was then multiplied by the total count of sea urchins in a quadrat (electronic supplementary material, table S1).

(b) Responses of reef state to altered reef conditions

Defining the envelope of possible combinations between reef state (macroalgal cover) and reef conditions (urchin biomass), the frequency distribution approach above provides an instantaneous snapshot of possible relationships from which alternative reef states may be inferred. Overlaying such distributions with observed shifts in reef state, in both magnitude and direction, to changes in 'reef conditions' informs the nature of regime-shift dynamics. Responses in macroalgal cover observed following natural or manipulated changes in sea urchin abundance were compiled by sourcing data from published and unpublished experimental and observational field studies. These studies documented macroalgal cover and sea urchin abundance both before and after a regime shift occurred. Where neither macroalgal cover nor sea urchin biomass was measured directly, conversions were performed as per the generation of frequency distributions described above. The frequency distributions of sea urchin biomass resulting in forward and reverse shifts were compared statistically using the non-parametric Kolmogorov–Smirnoff test and means were compared using 1-way ANOVA.

3. Results

Observed frequency distributions of macroalgal cover across sea urchin biomass were compiled for 13 globally representative rocky reef systems that are known to occur as algal bed or urchin barrens states (see map, electronic supplementary material, figure S2). Across reef systems, survey data showed clear separation of these alternative reef states and an abrupt collapse of macroalgal habitat to urchin barrens at high urchin biomass (figure 2a–m). Urchin barrens are maintained across a large range of urchin biomass and can occur at levels of urchin biomass less than those observed on macroalgal-dominated reefs. Observed magnitudes and directions of change within particular systems are indicative of hysteresis, as barrens formation (forward shift) typically occurs at much higher levels of urchin biomass than that for which macroalgal recovery (reverse shift) is observed to occur (cf. red and blue arrows, figure 2).

Pooling correlative data for all systems globally, the observed ceiling of macroalgal cover against increasing sea urchin biomass is consistent with expectations of a nonlinear threshold defining urchin barrens formation (cf. figures 1a and 3a). Compilation of a total of 57 observed regime-shift responses from rocky reefs studies worldwide (electronic supplementary material, table S2) shows that urchin barrens are created under conditions of moderate to high sea urchin biomass (red 'forward shift' arrows compiled from 17 observed shifts; figure 3b), whereas recovery of macroalgal habitat, once sea urchin barrens have formed, generally occurs at much lower levels of urchin biomass (blue 'reverse shift' arrows compiled from 40 observed shifts; figure 3b). Considering all studies reporting urchin barrens formation, the mean ($\pm$s.e.) urchin biomass for which macroalgal habitats are collapsed by overgrazing is 2640 ± 824 g m^{-2} (electronic supplementary material, table S2). Excluding high urchin biomass (more than 1500 g m^{-2}; figure 3b,c), a mean urchin biomass of 668 (± 115 g m^{-2}) can be considered to represent the minimum threshold for which overgrazing is observed for rocky reef systems globally (electronic supplementary material, table S2).

The frequency of observed forward-shift (urchin barrens formation) events shows a distinctly different distribution across the range of sea urchin biomass (right skewed red

distribution; figure 3c) compared with that of reverse-shift (macroalgal recovery) events (left skewed blue distribution; figure 3c). In contrast to the threshold for barrens formation, the mean threshold biomass of sea urchins that allows for macroalgal recovery is 34 ± 11 g m^{-2} (electronic supplementary material, table S2). While it is clear that a complete absence of sea urchins will enable kelp beds to recover, by excluding studies reporting macroalgal recovery at zero urchin biomass, the mean urchin biomass threshold allowing macroalgal recovery is estimated at 71 ± 20 g m^{-2} (electronic supplementary material, table S2). Upon reaching critical regime-shift thresholds, the mean ($\pm$s.e.) time observed for barrens formation and macroalgal recovery was 6.35 ± 1.2 and 18.5 ± 2.0 months, respectively (electronic supplementary material, table S2).

