Grazer behavior can regulate large-scale patterns of community states

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Abstract

Ecosystem patterning frequently arises either from environmental heterogeneity or in studies of homogeneous systems where biological feedbacks produce multiple persistent ecological states. However, density dependent changes in behavior can strongly regulate species interactions, raising the question of whether behavior can also affect large-scale community patterns. We resolve this empirically by fitting dynamical models to large-scale survey data on temperate rocky reefs predominated by herbivory and environmental variation. We find that increased urchin grazing activity at low kelp densities best explain observed community patterns. In our best-fitting models this feedback creates large-scale, alternatively stable kelp- and urchin-dominated states at 37% of reefs in California. In New Zealand, a more localized behavioral feedback and stronger gradients in wave stress on kelp limit this phenomenon to intermediate depths (3-8m), with only single states stable in shallower and deeper areas and long-term reef state depending little on initial kelp abundance. Our results highlight that behavior can predominantly pattern herbivore-dominated communities despite strong environmental variation, and emphasize that alternative stable states detected locally (here, 1-5m^2 samples) may not be relevant at larger scales.

Introduction

Patterned community regimes characterize many ecosystems. Much theory and experimental efforts focus on the processes that underlie fine-scale ($<$ 500m), mosaic patterns of community regimes in forests, shrublands, and intertidal marine communities (Rietkerk & Van de Koppel 2008). Other studies treat space implicitly and focus on predicting community regimes assumed to span much larger (>1km) scales of individual pastures or marine reefs (Scheffer *et al.* 2001). Transitions among such large-scale regimes raise greater concern because they often accompany loss of local populations or ecosystem properties targeted by conservation and management. In reality, the spatial scale of a given community regime can vary widely even within a given type of ecosystem, thereby determining the consequences of patterning for larger-scale processes. However, empirical studies largely remain system- or site-specific and rarely resolve the processes governing the spatial scale of ecosystem patterning.

Community patterns may be imposed externally by environmental heterogeneity or arise from local biotic feedbacks. Until recently, environmental variation in resources or stress was considered a predominant source of community patterning. This can include localized disturbances such as storms in coastal marine systems (Levin & Paine 1974; Reed *et al.* 2011) or lightning-induced fires in forest patches. Alternatively, patterns might arise when biological feedbacks reinforce distinct ecological states. Self-organized patterns occur in a wide array of systems with distance-dependent interactions, for instance when sessile individuals locally deplete resources (e.g., water in arid ecosystems) or displace growth-inhibiting factors such as snow in alpine forests or water currents in intertidal mussel beds (Rietkerk & Van de Koppel 2008). Distance-independent feedbacks can also pattern communities on large spatial scales by interacting with environmental heterogeneity. For instance, grasses predominate in areas of low-moderate herbivory but collapse from overgrazing in areas with high livestock densities (Noy-Meir 1975). In most ecosystems, however, feedback-induced patterning requires strong and often nonlinear species interactions.

Density-dependent changes in behavior can regulate the strength of species interactions. In predator-prey systems, higher prey densities can reduce predation through greater sharing of social information, even across prey species (Gil *et al.* 2018). Dense plant aggregations can likewise discourage herbivory, for instance when denser aspen stands reduce elk grazing activity by increasing the risk of predation by wolves (Laundré *et al.* 2001). Increased foraging rates might also frequently arise as declines in resources cause starvation. This raises the question of whether behavior can also affect large-scale community patterns.

Temperate rocky reefs exemplify patterned communities with a strong role of behavior-mediated herbivory and environmental variation. Patterning of two distinct ecological states, kelp forests and urchin-dominated barrens (Fig. 1a, b), can occur in these ecosystems at drastically different scales. For instance, forests and barrens span entire reefs (> 500m) in California but co-occur across adjacent depth zones along the coast of New Zealand, with barrens predominantly forming in shallow areas (Fig. 1c, d). This difference might arise from a greater sensitivity of the dominant kelp species in New Zealand to wave stress, which peaks at shallower depths, compared to the canopy-forming dominant kelp species in California. Alternatively, these regions may differ in the roles of behavioral feedbacks controlling urchin grazing activity. Two such feedbacks include increased grazing activity in locations where kelp densities are insufficient to physically deter urchins (Konar 2000) and increased grazing across the reef when low kelp densities lead to insufficient subsidies of kelp fronds drifting to urchins sheltering on the seafloor (Harrold & Reed 1985). Importantly, a greater role of feedbacks may indicate a greater likelihood that forests and barrens represent alternative stable states, where intense grazing prevents kelp forest recovery following natural or human-induced disturbances (Ling *et al.* 2015). However, quantifying the effects of biological feedbacks and environment at relevant spatial and temporal scales remains logistically intractable on most temperate rocky reefs (Petraitis & Dudgeon 2004).

Here, we quantify how community patterning observed in both regions depends on environment and behavior-mediated herbivory. We do this by comparing how well dynamical models incorporating the effect of each feature on kelp populations can explain observed kelp distributions in field data synthesized across large-scale surveys. We then analyze our best-fitting models to resolve the spatial patterns and potential for community-wide alternative stable states in each system.

Methods

2.1 Study systems

We focus our analysis on temperate rocky reefs in Northeast New Zealand and the northern California Channel Islands dominated by kelp (*Macrocystis pyrifera*, CA, and *Eklonia radiata*, NZ) or urchins (*Evechinus chloroticus* in NZ and *Strongylocentrotus purpuratus, S. franciscanus* in CA). Like many temperate reefs, high rates of kelp growth and urchin grazing characterize these systems: abundant urchins can denude kelp forests in weeks, while under low urchin densities kelp can recolonize barrens within a few months. By contrast, the abundance of comparatively longer-lived urchins (5-50 years) changes more slowly in response to urchin predator abundance and multi-year changes in ocean climate. This separation of time scales means that kelp reach steady state abundance under a given urchin density, whereas urchin density is largely independent of kelp abundance due to high demographic openness of urchin populations (Okamoto 2014).

Urchin grazing activity can strongly decline with either local- or reef-scale kelp density. Urchins typically remain in rock crevices that offer refuge from storms and predators, consuming only kelp fronds detached from plants by waves and carried to the bottom by currents over 100-1000m ('drift kelp' hereafter; Ebeling *et al.* 1985; Harrold & Reed 1985). When this long-distance subsidy becomes insufficient at low kelp and high urchin densities, urchins across the reef synchronously emerge from refugia to actively graze on kelp. Urchins can also reduce grazing activity in locally dense stands of kelp, which can physically abrase urchins as plants move with the motion of water waves (Konar 2000) or shelter urchin predators (Cowen 1983). Density-dependent consumption present in both feedbacks can theoretically create alternative stable states with either high or low resource abundance (Bate & Hilker 2014).

