

AN ABSTRACT OF THE THESIS OF

Zachary Howland Randell for the degree of Doctor of Philosophy in Integrative Biology presented
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Title: Grazer-resource Behavior, Interactions, and Feedbacks Control Kelp-forest Dynamics and Stability

Abstract approved: _____

Mark Novak

How the direct and indirect effects of species interactions cascade to affect community structure, functioning, and stability is a fundamental question in ecology. In temperate kelp forests, species interactions, in conjunction with environmental processes, produce rich spatiotemporal dynamics. Arguably the most dramatic of these are abrupt shifts in community state, where forested locations are grazed by herbivorous urchins to establish what is known as an “urchin barren”. The increasing frequency and intensity of perturbation events associated with climate change have increased the frequency of shifts towards the barren-state. Understanding not only the mechanisms precipitating state shifts but also those that stabilize both the forested and barren states is essential to guide effective kelp-forest conservation and management strategies.

Central to urchin barren establishment is a switch in behavior, where urchins leave cracks and crevices to move across the seafloor and graze upon kelp. While it is known that urchin predators can control urchin density and behavior, it is less clear how resource availability affects urchin behavior, or how the switch in behavior affects kelp-forest dynamics at large. This dissertation evaluated urchin behavior, the “bottom-up” processes controlling it, and the subsequent effects upon kelp-forest dynamics and stability from three distinct directions.

In *Chapter 2*, I analyzed 38 years of kelp-forest community data and found distinct spatiotemporal patterns: certain sites exhibited abrupt shifts in state, others exhibited resilient kelp-forest persistence. I suggest that substrate complexity (the rugosity of the benthic substrate) modified both “top-down” and “bottom-up” processes regulating urchin density and behavior. In particular, I suggest that substrate complexity altered the retention of drift algae (also known as kelp detritus, and henceforth, drift)—the senescent form of kelp that has detached from the seafloor. Urchins are believed to prefer drift, such that when drift is abundant urchin remain inactive, consume the drift, and do not graze live kelp. Variation in the retention of drift may thus in-part be responsible for

the urchin behavioral switch that leads to the establishment and stabilization of the barren state.

In *Chapter 3*, I used a one-consumer (urchins) two-resource (kelp and drift) model to test if and how a switch in urchin grazing can precipitate kelp-forest dynamics such as alternative stable states and the emergence of kelp population cycles. Under the assumption that urchins prefer drift over live kelp, results demonstrated that all shifts in state are associated with urchins switching between resources.

In *Chapter 4*, I experimentally tested the core assumption from *Chapter 3*, i.e., that urchins “prefer” drift. Specifically, I used a subtidal caging experiment to evaluate the density-dependent effects of drift and kelp upon urchin consumption rates. Results demonstrated a strong preference in urchins to consume drift, that kelp consumption is controlled by the availability of drift (not by kelp itself), and that urchins exhibit a rank switch—a switch in the proportion of resources consumed as total biomass increases—from kelp to drift.

Altogether, this dissertation used long-term monitoring, dynamical modeling, and subtidal experimentation to evaluate the influence of grazer-resource behavior, interactions, and feedbacks upon kelp-forest dynamics and stability. While urchin predators are predominantly thought to control the switch in urchin behavior, I demonstrate how resource availability can also control this behavioral switch. This may help explain shifts to the urchin barren state at locations where urchin predator abundances remain unchanged. Furthermore, my inferences involving substrate complexity and drift as a preferred urchin resource point towards potential strategies with which to conserve or restore kelp-forest ecosystems.

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Grazer-resource Behavior, Interactions, and Feedbacks Control Kelp-forest Dynamics and Stability

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Zachary Howland Randell

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Zachary Howland Randell, Author

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Academic

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CONTRIBUTION OF AUTHORS

Dr. Mark Novak assisted with the study design and writing of *Chapters 2, 3, and 4*. Mike Kenner, Joe Tomoleoni, and Dr. Julie Yee contributed to the writing of *Chapter 2*. Dr. Karen Abbott wrote the original version of the model analyzed in *Chapter 3*. Dr. Mark Carr, Casey Sheridan, and Jessica Bray contributed to the execution of field work, and Yi Zhang contributed to the analyses of *Chapter 4*.

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DEDICATION

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**Grazer-resource Behavior, Interactions, and Feedbacks Control Kelp-forest
Dynamics and Stability**

1 General Introduction

1.1 Conceptual motivation

Ecosystems exhibit rich and complex dynamics—defined here as changes in mean abundance or density—across space, time, and levels of organization. At the scale of an individual, sea otter dietary specialization and foraging behavior in response to a heterogenous landscape of limited prey can reinforce patchy community structure along the benthos (i.e. seafloor) (Tinker et al. 2008; Smith et al. 2021). At the scale of a single population, negative density-dependence such as intraspecific competition among life stages can produce periodic dynamics such as population cycles (Barraquand et al. 2017; Myers 2018). Consumer-resource interactions can exhibit multi-species density dependence, where predators lag prey and track changes in abundance through coupled and periodic phases of prey-escape and growth, predator over-exploitation, and prey and then predator collapse (May 1974; Murdoch et al. 2003). At the scale of an ecosystem, abrupt shifts in community state have been widely observed in terrestrial and aquatic environments in response to changing environmental conditions (phase shifts, Scheffer, Carpenter, et al. 2001a; Bestelmeyer et al. 2011) and with environmental conditions held constant (alternative stable states, Sutherland 1974; Beisner et al. 2003). Understanding these patterns requires understanding: (1) the precipitating mechanisms and regulatory processes at play, (2) the direct and indirect effects of these regulatory processes across levels of organization, and (3) how these cross-level effects feedback to affect the precipitating behavior or mechanism.

Understanding ecological patterns and the processes that drive them is essential for effective management and conservation. For example, within a single population, understanding that sea otters are resource limited across their current range can guide recovery efforts, even if only to emphasize that the existing range is unlikely to support significant further population growth. In the multi-species context, what was originally an opportunity to recover a Gray wolf population turned into invaluable ecological knowledge, as the direct and behavioral effects of the wolf population upon large herbivores cascaded to indirectly facilitate community structure and functioning (Ripple et al. 2012; Boyce 2018). The “landscape of fear”—how predators affect prey behavior—is now part of our intuition regarding the potential direct and indirect effects of (facilitated) consumer population recovery (Zanette et al. 2019). And finally, understanding the drivers of phase shifts versus the feedback processes stabilizing alternative stable states may provide an opportunity to reverse or stave off undesirable community shifts. As an example with a phase shift, Florida and

other parts of the gulf coast in the USA are inundated with “red tide” (toxic algal blooms from, e.g., *Karenia brevis*) causing massive fish, bird, and marine mammal mortality, and negative effects on human respiratory health (Kirkpatrick et al. 2004). Such drastic community shifts are likely to persist so long as the environmental conditions compounding their frequency and magnitude—in particular, high rates of nutrient outflow from agriculture—are sustained. In contrast, the existence of alternative stable states are dependent upon changes in the stabilizing processes affecting community structure. For example, alternative forested and shrub land states are dependent upon the abundance and canopy forming trees, and the associated effects upon fire frequency. Forest canopy cover reduces the growth of flammable species, providing stabilizing feedback via decreased fire occurrences. Shrub lands however are highly flammable, and young trees that could grow to establish a canopy are removed early and often by increased occurrences of fire (Wilson et al. 1992). Thus, varying fire dynamics as a function of community structure provide stabilizing feedback to either of the two alternative stable states. In this example, rather than controlling the mechanism of disturbance (fire), conservationists seek to preserve canopy forming trees and the stabilizing feedbacks they provide.

Focusing upon my study system, temperate kelp forests, this dissertation: (1) analyzed long-term subtidal monitoring of community structure to identify patterns of community resilience and stability, (2) used a dynamical model to study a key mechanism hypothesized to contribute to those community patterns of stability, and (3) experimentally evaluated *in situ* that same mechanism—closing the loop from the original empirical patterns and inferred processes.

Chapter 2 presents analyses of 38 years of long-term monitoring that uncovered distinct spatiotemporal patterns of community structure: (*a*) certain locations exhibited shifts in community state—including both directions of shift, and shifts “back-and-forth” at approximately the decadal scale; whereas other locations exhibited (*b*) a persistent and resilient single state of community structure through time. These distinct community dynamics manifested at locations near one another around a small island, and all locations experienced approximately the same set of environmental conditions. If shifts in community state occurred in response to changing environmental conditions, we would expect all sites to exhibit synchronous shifts in state. Instead, shifts were asynchronous, and certain sites did not shift at all. Therefore, I infer the observed shifts in state were not phase shifts, but rather alternative stable states. I demonstrate that variation in substrate complexity (the rugosity of the seafloor) associates with these distinct community dynamics. I hypothesize substrate complexity modifies multiple regulatory processes structuring the behavior

of herbivorous urchins, such that variation in this environmental variable associates with two distinct modes of grazing. That is, urchins switch between hiding in cracks and crevices consuming drift, to moving across the benthos grazing live kelp. Understanding how various processes affect this behavioral shift—and testing assumptions regarding the underlying mechanisms precipitating it—are the focus of *Chapters 3 and 4*.

Chapter 3 uses an analytically intractable model built to develop insight into the hypothesized switch in urchin grazing behavior, as well as the effects of various processes expected to influence the propensity of the system to shift between alternative stable states. Specifically, I modeled the interactions between a single grazer (urchins) and two alternative resources (kelp and drift) to test whether and how resource preference and switching between resources would affect system stability, including the propensity to switch between alternative stable states. Results of numerical analyses demonstrate: (1) the dependency upon resource availability to manifest the switch in urchin grazing behavior, (2) how resource switching is necessary for alternative stable states to emerge, i.e., bimodality (the existence of two attractors) is a function of the two modes of grazer behavior, and (3) the discontinuity between the two steady states is also associated with a dynamical shift between a fixed point regime and one exhibiting stable limit cycles.

Chapter 4 tested a core component of the urchin behavioral switch with a subtidal caging experiment. I evaluated the density-dependence between two alternative resources and the associated relative rates of consumption by an urchin species. This was a functional response experiment designed to measure how units of resources consumed varied with resource density. The experimental data indicates: (1) a strong preference by urchins to consume drift over kelp, (2) the availability of drift controls the consumption of kelp, and (3) a density-dependent rank switch from kelp to drift as the total biomass of the two resources increase. These results empirically support a key model assumption of *Chapter 3*, that urchin behavior is a function of drift availability. By fitting an ordinary differential equation system to our experimental data, I functionally characterized the density-dependent relationship between these two resources and their associated rates of consumption.

Chapter 5 concludes this dissertation by summarizing key findings and positing potential analytical and experimental avenues to build upon its results.

1.2 Kelp-forest dynamics

With the framework of the dissertation in place, I now turn to my specific system—temperate kelp forests. I provide an overview of community functioning, the role of perturbations in driving abrupt shifts, the regulatory processes structuring kelp forests at small and large spatial scales, and the potential for perturbations to alter the net-expression or realized strength of regulatory processes. This background material culminates with the assertion that the strength of local-scale processes—such as those inferred from *Chapter 2*, modeled in *Chapter 3*, and experimentally tested in *Chapter 4*—can be the difference between resilient community persistence following perturbation events, versus shifts between alternative stable states.

Kelp forests—comprised of macrophytes primarily in the Orders Laminariales and Fucales, henceforth “kelp”—are highly productive and diverse, and provide a myriad of ecological services both at the site of growth and through meta-ecosystem connectivity (Dayton 1985; Steneck, Graham, et al. 2002; Foster et al. 2010). Kelp forests provide key biological habitat for numerous invertebrates and fishes, and kelp canopy is particularly important habitat for fish larvae, especially rockfishes, transitioning from the pelagic dispersal phase (Carr 1991; Johnson 2006). Kelp exhibit rapid growth that has the potential to sequester significant amounts of carbon (Wilmers et al. 2012; Krause-Jensen et al. 2016), and detached forms of kelp known as drift algae or wrack provides nutrients through meta-ecosystem transport to deeper reefs, submarine canyons, and continental shelves, and onto intertidal and terrestrial systems (Hinojosa et al. 2010; Filbee-Dexter, Feehan, et al. 2016; Hawes et al. 2017). In addition to ecological functioning, these forests also have deep cultural significance to Tribes and First Nations (Swan 1855). Coastal populations cherish these forests for their aesthetic, recreational, and commercial value.

