

LETTER

Grazer behaviour can regulate large-scale patterning of community states

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Abstract

Ecosystem patterning can arise from environmental heterogeneity, biological feedbacks that produce multiple persistent ecological states, or their interaction. One source of feedbacks is density-dependent changes in behaviour that regulate species interactions. By fitting state-space models to large-scale (~500 km) surveys on temperate rocky reefs, we find that behavioural feedbacks best explain why kelp and urchin barrens form either reef-wide patches or local mosaics. Best-supported models in California include feedbacks where starvation intensifies grazing across entire reefs create reef-scale, alternatively stable kelp- and urchin-dominated states (32% of reefs). Best-fitting models in New Zealand include the feedback of urchins avoiding dense kelp stands that can increase abrasion and predation risk, which drives a transition from shallower urchin-dominated to deeper kelp-dominated zones, with patchiness at 3–8 m depths with intermediate wave stress. Connecting locally studied processes with region-wide data, we highlight how behaviour can explain community patterning and why some systems exhibit community-wide alternative stable states.

KEYWORDS

alternative stable states, behaviour, dynamical models, kelp forests, spatial patterning

INTRODUCTION

Spatial patterning in community types characterises many ecosystems. For example, in arid ecosystems patches of shrubs and barren soil 25 m in diameter form mosaic patterns (Klausmeier, 1999). On mountain ranges, strips of ribbon forests 500 m wide intersperse with wider bands of grassy meadows (Hiemstra et al., 2006). A longstanding focus of empirical and theoretical work has aimed to resolve the processes generating ecosystem patterns and their spatial scale.

Spatial patterning may occur due to underlying environmental heterogeneity, local biological feedbacks, or an interactive combination of both drivers (Rietkerk & Van de Koppel 2008). Examples of environment-driven patterns include gradients in desiccation stress

that zone intertidal communities from heat-tolerant to more sensitive species with increasing water depth (Dayton, 1971). Patterning can also arise when biological feedbacks reinforce distinct ecological states. If interactions change from positive to negative with the distance between individuals, self-organised patterns of populated and empty areas occur in homogeneous environments, as seen in shrub mosaics in arid ecosystems (Rietkerk & Van de Koppel 2008). Feedbacks that do not change sign with distance can also drive patterns over large scales by amplifying the effects of ecosystem heterogeneity. For instance grasses predominate in areas of low-moderate herbivory by diluting grazing across many plants while areas with elevated livestock densities exhibit a disproportional plant density collapse via overgrazing (Noy-Meir, 1975). In all cases,

feedback-induced patterning requires strong and often nonlinear species interactions.

One possible driver of biological feedbacks is density-dependent changes in behaviour (Peckarsky et al., 2008). Herbivory can decline in the presence of predators (McPeck & Peckarsky, 1998) or increase when herbivores form large groups that reduce predation risk (Gil et al., 2018). On coral reefs, for instance the activity of herbivorous fishes as part of schools can account for 68% of total consumption (Gil & Hein, 2017) and influence the potential for coral-dominated or algal-dominated community states (Gil et al., 2020). Density-dependent changes in behaviour could also create biological feedbacks, for example when dense plant aggregations increase predation risk and decrease herbivory rates, feeding back to increase local plant recruitment. This forms one possible mechanism for why plant stands expand after predator re-introduction (e.g. wolves in Yellowstone, Fortin et al., 2005) and recede around refugia from predation following herbivore recovery in the intertidal (Matassa & Trussell, 2011) and on coral reefs (Madin et al., 2019). However, because isolating the effects of behaviour from herbivore density is challenging over large scales (e.g. direct vs. indirect predator effects, Creel & Christianson, 2009), comparing models with and without behaviour can provide the next step towards understanding whether behaviour can underpin community patterning.

Temperate rocky reefs exemplify each of patterned communities, behaviour-mediated herbivory and environmental variation. Patterning of two distinct ecological states in these ecosystems, kelp forests and urchin-dominated barrens (Figure 1a, c), can occur at drastically different scales in different regions. Whereas large-scale (> 1 km) barrens and forests span all depths on California reefs (Figure 1d; Cavanaugh et al., 2014), in New Zealand metre-scale patchiness occurs at intermediate depths while kelp occupies deeper water and urchins shallower zones (Figure 1b; Parsons et al., 2004). This difference in patchiness scales might arise from a greater sensitivity of the dominant kelp species in New Zealand to wave stress in shallow areas (Grace, 1983) and more intensive, larger-scale pulses of urchin recruitment (Hart & Scheibling, 1988) or mortality (Lafferty, 2004) in California.

Regional differences in temperate reef patchiness could alternatively (or additionally) arise from differences in urchin behaviour. Urchins can exhibit two feeding modes: passive grazing on kelp fronds detached from plants and carried to the bottom by currents ('drift kelp' hereafter), typically while occupying cryptic habitats (e.g. crevices) protected from predators and physical stress, and active grazing on the open substrate (Dayton, 1985a; Harrold & Reed, 1985). In New Zealand, urchins switch to active grazing in local 1–5 m² patches when sub-canopy kelp densities become insufficient to deter active grazing via physical abrasion (kelp 'whiplash' effects, Konar, 2000) or by attracting urchin

predators (Cowen, 1983; Figure 2e). In California, giant kelp concentrates biomass in large canopies well above the seafloor, reducing local abrasion while increasing reef-wide drift kelp subsidies. A switch to active grazing can therefore happen synchronously across each reef in California when low kelp densities and low drift kelp subsidies to the seafloor cause reef-wide urchin starvation (Ebeling et al., 1985; Harrold & Reed, 1985; Figure 2d). As declines in kelp density increase grazing activity locally (in New Zealand) or reef-wide (in California) and feed back to further deplete kelp, we hypothesise that behaviour can create region-specific community patterning. The ability of behavioural feedbacks and distinct states to explain temperate reef spatial patterning also informs whether urchin barrens and kelp forests occur as alternative stable states, a long-debated phenomenon in rocky temperate reefs (Petraitis & Dudgeon, 2004).

Here we evaluate whether or not behaviour can affect large-scale community patterns in temperate rocky reefs by comparing observed patterns to predictions from models that incorporate environmental gradients, urchin density and behavioural changes in urchin grazing. We represent behavioural changes in urchin grazing using a functional response with decreased grazing rate at high kelp densities, as might occur with a shift in grazing mode from active to passive with increased kelp density. The kelp density that affects grazing can be local as urchins avoid predators or abrasion or reef-wide as urchins passively graze on drift kelp. First, we test whether accounting for behavioural feedbacks better explains observed data, both compared to and in combination with environmental gradients. Second, we test whether the best-fitting behavioural feedbacks differ in spatial scale between regions and produce observed differences in patterning between New Zealand and California. Third, we test whether the best-fit models include alternative stable states, and if so, at what spatial scale.

MATERIALS AND METHODS

In this section, we first describe our systems' data used to characterise kelp patterning and environmental drivers. Second, we describe our full model with environmental gradients, grazing and behaviour, from which we can exclude individual elements to explore processes alone or in combination. Third, we describe analyses of (a) which factors best explain the data, (b) how incorporating behaviour affects patterning in each region and (c) whether best-fit models include alternative stable states.