2.2 Model description

Here we describe the dynamical model of kelp abundance N_q and urchin behavior at the scale of individual sampling quadrats (1-5m). Throughout, we denote variables with uppercase letters and fitted parameters with lowercase symbols. Adult kelp N_q reproduce continuously during the year with a baseline per capita fecundity r. In California, fecundity can decline due to limitation of nitrate G that arises at high water temperatures; we model this dependence using a function that saturates to 1 at high nitrate levels, $g(G) = G(1 + vG)^{-1}$. Newly produced spores can disperse over short distances ($< 500m$ for *Macrocystis*, Reed et al. 1993), with a fraction γ of all spores dispersing across the local reef s. Thus, the density of spores arriving in a location q depends partly on kelp density averaged over the reef, $N_s = k^{-1} \sum_{q=1}^{k} N_q$, and on the fraction $1 - \gamma$ of locally produced spores that disperse $< 1 - 5m^2$.

Survival of settled juvenile kelp to adult stages depends on several factors. To model light limitation of juveniles by competitively dominant adults, we assume that light availability declines proportionally with adult density N_q from the baseline light availability L. Due to their greater palatability compared with adults, juveniles also experience high rates of grazing δ_J, which may depend on urchin behavior (*discussed below*). Several additional reef-scale factors can also mediate juvenile survival, including thermal stress or interspecific competition. We account for this survival stochasticity using a log-normally distributed random variable S_R with mean one and standard deviation σ, with S_R realizations identical

across all locations in each reef. Finally, given fast maturation (1-2 mo.) and high sensitivity of juveniles to competition and grazing, we assume recruitment of adult kelp is fast and rapidly adjusts to changes in adult density and urchin behavior.

Adult kelp can die from wave stress E and grazing by urchins δ_A, which may additionally depend on urchin behavioral feedbacks. To model high grazing at moderate kelp densities and very low grazing at high kelp densities, we use an inverse-quadratic decline in grazing with kelp density and a per-kelp grazing inhibition factor ξ_A. This conventional 'Type IV' functional response represents emergent prey or resource defense (Koen-Alonso 2007; Bate & Hilker 2014), and in our model depends on either N_q for the local feedback or average kelp density at the reef (N_s) in reef-scale feedbacks. To account for the possibility that high kelp densities might not completely prevent grazing, we additionally model the fraction of grazing activity that depends on behavior, f_b. Additionally, urchins may avoid active grazing outside of refugia from predators on reefs with high abundance of urchin predators P. Given a per-predator rate of grazing inhibition ξ_P, we integrate this inhibition over the entire year to arrive at the fractional decline in grazing due to density-dependent predator effects, $exp(-\xi_P P)$. Altogether, the behavior-mediated decline in urchin grazing is

$$b(N) = 1 - f_b + f_b \frac{exp(-\xi_P P)}{1 - (\xi_A N)^2}, \tag{1}$$

and the overall dynamics of local kelp abundance are

$$\frac{dN_q}{dt} = rg(G)(\gamma N_s + (1-\gamma)N_q)\frac{\sigma_R(L - dN_q)}{1 + \delta_R U b(N_q)} - \mu E N_q - \delta_A U b(N_q) N_q, \tag{2}$$

for the local grazing feedback and

$$\frac{dN_q}{dt} = rg(G)(\gamma N_s + (1-\gamma)N_q)\frac{\sigma_R(L - dN_q)}{1 + \delta_R U b(N_s)} - \mu E N_q - \delta_A U b(N_s) N_q, \tag{3}$$

for the reef-scale feedback.

2.3 Role of urchin behavior

We resolve how environment, urchin densities, and urchin behavior drive kelp densities by comparing how well dynamical models incorporating each feature can explain field data (Table 2). In addition to the full model (Eqn. 3), we construct a range of simpler models with one or two of these processes to resolve their independent and interactive effects; we also include a model with density dependence only as a baseline reference of model performance. Given that fast-growing kelp populations can quickly adjust to changes in abiotic conditions and urchin densities (see "Study system" above), we assume observed kelp densities are at steady-state and compare them with equilibria of fitted models. However, compared to New Zealand, California reefs experience more frequent extreme events in ocean climate (e.g., storms, heat waves) and recruitment and disease pulses of the short-lived *S. purpuratus* urchin. We therefore test our assumption of steady state kelp densities in California by fitting dynamical models to time series data and in both systems verify that the best-fitting parameter estimates in all models converge to steady state within one year.

We fit models to data using a maximum likelihood approach accounting for model mis-specification and observation errors. To account for mis-specification that occurs through

Table 1: Model components.

Parameter	**Description**
r, yr^{-1}	Adult kelp fecundity
v	Half-saturation constant of nitrate in fecundity
σ_R	Lognormal process error in recruit survival
γ	Fraction of kelp spores dispersing across reef
d, N^{-1}	Kelp competition for light inhibiting recruitment
μ, yr^{-1}	Kelp mortality from wave stress
δ_A, $\mathrm{U}^{-1}\mathrm{yr}^{-1}$	Max grazing intensity on adult kelp
δ_R, U^{-1}	Max grazing intensity on kelp recruits
f_b	Fraction of grazing activity affected by behavior
ξ_A, N^{-1}	Inhibition of grazing by kelp
ξ_P, P^{-1}	Inhibition of grazing by predators
Covariate	**Description**
L	Local (depth-dependent) light availability
E	Local (depth-dependent) wave stress
U	Local urchin density
G	Reef-scale nitrate availability (CA only)
P	Reef-scale urchin predator density

juvenile survival stochasticity S_R, we run each model under 30 values of S_R. We solve each model using a Runge-Kutta method in R 3.4.3 (R Core Team 2017), with kelp density initialized at the 5th and 80th percentiles of observed densities in order to resolve the potential presence of alternative stable states. We then compare these predicted kelp densities with observed kelp counts using a Poisson likelihood that accounts for observational errors. Averaging likelihood across the 60 simulations in each sample and summing the likelihood across all samples in each region, we arrive at the total likelihood of each model under a given parameter set. Note that in California we evaluate model fit to data collected across all years, although in preliminary analyses we found analogous results limiting the analysis to only a single sampling year from each reef.