Kelp forests are subject to both pulse-perturbations and gradual environmental changes associated with global climate change. In the Northeast Pacific, the effects of both are accentuated by the extirpation of sea urchin predators that, in-part, control excessive urchin grazing upon kelp (Filbee-Dexter and Scheibling 2014b; Rogers-Bennett and Catton 2019a). While the life histories of kelp are well suited to regular disturbance from large wave events, the increasing frequency and intensity of these events—and their correlation with other pulse-perturbations such as anomalous warm-water events—have increased the frequency and magnitude of kelp loss along large stretches of North America. These stochastic pulse-perturbations also occur concomitant with marine disease events such as the 2013-2014 Sea Star Wasting Syndrome (SSWS) event that decimated over

20 sea star species along the entire north-east Pacific Rim (Hewson et al. 2018).

When sufficiently perturbed, kelp forests exhibit abrupt, discontinuous movement (Hastings and Wysham 2010) to a different community state known as an urchin barren, where urchin overgrazing limits kelp recovery (Filbee-Dexter and Scheibling 2014b; Ling, Scheibling, et al. 2015a; Ling, Kriegisch, et al. 2019). While the precise mechanisms controlling these shifts vary latitudinally, generally they are thought to be brought about when urchins exhibit a switch in behavior, going from hiding in cracks and crevices and persisting on drift algae, to actively moving across the benthos and consuming live kelp (Harrold and Reed 1985a; Vanderklift and Kendrick 2005; Vanderklift and Wernberg 2008). This switch in behavior often manifests following localized disturbance, e.g., following a large-wave event that removes both drift algae and live kelp (Ebeling et al. 1985). However it is often unclear whether the urchin barren state is truly a “stable alternative,” or instead is a multiyear period of transient dynamics followed by kelp recovery (Fukami et al. 2011; Hastings, Abbott, et al. 2018; Hillebrand et al. 2020). The key to differentiating these two depends upon whether the strength of feedback processes stabilizing the forested state are sufficiently altered by the perturbation. If so, and in particular if this occurs across an entire coastline, e.g., see Filbee-Dexter, Feehan, et al. 2016, different stabilizing feedbacks may increase in strength to provide resilience to the urchin barren state. For example, increased urchin grazing reduces kelp cover, which reduces spore production, and leads to an increase in the cover of encrusting algae that facilitates settlement of sea urchin larvae (Taniguchi et al. 1994). The difference between alternative versus transient urchin barren dynamics is the difference between eventual “natural” kelp forest recovery versus active restoration efforts being required to cull urchin densities and restore kelp populations (Watanuki et al. 2010; Morris, Hale, et al. 2020).

The inherent dynamic complexity and spatiotemporal scales of kelp forest regulation presents a challenge given the differing spatial scales of kelp, invertebrate, and fish dispersal. Kelp, invertebrates, and fishes comprising healthy kelp forests are structured by different regulatory processes at different spatiotemporal scales (Cavanaugh, Kendall, et al. 2013), and pulse-perturbations can alter the predominant spatial scale of regulation (Edwards 2004; Reed, Rassweiler, et al. 2011). Giant kelp (*Macrocystis pyrifera*) release massive quantities of spores that produce gametophytes dispersed on the order of tens of meters to a few kilometers (Santelices 1990; Schiel et al. 2006), and thus meta-population theory predicts synchronous population dynamics at the spatial scale of dispersal (Fitness et al. 1986; Hastings and Harrison 1994). Instead, even contiguous stretches of reef exhibit kelp subpopulations that fluctuate asynchronously, akin to patches within a broader

network (Cavanaugh, Siegel, et al. 2014). While spore dispersal is key for enabling recolonization, particularly for distanced and smaller patches, localized extinction is often a stronger determinant of kelp dynamics (Castorani et al. 2015). This is because local heterogeneity in the form of variation in substrate and community composition drive local processes such as intra- and inter-specific competition for space to grow along the benthos, as well as herbivory and predatory consumer-resource interactions. The strength and resilience of these local-scale processes encompass many of the stabilizing feedbacks that provide resilience to the kelp forest state.

Local-scale of regulatory control is nonetheless subject to forcing from larger-scale processes such as storms (discussed below) and the pelagic dispersal of larvae. Marine propagules from invertebrates such as urchins and fishes can travel for tens to hundreds of kilometers with coastal currents (Kim 1992; Baetscher et al. 2019). Their dispersal processes operate at a much broader spatial scale relative to kelp spore dispersal, thus invertebrate and fish connectivity can synchronize populations along a coastline, a phenomenon known as the “Moran effect” (Ranta et al. 1997; Gouhier et al. 2010). This dynamic synchrony across space can occur when dispersal-enabled settlement overwhelms local heterogeneity by decoupling local rates of replenishment from the regulatory processes structuring adult individuals (Karatayev et al. 2020). For example, urchin barrens can persist despite high adult urchin mortality from density-dependent disease outbreaks because urchin settlement and recruitment are decoupled from both local larval output and from the top-down disease mortality affecting adults. In essence, dispersal-mediated stabilizing urchin barren feedbacks supersede the density-dependent urchin mortality locally structuring the adult population, enabling persistence of the urchin barren state. In contrast, widespread dispersal may not elicit spatial synchrony if local-scale feedback processes are sufficiently resilient, e.g., if the local community exerts high post-settlement mortality upon urchins.

Stochastic pulse perturbations such as warm-water, large-wave, or marine disease events modify the strength of local stabilizing feedbacks, thus predisposing kelp forests to dispersal-mediated synchrony of the urchin barren state. Kelp forests are stabilized through spore production, dispersal, growth, and the conversion through senescence of live kelp into drift algae, which sea urchins are believed to prefer to consume, and therefore losing kelp (i.e., losing the associated stabilizing feedbacks), particularly across large stretches of a coastline, reduces the short-term capacity of kelp to recover. If a perturbation occurs simultaneously or temporally lags by a couple years a strong urchin recruitment event, the combination can limit kelp recovery due to continual grazer pressure, and subsequent dispersal-mediated urchin recruitment can further stabilize the barren state.

1.3 Chapter summary

1.3.1 *Chapter 2: Kelp-forest dynamics controlled by substrate complexity*

This dissertation seeks to understand how local heterogeneity modifies species interactions and stabilizing feedback processes to either stabilize the forested state, or perpetuate switching between alternative stable states.

The objective of *Chapter 2* was to understand how kelp-forest community dynamics varied through time at a relatively small ($10m$) spatial scale. To do this, I analyzed 38 years of data from a long-term subtidal monitoring program around San Nicolas Island (SNI), southern California, USA. SNI is relatively small and experiences approximately homogenous exposure to environmental variables such as sea temperature and chlorophyll *a*. Because of this, I investigated how small-scale ($10m$) variation in substrate complexity associated with 38 years of community dynamics. I quantified the underlying rugosity of the seafloor with a magnetic surveyor's wheel and associated those measurements with a NMDS ordination of community structure. Reducing the dimensionality down to a single axis captured the community state of the system. Analyses indicate abrupt shifts between forested and urchin barren states only appeared at low-complexity sites. Similarly perturbed high-complexity sites exhibited 38 years of resilient urchin-kelp coexistence and persistence of the forested state. Furthermore, I demonstrate that shifts between states were high-velocity events, whereas within-state community movements consisted of low-velocity (relatively small) shifts in community structure. These results align with expectations for how a system responds to perturbations in relation to a stability landscape.

I hypothesize that substrate complexity modifies “top-down” processes regulating urchin behavior such as direct and behavioral effects of predators, as well as “bottom-up” processes such as the retention of drift algae upon which urchins are believed to preferentially consume. Regarding the latter, I hypothesize that low-complexity locations lack the physical heterogeneity necessary to “entrap” or otherwise retain drift algae during, e.g., a large wave event, such that low-complexity locations are subject to experiencing large shifts in urchin behavior—a switch from consuming drift to kelp—leading to urchin barren formation.

It is these assumptions—that urchins prefer to consume drift over kelp, and that the switch in urchin behavior is dependent upon the availability of drift—that I focus on for *Chapters 3* and *4*.

1.3.2 *Chapter 3: Urchin behavior controls system stability*

In *Chapter 3* I used a system of delayed-differential equations to simulate the interactions of a single consumer (urchins) grazing upon two resources (kelp and drift). My objectives were to explore if and how an urchin preference to consume drift and an associated behavioral switch could affect system stability, including the potential to exhibit alternative stable states. Urchin “preference” (i.e. the proportion of urchins grazing kelp) is dependent upon the availability (density) of drift. Changes in drift availability—either from urchin consumption or other sources of loss—feedback to affect kelp as urchins shift their grazing activity. I numerically analyzed the system with one- and two-dimensional (*1D* and *2D*) bifurcation analysis. Doing so allowed me to explore the effects of individual and pairs of parameters upon system dynamics, including how processes such as drift production, retention, and loss affected the propensity for the system to exhibit alternative stable states.

This model exhibited: (1) discontinuous movement between two steady states, (2) qualitative shifts in dynamics between a fixed point and stable limit cycles, and (3) alternative stable states. Shifts between alternative stable states were often characterized by both discontinuous movement between steady states and the qualitative change in dynamics. The model demonstrates how the processes involved in drift production, retention, and loss affect the capacity of the system to exhibit alternative stable states, and that all shifts in state in this model are predicated upon the switch in grazer activity. And this behavioral switch itself is dependent upon our assumption that the density of drift controls the behavior of urchins.

1.3.3 *Chapter 4: Drift algae controls the consumption of kelp*

The objective of *Chapter 4* was to experimentally evaluate the density-dependence of the relative rates of consumption upon kelp and drift. Doing so allowed me to evaluate whether urchins exhibit resource preference (where the proportion of a resource consumed exceeds its proportional availability), and switching behavior, such as positive and negative switching (a density-dependent shift in preference) or rank switching (where the proportion of a resource consumed changes with total, not relative, resource availability).

I experimentally evaluated these questions by teaming up with researchers at the University of California Santa Cruz in the Raimondi-Carr lab. Throughout the summers of 2018 and 2019, I conducted a subtidal caging experiment offshore of Hopkins Marine Station, Monterey, California, USA. I measured kelp and drift consumption across three 48hr periods—restocking resources back

up to their initial conditions at end of each period—producing a three-period temporal sequence of consumption observations. This experiment was repeated four times. To analyze these data, I fit an ordinary differential equation (ODE) system to the observed values of drift consumed to estimate key parameters such as resource preference. I also used “gut fullness” as a latent variable to model the manner in which urchin consumption declined as net-consumption increased across the three-period sequence.

Notable results include: (1) drift consumption increased with drift availability. In contrast, (2) kelp consumption was unrelated to kelp availability, and instead was controlled by the availability of drift. Furthermore, (3) urchins exhibited a preference for drift. They also (4) exhibited rank switching from kelp to drift as the total availability of the two resources increased. Model fitting and simulations (5) reproduced these experimental patterns, and while our model for gut fullness is likely incomplete in that it does not reproduce a (continual) gradual temporal decline in consumption, it succeeded in addressing the focal questions of interest regarding resource preference and switching.

1.3.4 *Chapter 5: Concluding remarks*

I conclude this dissertation with a summary of key findings from each chapter. I also touch upon future potential avenues of research—both analytical and experimental—that could expand upon our results.

2 Kelp-forest dynamics controlled by substrate complexity

2.1 Abstract

The factors that determine why ecosystems exhibit abrupt shifts in state are of paramount importance for management, conservation, and restoration efforts. Kelp forests are emblematic of such abruptly-shifting ecosystems, transitioning from kelp-dominated to urchin-dominated states around the world with increasing frequency, yet the underlying processes and mechanisms that control their dynamics remain unclear. Here, we analyze four decades of data from biannual monitoring around San Nicolas Island, CA, USA, to show that substrate complexity controls both the number of possible (alternative) states and the velocity with which shifts between states occur. The superposition of community dynamics with reconstructions of system stability landscapes reveals that shifts between alternative states at low-complexity sites reflect abrupt, high-velocity events initiated by pulse perturbations that rapidly propel species across dynamically-unstable state-space. In contrast, high-complexity sites exhibit a single state of resilient kelp-urchin coexistence. Our analyses suggest that substrate complexity influences both top-down and bottom-up regulatory processes in kelp forests, highlight its influence on kelp-forest stability at both large (island-wide) and small (< 10m) spatial scales, and could be valuable for holistic kelp forest management.