Study systems

We focus our analysis on temperate rocky reefs in Northeast New Zealand (NZ) and the California

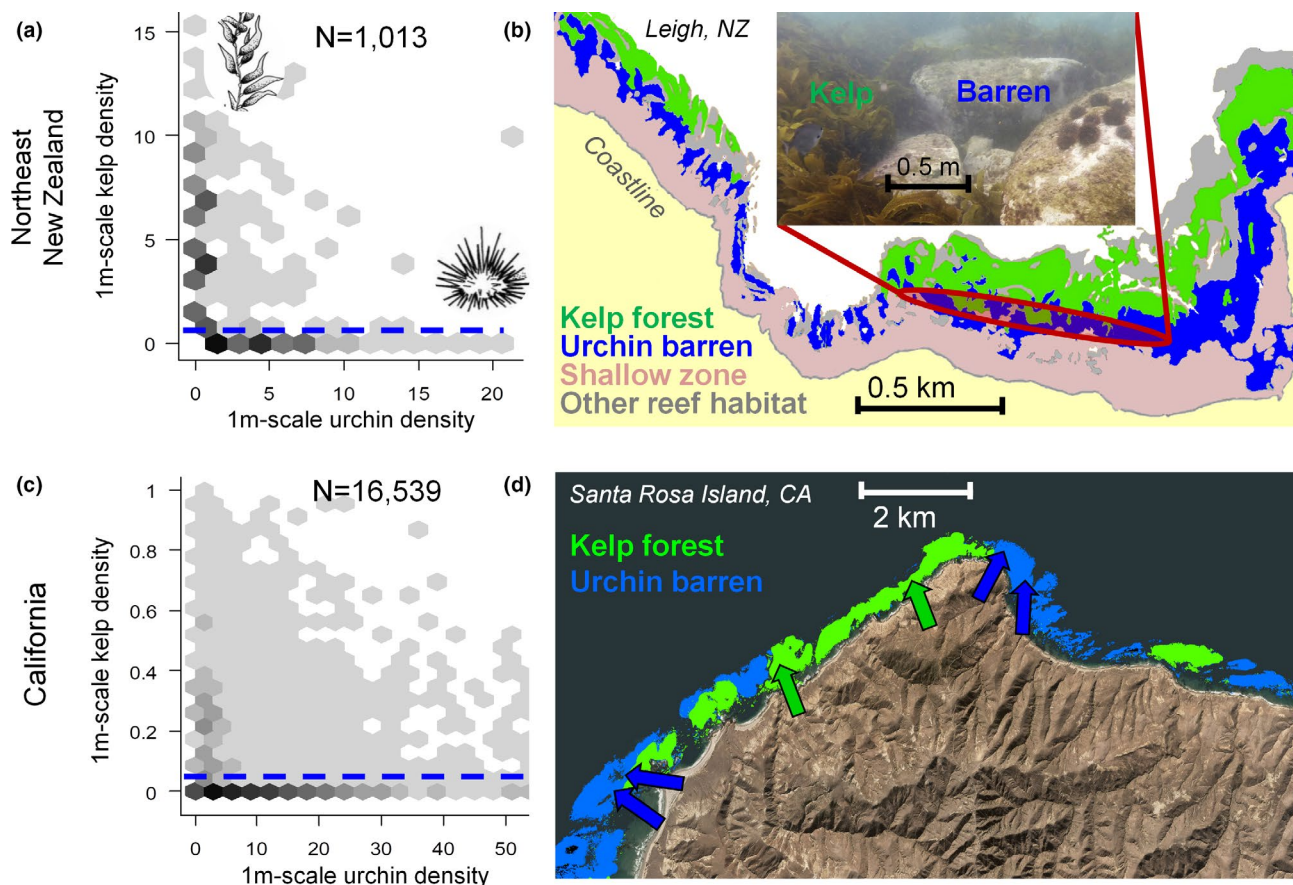


FIGURE 1 Visualisation of kelp and urchin density in New Zealand (a, b) and California (c, d). (a, c) Region-specific distribution of kelp- and urchin-dominated states with N indicating total numbers of samples. Dashed lines in (a, c) denote kelp threshold densities used to categorise community regimes as forested (i.e. exceeding the 10th quantile of kelp densities in samples with kelp in each region) and barren otherwise. (b) Depth zonation of New Zealand reef communities 2 years after the establishment of the Leigh Marine reserve, reproduced from Leleu et al. (2012). Inset in shows the local kelp and barren patchiness in mid-depth zones, and ‘shallow zone’ denotes intertidal and shallow sub-tidal areas dominated by wave-tolerant brown algal species other than *Ecklonia*. (d) Reef-scale patchiness of forest and barren community states at Santa Rosa Island, California in 2016 from satellite imagery (shaded areas) and 6 monitoring sites (arrows, with arrow colour denoting site state). See Appendix A for details on state estimation from satellite imagery and density measurements in (a, c). Note that exact state classifications may differ between panels (a) vs. (b) and (c) vs. (d)

Northern Channel Islands (CA) dominated by kelp (*Macrocystis pyrifera*, CA, and *Ecklonia radiata*, NZ) or urchins (*Strongylocentrotus purpuratus*, *Mesocentrotus franciscanus* in CA and *Evechinus chloroticus* in NZ). Like many temperate reefs, fast kelp growth and intense urchin grazing characterise these systems: abundant urchins can denude kelp forests in weeks, while under low urchin densities kelp can recolonise barrens within a few months (Ebeling et al., 1985). In contrast, urchin populations experience lower turnover and fluctuate more gradually in response to urchin predator abundance and multi-year changes in ocean climate (Okamoto, 2014; Shears et al., 2012). This difference in time scales means that kelp abundance and urchin grazing activity can reach steady state under a given urchin density, whereas urchin density depends little on local kelp abundance due to demographic openness (Okamoto, 2014) and can remain high in the absence of kelp (Filbee-Dexter & Scheibling, 2014; Ling et al., 2015).

Data for kelp spatial patterns and environmental drivers

We use surveys of kelp density spanning 200–300 km coastlines in each region, with 71 reefs sampled in 2001 in New Zealand (Shears & Babcock, 2004) and 93 reefs sampled over 5–30 years in California (Caselle et al., 2018; Kushner et al., 2013). This geographical extent allows us to disentangle the effects of multiple processes by sampling a wide range of environments and increases the robustness of our results to inter-annual variation in the environment by exceeding the spatial scales of storms, upwelling variability or recruitment pulses (8–50 km; Cavanaugh et al., 2013; Karatayev & Baskett, 2020).