For each model, we find the set of best-fitting parameters using the DIRECT algorithm (Jones et al. 1993) in the package nloptr (Johnson 2019). We then compare model performance using the Akaike Information Criterion (AIC), where AIC difference of > 4 suggests improved model fit (Bolker 2008), and also calculate the correlation between predicted and observed kelp presence for a more intuitive reference of model fit. We also record the frequency of alternative stable states as the fraction of samples and iterations of S_R where simulations starting from the two initial conditions have different steady state kelp densities.

2.4 Data

We use survey data sampling 200-300km coastlines in each region, with 71 reefs sampled in 2001 in Northeast New Zealand (Shears & Babcock 2004) and 93 reefs sampled over 5-30 years in the California Channel Islands (Kushner *et al.* 2013; PISCO *et al.* 2011). This geographic extent spans a wide range of environmental conditions and urchin densities, allowing us to independently estimate the effects of each model process. This spatial scale also makes our

findings robust to inter-annual variation in the primary environmental drivers (e.g., storms, temperature, upwelling) because these factors are correlated at smaller spatial scales in both systems (10-50km; Cavanaugh *et al.* 2013). Additionally, availability of long-term data at California reefs (10 years at each reef on average) allows us to verify our assumption that kelp reach steady states within a single year (see "Role of behavioral feedbacks" below). Samples in both systems were collected at the end of the growing season, when kelp reach peak abundance levels (July-August in CA, March-June in NZ).

Samples in each system span c.a. 500m^2 of each reef. Data measured at the scale of entire reefs include total urchin predator density (2 species in NZ, 3 species in CA), wave stress based on wind fetch (NZ) or year-specific maximum wave height (CA), light penetration in the water (i.e., visibility), and nitrate concentrations derived from water temperature (CA only; Bell *et al.* 2018). Each reef is sampled using transects with 15-50 1-5m^2 quadrat samples that span a 2-20m water depth gradient, translating to 1,273 samples in NZ and 14,955 samples in CA. Data collected in each quadrat include densities of adult kelp and urchins of sufficient size to consume kelp (>25mm test diameter), sample location along transect, and depth. Given that water depth attenuates both wave stress and light, we adjust these estimates to the depth of each sample. For this we use the standard relations of light extinction and dissipation of wave energy (Bekkby *et al.* 2008), and in each systems use a fitted parameter to adjust the wave stress-depth relation into realized kelp mortality.

To compare the spatial extent of kelp- and urchin-dominated regimes in New Zealand and California, we categorize the community state in each sample (Fig. 1a, b). Given that low urchin densities can maintain barren regimes, we classify samples containing urchins and few kelp (< 0.05 ind m^{-2} in CA, < 0.5 ind m^{-2} in NZ) as urchin-dominated and kelp-dominated otherwise (following Ling *et al.* 2015). We then calculate the scale of patterning (Fig. 1c, d) as the distance at which Pearson correlation in community state κ, calculated over a 5km window moving by 0.5km, declines to zero (with standard error $\sqrt{(1-\kappa^2)/(n-2)^{-1}}$ given n comparisons).

2.5 Drivers of community patterning

We resolve how wave stress, grazing, and behavior might affect community patterns by analyzing our best-fitting models in each region (Fig. 2). To resolve the effect of grazing we simulate 40 reefs with reef-scale urchin densities spanning the range of values observed in each system. Given that wave stress predominantly depends on water depth rather than reef-scale characteristics, at each reef we additionally simulate 30 locations spanning the range of depths in data. We also denote whether alternative stable states arise from behavioral feedbacks in model dynamics. Throughout, we set urchin distribution across depths and reef-scale exposure, light availability, and predator density to the average values observed in data. We then determine the scale of community patterns based on whether predicted kelp density predominantly varies across reefs or across depths within reefs. As a reference, we additionally plot observed patterns in kelp abundance smoothed using 2-d splines using the mgcv package.

2.6 Presence of alternative stable states

We evaluate the role of alternative stable states in explaining observed patterns by tracking how the fit of models with behavioral feedbacks corresponds to the predicted frequency of alternative stable states across samples (Fig. 3). For this we fix grazing inhibition by

kelp ξ_A at levels increasing from 0 (i.e., no feedback) and optimize all other parameters for best fit (i.e., likelihood profiles; Bolker 2008). Additionally, we compare how differences in predictions of best-fitting models with and without behavioral feedbacks correspond to differences in these models' performance.

To evaluate the potential for alternative stable states spanning entire communities, we analyze how predicted kelp density, averaged across all depths, depends on average urchin density at the reef (Fig. 4). We focus on this parameter because urchin density typically depends on reef-scale factors, including oceanographic variability and predator densities. Additionally, management efforts might indirectly reduce urchin density by limiting fishing intensity on urchin predators or through urchin harvest (Hamilton and Caselle 2015; House 2017). For reference, we compare predictions from our best-fitting models both with and without the behavioral feedbacks, and also with the reef-scale average frequency of kelp- and urchin-dominated regimes as determined in Figure 1a, b.

Results

3.1 Role of urchin behavior

Behavior-mediated grazing in California and an interactive effect of behavior-mediated grazing and environmental variation in New Zealand predominantly explain patterns in field data (Table 2). Best-fitting models in both regions include environment, grazing, and behavior, and meaningfully reproduce observed patterns ($R^2 = 0.35$ in NZ and 0.54 in CA). In California models with grazing and behavioral feedbacks alone outperform models with only grazing and environment. This contrasts New Zealand, where models with environment alone better explain the data than models with only grazing and behavior; however, a model incorporating all three processes strongly outperforms all other models. In both regions, models with behavior outperform models without behavior because they can explain the co-occurrence of high and low kelp densities at intermediate urchin densities (Fig. 3). Identical model ranking and comparable parameter estimates also arise in temporally explicit model fits in California, despite the stronger temporal variation in abiotic conditions and urchin densities in this region.

Comparison of models with behavior strongly indicates local-scale grazing feedbacks in New Zealand and reef-scale grazing feedbacks in California (Table 2). In New Zealand models attain much better fit when assuming a decline in grazing with localized kelp density rather than a decline in grazing with kelp density averaged over entire reefs; in California, models of feedbacks with reef-scale kelp density outperform models with local kelp density. In all model fits, accounting for behavioral declines in grazing activity with predator density has relatively weak but significant increase on model performance.