2.2 Introduction

Kelp-forest ecosystems exhibit rich and varied spatiotemporal dynamics. Prominent among these are dramatic shifts between kelp-dominated forests and so-called urchin barrens from which macroalgae are almost entirely absent due to intense urchin grazing (Filbee-Dexter and Scheibling 2014b; Ling, Scheibling, et al. 2015b). Phase shifts between kelp and barren states have long been associated with structural changes to kelp-forest communities, such as the addition or removal of sea-urchin predators (Estes and Palmisano 1974; Ling, Johnson, et al. 2009), or changes in the environment such as shifting water temperatures (Tegner et al. 1991; Dayton, Tegner, Edwards, et al. 1998; Ling, Johnson, et al. 2009; Johnson et al. 2011). Kelp forests are also subject to stochastic perturbations such as large wave, marine disease, and anomalous warm water events that perturb kelp forests between alternative stable states (Reed, Rassweiler, et al. 2011; Rogers-Bennett and Catton 2019b). However, distinguishing phase shifts and alternative stable states is a major challenge (Dudgeon et al. 2010). This is partially because both slow environmental change

and relatively rapid stochastic perturbations often appear to act synergistically and with episodic urchin recruitment events which, due to their large regional extent, decouple rates of urchin grazing from the local density-dependent regulation of their populations (Uthicke et al. 2009; Karatayev et al. 2020).

Although consensus is emerging that the maintenance of kelp-dominated forests is driven by a combination of top-down and bottom-up processes, the mechanisms underlying these processes—and hence the optimal means to control and avoid tipping points to the urchin barren state—appear varied and often unclear (Ling, Scheibling, et al. 2015b; Krumhansl et al. 2016). For example, top-down processes contributing to kelp-forest stability include the effects of predators and disease on sea-urchin grazing behavior and mortality rates (Lafferty 2004; Hamilton et al. 2015; Burt et al. 2018; Eisaguirre et al. 2020; Smith et al. 2021), emphasizing the need for management strategies that preserve or restore top-down forms of urchin control (Ling, Ibbott, et al. 2010; Estes, Terborgh, et al. 2011). On the other hand, bottom-up processes affecting kelp growth and senescence rates, and the retention of drift algae which urchins prefer to consume, are also known to contribute to kelp-forest stability, emphasizing management strategies that differ from those of direct urchin control (Harrold and Reed 1985b; Vanderklift and Kendrick 2005; Vanderklift and Wernberg 2008; Foster et al. 2010; Kriegisch et al. 2019)

Here we apply the perspective of stochastic dynamical systems to the study of kelp forests to determine not the specific mechanisms or feedbacks that underlie kelp-forest dynamics but rather to infer an environmental variable that influences their relative strength and net expression. The dynamical-systems perspective conceptualizes a system's community states and dynamics using the ball-in-cup heuristic of stability and resilience (Holling 1973; Scheffer, Carpenter, et al. 2001b), formally described by a (quasi-)potential stability landscape (Zhou et al. 2012; Nolting et al. 2016). A system with alternative stable states exhibits a multi-modal landscape with two or more basins of attraction (cups) over which it travels in time due to endogenous drivers (e.g., species interactions) and external perturbations. Because most perturbations are directionally random and small, communities spend more time in states at the bottom of the attracting basins than they do on their slopes and cusps, with deeper and steeper-sloped basins corresponding to more stable and resilient community states whose dynamics are dominated by negative feedbacks (Nolting et al. 2016). Previous work has utilized this characteristic of stochastic dynamical systems to make use of large-scale spatial variation in community structure to infer what biotic and environmental conditions may alter the stability of various ecological systems, including tropical and temperate

forests and desert biomes (Ling, Johnson, et al. 2009; Hirota et al. 2011; Staver et al. 2011; Aleman et al. 2020). For example, (Scheffer, Hirota, et al. 2012) used satellite-derived spatial variation in the frequency-distributions of percent tree cover values to infer that boreal biomes exhibit between one and three different alternative stable states whose number and nature depend on mean July temperature, where empirical system state frequency histograms represent negative potential, i.e., a mirror image of a ball-in-cup stability landscape reflected across the x-axis. Similarly, (Ling, Johnson, et al. 2009) combined spatial survey data with translocation experiments to infer bistability in response to urchin densities in Tasmanian kelp forests. The approach underlying these inferences has been referred to as potential analysis (Livina et al. 2010).

Using spatially-fixed and replicated long-term time series of kelp-forest community dynamics around San Nicolas Island, CA, we extend the application of potential analysis to include the temporal domain to more rigorously infer their condition-dependent stability landscapes and movement. Our analyses reveal kelp-forest communities around San Nicolas Island that exhibit dramatic, perturbation-induced shifts between kelp-dominated forests and urchin barren states only when the complexity of the underlying substrate is low, and that similarly-perturbed high-complexity substrates permit only a single persistent state of resilient kelp-urchin coexistence. Substrate complexity at San Nicolas Island controls the relative strength of the many negative and positive feedbacks that have been described in kelp forests, and therefore understanding complexity is likely to increase the effectiveness of management efforts seeking to conserve and restore their existence.

2.3 Methods and Results

2.3.1 Multimodality and velocities of community movement

San Nicolas Island is located in the Channel Islands off the southern Californian coast (N 33.25°, W 119.50°). We analyzed 38 years of biannual community data from 1980 to 2018 at six subtidal sites installed around the island at depths of 10 – 14m. Each site comprises five fixed-location benthic transects (10 x 2m) in which the abundance of seven key invertebrates and seven dominant macroalgae species (henceforth “kelp” for brevity) were monitored (Kenner, Estes, et al. 2013). We quantified the substrate complexity of each transect as its lengthwise linear relief measured using a 13cm circumference electronic surveyor’s wheel (Wilding et al. 2007). Because some sites exhibit informative variation in substrate complexity and dynamics among their transects, we present the results of analyses conducted at the transect scale rather than the site scale.

To reconstruct transect-level stability landscapes and evaluate their multi-modality using potential analysis, we expanded upon (Kenner and Tinker 2018) and used non-metric multidimensional scaling (NMDS, (Kruskal 1964)) to obtain a two-dimensional ordination of all transect-level species abundances through time. Axis-1 of this ordination encompassed 61.2% of the variation and effectively captured the predominant gradient of community structure ranging from kelp-dominated with almost no urchins (Fig. 2.1*a*), to a broad mixture of kelp and urchins centered around the axis origin (Fig. 2.1*a,b*), to urchin barrens comprised almost exclusively of urchins and no macroalgae (Fig. 2.1*b*). Axis-2 was primarily associated with non-grazing, predatory invertebrates, specifically sea stars (inset of Fig. 2.1*c*) and captured an additional 23.9% of variation. Due to their length and sampling-frequency, each transect-level time-series evidenced ample and consistent community variation relative to the broader range of community structure across all sites to reconstruct robust frequency distributions of community state. The multi-modality of these frequency distributions along Axis-1 was visualized using kernel densities and formally evaluated using Gaussian mixture models. In concordance with (Kenner and Tinker 2018), these provided strong evidence for both uni-modal and multi-modal community state distributions among the thirty transects (Fig. 2.2*a-f*; Table A1, Fig. A2).

As inferred by potential analysis, some transects exhibited alternative stable states while others exhibited only a single stable state. Prior inferences based on potential analysis have relied on the assumption that low-frequency states reflect transient states en route to regions of stability. This assumption is not always warranted given the possibility of multi-generational transients and population cycles (Jäger et al. 2008; Hastings, Abbott, et al. 2018), particularly in multi-dimensional systems (Rodríguez-Sánchez et al. 2020). Therefore, and because our time-series span many generations of the dominant kelp species, we next quantified velocities of community movement through two-dimensional ordination space to gain insight into the state-dependent nature of within- and between-basin perturbation effects and feedbacks. We expected rates of community change to be lowest and directionally-random in regions of Axis-1 reflecting centers of high-frequency community states, and highest and directional (towards high-frequency centers) in regions reflecting low-frequency community states (Lamothe et al. 2019). These expectations were realized in all cases associated with urchin barren and mixed kelp-urchin community states (Fig. 2.2*a-f*; see Fig. A2 for directionality), indicating that these high-frequency states indeed represent stable attractors resilient to most perturbations. Transitions between these states consistently entailed high-velocity, directional events (Fig. A1*a,b*), the mechanisms of which we return to below.

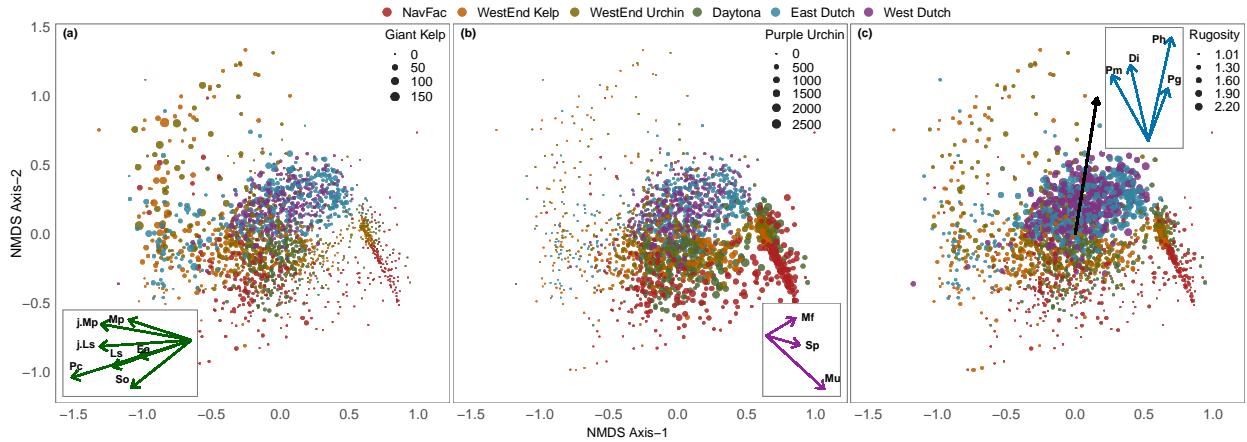


FIGURE 2.1: Ordination of kelp forest community dynamics in two-dimensional species-space. Each point reflects community composition of a transect at a given time-point. Point color identifies the transect's site. Point size reflects a different variable in each panel: (a) giant kelp (*Macrocystis pyrifera*) abundance, negatively associated with Axis-1 (inset: the direction and strength of association of all algal taxa with ordination axes relative to the ordination center); (b) purple urchin (*Strongylocentrotus purpuratus*) abundance and presence positively associated with Axis-1 (inset: the association of all grazing invertebrates with ordination axes); (c) substrate rugosity is positively associated with Axis-2 (main panel black arrow reflects the linear correlation of substrate rugosity with ordination axes; inset: the association of non-grazing and predatory invertebrate taxa with ordination axes). The 14 benthic taxa were purple [Sp] and red (*Mesocentrotus franciscanus*) [Mf] urchins, one gastropod grazer (*Megastraea undosa*) [Mu], four sea stars: the Sunflower star (*Pycnopodia helianthoides*) [Ph], the Giant spined star (*Pisaster giganteus*) [Pg], the Leather star (*Dermasterias imbricate*) [Di], and the Bat star (*Patiria miniata*) [Pm], one macroalgal species in the Order Fucales (*Stephanocystis osmundacea*) [So], and six macroalgae in the Order Laminariales, including two juvenile stages: Giant kelp (*Macrocystis pyrifera*) [Mp], juvenile (< 1m) Giant kelp [j.Mp], (*Pterygophora californica*) [Pc], (*Eisenia arborea*) [Ea], Laminaria spp. [Ls], and young Laminariales [j.Ls].