Samples in both systems were collected at the end of the kelp growing season (July–August in CA, March–June in NZ) and span 100–500 m² of each reef s (see Appendix A for details on dataset and sampling methodologies). At the reef scale, we account for potential

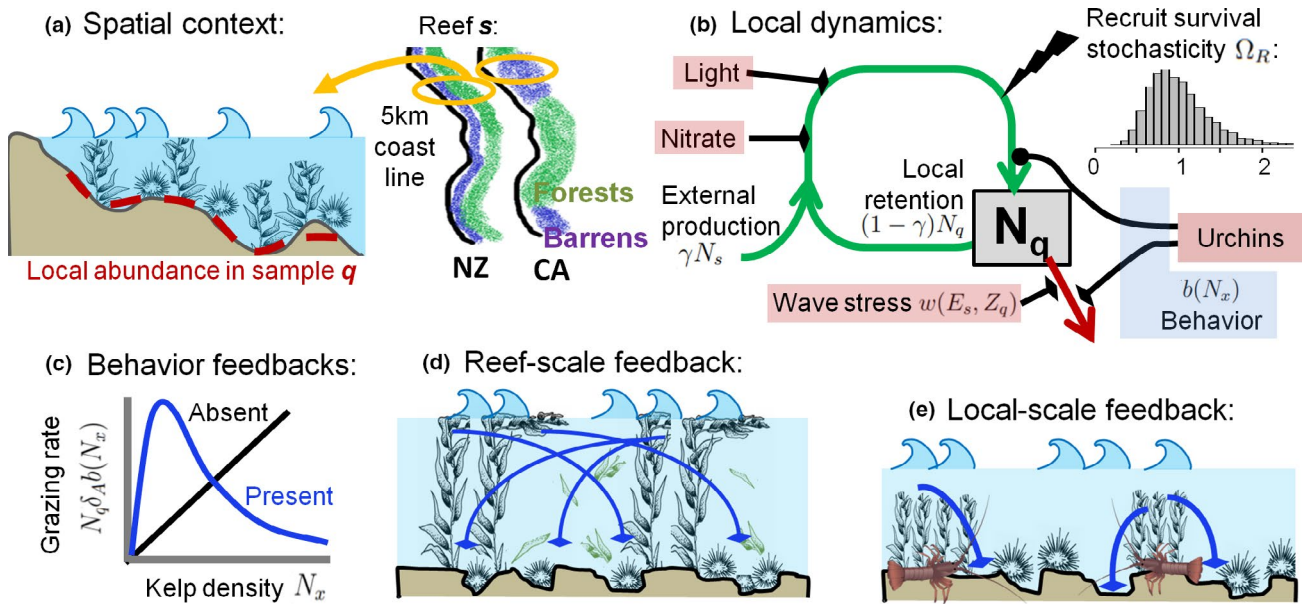


FIGURE 2 Model layout. (a) Local samples (red bars) on each reef span a depth gradient that influences wave intensity and light attenuation. Across reefs, forested and barren community types follow depth zonation in New Zealand but span entire reefs in California. (b) Dynamics of local kelp abundance N_q depend on environmental factors (red boxes), stochasticity and urchin behaviour (blue box) that affect adult survival (red arrow) or recruitment (green arrows). Circular endpoints on lines denote negative effects and flat endpoints denote positive effects; stochasticity in recruit survival Ω_R (lightning bolt and inset distribution) can have positive ($\Omega_R > 1$) or negative ($\Omega_R < 1$) effects. (c) Functional form of grazing with behavioural feedbacks absent (black) or present (blue), where grazing rate declines with either local ($N_x = N_q$) or reef-wide ($N_x = N_s$) kelp density through urchin shifts from active to passive grazing. (d) Reef-scale feedbacks where passive drift kelp subsidies at high kelp densities N_s reduce urchin grazing across the reef (blue lines), as expected to be relevant in California. (e) Local-scale feedbacks where predators and physical abrasion in dense kelp stands deter grazing locally (blue lines), as expected to be relevant in New Zealand

environmental drivers of kelp dynamics, including total urchin predator density P_s (Caselle et al., 2018; Shears et al., 2008), wave stress E_s (Cavanaugh et al., 2011) and temperature-derived nitrate concentration G_s (Table S1). In the model below we omit nitrate limitation, which did not affect preliminary fits (Appendix A). Each reef was sampled using transects with 15–50 1–20 m² quadrat samples spanning a ~15 m water depth gradient (2018 NZ samples, 16,539 CA samples). Within each quadrat q , we account for densities (ind m⁻²) of adult kelp plants and urchins (> 25 mm test diameter, U_q), water depth Z_q (which attenuates waves) and near-bottom light availability L_q . While *Ecklonia* can inhabit shallower depths than *Macrocystis*, in New Zealand we omitted 228 shallow (< 3 m) samples where wave-tolerant algae displaced both *Ecklonia* and urchins (Appendix A); we also omitted 777 samples along continuous transects that recorded *Ecklonia* presence but not density.

Model description

Our model follows the dynamics of adult kelp abundance N_q in 1–5 m² locations q across a 0.1–0.5 km² reef s (Figure 2a). We model kelp reproduction, spore survival and adult survival as they depend on either local kelp density or kelp density averaged across the reef $N_s = k^{-1} \sum_{q=1}^k N_q$ and reef-wide or local environmental

factors. This model structure can produce kelp- and urchin-dominated regimes that form localised mosaics, gradients along depth-dependent environmental factors, or one regime spanning an entire reef. Below we describe the full model with all drivers, where zeroing out individual dynamics yields sub-models with different driver combinations.

Kelp reproduces continuously during the year with a baseline fecundity m . Newly produced spores can disperse over short distances (< 500 m for *Macrocystis*, Anderson & North, 1966; Reed et al., 1992). Therefore, we model the amount of spores r arriving in a location q as (1) the proportion γ of all spores dispersing throughout the reef plus (2) the proportion $1 - \gamma$ of locally produced spores dispersing < 5 m:

$$r(N_q, N_s) = m(\gamma N_s + (1 - \gamma) N_q). \quad (1)$$

Survival of settled zygotes into adult sporophyte stages depends on both local and reef-scale factors. To incorporate the environmental gradient in light, we assume light availability increases with measured visibility L_q given proportionality constant g_L and declines with local density dominant adults N_q given proportionality constant d (Dayton, 1985a). Due to their greater palatability compared with adults, juveniles also experience high rates of urchin grazing δ_R proportional to local urchin density U_q , which can depend on behaviour according to the

function $b(N_x)$, as described below. We account for environmentally driven stochasticity in survival, as might be due to thermal stress or interspecific competition, using a log-normally distributed random variable Ω_R . Finally, given fast maturation (2–3 months) and high sensitivity of juveniles to competition and grazing, we assume juvenile abundance quickly reaches steady state on the time scale of adult kelp abundance, so that overall recruit survival is

$$S_R(N_q, N_x) = \frac{\Omega_R(1 - g_L + g_L L_q - dN_q)}{1 + \delta_R U_q b(N_x)}. \quad (2)$$