3.2 Drivers of community patterning

The local scale of behavioral feedbacks and a decline in wave stress with depth together explain the much smaller scale of community patterning in New Zealand. In this region, our best-fitting model predicts barrens as the only stable state in shallow areas ($< 3m$) due to a combination of grazing and high wave stress (Fig. 2). At greater water depths that largely attenuate waves ($> 8m$), forests are the only stable state because kelp quickly form dense stands that inhibit grazing. At intermediate wave stress between these zones, alternative stable states spanning 1-5m^2 patches arise as urchins largely avoid grazing in dense kelp

stands and graze intensively elsewhere. This interface occurs at greater depths and urchin barrens cover a larger fraction of the system at reefs with greater overall urchin densities. In California community regimes simultaneously span all reef depths due to the weaker role of wave stress and the larger scale of grazing feedbacks (Table 2).

3.3 Presence of alternative stable states

Our best-fitting models predict that alternative stable states occur locally in both regions (40% of CA samples, 18% of NZ samples, Fig. 2, 3), but at the scale of entire reefs are relevant only in California (Fig. 4). In this region, final community state strongly depends on the initial kelp abundance over a wide range of reef-scale urchin densities, as urchins graze either passively on drift kelp or actively on kelp plants. Aggregating community state across all depths in New Zealand, however, leads to a small difference in outcomes due to the fact that alternative stable states occur over only a narrow range of depth-dependent wave stress intensities. Consequently, our best-fitting models in this system predict potentially large-scale forests and barrens but only small-scale shifts between these regimes.

Discussion

Our results show that behavior can determine the presence and scale of community patterning by mediating consumer-resource interactions. This potential requires feedbacks where density-dependent changes in behavior amplify consumption when resources decline at a particular spatial scale. In heterogeneous environments, this feedback scale then determines the spatial extent of the resulting resource- or consumer-dominated community regimes. Specifically, we find that forests and barrens spanning entire reefs in California are most consistent with large-scale grazing feedbacks, wherein urchins actively graze whenever low kelp densities across large (> 500m) scales lead to insufficient subsidies of kelp fronds to the bottom (Table 2; Harrold & Reed 1985). By contrast, in New Zealand localized feedbacks involving short-distance physical deterrence of grazing by kelp (Konar 2000) can explain fine-scale patterning (1-5m) of community regimes that is organized into distinct depth zonation by a gradient in wave stress.

Regional differences in the scale of alternative stable states also suggest that the relevance of this phenomenon at ecosystem scales requires either spatially homogeneous environments or a high mobility of matter or organisms involved in ecological feedbacks. Whereas our best-supported models predict alternative stable states in both regions (37% of samples in CA, 15% in NZ; Table 2), in New Zealand eventual state of the reef depends little on initial kelp abundance (Fig. 4) because alternative stable states span only a narrow range of depths (Fig. 2). Conversely forests and barrens span entire reefs in California, where urchin grazing activity depends on drift kelp carried by water motion over long distances and across all depths. This provides empirical support for existing theory predicting that alternative stable states occur either in relatively homogeneous environments or when matter or organisms move freely over large scales (van Nes & Scheffer 2005). Otherwise, heterogeneity restricts shifts between ecological states to a narrow range of environments. Across space, such localized states average out to produce a gradual system-wide response to environmental change and little-no dependence of the overall system state on initial conditions.

4.1 Consequences for detection of alternative stable states

Our results predicting relevance of alternative stable states only at small (1-5m^2) spatial scales in New Zealand can help explain the debated presence of this phenomenon in many systems. Studies most commonly detect alternative stable states based on bimodality (here, Fig. 4d) or initial-condition dependency of ecological states under the same environmental conditions (Mumby *et al.* 2007). System-specific reviews increasingly find evidence for this phenomenon across many regions (e.g., Staver *et al.* 2011, savannas and forests; Ling *et al.* 2015, rocky temperate reefs). Our results demonstrate that empirical tests conducted at local scales provide insufficient evidence for the practical relevance of alternative stable states. We emphasize that analyses of bimodality in field data additionally quantify the scales of identified states. Analogously, we suggest that manipulative experiments focus on quantifying feedback processes that involve either mobile species or environmental features synchronized across entire communities, for instance the supply of drift kelp or aggregate forest flammability in terrestrial landscapes.

Our analysis also represents a novel approach to quantify empirical support for alternative stable states. Preceding studies based on mechanistic models detect this phenomenon in field data by fitting model dynamics to time series (e.g., Ives *et al.* 2008). However, such studies remain rare because long-term monitoring data is available for only a few systems thought to exhibit alternative stable states. Instead, we fit the steady states of dynamical models of kelp abundance and urchin behavior to spatial survey data by utilizing the time scale separation between these processes and comparatively slow, longer-term changes in urchin abundance and the environment. This compensates for an absence of adequate time series by leveraging spatial replication of field data across gradients in urchin density and the environment. We also show that this approach can yield model ranking and parameter estimates analogous to conventional time series approaches in California, where the 'slower' variables exhibit more interannual variation compared to New Zealand.

4.2 Community patterning on temperate rocky reefs

The regional differences in the scale of alternative stable states here suggest that feedbacks involving drift kelp or mobile species are more likely to drive reef-scale alternative stable states. Our results complement preceding observational support for reef-scale alternative stable states in California (Dayton *et al.* 1984; Harrold & Reed 1985) by estimating the frequency of this phenomenon (37%) across the region and decades of monitoring. High levels of drift kelp that likely underlie the behavioral feedbacks in this system also occur in Chile, where the dominant urchin relies predominantly on passive grazing (Vásquez *et al.* 1984). Feedbacks in kelp-urchin interactions might also underlie reef-scale alternative stable states when kelp facilitate recruitment urchin predators that freely forage across entire reefs (Smith & Herrkind 1992; Karatayev and Baskett 2019). Our results highlight how behavior might strengthen this feedback by resolving declines in grazing activity with predator density in both regions (Table 2), complementing analogous findings in California (Ebeling *et al.* 1985; Caselle *et al.* 2018). Conversely, the ubiquity of depth gradients in wave stress suggests a limited potential for reef-scale alternative stable states to arise from feedbacks involving local processes. This may include feedbacks where kelp physically deter grazing ('whiplash'), hinder urchin movement, or reduce survival of urchin larvae compared to barren areas. Our model predictions in New Zealand indicate that such local feedbacks may however explain the distinctive, patchy boundaries between kelp- and urchin-dominated areas frequently observed locally on temperate rocky reefs (Vásquez & Buschmann 1997).