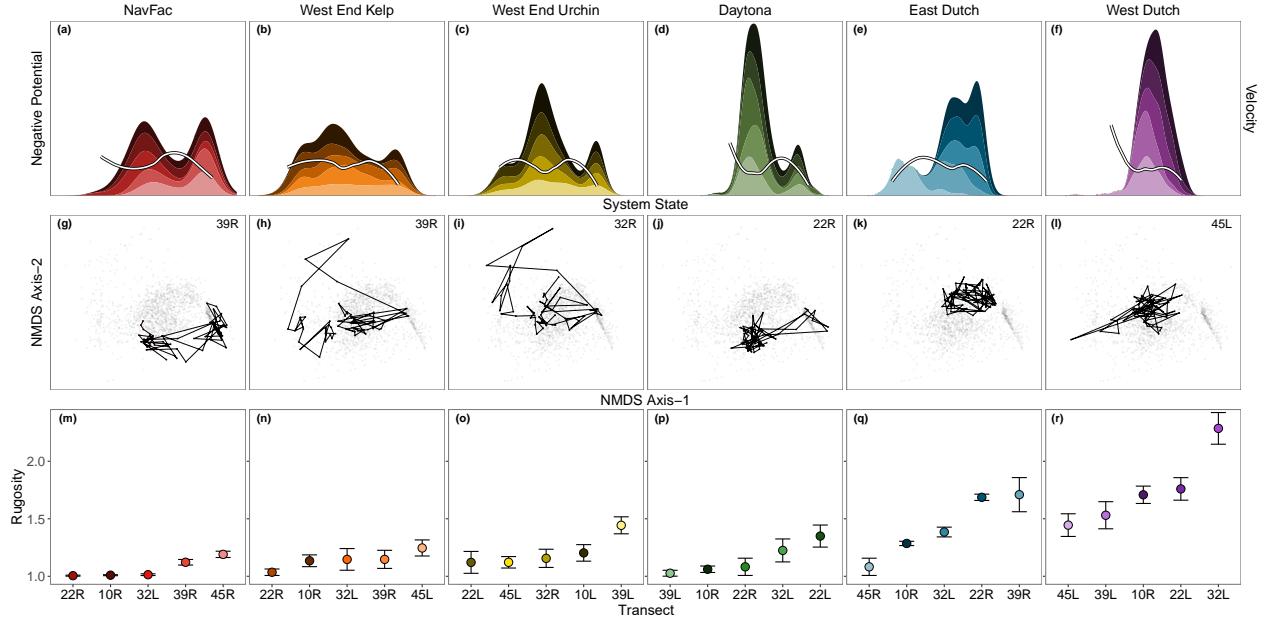


FIGURE 2.2: Row 1: Transect-specific stability landscapes stacked by site (transects differentiated by color hue) and state-dependent velocities of community movement (white lines loess-smoothed with a span of 0.75). Row 2: Ordination of site-specific community dynamics in species-space (as in Fig. 2.1) with the temporal dynamics of one focal transect visualized to highlight within-and between basin movement. Row 3: Transect-specific estimates of substrate complexity (mean \pm 1 SE).

In contrast, our expectations were not realized for 10 transects across two sites inferred by potential analysis to exhibit the third high-frequency state, the algal-only state in which urchins were almost entirely absent (Fig. 2.2*h,i*). This state was also observed by (Kenner and Tinker 2018). It persisted for 2-8 years following large and rapid urchin declines, likely due to disease, and invariably transitioned back to the mixed kelp-urchin state in a smooth and continuous fashion (Fig. 2.3*b,c*). We interpret the dynamics of these algal-only transects as reflecting multi-generational transient dynamics (Frank et al. 2011; Hastings, Abbott, et al. 2018), a finding potential analysis alone would not have resolved. One additional low complexity transect (East Dutch 45R, Fig. 2.2*e*) exhibited the algal-only state for the entire duration of the time-series, in marked contrast to the four other high-complexity transects of the same site which persistently exhibited the mixed kelp-urchin state (Figs. 2.2*e,q* & 2.3*e*).

2.3.2 Multimodality determined by substrate complexity

Transect-level estimates of substrate complexity (surface rugosity) varied markedly across the thirty transects, ranging from being highly structured and complex (linear relief = 24m) to flat

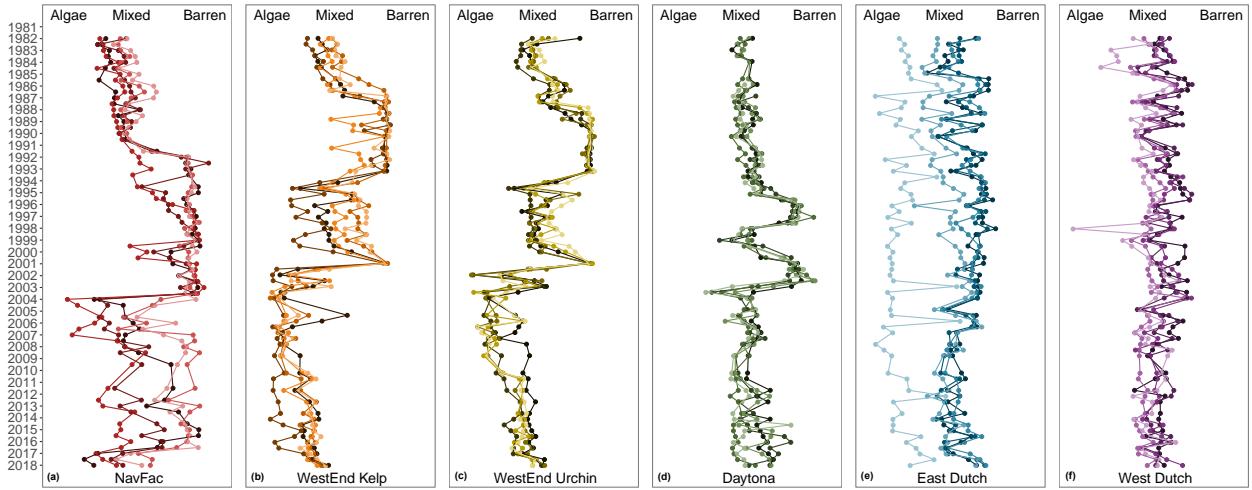


FIGURE 2.3: The temporal dynamics of system state (NMDS Axis-1), with sites ordered from left to right by their average substrate complexity and where individual lines correspond to individual transects. Transitions between urchin barren (“Barren”) and mixed kelp-urchin (“Mixed”) states (*a-d*), as well as from the urchin barren state to the algal-only (“Algae”) state (*a-c*), represent high-velocity shifts. In contrast, transitions from the algal-only state to the mixed kelp-urchin state are smooth and continuous (*b* and *c*) after 2004. All types of shifts entail both synchronous and asynchronous events among transects and sites. The persistent algal-only state of the exceptional transect (light blue in *e*) is addressed in the *Discussion*.

(linear relief = 10m) (Fig. 2.2*m-r*). Transects within a site tended to exhibit similar magnitudes of substrate complexity, but this was not always the case (e.g., Fig. 2.2*q,r*). Substrate complexity was clearly associated with Axis-2 of the NMDS ordination (Pearson’s $r^2 = 0.22$), particularly for transects exhibiting the urchin barren and mixed kelp-urchin community states (Fig. 2.1*c*).

Ordering sites and transects by their average substrate complexity suggested that complexity is predictive of the kelp-forest stability landscape (Fig. A1*a*). While high-complexity transects ($> 15m$ linear relief, rugosity > 1.5) exhibited uni-modal landscapes of persistent kelp-urchin coexistence, low-complexity transects ($< 15m$ linear relief, rugosity < 1.5) exhibited multi-modal landscapes reflective of alternative stable states. Moreover, all transects exhibiting the algal-only transient state were low-complexity transects, including the single East Dutch 45R transect that exhibited a persistent algal-only state.

2.4 Discussion

At San Nicolas Island (SNI), high-complexity sites and transects did not exhibit alternative stable states of community composition, instead exhibiting 38 years of stable kelp-urchin coexistence

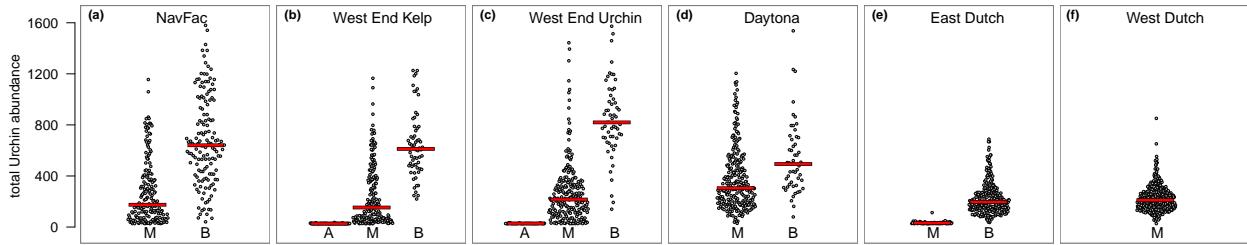


FIGURE 2.4: Total red and purple urchin abundances partitioned by system state (transects combined by site) with sites arranged by increasing mean substrate complexity from left to right. Within each panel the algal-only state is represented by the letter A, the mixed kelp-urchin state by M, and the urchin barren state by B. Red line segments delineate median urchin abundances. A high degree of overlap between the mixed kelp-urchin and urchin barren states indicates that urchin density is not the exclusive driver of kelp-forest states.

resilient to perturbation. Urchins were not common in these transects (Fig. 2.4e,f), but rather than forming fronts or grazing actively in the open, as urchins are known to do during urchin barren formation (Harrold and Reed 1985b), these urchins were consistently hiding in crevices and self-created pits (Russell et al. 2018). In contrast, low-complexity transects exhibited both mixed kelp-urchin and urchin barren states that persisted for up to 12 years, with transitions between them being higher-velocity events in both directions (Figs. 2.3, A1, A2, & A3). Urchins in these transects were observed to exhibit sedentary behavior when in the mixed kelp-urchin state, with urchin densities seen during mixed kelp-urchin periods overlapping considerably with those seen during urchin barren periods (Fig. 2.4a-d). Because high and low-complexity sites are interspersed around the island, with adjacent sites of differing substrate complexity experiencing equivalent oceanographic conditions, these patterns are unlikely to be caused by un-assessed covariates (see *Supplementary Materials* for discussions of chlorophyll *a* (Fig. A4), sea temperature (Fig. A5), wave height (Fig. A6), and sea urchin predator abundance (Fig. A7)). Instead, we hypothesize high substrate complexity permits stable kelp-urchin coexistence because it modifies the relative strength of both top-down and bottom-up regulatory feedbacks through an interplay of behavioral, inter-specific, and oceanographic processes.

2.4.1 Complexity modifies the strength of urchin-regulating feedbacks

We hypothesize that substrate-induced covariation between top-down and bottom-up effects on urchin behavior, recruitment, and mortality determine the propensity of kelp-forest communities to exhibit a single, resilient state versus multiple, alternative stable states between which tipping-point switches occur. Urchin predators, such as sea stars and California (CA) sheephead

(*Semicossyphus pulcher*), positively associate with high complexity at SNI (Fig. 2.1c and Fig. A7). Their presence exerts direct mortality on urchins and modifies urchin behavior through a “landscape of fear” (Cowen 1983; Burt et al. 2018; Eisaguirre et al. 2020). High-complexity substrate also entraps drift algae in cracks, below ledges, and at the base of rocky outcrops. High-complexity substrate thereby retains and stabilizes the supply of drift, which urchins prefer to consume over live kelp, particularly during large wave events that otherwise result in net drift export (Vanderklift and Wernberg 2008; Figurski 2010a). Urchins persist during periods of relatively low drift availability following storms due to their high longevity even when starved (Rogers-Bennett 2007). For low-complexity substrates, the net loss of drift during storms elicits the urchin behavioral shift to actively wander and graze upon live kelp (Harrold and Reed 1985b; Vanderklift and Kendrick 2005; Kriegisch et al. 2019). Because lower-complexity substrates also have lower abundances of slow-to-reproduce predators, active urchin grazing following drift loss proceeds largely unchecked, with increasingly strong feedback mechanisms—including lower local production of drift and a greater cover of encrusting algae which acts as a cue for urchin settlement (Taniguchi et al. 1994)—stabilizing the urchin barren state. Once in the urchin barren state, large, density-dependent but stochastic disease outbreaks at high urchin densities (Lafferty 2004) permit opportunities for kelp recovery. Low-complexity substrates are thereby predisposed to alternative stable states because the combination of low drift retention and low predator abundance promotes persistent changes in urchin behavior and demography.

Substrate complexity determines not only the number of kelp-forest alternative stable states but also how perturbations cause shifts between them. The high velocity required to shift between alternative stable states (Figs. 2.2 & A2) indicates that low-complexity transects exhibit a time-invariant, bimodal stability landscape with alternative stable attractors separated by dynamically unstable space (Fig. A1a). That is, transitions from one stable attractor to another require a pulse perturbation, such as rapid kelp and drift loss due to large wave events or urchin mass-mortality due to disease (Miles et al. 1990; Reed, Rassweiler, et al. 2011). Shifts between states occurred in both directions and occurred both synchronously and asynchronously at low-complexity sites around the island, even as high-complexity transects exhibited stable persistence (Figs. 2.3 & A2). It is therefore unlikely that the existence of alternative stable states at low-complexity sites reflects forcing from changes in environmental drivers, including gradual press perturbation changes that alter the shape of the stability landscape itself. Instead, our results indicate that the localized effects of stochastic pulse perturbations are state dependent and are modified at small scales by

the stabilizing feedbacks associated with substrate complexity.