Adult mortality depends on local-scale urchin grazing and wave stress E_s . To incorporate the environmental gradient in wave stress, we model wave stress dissipation by depth Z_q at more exposed sites following Bekkby et al. (2008). Dissipation depends on region-specific oceanographic features and weakens at exposed sites, represented by f_w and scaling factor μ . Per-capita adult mortality to wave stress is then

$$w_q(E_s, Z_q) = \mu E_s \exp(-f_w Z_q E_s^{-1}). \quad (3)$$

Grazing on adults occurs at a per-urchin rate δ_A , as with recruit survival can depend on behaviour according to $b(N_x)$ described below. Thus, per-capita adult mortality from grazing is

$$v_A(N_x) = \delta_A U_q b(N_x). \quad (4)$$

To incorporate a feedback between kelp density and urchin behaviour in grazing, we assume urchin density is constant on the time scale of annual kelp dynamics but grazing rate can dynamically depend on adult kelp density ('behaviour feedbacks' hereafter). Specifically, we incorporate the potential for a decline in grazing rate at high kelp densities, as might occur due to a switch from active to passive grazing mode, with a per-kelp grazing inhibition factor ξ_A in a generic 'Type IV' functional response (Bate & Hilker, 2014; Koen-Alonso, 2007). Dependence of this function on local-scale kelp density $N_x = N_q$ represents local-scale feedbacks involving physical abrasion (expected in NZ), and dependence on reef-scale kelp density $N_x = N_s$ represents reef-scale feedbacks where drift kelp availability affects cryptic urchin behaviour and associated direct grazing on kelp (expected in CA). Urchins may additionally avoid active grazing on reefs with high predator abundance P_s . We integrate a per-predator grazing inhibition rate ξ_P over the entire year to arrive at the proportional decline in grazing due to predator avoidance, $\exp(-\xi_P P)$ (see Appendix B for separating predator effects on density vs. behaviour). Altogether, behaviour-mediated decline in urchin grazing is

$$b(N_x) = \frac{\exp(-\xi_P P)}{1 + \xi_A N_x^2}. \quad (5)$$

The overall dynamics of local kelp abundance are then

$$\frac{dN_q}{dt} = r(N_q, N_s) S_R(N_q, N_x) - w_q(E_s, Z_q) N_q - v_A(N_x) N_q. \quad (6)$$

Role of urchin behaviour

To compare the role of potential drivers (environmental, urchin density, behavioural), we compare the best fit of the full model (Eqn. 4) and simpler models that omit the effects of environmental factors ($\mu = g_L = 0$), grazing ($\delta_i = 0$), urchin predator avoidance ($\xi_P = 0$) and kelp-density feedback on urchin grazing rate ($\xi_A = 0$), each individually and in combinations. In Appendix C, we additionally evaluate whether herbivory dilution in a saturating Type II functional response, a behaviour-independent feedback, can explain kelp patterning. We separate fits by region to estimate region-specific parameters. Given high kelp growth rates and our end-of-growing-season surveys (see 'Study system'), we assume kelp densities reach steady state within one year. Therefore, we fit model equilibria to observed kelp abundance (i.e. a state-space model) and verify that best-fit models reach equilibrium within one year in Appendix D. Our approach assumes kelp densities at a reef are independent among consecutive years, an approximation we verify in Appendix E.

To evaluate model performance, we numerically solve models for the steady-state kelp abundance under the observed conditions (Table S1) in each sample and year, and then compare these predictions with observed kelp densities. We use a Runge–Kutta solver (R 3.4.3, deSolve package) with initial kelp abundance across the reef initially high or low (80th and 5th quantiles of observed densities in samples with kelp). Low initial abundance can occur when senescence pulses (in NZ) or storms (in CA; Cavanaugh et al., 2011) precede the growing season. To account for a range of possible recruitment conditions over the preceding year, we additionally solve the model under 10 realisations of Ω_R starting from each initial condition (i.e. 20 total realisations, Figure 2c; Ω_R realisations identical across samples and models). To implicitly account for multiple secondary factors that allow kelp to occur in apparently adverse conditions (e.g. microsubstrate), we round predicted densities of 0 to 0.01.

For each quadrat, we compute the Poisson probability of the observed kelp count under each realisation, and average these probabilities across realisations to reflect that observed densities can arise from any combination of initial abundance and recruitment conditions (Gelman et al., 2013). We then calculate the logarithm of this marginal likelihood and, summing across all samples in the region, arrive at the total model log likelihood under a given parameter set. We find the best-fitting parameter sets using the DIRECT (global) followed by COBYLA (local) optimisation algorithms in nloptr (Jones et al. 1993; Johnson, 2019) and compare models

based on Bayesian Information Criterion differences (ΔBIC), where $\Delta\text{BIC} > 4$ indicates improved model fit (Bolker, 2008). We additionally calculate the squared correlation between predicted and observed (1) kelp densities R_N^2 and (2) reef states (as defined below) R_S^2 averaged across S_R realisations, choosing best-fitting initial conditions when models predicted two stable states.

As outlying kelp density observations favoured maximal variation in Ω_R , in the main analysis, we set the Ω_R distribution mean to 1 and standard deviation to $\sigma_R = 0.35$ based on year-long recruitment experiments Moreno and Sutherland (1982) (i.e. distribution parameters $\mu = \log(\sigma_R^2 + 1)^{-0.5}$, $\sigma = (\log(\sigma_R^2 + 1))^{0.5}$). In Appendix E, we evaluate model ranking robustness to $\pm 30\%$ changes in σ_R , urchin-species-specific grazing, site effects and temporal autocorrelation.

Drivers of community patterning and presence of alternative stable states

To resolve how grazing and wave stress gradients can jointly pattern communities, we use the best-fitting models from each region to project predicted kelp abundance over the observed range of reef-scale urchin densities. Within each reef, we simulate 30 locations spanning the sampled depth range. Throughout, we set urchin distribution across depths and reef-scale wave stress, light availability and predator density to the average values observed in the data. We compare model projections with observed kelp patterns smoothed using 2-D splines.

To evaluate the role of behaviour in explaining specific aspects of observed community patterns, we compare survey results with predictions of our best-fitting models with and without behavioural feedbacks. For this, we first categorise the community state in each sample and model prediction (Figure 1a, c). Given that urchins can maintain barrens even when rare (Ling et al., 2015), we classify samples and predictions with urchins and few kelp (CA: ≤ 0.05 individuals m^{-2} , NZ: ≤ 1 individual m^{-2} , 10th density quantiles in samples with kelp, Figure 1a,b) as urchin-dominated, omit samples with no urchins and few kelp (NZ: 10% of samples, CA: 2%) and classify remaining samples as kelp-dominated. For within-reef patterning, we focus on a subset of reefs sampled by placing quadrats end-to-end in contiguous line transects (777 NZ samples, 5644 CA samples) and quantify patch sizes as the number of adjacent samples with the same community regime.

RESULTS

Role of urchin behaviour

Behaviour-mediated grazing in California and an interactive effect of behaviour-mediated grazing and environmental variation in New Zealand predominantly

explains patterns in field data (Table 1). Best-fitting models in both regions include all three of environment, grazing and behaviour, and explain much of the variation in community states (NZ $R_S^2 = 0.47$; CA $R_S^2 = 0.49$). In models with behaviour, local-scale grazing feedbacks (i.e. kelp-density-mediated grazing) in New Zealand and reef-scale grazing feedbacks in California best explain the data (Table 1). In California, models with grazing and behavioural feedbacks only outperform models with grazing and environmental factors only ($\Delta\text{BIC} = 567$). In both regions, models with behaviour feedbacks outperform models without behaviour because they can explain the co-occurrence of high and low kelp densities at intermediate urchin densities (Figure 3). We find a similar model ranking when controlling for higher red urchin grazing rates, temporal autocorrelation, site effects and different levels of σ_R (Appendix E). We did not find support for Type II grazing saturation (Appendix C).