4.3 Results robustness

To avoid model over-fitting, our approach leaves out several secondary urchin behaviors that can increase the role of behavioral feedbacks in both regions. First, our model tracks urchin grazing activity but omits local-scale urchin movement in response to kelp density, which in New Zealand might explain higher urchin densities in shallower areas. On some temperate rocky reefs, urchin aggregations in mobile grazing fronts can produce shifts to large barren areas (Silliman *et al.* 2013; Filbee-Dexter & Scheibling 2014). However, the role of kelp in spatial urchin distributions in New Zealand is unclear because expansion of barren areas does not appear to follow periods of synchronous, senescence-induced kelp declines. Second, we limited model comparison to select a single behavioral feedback that best explains patterns in each region, whereas in reality both physical deterrence and drift subsidies might influence grazing activity (van de Leemput *et al.* 2016). Finally, available data likely underestimates urchin densities at low grazing activity in California because urchins sheltering in rock crevices are harder to detect; in turn, our model fits might underestimate the role of behavioral feedbacks in limiting urchin grazing in kelp forests. However, in a preliminary analysis we find a weak effect of sampling intensity on estimated urchin densities.

We also omit species interactions that might increase the potential for alternative stable states compared to our estimates based on behavioral feedbacks only. First, we do not consider competition among primary producers, which might displace competitively inferior juvenile stages of *Eklonia* and *Macrocystis*. However, few samples in our data indicate competitive exclusion by lacking both kelp and urchins ($< 10\%$); additionally, our approach might implicitly account for competition with more wave-tolerant species in shallower areas by over-estimating the direct role of depth-dependent wave stress. Second, our focus on kelp and behavioral dynamics ignores longer-term feedbacks affecting consumer abundance. For instance, kelp cover facilitates recruitment of urchin predators (Smith & Herrkind 1992), whereas crustose corralline algae present in barrens promotes urchin recruitment (Baskett & Salomon 2010).

Figure 1: (a, b) Distribution of kelp- and urchin-dominated states across regions. (c, d) Spatial scales of correlation in community state (defined as kelp presence). Red points in (c) indicate mean correlation; lines in (d) denote mean correlation ±99% confidence intervals. In (a, b) dashed blue lines divide kelp- and urchin-dominated states and N indicate sample size.

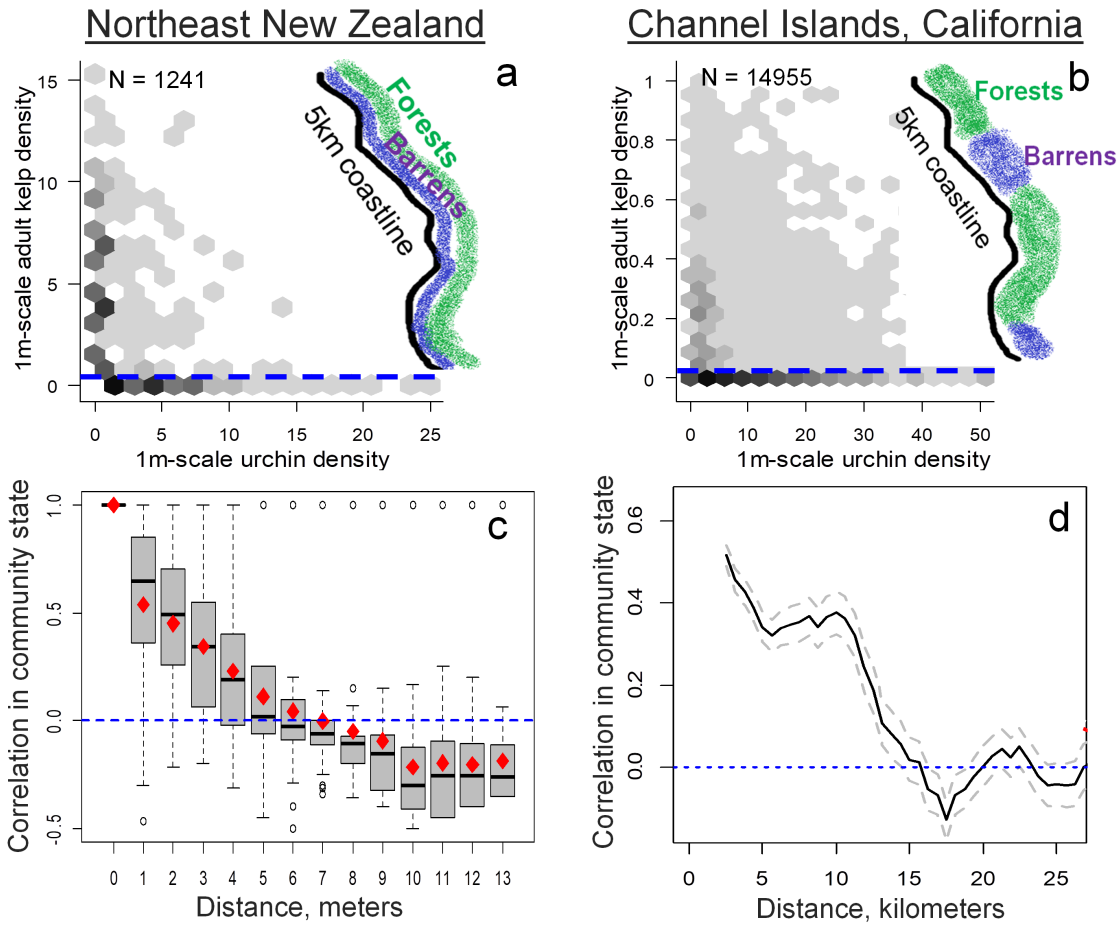

Figure 2: Best-fitting models with behavioral feedbacks reproduce patterns of kelp abundance (colors) in both regions. (a, c) show patterns in observed kelp density across depths on each reef (y-axes) and across reefs with increasing average urchin density. (b, d) show kelp densities predicted by best-fitting models in each region, with secondary y-axes denoting the best-fit, depth-dependent estimates of mortality induced by wave stress. Gray dots in (a, c) denote the sample coverage across these conditions and hashed boxes in (b, d) denote conditions for which best-fitting models predict alternative stable states with kelp present or absent.