4. Discussion

(a) A globally coherent discontinuous regime shift

Our global compilation of empirical patterns across rocky reef systems prone to urchin grazing is consistent with expectations of discontinuous 'catastrophic' regime-shift dynamics. Results show that sea urchins become incapable of maintaining sea urchin barrens at a biomass below approximately 70 g m^{-2}, whereas the biomass of sea urchins required to form barrens in the first instance is approximately 700 g m^{-2}. Thus, by definition, the hysteresis evident for this regime shift is approximately one order of magnitude of sea urchin biomass. Simply put, the available empirical evidence for rocky reef systems worldwide reveals that the abundance of sea urchins required to form barrens is greater than that required to maintain a barren and that recovery of productive macroalgal beds requires virtually all urchins to be removed.

Notably, while macroalgal bed recovery occurs consistently when urchins are absent or at low biomass, overgrazing of macroalgal beds occurs over a much wider range of urchin biomass (figure 3b,c). This probably reflects the more heterogeneous structure of kelp bed habitats across the globe and passive versus active modes of urchin grazing which occur within macroalgal beds [29] relative to the homogeneous barrens state, which shows much greater structural consistency (see electronic supplementary material, figure S1) and is maintained by a more consistent biomass and grazing behaviour of urchins (figure 3b,c). In addition, while the catastrophic regime-shift dynamic appears generally applicable across urchin-grazing systems, there is a dearth of information on forward and reverse shift dynamics within particular rocky reef systems (figure 2 and electronic supplementary material, table S2). Thus, while general dynamics and threshold values are reported here, further experimental manipulations and modelling studies [20] are clearly warranted to quantify dynamics and identify thresholds and options for reef management within particular urchin-grazing systems.

While sea urchin grazing dynamics are evidently catastrophic in nature, with macroalgal beds and urchin barrens representing the alternative stable states of rocky reef ecosystems (see also [3]), there is high variability across different urchin-grazing systems, particularly with respect to the range of urchin biomass and the degree of transitory dynamics in macroalgal cover (figure 2). Therefore, further exploration of the rates of macroalgal primary production, urchin grazing, and predation on sea urchins is warranted
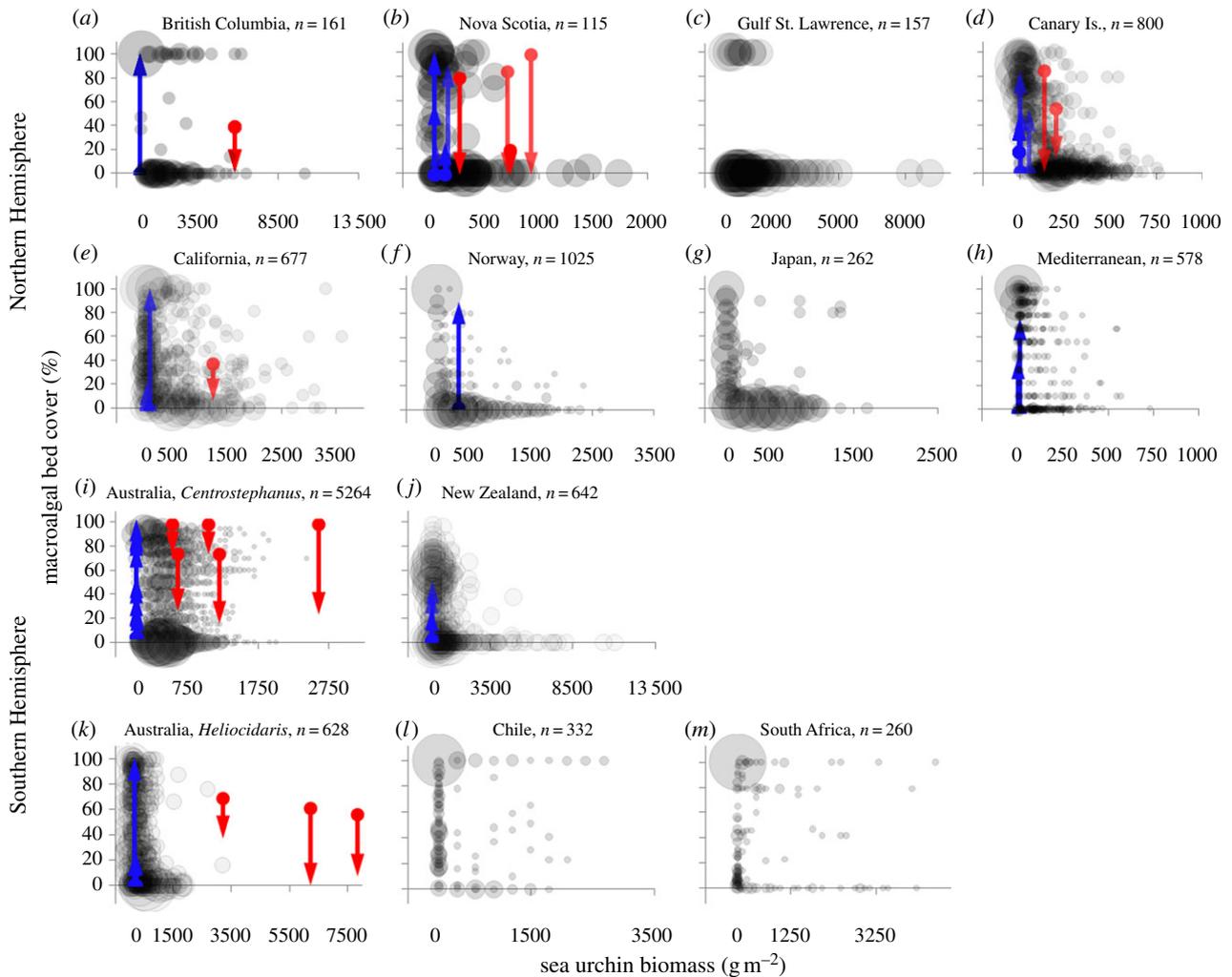
Figure 2. Regime-shift dynamics between macroalgal beds and sea urchin-dominated barrens on 13 rocky reef systems worldwide. (*a−h*) Northern Hemisphere and (*i−m*) Southern Hemisphere; *n*, no. quadrat samples (after electronic supplementary material, table S1; see also world map in the electronic supplementary material, figure S2). As per figure 1, semi-transparent bubbles represent relative frequency of particular combinations of urchin biomass (g m^{-2}) and macroalgal cover (%). Where available for particular regions, overlaid arrows show the direction and magnitude of regime shifts (forward shift, red arrows; reverse shift, blue arrows) observed following natural and manipulated change in sea urchin biomass (after electronic supplementary material, table S2). Note that *x*-axes vary in scale across regions.