In both regions, behaviour improved model fit predominantly through kelp-density feedbacks as compared to predator-density-mediated behaviour. Models with environment and kelp-density-mediated behaviour outperformed models with environment and predator-density-mediated behaviour (CA $\Delta\text{BIC} = 7561$; NZ $\Delta\text{BIC} = 415$). Nevertheless, best-fit declines in grazing via predator avoidance appeared strong (up to 78% in CA, 26% in NZ) and strongly improved model fit in California ($\Delta\text{BIC} = 2272$). Lower support for predator avoidance in New Zealand possibly arose because few reefs had abundant predators or because predators congregate in kelp stands, an effect already captured by local kelp-density feedbacks.

Drivers of community patterning

The local scale of kelp-density behavioural feedbacks, combined with a decline in wave stress with depth, best explains the much smaller scale of community patterning in New Zealand than in California. In New Zealand, our best-fitting model predicts barrens as the only stable state in shallow areas (< 3 m) due to a combination of grazing and high wave stress (Figure 4b). At greater water depths that largely attenuate waves (> 8 m), we predict forests are the only stable state because kelp quickly forms dense stands that inhibit grazing. At intermediate wave stress between these zones, we predict that alternative stable states span $1\text{--}5\text{m}^2$ patches, where urchins concentrate grazing outside of dense kelp stands. This interface occurs at greater depths and urchin barrens cover a larger fraction of the system on reefs with greater overall urchin densities. In California, we predict that community regimes simultaneously span all reef depths due to the larger scale of grazing feedbacks (Figure 4d, Table 1).

TABLE 1 Results of model fitting and model comparison in California (top half) and New Zealand (bottom half)

E	U	B _L	B _R	B _P	m	γ	d	μ	δ_A	δ_R	ξ_P	ξ_A	f _w	g _L	BIC	Δ BIC	R _S ²	R _N ²	pA.S.S.
✓	✓		✓	✓	10.2	0.6	4.6	2.6	9	10.6	1.5	10.3		0.2	73811	0	0.49	0.22	0.32
✓	✓		✓		10.4	0.7	2.7	4.8	8.6	10		11.1		0.1	76083	2272	0.44	0.16	0.35
✓	✓	✓			8.1	0.7	4.4	4.5	9	12		12		0.2	77783	3972	0.38	0.18	0.36
✓	✓	✓		✓	8.1	1	5.4	3.1	8.9	11.6	0.9	11.8		0.2	78153	4342	0.43	0.19	0.37
	✓	✓			7.5	1	7.2		9	12		11			83162	9351	0.54	0.3	0.47
✓	✓			✓	12.1		4.2	5.5	0.5	0.2	1.5			0.3	83644	9833	0.14	0.07	0
✓	✓				6	1	4.4	2.7	0.4	0.2				0.3	83729	9918	0.14	0.08	0
	✓		✓		6	1	7.3		9	12		10.9			87028	13217	0.5	0.23	0.33
		✓			19.8	1	4.7		0.7	0.2					89557	15746	0.16	0.12	0
✓					9.5	0.8	3.3	6.8							103765	29953	0	0.01	0
✓	✓	✓		✓	6.6	0	0.3	3.5	1.7	2.2	0.3	2.3	0.2	0.4	4322	0	0.47	0.41	0.28
✓	✓	✓			6.2	0	0.3	3.5	1.7	2.2		2.3	0.2	0.4	4322	0	0.47	0.41	0.29
✓	✓				8.9	0.3	0.3	6.8	1.1	0.3			0.6	0.2	4644	322	0.27	0.32	0
✓	✓			✓	8.9	0	0.2	3.6	0.8	0.2	0.5		0.3	0.2	4737	415	0.24	0.31	0
	✓	✓			12.8	0	0.2		5.8	2.4		2.1			4803	482	0.55	0.36	0.44
	✓	✓		✓	6	0	0.3	3.8	1.7	4.5		1	0	0.4	5053	731	0.13	0.13	0.05
✓	✓		✓	✓	8.2	0	0.3	4	1.7	5.8	0.5	1	0	0.3	5110	788	0.21	0.14	0.04
	✓				6	0.3	0.2		1.2	0.2					5296	974	0.2	0.21	0
✓					13.5	0	0.2	6.9					0.1		5438	1116	0.07	0.11	0
	✓		✓		6.6	0	0.3		1.8	0.6		0			5487	1165	0.14	0.13	0.08

Check marks denote whether models include environmental factors (E), urchin grazing (U), local-scale behaviour feedbacks (B_L), reef-scale behaviour feedbacks (B_R) and predator avoidance (B_P). pA.S.S. denotes the proportion of observations for which each model predicts alternative stable states. Δ BIC denotes BIC difference compared to the best-fitting model in each region. R² columns denote squared correlation between observed and predicted reef states (R_S²) and kelp density (R_N²). Covariate units are metres for Z_{gr} and L_{gr}, E_s and P_s are proportions of their region-specific maximum values. See Appendix E for model-fitting details and sensitivity.

Presence of alternative stable states

Our best-fitting models predict that alternative stable states can occur in both regions (32% of CA samples, 28% of NZ samples, Figures 3, 4b, d). In California, predicted alternative stable states occur at the scale of entire reefs (Figure 5b, d). In New Zealand, alternative stable states occur over only a narrow range of depth-dependent wave stress intensities, such that our best-fitting model predicts that the final reef state depends little on initial kelp abundance (Figure 5a). In this region, the small scale of kelp- and urchin-dominated patches observed in data arises only in models with local-scale behaviour feedbacks (Figure 5c). This shows that the spatial scale of behavioural feedbacks can determine the scale of patterning when feedbacks produce alternative stable states.

DISCUSSION

We show that behaviour can determine the presence and scale of community patterning by mediating consumer-resource interactions in temperate rocky reefs. This potential occurs through feedbacks where kelp-density-dependent changes in urchin grazing rate amplify

consumption when resources decline, as might occur through a shift from passive to active grazing modality. The scale of this feedback determines the spatial extent of the resulting resource- or consumer-dominated community regimes. Specifically, kelp forests and urchin barrens spanning entire reefs in California Channel Islands are most consistent with large-scale feedbacks, as might occur when drift kelp are transported over large distances and starvation-induced active grazing occurs when kelp densities decline across entire reefs (Figures 4d, 5b; Table 1; Harrold & Reed, 1985). In contrast, in Northeast New Zealand feedbacks that deter grazing locally, as might occur when kelp stands increase predation or physical abrasion (Ebeling et al., 1985; Konar, 2000), can explain fine-scale patterning of community regimes organised into distinct depth zonation by a gradient in wave stress (Figures 4b, 5a). Thus, feedbacks in consumer behaviour interact with environmental heterogeneity to pattern communities at specific scales.