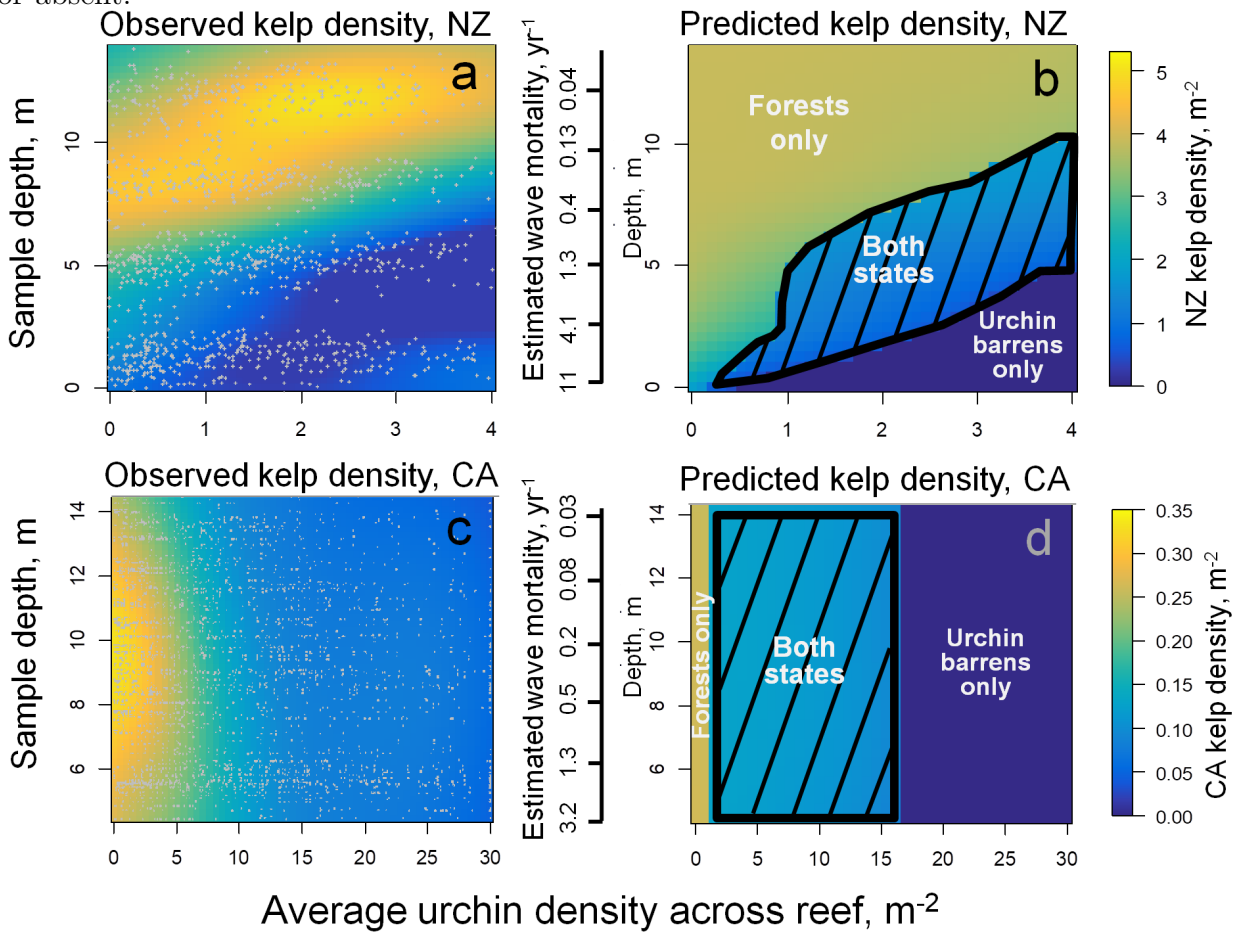

Figure 3: Behavioral feedbacks best explain observed patterns by predicting alternatively stable kelp- and urchin-dominated states. (a, b) show kelp density predicted by best-fitting models without behavior (gray lines) and models with behavior (black lines) for simulations with initially high (solid lines) and initially low kelp densities (dashed lines, not visible without behavior). Blue lines in (a, b) denote the average difference in log likelihood between models with and without behavior, with positive differences denoting better fit. (c, d) show performance of models with behavior in each region (black lines) and the fraction of all samples for which models predict alternative stable states (blue lines). 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 2).