to identify processes operating across systems that result in either a build-up of urchin biomass towards a forward-shift threshold, or a decline in biomass to below a reverse-shift threshold, that determine the dynamics of regime shift [30]. For example, although urchin populations can reach high biomass in South Africa and the general dynamic of overgrazing applies across this productive kelp system (figure 2*j*), urchin-dominated patches are observed to remain as highly localized features (10^0–10^1 m) devoid of the negative ecological impacts reported for extensive urchin barrens elsewhere [31].

(b) Time asymmetry in discontinuous dynamics?

Once critical tipping points in sea urchin biomass are reached, barrens formation occurs in one third of the time (forward shift approx. six months) that is required for recovery of kelp bed habitats (reverse-shift approx. 18 months; electronic supplementary material, table S2). But while overgrazing of kelp beds is a relatively abrupt event, many years may be required for urchin populations to build towards this critical biomass threshold. For example, the sea urchin *C. rodgersii* has a planktotrophic larvae that develops over three months (see [10]) before settling to the reef, after which

another 5–7 years elapse before the urchins emerge from crypsis to graze macroalgae on the reef surface [10,12,16]. Furthermore, in situations where sea urchins from adjacent deep-living populations aggregate at the lower margin of kelp beds (e.g. *Strongylocentrotus droebachiensis* in the NW Atlantic), typically it is the larger size-classes that dominate urchin biomass at mobile grazing 'fronts' [28]. So while the time taken for overgrazing may be relatively sudden, the time necessary to build urchin populations towards a critical threshold in abundance can be protracted.