2.4.2 The algae-only state as a multi-generational long transient

Potential analysis indicated the existence of a third alternative algal-only state (Fig. 2.2*b,c*), but the velocity dynamics indicate this to be a multi-generational period of transient dynamics that inevitably and smoothly leads to the mixed kelp-urchin stable state upon the demographic recovery of urchins. For all but a single exceptional transect (discussed below), this algal-only state followed disease-related urchin mass-mortality. Lacking nearly any observable urchins when in the algal-only state (Fig. 2.4*b,c*), transects exhibited wide fluctuations in kelp abundance, producing numerous cases where within-state high-velocity community movement that represent the vast majority of instances where transect position along Axis-2 was not associated with substrate complexity (Figs. A2 & A3). Fluctuations in kelp abundance decreased as urchins began recovering approximately 6-8 years following their crash (Fig. 2.3*b,c*; (Kenner, Estes, et al. 2013)). Whereas kelp reproduce and grow annually, urchins require several years to reach adult size (Ebert 2010); thus, we hypothesize these transient dynamics to be driven by the temporal lag between urchin mass mortality and the years required for local urchin recovery. Such dynamics are expected for slow-fast systems with strongly differing consumer and resource generation times (Hastings, Abbott, et al. 2018). The multi-year nature of this transience highlights the limitation of potential analysis when additional temporal insight is lacking (Bestelmeyer et al. 2011), and emphasizes the need for long-term monitoring to provide context for shifts in state and to guide kelp-forest management and conservation (Krumhansl et al. 2016; Hughes et al. 2017; Francis et al. 2021).

2.4.3 Low-complexity dynamics conditional upon surrounding heterogeneity

Performing analyses at the transect level provided insight into variation that potential analysis would not have revealed at the site level (Kenner and Tinker 2018), but also raises a question regarding the behavior of an exceptional transect. The transect, East Dutch 45R, is the only low-complexity transect to exhibit a persistent algal-only state (Fig. 2.2*e,q*). It experienced repeated perturbations from which it returned to the algal-only state with high velocity (Figs. 2.3*e* & A2). These dynamics suggest that this transect's algal-only state reflects a third stable attractor, rather than a long-transient. This is an exception to our inference that substrate complexity is alone predictive of kelp-forest stability at SNI, as we would expect this low-complexity transect to exhibit multi-modality. We contend, however, that this exceptional transect reflects a deeper nuance

to kelp-forest dynamics related to spatial scale, as it is the only low-complexity transect that is surrounded by otherwise high-complexity substrate. We hypothesize that the stabilizing effects of adjacent complex substrate spill over to confer this transect's resilience. Larger expanses of low-complexity substrate—as surrounds all other low-complexity transects and sites of our analyses—lack this stabilizing spatial spillover. Manipulative experiments, such as urchin-additions or the continual removal of drift from similar low-complexity areas that are surrounded by high-complexity substrate are needed to test this hypothesis and determine the spatial scales to which the mechanism may apply.

2.4.4 Conclusions

The processes and feedbacks which associate with substrate complexity undoubtedly extend well beyond those which we have discussed. For example, high-complexity transects are more species-rich and exhibit a greater coverage of foliose red algae and sessile invertebrates than do low-complexity transects (Kenner, Estes, et al. 2013). As such, our results add to a rich ecological literature detailing the many means by which physical and biological complexity can modify species coexistence and the dynamics and functioning of ecological communities (MacArthur et al. 1961; May 1974; Dayton 1985; Bodkin 1988). It nonetheless remains an open question how globally widespread the importance of substrate complexity is, as changes in kelp-forest state certainly do occur irrespective of substrate complexity, especially at higher latitudes (Hagen 1983; Scheibling 1986; Ling, Johnson, et al. 2009; Steneck, Leland, et al. 2013). We speculate many of these large-scale changes in kelp-forest state to be driven by phase shifts rather than switches between alternative stable states.

That said, our findings bear two points of consideration for management and restoration efforts that seek to mitigate or reverse kelp-forest loss (Watanuki et al. 2010; Morris, Hale, et al. 2020; Gleason et al. 2021).

First, our work implies that both natural and artificial high-complexity reefs offer a means to increase the strength of stabilizing kelp-forest feedbacks. Reefs could be selected for conservation efforts or constructed to maximize the entrapment of locally-produced and delivered drift algae, provide structure for urchins to shelter, and support a diversity of urchin-controlling predators. In the context of artificial reefs, we acknowledge there is no quick fix for ecological restoration (Hilderbrand et al. 2005), and that multiple interests are often at play (e.g., the desire to minimize man-made structures in marine protected areas). However, given our evidence that kelp-forest

stability can vary at the scale of a $10 \times 2m$ transect, and strong evidence that meta-population dynamics driving kelp spore dispersal operate at much larger scales (Graham 2000), we submit that strategically-placed patchworks of natural and artificial reefs could serve as hotspots of emergent kelp-forest resilience.

Second, the large overlap between urchin densities in the mixed kelp-urchin and urchin barren states (Fig. 2.4) emphasizes that urchin density alone is an insufficient predictor of urchin behavior and state stability. In particular, the rapid timescales of kelp and drift algae loss, and the rapid manner with which urchin behavior responds (Harrold and Reed 1985b), indicate that bimodality in system state mirrors a bimodality in urchin grazing activity. Hence, the common practice of removing or culling urchins to reduce their abundance will decrease grazing rates only in the short term and will not alone restore feedback processes that confer kelp-forest stability. More specifically, the processes of kelp growth, reproduction, dispersal, senescence and drift production, which are critical for achieving and stabilizing the mixed kelp-urchin state, as well as the counteracting processes of urchin immigration, settlement, and recruitment, which stabilize the barren state, are not affected by such direct, short-term means of urchin control. Instead, urchin removal is likely to be most effective for jump starting kelp recovery when efforts are focused upon high-complexity substrate and paired alongside local kelp-focused restoration (e.g., outplanting) and short-term drift enhancement to strategically protect out-planted kelp until local kelp growth and drift-production are reestablished.

2.5 Methods

2.5.1 Time-series and community analysis

Five fixed-location transects at each of six sites around SNI were biannually surveyed from 1980 to 2018, yielding 30 location-specific time series of 14 taxa (1973 transect surveys total due to some missed survey periods). See (Kenner, Estes, et al. 2013) and (Kenner and Tinker 2018) for additional details on the spatiotemporal structure of these data. Species abundances in the 1973×14 community matrix were $\log(x + 1)$ transformed to down-weight the influence of highly abundant purple urchins prior to calculation of a Bray-Curtis dissimilarity matrix. Nonmetric multidimensional scaling was performed on this dissimilarity matrix using the *vegan* package (v.2.5-4, (Dixon 2003)) in R v.3.5.3 (R Core Team 2017) and exhibited a stress of 0.18. Coefficients of determination (r^2) were used to quantify the variance represented along each ordination axis and

were obtained using PC-ORD v.7 (McCune et al. 2016).

2.5.2 Linear relief measurements

We used a 13cm-circumference electronic surveyor’s wheel to measure the linear relief of each transect, averaging three replicate measurements per transect: down the lengthwise center and 1m away on each side of the center. The association of mean complexity with Axis-2 of the ordination was calculated using Pearson’s linear correlation coefficient in the *vegan* R-package (Dixon 2003).

2.5.3 Potential analysis and multi-modality

Stability landscapes were represented as kernel density plots using the *geom_density* function of *ggplot2* (Wickham 2016a) with the default bandwidth (adjust = 1.0) for all but the two WestEnd sites (adjust = 0.8, to better visualize the algal-only state); other bandwidths produced qualitatively-similar results. Multimodality along Axis-1 was formally evaluated univariately by Gaussian mixture models with the *mclust* package (v5.4.3) (Scrucca et al. 2016) allowing variable variances among the clusters (model option “V”). We also repeated our analyses after restricting the time-series to either only fall or spring surveys and obtained qualitatively-similar results. State categorizations in Fig. 2.4 were delineated by maximum and minimum kernel density values.

2.5.4 Velocities of community movement

Velocities were calculated in two-dimensional ordination space by dividing the Euclidean distance between two sequential sample points by the number of days elapsed between them. Their midpoint along Axis-1 determined the community state against which velocities were plotted in Fig. 2.2.

2.6 Acknowledgments

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Studies of Coastal Oceans. All code and data used in the analysis are available at: https://github.com/zhrandell/Substrate_Complexity. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

3 Kelp-forest stability controlled by drift algae and the urchin behavioral shift

3.1 Abstract

The mechanisms that drive shifts in community state and those that limit such shifts by providing stabilizing feedback are of keen interest to ecologists and those involved in conservation. Kelp forests exhibit both a forested state where stage-structured kelp competition can produce periodic dynamics, and an urchin barren state where urchin consumption of kelp provides stabilizing feedback against recovery of the forested state. Central to the establishment of urchin barrens is behavioral shift, where urchins switch from residing in cracks and crevices consuming drift algae to actively moving and grazing upon live kelp. Here we present a delayed-differential equation model representing urchins grazing upon live kelp and drift algae. We modeled consumption of the two resources as a function of resource availability, where urchins prefer drift and switch to consume kelp when drift is scarce. Numerical analyses of our model indicate discontinuous movement between two steady state attractors: one where kelp exhibit stable limit cycles and produce abundant drift which urchins primarily consume, and another where kelp exhibit a low-density fixed point, little drift is produced, and urchins graze upon and limit kelp. Increasing the initial conditions of drift in certain low-kelp fixed point parts of parameter space switches urchins to consume drift, raising the kelp equilibrium, which in turn increases drift production and reinforces urchin consumption upon drift—all of which shifts the system to the high-kelp state where kelp exhibit limit cycles. These results therefore provide mathematical support for the hypothesis that alternative forested and urchin barren states can be dependent upon (1) the capacity for urchins to switch between resources, (2) a preference to consume drift, and (3) drift availability.

3.2 Introduction

Consumer-resource interactions determine the flux of energy across trophic levels, and both empirical and theoretical research has described how these interactions affect species diversity and community structure and stability (May 1974; Murdoch et al. 2003; Terborgh et al. 2010; Estes, Terborgh, et al. 2011). However, these interactions are not fixed but rather are dynamic, can have indirect downstream effects, and can feedback to modify interaction strength (Strauss 1991; Wootton 1994; Clark et al. 2020). For example, research involving the “landscape of fear” has shown how predators modify both prey density and grazing behavior, thereby indirectly affecting

primary production and community structure and function (Ripple et al. 2012; Boyce 2018). Other research provides an example of a behavioral feedback, where herbivorous fish forage at higher per capita rates when at high population densities, predisposing the reef to fishery-mediated ecosystem collapse (Gil et al. 2020). Understanding the mechanisms underlying indirect consumer-resource interactions and behavioral feedbacks is particularly important for ecosystems where positive and negative feedback processes may lead towards—or help resist—abrupt shifts in community state (Thomas 1981; Scheffer, Carpenter, et al. 2001b; Bestelmeyer et al. 2011).

3.2.1 Two modes of kelp-forest dynamics

In temperate rocky-reef kelp forests, intraspecific, grazer-resource, and predator-prey interactions are strong determinants of community structure and stability (Steneck, Graham, et al. 2002). Macrophytes in the Order Laminariales (henceforth “kelp”) such as Giant kelp (*Macrocystis pyrifera*) have been observed to exhibit fluctuations in density at various temporal scales, particularly from the annual scale out to about 5 – 10 years (Dayton, Currie, et al. 1984). Classically considered as evidence of density-dependence, various mechanisms have been proposed to explain these fluctuations, including: (1) the combination of optimal growing conditions and sufficient adult individuals for spore production and successful recruitment (Deysher et al. 1984), (2) stochastic and periodic effects from oceanographic processes (Tegner et al. 1987), and (3) intraspecific, stage-structured competition, where large canopy forming individuals shade and inhibit younger kelp recruits (Santelices 1990). Experiments and correlative studies indicate the latter mechanism is particularly important, as expansive canopy densities are associated with lower understory kelp recruitment and growth (Reed and Foster 1984; Carr 1989; Reed 1990).

This mechanism was modeled by Nisbet et al. 1989, demonstrating that age-structured and density-dependent competition could produce stable limit cycles approximating empirical observations of the time. Wavelet analyses of ongoing long-term subtidal monitoring at SNI (the same dataset analyzed in *Chapter 2*) reveals similar periodic patterns (Fig. 3.1a,c) relative to those documented by Dayton, Currie, et al. 1984 when urchins are scarce. This suggests that stable limit cycles may manifest intrinsically when a kelp population is relatively free from urchin grazing pressure and dislodgement by large waves.