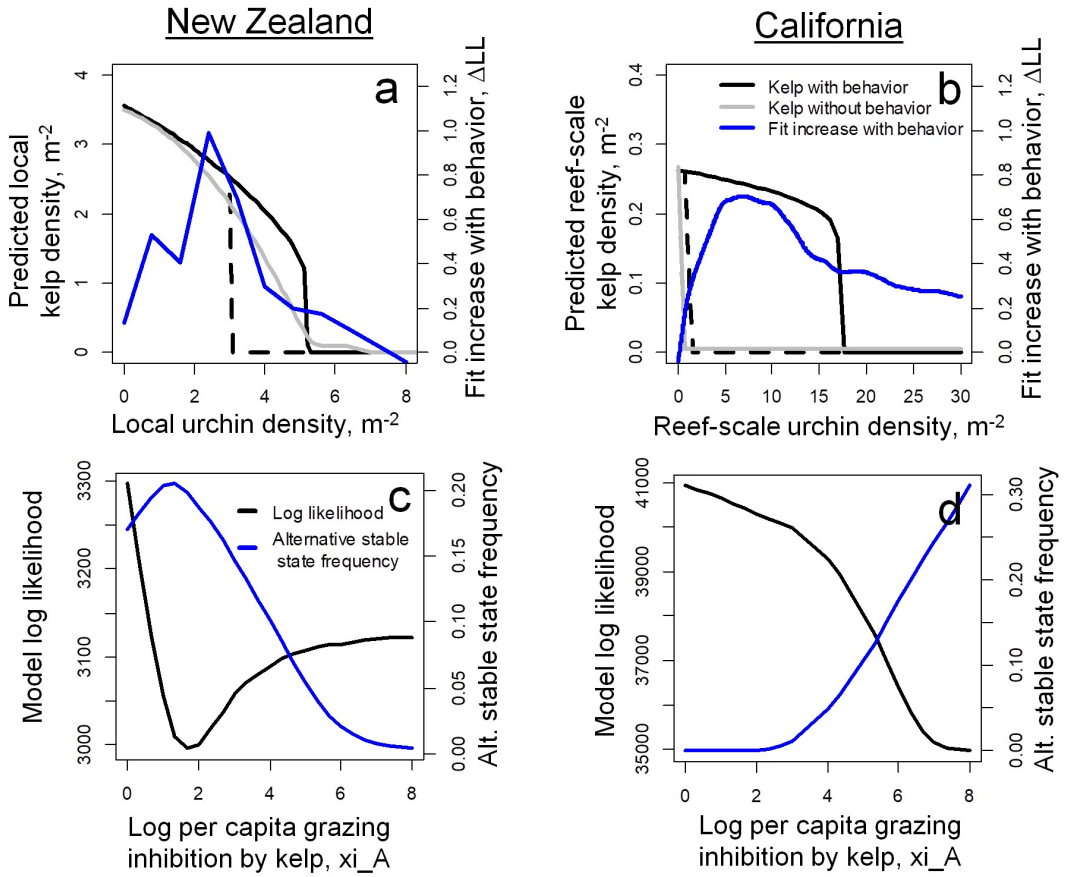

Figure 4: Best-fitting models with behavioral feedbacks predict a relevance of reef-wide alternative stable states with increasing reef-scale urchin densities in California (b) but not in New Zealand (a). (a, b) show frequency of kelp presence across reef predicted by best-fitting models without behavior (red lines) and models with behavior (black lines) for simulations with initially high (solid lines) and initially low kelp densities (dashed lines, not visible without behavior). Blue dots show frequencies of kelp presence across all samples on each reef, with different dots representing different reefs and reefs in different years (b only).

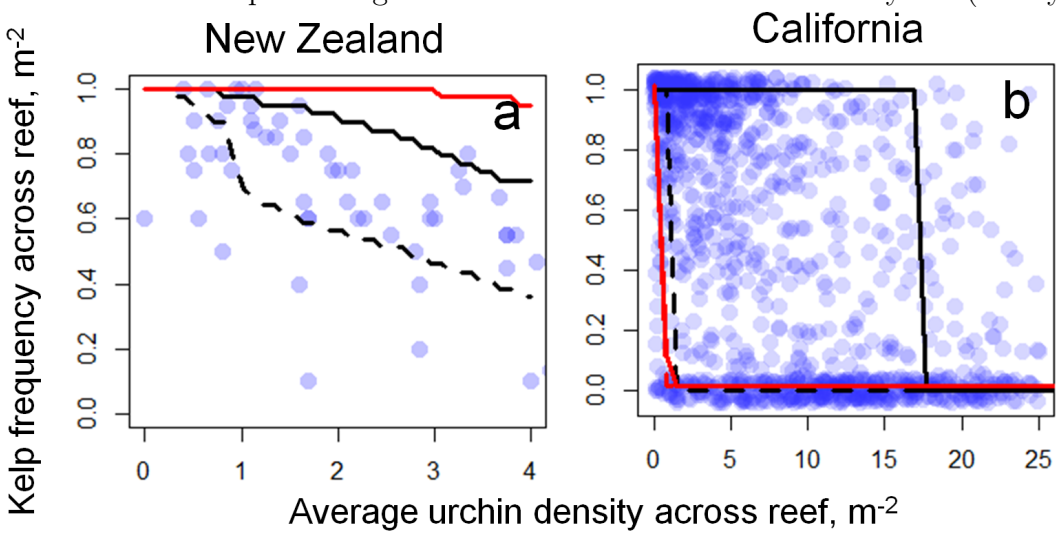

Table 2: Results of model fitting and model comparison in New Zealand (top half) and California (bottom half). Capital letters denote models including environment (E), urchin grazing (U), urchin behavior (B), or density dependence only (DD, present in all models). Subscripts further denote whether behavior includes predator avoidance (P), local-scale feedbacks (Local), or reef-scale feedbacks (Reef). R^2 denotes squared correlation between observed and predicted kelp presence, and pA.S.S. denotes the proportion of observations for which each model predicts alternative stable states.

Model	r	σ_R	γ	d	μ	δ_A	δ_R	f_b	ξ_A	ξ_P	AIC	ΔAIC	R^2	pA.S.S.
E,U,B$_{Local,P}$	18.0	0.34	0	0.4	2.65	1.53	4.79	0.97	1.94	9.65	2899	0	0.22	0.24
E,U,B$_{Reef,P}$	16.0	0.34	0	0.5	2.66	2.45	4.18	0.84	48.9	11.0	3075	176	0.22	0.00
E,U	19.1	0.34	0	0.5	0.88	0.75	1.78				3394	496	0.14	0
E	14.0	0.14	0	0.3	2.66						3423	525	0.13	0
U,B$_{Local}$	16.9	0.34	0	0.3		1.40	4.51	0.85	52.7		3435	536	0.10	0.12
U	19.5	0.34	0	0.3		0.48	2.35				3508	609	0.11	0
U,B$_P$	19.5	0.34	0	0.3		0.51	2.29			10.8	3511	613	0.11	0
U,B$_{Reef}$	18.0	0.34	0	0.3		1.55	2.66	0.77	85.1		3526	627	0.10	0.00
DD	18.0	0.06	0	0.4							3936	1038	0.00	0
E,U,B$_{Reef,P}$	11.0	0.34	1	3.3	1.52	1.11	3.33	0.97	4160	8.66	33501	0	0.12	0.24
E,U,B$_{Local,P}$	11.0	0.34	1	3.9	1.52	1.11	3.33	0.97	4160	11.7	34290	789	0.15	0.20
U,B$_{Local}$	18.3	0.34	1	4.5		1.48	2.54	0.98	2109		36386	2885	0.11	0.35
U,B$_{Reef}$	10.8	0.34	1	5.2		1.45	2.59	0.98	2538		36952	3451	0.09	0.27
E,U	12.1	0.34	1	3.9	0.78	0.37	0.37				39529	6028	0.15	0
U,B$_P$	19.3	0.34	1	4.1		0.48	0.75			11.1	41168	7667	0.12	0
U	19.3	0.34	1	4.1		0.47	0.50				41186	7685	0.12	0
DD	2.00	0.34	1	8.3							49484	15983	0.00	0

References

Baskett, M.L. & Salomon, A.K. (2010). Recruitment facilitation can drive alternative states on temperate reefs. *Ecology*, 91, 1763–1773.

Bate, A.M. & Hilker, F.M. (2014). Disease in group-defending prey can benefit predators. *Theoretical Ecology*, 7, 87–100.

Bekkby, T., Isachsen, P.E., Isæus, M. & Bakkestuen, V. (2008). Gis modeling of wave exposure at the seabed: a depth-attenuated wave exposure model. *Marine Geodesy*, 31, 117–127.

Bell, T.W., Reed, D.C., Nelson, N.B. & Siegel, D.A. (2018). Regional patterns of physiological condition determine giant kelp net primary production dynamics. *Limnology and Oceanography*, 63, 472–483.