In contrast, providing urchin grazing pressure is sufficiently relaxed and connectivity to local spore sources exists, macroalgal life-history strategies enable a more immediate local response in recruitment and growth through to mature stands within the estimated approximately 18 months required for the system-wide reverse shift (see electronic supplementary material, table S2). The age structure of populations of *C. rodgersii* across eastern Tasmania [10] provides evidence of gradual building towards a critical transition in the rate of herbivory, as urchin populations approach the average age (approx. 20 years old) at which overgrazing occurs [12,20]. This protracted onset is evident in comparing size–frequency distributions of populations in Tasmania with those in New South Wales,
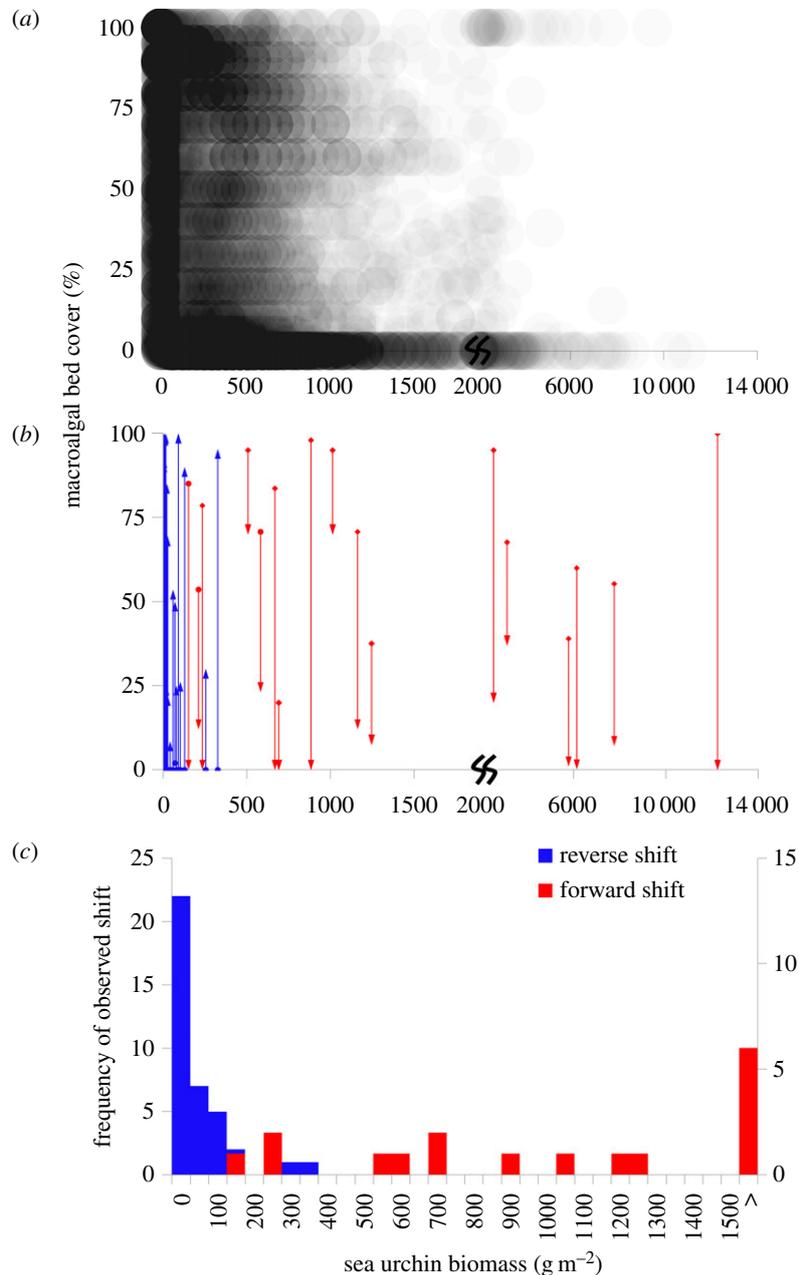
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Figure 3. Global regime-shift dynamics between cover of macroalgal beds and sea urchin barrens across increasing urchin biomass. (*a*) Macroalgal bed cover versus sea urchin biomass; presented as a scatter plot with intensity of shading representing frequency of particular macroalgal cover/urchin biomass combinations for all available rocky reef quadrats ($n = 10\ 151$) sourced from 13 regions globally (after electronic supplementary material, table S1). (*b*) Observed direction and magnitude of shifts in macroalgal cover versus sea urchin biomass; red arrows indicate forward shift from macroalgal beds to urchin barrens; blue arrows indicate reverse shift recovery from urchin barrens back to healthy macroalgal beds, $n = 57$ observations globally (after electronic supplementary material, table S2); (*c*) frequency histogram of studies observing forward (red, $n = 17$) and reverse (blue, $n = 40$) regime shifts across increasing sea urchin biomass; frequency distributions were significantly different (Kolmogorov–Smirnov test; $D = 0.95$, $p < 0.0001$), as were means (1-way ANOVA, stabilizing transformation = urchin biomass$^{0.2}$, $F_{1,55} = 100.4$, $p < 0.0001$). Note that to effectively display the full range of urchin biomass in (*a,b*), *x*-axis tick marks increase by units of 500 until axis break, with units of 4000 thereafter.