Our findings expand the results of prior behaviour-induced patterning studies in two ways. First, our approach disentangles the role of grazer density from behaviour by showing that models with environmental gradients and grazer densities do not predict observed patterns without also accounting for behavioural feedbacks

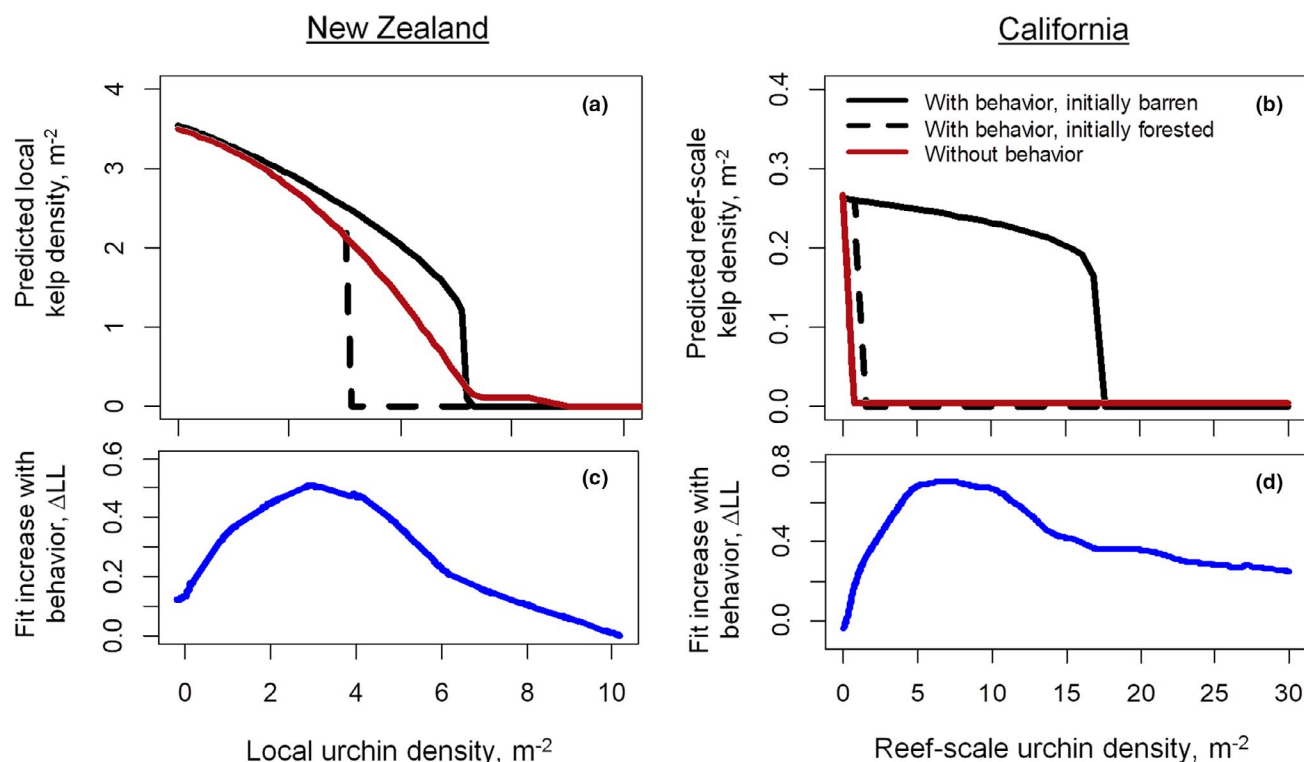


FIGURE 3 Behavioural feedbacks best explain observed patterns by predicting alternative stable kelp- and urchin-dominated states under moderate urchin densities. Here behavioural feedbacks occur through a decline in grazing rate at high kelp densities, as might occur through a shift from active to passive grazing. (a, b) Kelp density predicted by best-fitting models without behaviour (red lines) and models with behaviour (black lines) for simulations with initially high (solid lines) and initially low kelp densities (dashed lines; without behaviour, identical to the solid line). Note the comparison of local kelp densities in (a) and reef-scale kelp densities in (b), reflecting the region-specific scale of feedbacks in our best-fitting models (Table 1). (c, d) Average difference in log likelihood between models with and without behaviour. Note that lines in (a, b) denote deterministic equilibria under average environments; lower or higher levels of predators, visibility and wave stress in specific samples broaden the range of urchin densities at which models with behaviour predict alternative stable states and outperform models without behaviour

(Table 1, Figures 3, 5). Second, our best-supported models predict that behavioural feedbacks alone can create alternative stable states. Whenever localised pulse disturbances affect plant abundance (e.g. kelp loss in storms, Cavanaugh et al., 2011), this dynamic can produce persistent patterning in communities with spatially homogeneous environments and grazer densities. This extends results found in spatially heterogeneous systems, which show that behaviour can mediate boundaries between community states (e.g. grazing halos, Burkholder et al., 2013; Madin et al., 2019; Matassa & Trussell, 2011) but leave open the question of whether behaviour feedbacks generate patchiness *de novo* in uniform environments.

While our results are built around temperate rocky reef systems, the Type IV functional response in urchin grazing behaviour we include here can arise from the commonly observed phenomena of starvation-induced consumption at low resource densities or group defence at high resource densities. Starvation-induced active urchin grazing might create persistent patterns observed in California because, after overgrazing kelp, urchins can survive for decades with little food due to low metabolic costs (Filbee-Dexter & Scheibling, 2014; Ling et al., 2015). In other grazer taxa, however,

starvation might not create persistent patterns if high metabolic costs cause starvation-induced mortality or grazers emigrate to higher resource areas, and declining grazer densities allow eventual resource recovery. Group defence can arise through resource behaviour when prey forms schools or herds or, alternatively, through consumer behaviour when herbivores avoid increased predation risk (Fortin et al., 2005) or environmental stress (Konar, 2000) in dense vegetation. Persistent patterning of sparse and abundant resources, as in New Zealand reefs, can then arise when prey or plants in high-density patches exhibit group defence that shifts predation or herbivory to locations where resources are sparse (Schneider & Kefi, 2016). As with our spatial model, Type IV functional responses from either factor can lead to alternative stable consumer- or resource-dominated states in a suite of spatially implicit models where consumer density depends on resource availability (Bate & Hilker, 2014; Koen-Alonso, 2007). Therefore, in addition to expanding empirical support for Type IV functional responses, our model suggests that Type IV functional responses might warrant exploration in other consumer–resource systems as a driver of spatial patterning.