Bolker, B.M. (2008). *Ecological models and data in R*. Princeton University Press.

Caselle, J.E., Davis, K. & Marks, L.M. (2018). Marine management affects the invasion

success of a non-native species in a temperate reef system in california, usa. *Ecology Letters*, 21, 43–53.

Cavanaugh, K.C., Kendall, B.E., Siegel, D.A., Reed, D.C., Alberto, F. & Assis, J. (2013). Synchrony in dynamics of giant kelp forests is driven by both local recruitment and regional environmental controls. *Ecology*, 94, 499–509.

Cowen, R.K. (1983). The effects of sheephead (*Semicossyphus pulcher*) predation on red sea urchin (*Strongylocentrotus franciscanus*) populations: an experimental analysis. *Oecologia*, 58, 249–255.

Dayton, P.K., Currie, V., Gerrodette, T., Keller, B.D., Rosenthal, R. & Tresca, D.V. (1984). Patch dynamics and stability of some california kelp communities. *Ecological Monographs*, 54, 253–289.

Ebeling, A.W., Laur, D.R. & Rowley, R.J. (1985). Severe storm disturbances and reversal of community structure in a southern california kelp forest. *Marine Biology*, 84, 287–294.

Filbee-Dexter, K. & Scheibling, R.E. (2014). Sea urchin barrens as alternative stable states of collapsed kelp ecosystems. *Marine Ecology Progress Series*, 495, 1–25.

Gil, M.A., Hein, A.M., Spiegel, O., Baskett, M.L. & Sih, A. (2018). Social information links individual behavior to population and community dynamics. *Trends in Ecology & Evolution*, 33, 535–548.

Harrold, C. & Reed, D.C. (1985). Food availability, sea urchin grazing, and kelp forest community structure. *Ecology*, 66, 1160–1169.

Ives, A.R., Einarsson, Á., Jansen, V.A.A. & Gardarsson, A. (2008). High-amplitude fluctuations and alternative dynamical states of midges in lake myvatn. *Nature*, 452, 84.

Johnson, S.G. (2019). The nlopt nonlinear-optimization package. URL `http://ab-initio.mit.edu/nlopt`.

Koen-Alonso, M. (2007). A process-oriented approach to the multispecies functional response. In: *From energetics to ecosystems: the dynamics and structure of ecological systems*. Springer, pp. 1–36.

Konar, B. (2000). Seasonal inhibitory effects of marine plants on sea urchins: structuring communities the algal way. *Oecologia*, 125, 208–217.

Kushner, D.J., Rassweiler, A., McLaughlin, J.P. & Lafferty, K.D. (2013). A multi-decade time series of kelp forest community structure at the california channel islands: Ecological archives e094-245. *Ecology*, 94, 2655.

Laundré, J.W., Hernández, L. & Altendorf, K.B. (2001). Wolves, elk, and bison: reestablishing the" landscape of fear" in yellowstone national park, usa. *Canadian Journal of Zoology*, 79, 1401–1409.

Levin, S.A. & Paine, R.T. (1974). Disturbance, patch formation, and community structure. *Proceedings of the National Academy of Sciences of the United States of America*, 71, 2744–2747.

Ling, S.D., Scheibling, R.E., Rassweiler, A., Johnson, C.R., Shears, N., Connell, S.D. *et al.* (2015). Global regime shift dynamics of catastrophic sea urchin overgrazing. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 370.

Mumby, P.J., Hastings, A. & Edwards, H.J. (2007). Thresholds and the resilience of caribbean coral reefs. *Nature*, 450, 98–101.

Noy-Meir, I. (1975). Stability of grazing systems: an application of predator-prey graphs. *Journal of Ecology*, 459–481.

Okamoto, D.K. (2014). *The role of fluctuating food supply on recruitment, survival and population dynamics in the sea*. University of California, Santa Barbara.

Petraitis, P.S. & Dudgeon, S.R. (2004). Detection of alternative stable states in marine communities. *Journal of Experimental Marine Biology and Ecology*, 300, 343–371.

PISCO, Carr, M. & Caselle, J. (2011). Pisco: Subtidal: Community surveys: Swath surveys. URL {http://search.dataone.org/view/doi:10.6085/AA/pisco_subtidal.151.2}.

R Core Team (2017). R: A language and environment for statistical computing.

Reed, D.C., Rassweiler, A., Carr, M.H., Cavanaugh, K.C., Malone, D.P. & Siegel, D.A. (2011). Wave disturbance overwhelms top-down and bottom-up control of primary production in california kelp forests. *Ecology*, 92, 2108–2116.

Rietkerk, M. & Van de Koppel, J. (2008). Regular pattern formation in real ecosystems. *Trends in Ecology & Evolution*, 23, 169–175.

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C. & Walker, B. (2001). Catastrophic shifts in ecosystems. *Nature*, 413, 591–596.

Shears, N.T. & Babcock, R.C. (2004). *Community composition and structure of shallow subtidal reefs in northeastern New Zealand*. Department of Conservation Wellington.

Silliman, B.R., McCoy, M.W., Angelini, C., Holt, R.D., Griffin, J.N. & van de Koppel, J. (2013). Consumer fronts, global change, and runaway collapse in ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, 44, 503–538.

Smith, K.N. & Herrkind, W.F. (1992). Predation on early juvenile spiny lobsters panulirus argus (*Latreille*): influence of size and shelter. *Journal of Experimental Marine Biology and Ecology*, 157, 3–18.

Staver, A.C., Archibald, S. & Levin, S.A. (2011). The global extent and determinants of savanna and forest as alternative biome states. *Science*, 334, 230–232.

van de Leemput, I.A., Hughes, T.P., van Nes, E.H. & Scheffer, M. (2016). Multiple feedbacks and the prevalence of alternate stable states on coral reefs. *Coral Reefs*, 35, 857–865.

van Nes, E.H. & Scheffer, M. (2005). Implications of spatial heterogeneity for catastrophic regime shifts in ecosystems. *Ecology*, 86, 1797–1807.

Vásquez, J.A. & Buschmann, A.H. (1997). Herbivore-kelp interactions in chilean subtidal communities: a review. *Revista Chilena de Historia Natural*, 70, 41–52.

Vásquez, J.A., Castilla, J.C. & Santelices, B. (1984). Distributional patterns and diets of four species of sea urchins in giant kelp forest(macrocystis pyrifera) of puerto toro, navarino island, chile. *Marine Ecology Progress Series*, 19, 55–63.