where long-established urchin populations appear to have driven down kelp abundance to a greater extent. It suggests that the time required for urchin populations to build to threshold levels for overgrazing, in addition to the time course of transition from kelp to barrens itself, is much longer than commonly perceived (see 'Living on borrowed-time concept' [32]). Once a trajectory of rapid population growth and accumulation of urchin biomass on rocky reefs is initiated, overgrazing is likely to ensue unless urchin abundance is somehow held below the threshold for barrens formation. Thus, the current state of the ecosystem and its resilience to external stressors, including influx of settling urchins, are key determinants of the likelihood of regime shift.

(c) Reinforcing feedbacks and stressors eroding resilience

Rocky reef systems are influenced by myriad complex interactions between physical and biological processes acting across a wide spectrum of spatial and temporal scales (reviewed by [2,3,11]). For systems that exhibit discontinuous 'catastrophic' regime-shift dynamics between alternative states, understanding the self-maintaining positive-feedback mechanisms that confer resilience (i.e. persistence stability [33]) of a state to external stressors is critically important [9,20]. Various positive feedback mechanisms maintain the stability of macroalgal and urchin barrens states (table 1*a*; see also [3]), and the stressors

Table 1. Feedbacks and stressors of alternative macroalgal-dominated and urchin barren rocky reef states. (a) State-dependent mechanisms creating positive feedbacks reinforcing resilience of each alternative reef state (see also review by Filbee-Dexter & Scheibling [3]). (b) State-dependent processes that erode resilience of each alternative reef state. Panels shaded in blue indicate feedbacks and processes favouring maintenance and recovery of desirable macroalgal beds; red shading indicates unfavourable regime shift and maintenance of the unwanted urchin barrens state. Note that human-derived stressors are indicated by asterisks and that multiple stressors, both human-derived and natural processes, may interact to either maintain or erode resilience in additive, synergistic or antagonistic manners (e.g. asterisks within parentheses indicate physical processes influenced by anthropogenic-forcing on global climate).