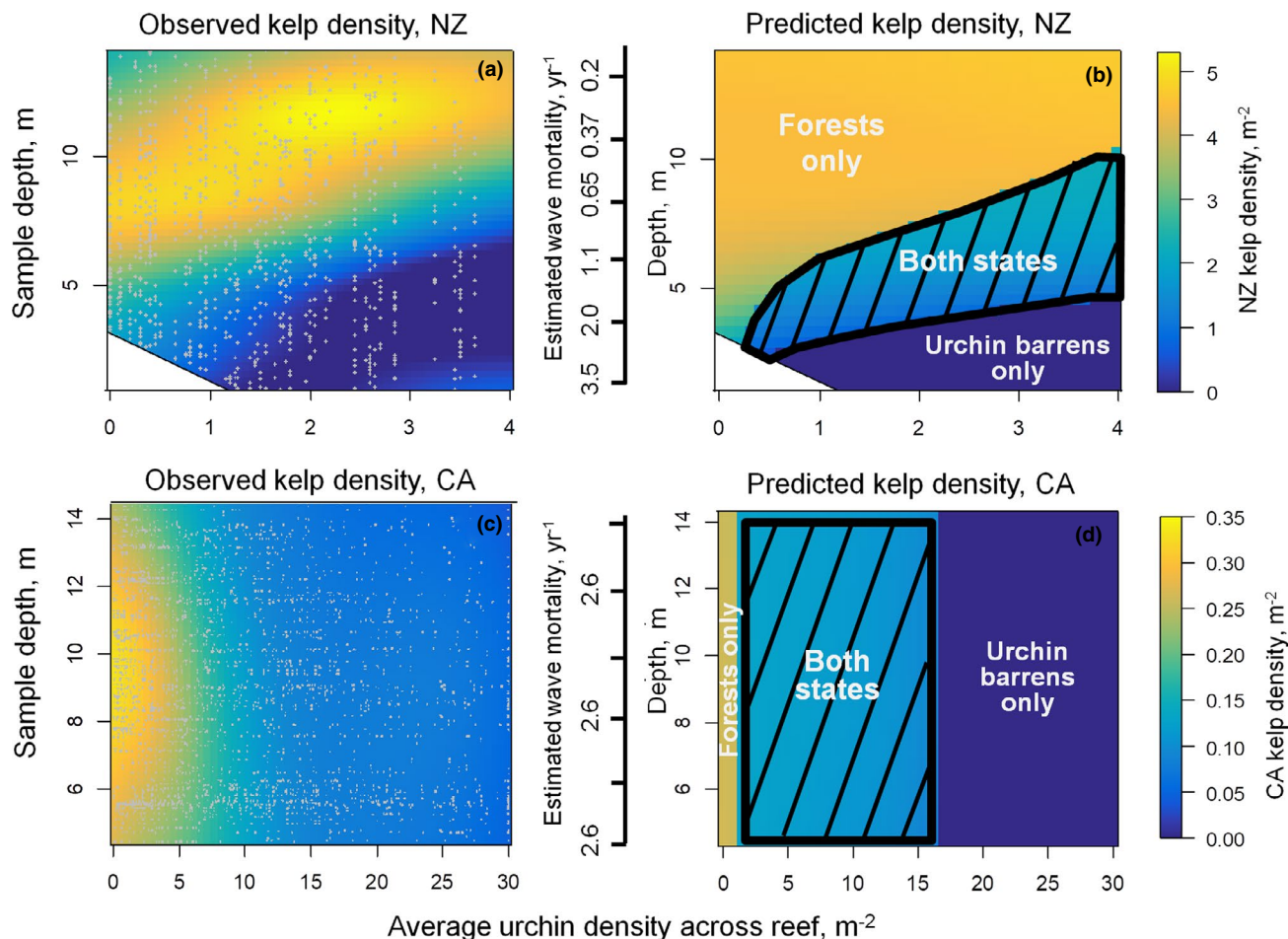


FIGURE 4 Regional differences in kelp distribution are best explained by a smaller scale of behavioural feedbacks and stronger wave stress gradients in New Zealand (a, b) compared to California (c, d). (a, c) Patterns in observed kelp density across depths on each reef (y-axes) and across reefs with increasing average urchin density. (b, d) Kelp densities predicted by best-fitting models in each region, with secondary y-axes denoting the best-fit, depth-dependent estimates of mortality induced by wave stress. Grey dots in (a, c) denote the sample coverage across these conditions, with kelp density interpolated using 2-d splines. Hashed boxes in (b, d) denote conditions for which best-fitting models predict alternative stable states with kelp present or absent

Community patterning on temperate rocky reefs

While we fit models to New Zealand and California data, our findings can inform the drivers of community patterns in temperate rocky reefs globally. Mosaics separating urchin- and kelp-dominated depth zones found in New Zealand (Figures 1, 4b, 5c) also occur in other systems dominated by sub-canopy kelp species, including northern Chile (Vásquez & Buschmann, 1997), South Africa (Ling et al., 2015) and Nova Scotia (Dayton, 1985a). Compared to canopy-forming kelp, sub-canopy kelp might reduce long-distance drift subsidies through lower total biomass (here, 0.05 kg m^{-2} in NZ vs. 2 kg m^{-2} in CA; Shears & Babcock, 2004; Cavanaugh et al., 2011) but increase short-distance urchin deterrence (e.g. ‘whiplash’, sheltering predators) as plants concentrate biomass near the bottom. Ubiquitous depth gradients in wave stress might also affect sub-canopy kelp more strongly than canopy-forming kelp because sub-canopy species can inhabit more exposed ($<2 \text{ m}$) depths while

simultaneously being largely sheltered from wave stress in deeper ($>10 \text{ m}$) areas. However, kelp-urchin zonation may be reversed with barrens forming in deeper habitats when urchins are more sensitive to wave action than kelp (e.g. Chile, Nova Scotia; Dayton, 1985a, b).

Large drift subsidies from canopy-forming kelp modelled here could underlie reef-scale grazing feedbacks and patchiness along the North American west coast. However, we expect behaviour-driven patchiness to be less prevalent where grazing has weaker effects on kelp due to greater storm disturbance (e.g. central California, Cavanaugh et al., 2011), heat stress (southern and Baja California, Bell et al., 2018), urchin disease (Lafferty, 2004) and predator densities (e.g. marine protected areas, Hamilton & Caselle, 2015). Similarly, on *Macrocystis*-dominated reefs of central Chile, urchins rely primarily on passive grazing (Vásquez et al., 1984) but in other areas can form barrens. A second reef-scale feedback that can contribute to reef-scale forests and barrens arises when kelp facilitates the recruitment of urchin