An altogether different pattern emerges when herbivorous urchins overgraze kelp to establish and maintain a deforested urchin barren (Fig. 3.1b,d, Hagen 1983; Filbee-Dexter and Scheibling 2014b; Ling, Scheibling, et al. 2015b). Increased grazing pressure suppresses kelp growth, a behav-

ioral feedback limiting future kelp recruitment and recovery (Ling, Kriegisch, et al. 2019). Urchin barrens can persist for years and at times over a decade, and are often considered an alternative stable state to kelp forests (Filbee-Dexter and Scheibling 2014b). In contrast to phase shifts, where environmental variables change or urchin predators are removed/introduced to drive an associated community shift (Tegner et al. 1991; Dayton, Tegner, Edwards, et al. 1998; Ling, Johnson, et al. 2009; Johnson et al. 2011), alternative stable states are defined as existing with conditions held constant (Connell et al. 1983; Dudgeon et al. 2010). And whereas phase shifts reverse when the precipitating environmental variable changes, the persistence of alternative stable states is predicated upon stabilizing feedback that inhibits (or provides inertia against) recovery (Thomas 1981). In addition to continual urchin grazing, other urchin barren stabilizing feedbacks include the expansion of encrusting coralline algae which produce a chemical cue for urchin recruitment (Pearce et al. 1990; Taniguchi et al. 1994), and that young urchin recruits may have higher survival rates when sheltering near or within the protection of spines on adult individuals (Hernández et al. 2010). Furthermore, because urchin recruitment is open (i.e. the source of larvae is often far away from the site of recruitment), the processes regulating adult urchins at any one location can be decoupled from the rates of recruitment, further stabilizing the barren state (Uthicke et al. 2009; Karatayev et al. 2020).

3.2.2 Two modes of sea urchin grazing

Central to the formation of urchin barrens is a presumed behavioral switch between two distinct modes of sea urchin grazing: (1) urchins are largely hidden in cracks and crevices and graze upon drift algae—detached macrophytes also known as kelp detritus; and (2) urchins leave cracks and crevice and graze upon live kelp leading to urchin barren formation. Particularly in high-latitude kelp forests, predators are essential for regulating urchin density and behavior such that the presence or absence of urchin predators is the difference between the forested or urchin barren state (Estes and Duggins 1995; Watson et al. 2011; Burt et al. 2018). In lower latitudes however, instances of kelp-urchin coexistence—that is, relatively large urchin populations that do not form urchin barrens—have been observed independent of changes in the urchin predator populations (Fig. 2.4). In such cases, resource availability is believed to regulate urchin behavior.

Beyond just considering the standing stock of live kelp however, observational and experimental research suggests drift algae can regulate the urchin behavioral shift. For example, in southern California, Harrold and Reed 1985a inferred that large wave events associated with a winter storm

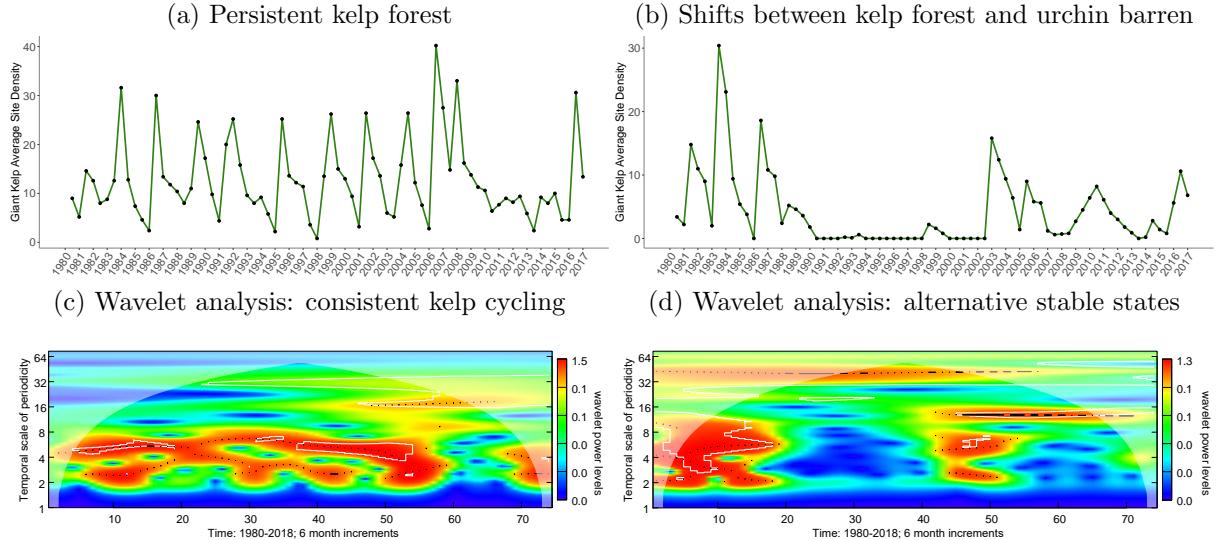


FIGURE 3.1: Two modalities of kelp-forest dynamics: persistent, cyclic kelp dynamics (*a,c*) versus switching between the forested and urchin barren state (*b,d*). Biannual time series of Giant kelp average density at (*a*) East Dutch and (*b*) NavFac, two subtidal sites located at San Nicolas Island, California, USA (*Chapter 2*). (*c*) Bottom panels show wavelet analysis results for the Giant kelp time series at East Dutch, where kelp exhibit persistent periodic dynamics at the 2 – 4 yr scale (red regions). The x-axis of these wavelet figures depicts linear time in 6 mo increments. The y-axis represents the temporal scale at which the wavelet function is applied to the data. (*d*) Kelp also exhibit cyclic dynamics at NavFac, but the forested state exhibited a shift to the urchin barren state (where kelp drop to 0). Blue regions represent the lack of periodic dynamics at any temporal scale. Wavelet analyses were completed in *R* using the *waveletcomp* package (Roesch 2018).

removed drift, whereupon they observed urchins actively moving and grazing upon kelp, leading to the formation of an urchin barren. Experiments indicate urchins will forgo consuming kelp when drift is available, and likewise will move towards and then “hunker down” with drift, restraining it with their spines and tube feet to consume it (Vanderklift and Kendrick 2005; Vanderklift and Wernberg 2008; Kriegisch et al. 2019). Finally, and as presented in *Chapter 2*, analyses of long-term subtidal monitoring data indicate substrate complexity modifies both “top-down” processes such as urchin behavior and mortality via predation and disease, as well as “bottom-up” processes such as the retention of drift algae along complex benthic substrate. Based on the assumption that urchins prefer to consume drift, the processes of drift production, retention, and transport are all believed to influence the urchin behavioral shift. Drift-influencing processes may therefore cascade to affect kelp-forest community stability, including whether kelp exhibit the forested state and have the potential to exhibit stable limit cycles, versus shifts between alternative forested and urchin barren states as urchins switch behavior.

3.2.3 Model objectives

My objective was to develop a mathematical model describing the consumer-resource interactions of urchins grazing upon two resources of live kelp and drift algae. We focused upon two trophic levels to understand if and how the rates of kelp recruitment, and drift production, retention and loss, and the capacity for urchins to switch between kelp and drift resources could explain the two modalities of kelp-forest dynamics exhibited in Fig. 3.1. Specifically, we asked under what conditions an urchin preference to consume drift could produce a switch in urchin behavior, and whether that switch associated with shifts between: (1) stable persistence of the forested state in which urchins graze upon drift and kelp exhibit stable limit cycles, and (2) a barren state in which urchins graze upon kelp as drift production is limited. In this low-kelp urchin barren state, increasing the initial conditions of drift should elicit the urchin behavioral switch back to consuming drift, enabling a shift to the high-kelp, forested state, whereupon kelp have the potential to once more cycle.

3.3 Methods – the system

3.3.1 System overview

This methods section summarizes the model and explains the biological motivation underlying individual functions and parameters. We then motivate the numerical methods used to computationally analyze select aspects of this model.

The system contains three delayed-differential equations modeling the interplay among state variables $A[t]$, $S[t]$, $H[t]$ representing the state (abundance) kelp, drift, and urchins, respectively, at time t . The model incorporates the processes of recruitment, loss, and species interactions that together determine rates of population change $\frac{dA}{dt}$, $\frac{dS}{dt}$, $\frac{dH}{dt}$.

$$\begin{aligned} \frac{dA}{dt} &= R_{A[t-\tau]} - Q_S * F_A * H[t] - d_A * A[t] \\ \frac{dS}{dt} &= k_S * d_A * A[t] - (1 - Q_S) * F_S * H[t] - d_S * S[t] \\ \frac{dH}{dt} &= r_H - F_H * H[t]. \end{aligned} \tag{3.1}$$

See Table 3.1 for the primary and constituent functions comprising this system, and see Table 3.2 for an interpretation of each parameter along with the baseline values used in all analyses. Regarding

symbology: Functions are capitalized and the subscript denotes the state variable that (1) the function depends upon (e.g., kelp recruitment R_A is dependent upon $A[t]$), or (2) the state variable proximally affected by the function (e.g., F_H denotes urchin loss). Similarly, lowercase parameters have subscripts identifying the state variable they affect (e.g., urchin recruitment r_H) (Several functions nested within other functions break with this later standard and are represented in the manner described for parameters, e.g., c_R , b_R , c_Q , and b_Q ; the subscript for these functions denotes the parent function; these functions are described within in Appendix A2.1.

The kelp equation $\frac{dA}{dt}$ in Eqn. 3.3.1 contains a recruitment function R_A (Fig. A8) and consumption via urchin grazing $-Q_S * F_A * H[t]$ where Q_S (Fig. A9) is the proportion of urchins grazing upon kelp and F_A is the functional response of kelp consumed by urchin grazing (Fig. A10). Background kelp mortality independent of grazing is $d_A * A[t]$, where d_A is a key parameter that also determines drift production.

The drift equation $\frac{dS}{dt}$ in Eqn. 3.3.1 contains the same three basic components: $k_S * d_A * A[t]$ represents drift production via grazing-independent kelp mortality. k_S represents the proportion of senescent kelp biomass that becomes drift and is retained within the system (i.e., not lost by transport to adjacent or deeper habitats offshore). Drift consumed by urchins is structured to kelp consumption, where $(1 - Q_S) * F_S * H[t]$ is removed by urchin grazers. $d_S * S[t]$ reflects other sources of loss, such as decomposition or removal from large-wave events (Harrold and Reed 1985b; Reed, Rassweiler, et al. 2011).

Though multiple feedbacks involving urchin recruitment have been documented (Taniguchi et al. 1994; Baskett et al. 2010; Hernández et al. 2010), we did not believe these would be necessary to elicit the hypothesized switch in urchin grazing and associated kelp-forest dynamics. Nor did we want the additional complexity associated with urchin recruitment dynamics to confound or obscure the core questions surrounding kelp recruitment and drift production, retention, and loss. Therefore, we modeled urchin recruitment within $\frac{dH}{dt}$ in Eqn. 3.3.1 as a density-independent parameter r_H .

Eqn. 3.3.1 is comprised of five functions, though only two distinct functional forms are present. The first is a declining logistic used to model kelp recruitment R_A , the proportions Q_S of urchins grazing upon kelp, and urchin mortality F_H . The second is a Holling Type II functional response (Holling 1973), an asymptotically increasing function that relates the amount (number or biomass) of resources consumed per consumer to their abundance. Type II saturating feeding curves are used here to model kelp F_A and drift F_S removed by urchin grazing. We examine each of these five functions in turn.