(a) state-dependent feedbacks reinforcing resilience		(b) state-dependent stressors decreasing resilience	
macroalgal beds	**reference**	**macroalgal beds to urchin barrens**	**reference**
presence of functional urchin predators		*overharvesting of urchin predators	[4,9,34–36,38]
—macro-predators	[4,9,34–38]	multi-trophic consequences of prey-switching	
—micro-predators	[39]	by natural predators	[62]
*presence of human urchin harvest/urchin culling	[40]	*kelp disease/overgrowth by invasive algae/epiphytes	[28,61]
(*)presence of urchin disease	[28]	*direct removal of kelp	
high macroalgal productivity		—human harvest	[63]
—local standing macroalgae	[29]	(*)acute physical change	
—distant allochthonous inputs	[41,42]	—storms/ extreme weather	[63]
large macroalgal bed biomass (patch-size dynamics)	[16,19,43]	—warm periods promoting sea urchin larval survival	[64]
propagule supply (connectivity)	[4,44]	—cool periods promoting sea urchin recruitment	[65]
natural barriers to urchin movement		(*)chronic physical change	
—high swell/ current exposure	[45]	—declining algal productivity due change in oceanography/ catchment processes	[63,66]
—macroalgal whiplash	[16,46]	—declining algal productivity of allochthonous macroalgal 'drift' supply	[67]
		—range-extension of urchins	[10,68]
		other mesograzers	[60,69]
urchin barrens	**reference**	**urchin barrens to macroalgal beds**	**reference**
diet switching from large macroalgae to encrusting/ filamentous forms	[4]	presence of functional urchin predators	[9,34–36,38,70,71]
*continued harvesting of urchin predators	[35,47]	*human urchin harvest/urchin culling	[40,72]
increased urchin foraging rates causing high mortality of juvenile kelp	[4,48–51]	(*)increasing macroalgal productivity due to strengthening wave conditions	[48,73]
reduced urchin dislodgement due to absence of kelp whiplash	[16,46]	urchin disease	[74,75]
increased urchin recruitment in absence of macroalgae	[10,16,52,53]	(*)acute physical change	
reduced predation in absence of kelp:		—hurricane events leading to increased urchin disease	[76]
—increased spine length	[16]	—freshwater flood events	[77]
—decreased palatability for human harvest and/or natural predators	[16,52,54,55]	(*)chronic physical change	
facilitation of juvenile survival by adults:		—increasing temperature increasing urchin disease	[78]
—reducing micro-predator abundance by eliminating macroalgae	[39]	—increasing temperature reducing urchin settlement	[79]
—offering refugia under adult urchin spine canopy	[56–59]	— increasing temperature causing range-extension of urchin predators	[80]
increasing barren size (patch-size dynamic)	[43]		
reduced macroalgal propagule supply	[44]		
increased abundance of mesograzing invertebrates	[60]		
*local presence of invasive algae/ ephemeral algae and epiphytes restricting kelp re-growth	[61]		

capable of eroding resilience are also state-dependent (table 1b). While state-dependent stressors can be identified separately, they rarely act in isolation. Therefore, predicting interactions among multiple stressors, including anthropogenic climate change [81] and overfishing [9,18], is fundamental for managing systems prone to catastrophic regime-shift dynamics (table 1).

The ability of sea urchin predators to control sea urchin abundance, and to effect trophic cascades, underscores the importance of state-dependent feedbacks and hysteresis in the urchin-grazing system (table 1). That is, hysteresis in this system means that approximately one order of magnitude more urchin biomass must be consumed by predators to revert barrens to macroalgal beds compared with that required to maintain the macroalgal-dominated state by keeping urchin density just below the critical forward-shift threshold. Furthermore, this hysteresis is compounded as urchins are less vulnerable to predation when occurring on barrens owing to longer protective spines, a greater abundance of individuals for a given biomass, decreased palatability and an overall reduction in predator abundance on rocky reefs in the absence of macroalgal habitat (table 1). Thus, while the role of predators in controlling the abundance of sea urchins features extensively in the literature [2,13], this pivotal hysteresis has not been considered. Our global synthesis indicates that

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management of urchin grazing, including attempts to remedy urchin grazing by facilitating recovery of urchin predators, must be squarely underpinned by this hysteresis effect. Implementing such management can be achieved by employing a 'resilience-based approach' focused not only on building resilience of the desirable macroalgal bed state, but also committing to the more difficult task of eroding resilience of the unwanted urchin barrens state once it has formed (table 1; see also [82,83]).

5. Conclusion

Globally, the occurrence of urchin barrens on rocky reef represents an unwanted regime shift from the desirable kelp bed state, which proves difficult to reverse. Hence, onus must be squarely placed on understanding when this type of system is approaching its tipping point, so that collapse of desirable ecosystem states may be avoided. For ecosystems displaying such discontinuous 'catastrophic' regime-shift dynamics, increasing resilience of desirable ecosystem states before a shift occurs will be much more effective than attempts to break resilience of unwanted ecosystem states once the system has moved to a new self-reinforcing regime (table 1). That is, the herein defined globally coherent catastrophic regime shift supports a general rule that small amounts of prevention will be far more effective than large amounts of

cure for collapsed ecosystems. Defining such regime-shift dynamics and the potential state-dependent feedback mechanisms at play is therefore crucial for any attempt to manage this type of system for maximum social and ecological benefit [83]. Such practical understandings are urgent in an era of increasing human-derived stressors, many of which interact (table 1) to accelerate the frequency, extent and irreversibility of ecosystem change from local to global scales.

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