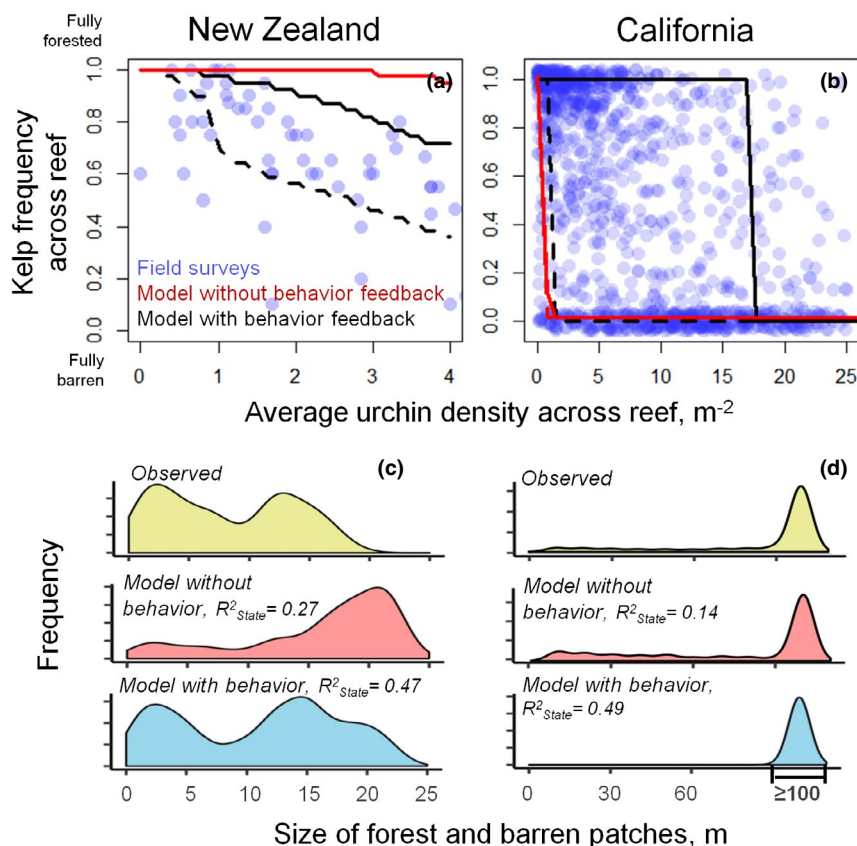


FIGURE 5 Best-fitting models with behavioural feedbacks predict alternative stable states that span a fraction of each reef in New Zealand (a) and entire reefs in California (b). (a, b) Frequency of kelp presence across reef predicted by best-fitting models without behaviour (red lines) and models with behaviour (black lines) for simulations with initially high (solid lines) and initially low kelp densities (dashed lines, identical to the solid line in the model without behaviour). Blue dots show frequencies of kelp presence across all samples on each reef, with different dots representing different reefs and (in b) reefs in different years. (c, d) Sizes of barren and forested patches in data (yellow) and in best-fitting models without (red) and with (blue) behaviour, with most patch sizes in California exceeding 100 m due to limited spatial extent of sampling. R^2_{pres} in (c, d) is the squared correlation between predicted and observed kelp presence (Table 1)

predators (Karatayev & Baskett, 2020), which freely forage across entire reefs (Topping et al., 2005). Our results highlight that behaviour might strengthen this feedback in both regions as predators deter active grazing, complementing analogous findings in California (Caselle et al., 2018; Ebeling et al., 1985). Altogether, our results suggest that large-scale patchiness in systems characterised by canopy-forming kelp could arise from shifts in feeding modality among already-present urchins rather than urchin density changes via recruitment pulses and die-offs.

Model assumptions

To avoid model over-fitting, our approach leaves out additional potential dynamics that might drive alternative stable states and therefore patterning in temperate rocky reefs. First, we do not consider competition among primary producers which might displace competitively inferior juvenile stages of *Ecklonia* and *Macrocystis*, although <10% of samples indicate competitive exclusion by lacking both kelp and urchins (Figure 1). Second, in our focus on whether or not behaviour can explain observed patterns,

we ignore many additional feedbacks hypothesised to drive (alone or in combination) alternative stable states in kelp forests (Ling et al., 2015). These additional feedbacks could increase the potential for patchiness. Furthermore, we assume kelp abundance correlates with drift kelp that drives reef-scale grazing feedbacks; future biomass data may allow more mechanistic models of grazing. Finally, seasonality in wave-induced mortality (predominantly in winter) and recruitment (predominantly in spring) might weaken our assumption that kelp abundance reaches steady state within a year. Seasonal transients can obscure distinct equilibria (Mumby et al., 2013) and cause under-estimation of alternative stable states.

We also omit several secondary urchin behaviours that in both regions can increase the role of behavioural feedbacks in particular. Available data likely underestimate California urchin densities because cryptic urchins are harder to detect, causing best-fit models to underestimate the role of behaviour in limiting grazing. Our model also omits urchin movement across the reef in response to kelp density, which can produce moving or stationary grazing fronts (Silliman et al., 2013) and in New Zealand might explain higher urchin densities in

shallower areas. However, how kelp affects urchin movement in New Zealand remains unclear because barrens do not expand following regular *Eklonia* senescence pulses. Given the strong role of behaviour in community patterning found here, we suggest future experiments and more detailed spatial models explore the drivers of urchin movement.

Detection of alternative stable states

Behavioural feedbacks drive patchy spatial patterning in our best-supported models by giving rise to alternative stable states. Therefore, our results support the relevance of this phenomenon across both regions, especially in California where large-scale feedbacks can produce alternative stable states spanning entire reefs (Figure 5b). In New Zealand, the localised scale of feedbacks limits alternative stable states to reef depths with intermediate wave stress on kelp (Figure 4). These localised states average out to produce a gradual reef-wide response to changes in urchin density and little dependence of reef state on initial kelp abundance (Figure 5a). This result supports existing theory (van Nes & Scheffer, 2005) predicting greater relevance of alternative stable states at ecosystem scales either in spatially homogeneous environments or when biological feedbacks span large scales by involving mobile matter (e.g. drift kelp) or organisms.

The region-specific scales of alternative stable states found here can also help explain the debated presence of this phenomenon on temperate rocky reefs. Empirically demonstrating alternative stable states is challenging because of the limited spatiotemporal scales of experimental manipulations and measurements of biological feedbacks (Petraitis & Dudgeon, 2004). Our results suggest one explanation for this debate: that the scale of alternative stable states is system-dependent. Future studies can estimate the potential scale of alternative stable states by quantifying the smallest observed areas of each state or the spatial scale of underlying ecological feedbacks.

Our analysis additionally expands on previous approaches to detecting alternative stable states. Studies most commonly test for this phenomenon based on whether distinct ecological states (e.g. Figure 5b) or initial-condition dependency occur under the same levels of an environmental driver (Mumby et al., 2013; Petraitis, 2013) by pooling observations or experiments across space or time. However, **environmental heterogeneity may obscure distinct stable states** (Mumby et al., 2013): for instance our best-fit models predict that kelp densities in forested states double from 5 to 10m depths (Figure 4b). Fitting dynamical models to time series can explicitly account for the expected effects of environmental variation (e.g. Ives et al., 2008), but requires long-term monitoring data. Instead, here we fit model steady states

to data from large spatial surveys. Our analysis capitalises on time scale differences between kelp abundance and comparatively slow changes in the environment and urchin abundance, a feature utilised in previous kelp-urchin studies (Ling et al., 2015). We caution that this approach may produce biased interaction estimates by assuming population densities are independent among years. This approach additionally assumes that ecological interactions not modelled or measured explicitly vary little across locations and time; such variation can be accounted for using hierarchical modelling and model averaging techniques (Bolker, 2008). Altogether, our work highlights how combining spatial surveys, mechanistic models and statistics could predict the likelihood, given the uncertainty and variable environments, that alternative stable states underlie observed ecological patterns.

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AUTHORSHIP

VAK and MLB conceived the study; VAK took the lead on designing the approach, performing the analysis and writing the manuscript, with substantial input from all authors.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ele.13828>.

DATA AVAILABILITY STATEMENT

We use published data available from cited sources. Simulation and model fitting code available at: github.com/VadimKar/BehaviorPatternsCommunities (<https://doi.org/10.5281/zenodo.4750732>).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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