TABLE 3.1: Primary and constituent functions

process	function	expression	details
kelp recruitment	R_A	$R_A = r_R + (m_R - r_R) * e^{-c_R * A[t-\tau]^{b_R}}$	A8
	b_R	$(b_R - 1) * e^{[-(b_R-1)] / b_R} = \frac{s_R * i_R}{m_R - r_R}$	A2.1
	c_R	$c_R = \frac{(b_R-1)}{b_R * (i_R^{b_R})}$	—
proportion of urchins grazing kelp	Q_S	$Q_S = e^{-c_Q * S[t]^{b_Q}}$	A9
proportion of urchins grazing drift	$Q_S - 1$	—	—
—	b_Q	$(b_Q - 1) * e^{[-(b_Q-1)] / b_Q} = s_Q * i_Q$	—
	c_Q	$c_Q = \frac{(b_Q-1)}{b_Q * (i_Q^{b_Q})}$	—
kelp consumed by urchins	F_A	$F_A = \frac{a_A * A[t]}{1 + a_A * h_A * A[t]}$	A10
drift consumed by urchins	F_S	$F_S = \frac{a_S * S[t]}{1 + a_S * h_S * S[t]}$	—
urchin mortality	F_H	$F_H = d_F + (m_F - d_F) * e^{-c_F * (\frac{A[t] + S[t]}{H[t]})^{b_F}}$	A11
	b_F	$(b_F - 1) * e^{[-(b_F-1)] / b_F} = \frac{s_F * i_F}{m_F - r_F}$	—
	c_F	$c_F = \frac{(b_F-1)}{b_F * (i_F^{b_F})}$	—

TABLE 3.2: Parameters, baseline values used in analyses, and interpretation

parameter	value	interpretation
r_R	5	minimum kelp recruitment
m_R	15	maximum kelp recruitment
i_R	35	inflection point of kelp recruitment R_A ; capacity for kelp to cycle
s_R	3	slope of kelp recruitment R_A
τ	2	temporal lag i.e. kelp recruitment competition
d_A	0.25	kelp mortality i.e. drift creation
k_S	0.7	proportion of drift retained
d_S	0.3	drift mortality
r_H	10	urchin recruitment
d_F	1	minimum urchin mortality
m_F	4	maximum urchin mortality
i_F	10	inflection point of urchin mortality F_H
s_F	1	slope of urchin mortality F_H
a_A	3	urchin encounter rate upon kelp
a_S	3	urchin encounter rate upon drift
h_A	0.2	inversed maximum feeding rate upon kelp
h_S	4	inversed maximum feeding rate upon drift
i_Q	5	inflection point for the proportion Q_S of urchins grazing kelp
s_Q	1	slope around the proportion Q_S of urchins grazing kelp

3.3.2 Kelp recruitment R_A

R_A is modeled with a declining logistic function (Fig. A8)

$$R_A = r_R + (m_R - r_R) * e^{-c_R * A[t-\tau]^{b_R}} \quad (3.2)$$

which itself is comprised of two exponential functions, b_{R_A} and c_{R_A} , with four parameters: maximum kelp recruitment m_R , minimum kelp recruitment r_R , the inflection point i_R , and the slope s_R around that inflection point. This motif of a declining logistic containing two exponentials is retained across the three logistics R_A , Q_S , and F_H , and see Appendix A2.1 for a full explanation of how these functions work.

Following Nisbet et al. 1989, we modeled the stage-structured competition exhibited by canopy forming kelp, where surface canopy shades the benthos and limits kelp recruitment and growth. When adult kelp are at low abundance their canopy does not obscure light such that young recruits can grow unimpeded resulting in a larger adult population sizes at future time points. The kelp recruitment function R_A models an expected biological pattern of recruitment: as kelp density increases, fewer kelp recruit. Instead of explicitly incorporating stage-structured kelp growth, I instead model the implicit temporal nature of this intraspecific competition with the lag parameter τ . Thus we only consider the adult population, as the processes of reproduction, dispersal, and state-structured growth are all subsumed within the delay between current density of kelp and future kelp growth. For example, $\tau = 0$ equates to no temporal effect, where the current level of kelp $A[t]$ instantaneously results in kelp recruitment $R_A[A[t]]$. In contrast, $\tau = 4$ introduces a temporal delay, such that the current adult kelp population $A[t]$ determines kelp recruitment $R_A[A[t+4]]$ four time steps in the future. Rephrased, current kelp recruitment (i.e. the production of adults, given that there is no stage-structure) is a function of the kelp population τ steps ago, and the state variable $A[t]$ within Eqn. 3.3.2 takes the form $A[t - \tau]$.

Biologically speaking, the inflection point i_R (Fig. A8) can be thought of as the parameter (in conjunction with slope s_R and time-lag τ) that dictates the capacity for intraspecific kelp competition to produce kelp cycling, i.e., how many adults are necessary to suppress kelp recruits.

3.3.3 Proportion Q_S of urchins feeding upon kelp

Q_S is another declining logistic (Fig. A9), but with output ranging between 0 – 1 such that there are no max and min parameters:

$$Q_S = e^{-c_Q * S[t]^{b_Q}}. \quad (3.3)$$

Q_S determines the proportion of urchins grazing upon kelp, and accordingly $(1 - Q_S)$ is the proportion of urchins grazing upon drift. Q_S is a function of drift; as $S[t] \rightarrow \infty$, $Q_S \rightarrow 0$, such that all urchins graze drift instead of kelp. Likewise, as $S[t] \rightarrow 0$, $Q_S \rightarrow 1$, such that all urchins graze upon kelp. This function encapsulates observations that the urchin behavioral switch is controlled by the density of drift (*Chapter 4*). Q_S contains exponentials b_Q and c_Q whose purpose mirror those of b_R and c_R in R_A (Appendix A2.1). However, as Q_S lacks min and max parameters, its functional form is set by the two parameters controlling the inflection point i_Q and the slope s_Q around that point. As with R_A , the placement of i_Q and slope s_Q determine the density of drift at which the switch in grazing behavior occurs and the strength and speed (i.e., nonlinearity) of that shift.

3.3.4 Urchin loss F_H

The third and final declining logistic function (Fig. A11) models urchin loss as

$$F_H = d_F + (m_F - d_F) * e^{-c_F * (\frac{A[t] + S[t]}{H[t]})^{b_F}}. \quad (3.4)$$

Urchin loss is a function of the ratio of total resource density (drift and kelp) to urchin abundance $\frac{A[t] + S[t]}{H[t]}$. We used this ratio both because of the underlying biological interpretation and from a modeling practicality standpoint. Urchins being highly abundant relative to kelp and drift can be thought of as high urchin mortality associated with the urchin barren state: at such an extreme, the value of $\frac{A[t] + S[t]}{H[t]} \rightarrow 0$, such that $e^{-c_F * \frac{A[t] + S[t]}{H[t]}^{b_F}} \rightarrow 0$ and $F_H \rightarrow d_F$, where d_F is max urchin mortality (Fig. A11). This is biologically interpreted as urchins actively wandering in a barren, starving, susceptible to disease and/or large wave events, and vulnerable to predators. In contrast, when urchins are scarce relative to kelp and drift, $\frac{A[t] + S[t]}{H[t]} \rightarrow A[t] + S[t]$, such that $e^{-c_F * \frac{A[t] + S[t]}{H[t]}^{b_F}} \rightarrow 1$ and $F_H \rightarrow m_F$, the parameter for minimum urchin mortality. This is biologically interpretable as a kelp forest where urchins choose to hide in cracks and crevices, have lower incidences of density-dependent disease mortality, are protected from large wave events, and are relatively sheltered from predators. This density-dependence of F_H provides regulatory bounding upon urchin population size: increased mortality at high urchin densities provides negative feedback against runaway urchin population growth and subsequent resource over-exploitation. Likewise, lower mortality at low urchin densities provides negative feedback against extinction when their density is low.

3.3.5 Functional responses F_A and F_S specifying kelp and drift consumed

The second functional form used in the system is the Holling Type II functional response (Fig. A10). This models the saturating relationship between the units of resources available and the corresponding units of resources consumed per unit of urchin per unit time. Separate functions specify the kelp F_A and drift F_S mortality as

$$F_A = \frac{a_A * A[t]}{1 + a_A * h_A * A[t]}, \quad F_S = \frac{a_S * S[t]}{1 + a_S * h_S * S[t]}. \quad (3.5)$$

Each of these Type II functions contains two parameters, a and h . The slope at the origin is controlled by a , such that a is commonly interpreted as the attack or encounter rate, where higher values of a equate to greater resource loss as resource availability increases. We selected parameter values such that $a_A = a_S = 3$, which equates to grazers having equal access to consume either kelp or drift, with their “choice” dependent upon Q_S , where Q_S itself dependent upon the density of drift.

The second parameter h controls how consumption rates saturate, such that the functions F_A and F_S asymptotically approach $\frac{1}{h_A}$ and $\frac{1}{h_S}$, respectively. h is commonly referred to as the handling time required to catch, consume, and digest resources, but more broadly subsumes any such rate-limiting processes. It is useful to think of h_A and h_S as the inverse of the maximum consumption rate. We set $h_S = 4$ and $h_A = 0.2$, such that urchins slowly remove drift and rapidly remove kelp at maximum consumption. This aligns with observed aspects of urchin foraging: urchins often graze at the base of a kelp individual (just above the holdfast), which can detach the kelp from the benthos. This results in a greater rate of kelp loss relative to the same density of inactive urchins consuming drift. (Note that this assumption of $h_A \neq h_S$ does not influence urchin growth rates as these are decoupled from the amount of resources they consume; see $\frac{dH}{dt}$ in Eqn. 3.3.1, and urchin recruitment r_H in Table 3.2).

3.4 Methods – computational analyses

Due to the temporal lag parameter τ in kelp recruitment R_A (Eqn. 3.3.2), standard methods of evaluating dynamical stability were not possible. A closed-form analytic solution to this model is unknown to us. Therefore, we relied upon computational power to numerically solve our system and tracked the steady-state change in state variables in response to varying one or two focal

parameters (i.e., we performed one- and two-dimensional bifurcation analysis). With 19 parameters, the possible combinations of unique parameter values renders a complete exploration of parameter space untenable. Thus we strategically investigated parts of parameter space of *a priori* interest.

3.4.1 Baseline parameter values

We first established a baseline set of parameter values (Table 3.2) reflecting our core assumptions regarding drift production, retention, and loss, as well as those involving kelp recruitment and urchin grazing. Given the high level of abstraction codified by our model, we did not explicitly rely on literature to inform these parameter values. Instead, we selected parameter values that: (1) expressed belief about nonlinear relationships within the system (e.g., the slope of kelp recruitment S_R expresses our mathematical approximation of the empirical processes of intraspecific competition among kelp age classes); (2) calibrated a function to a certain range of equilibrium state values, thereby rendering the function/process relevant (e.g., i_R and i_Q need to overlap with state values of kelp and drift for their nonlinear sigmoidal components to be expressed); (3) bounded the approximate minimum and maximum recruitment rates to express biological expectation regarding relative population size (e.g., maximum kelp recruitment m_R was greater than maximum urchin recruitment r_H , given that kelp have far more biomass relative to urchins). The effects of individual and pairs of parameters are discussed in subsequent sections, contextualized by the effects of these baseline values. While this approach does not have precise application to any one location or species, we trade specificity for an abstract and generalized inquiry into the effects of our core questions regarding urchin switching behavior, kelp recruitment, and drift production, retention, and loss.

3.4.2 Numerical bifurcation analysis

With a baseline set of parameters established, we performed one- ($1D$) and two-dimensional ($2D$) bifurcation analysis to explore the effects of individual and paired parameters upon the equilibrium values of the three state variables and the qualitative dynamics exhibited by the system. Equilibrium values were obtained from the last 20 time steps of the model simulated to a total of 500 time steps. (Simulating out to $t = 10,000$ verified that $t = 480$ approximated steady state. Likewise, simulations verified that the range was $t = 480 - 500$ captured at least two cycle periods across a range of parameter values that affected kelp cycling).

Parameters were systematically varied across a range of 100 values regardless of their scale.

(For example, the proportion k_S of drift retained ranged from 0 – 1 and was sampled in steps of 0.01, and urchin recruitment r_H ranged 0 – 90 and was sampled in steps of 0.9). Our $2D$ analyses therefore are comprised of $100 * 100 = 10,000$ separate solutions of the system.

The analyses focused upon the following parameters (Table 3.2): (1) d_A , non-urchin sources of kelp mortality (i.e. drift creation); (2) k_S , the proportion of kelp mortality that is retained as drift; (3) d_S , non-urchin sources of drift mortality; (4) i_R , the inflection point of kelp recruitment that represents the capacity for kelp to cycle; (5) h_A , the maximum grazing rate upon kelp; (6) h_S , the maximum grazing rate upon drift; (7) i_Q , the density of drift required for urchins to switch resources; and finally (8) r_H , urchin recruitment.

3.4.3 Testing for alternative stable states

We tested for the existence of alternative stable states for each of the 100 points in $1D$ space and 10,000 points in $2D$ parameter space. The default initial conditions used for the $1D$ and $2D$ analyses were $A[0] = 1$, $S[0] = 0$, and $H[0] = 1$, where drift is subsequently created from kelp senescence once $t > 0$. To simulate an increase in drift availability, we repeated the $2D$ analysis described above but with $S[0] = 20$. This simulates a change in the initial conditions of the state variable but where the system itself (i.e., the environmental conditions, or specifically, all parameter values) are held constant. To evaluate sensitivity we tried other combinations of varied initial conditions (i.e., also altered $A[0]$, $H[0]$) and found that $S[0] = 20$ captured all (the only) alternative stable state. The system of delayed-differential equations was numerically evaluated with the *NDSolve* function in *Mathematica V12.2* using the Runge-Kutta iterative method.

3.5 Results

3.5.1 Summary of results

The system exhibited both smooth and discontinuous movement between two steady state attractors: a “low kelp” and “high kelp” state that we designate *Low* and *High*, respectively. Discontinuous switching between steady states often included a qualitative shift in dynamics when varying parameter values (Fig. 3.2a,b). For example, the *Low* state (almost) exclusively exhibited an equilibrium point attractor (or fixed point), whereas the *High* state often (but not always) exhibited stable limit cycles when both the lag parameter τ and the slope s_R of kelp recruitment were sufficiently high (Fig. 3.2c-f within each pane). The system also switched between the two

steady state attractors while holding all parameters constant and when varying the initial conditions of drift, and therefore the system exhibited alternative stable states (Fig. 3.2*c,d* and *e,f*). (See Figs. A12 for examples of the temporal and phase space dynamics described above and A13 for additional *1D* analyses of parameters).

We first present two key parameters that influenced both the equilibrium value of kelp and the qualitative dynamics exhibited at the two steady state attractors. We demonstrate how the inflection point i_R of kelp recruitment creates the nonlinear structure by which stable limit cycles can emerge, and that kelp mortality d_A subsequently determines whether cyclic kelp dynamics appear (Figs. 3.3*c,d* & 3.4).

With this *2D* overview of kelp mortality d_A and the capacity to cycle i_R in place, we turn off functions and processes (i.e., we present results where we set certain parameters to very low values). Doing so provides insight into how individual and interacting processes such as kelp recruitment and urchin grazing enable the system to exhibit one vs two attractors, cyclic dynamics vs a point equilibrium, continuous versus discontinuous movement between the two attractors, and alternative stable states. Unexpected regions of cyclic dynamics within *2D* parameter space emerged (e.g., Fig. 3.3*c,d*), and we discuss how these structures are a product of the interaction between two or more processes, specifically kelp recruitment R_A , the proportion of urchins grazing kelp Q_S , and kelp F_A and drift F_S loss to urchin grazing.

Regarding the effects of drift: results demonstrate how the capacity for urchins to switch between kelp and drift resources enables the existence of the *High* state, and that all shifts in state are a function of the underlying shift in urchin grazing activity (Fig. 3.5*a,b*). Furthermore, discontinuous switching between the two alternative states is dependent upon a large differential in the relative ratio between inverse maximum feeding rates upon drift h_S and kelp h_A , where a rapid feeding rates upon kelp ($h_A < 0.3$) is necessary for discontinuous movement. In the *Discussion* we argue these two parameter values mirror the two modes of urchin grazing that have been empirically observed to lead to the barren state.

Finally, we close the *Discussion* by returning to the parameters controlling drift production, retention, and loss, and demonstrate how the processes affecting drift dynamics scale and feedback to affect urchin behavior, the kelp equilibrium, and thus kelp-forest dynamics at large.

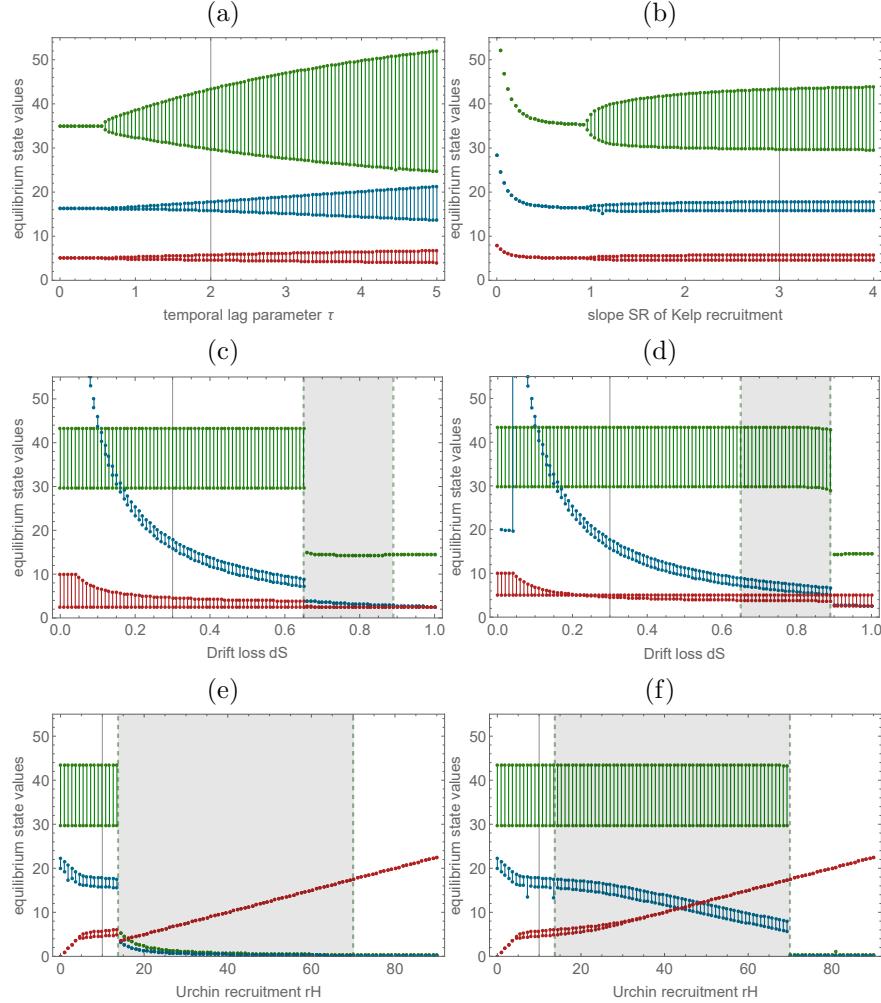


FIGURE 3.2: *1D* bifurcation analyses depicting three distinct dynamical properties. Colors represent the steady state solutions for **kelp**, **drift**, and **urchins**. (1) A critical point (*a, b*) as the parameter values of τ and s_R change (across the x-axis), and the system shifts from a fixed point to exhibiting stable limit cycles. The single solid and narrow gray line delineates the baseline value of each parameter used in all numerical analyses. (2) Discontinuous movement between two steady states as parameter values change is exhibited by (*c-f*). This dynamical shift is *both* a discontinuity between two attractors *and* a qualitative shift in dynamics from a fixed point to the onset of limit cycles. (3) Alternative stable states are exhibited both by (*c, d*) and (*e, f*) as parameter values are held constant and as drift initial conditions are varied ($S[0] = 0$ & $S[t] = 20$). That is, compare the equivalent location along the x-axis between the following pairs of plots: between (*c, d*) for drift mortality d_S , where the green dashed lines and grayed area delineate the parts of d_S parameter space exhibiting alternative stable states. In the case of d_S , the region in question can exhibit a stable point equilibrium (*c*) or periodic dynamics at a different steady state (*d*) depending upon the initial conditions of drift. (*e, f*) Also exhibit alternative stable states for urchin recruitment r_H , providing mathematical evidence that equivalent densities of urchins can associate with dramatically different system dynamics depending upon the availability of drift. These predictions align with the empirical observations of urchins at equivalent densities within the mixed kelp-urchin and urchin barren state (Fig. 2.4).

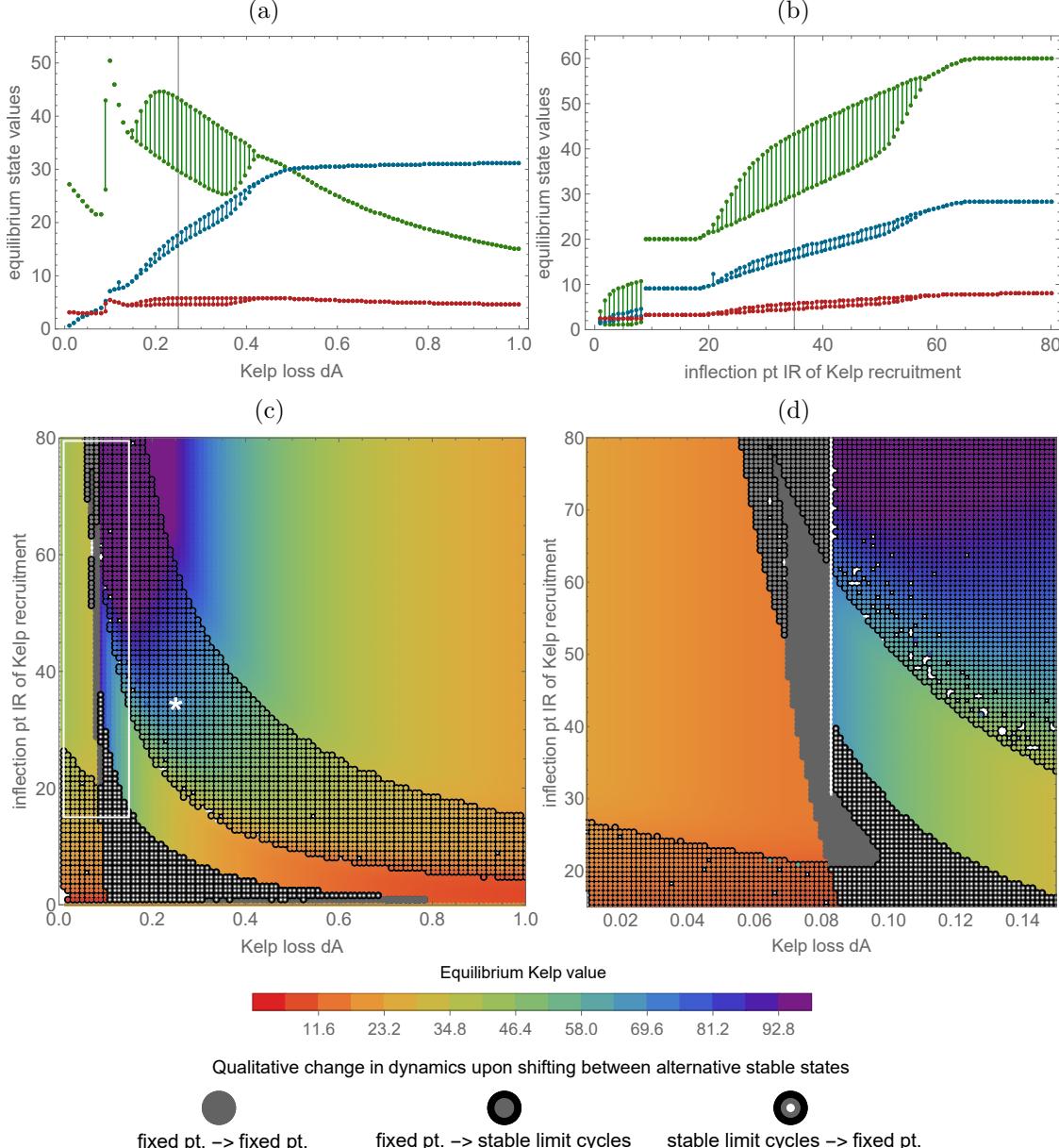


FIGURE 3.3: (a) 1D bifurcation map of kelp mortality d_A and (b) the inflection point i_R of kelp recruitment that determines the capacity of kelp to cycle. Both parameters affect the kelp equilibrium value and emergent dynamics (fixed point vs limit cycles). (c) d_A and i_R in 2D represent a map of system dynamics, and (d) zooms in to the white rectangle in the upper left corner of (c). The white dot denotes the baseline parameter values used in all other analyses (the 2D equivalent of the gray vertical lines in (a,b)). The gray shaded dots denote alternative stable states, and the exact symbol represents the change in dynamics exhibited upon switching from the *Low* to the alternative *High* state.

3.5.2 Kelp mortality d_A and the inflection point i_R

Kelp mortality d_A and the inflection point i_R of kelp recruitment are the two most important parameters in the model because they both directly control (1) the equilibrium value of kelp and (2) the qualitative dynamics that emerge at any given equilibrium value (Fig. 3.3a,b). The equilibrium value of kelp in turn controls the production of drift, which itself controls the urchin switch in grazing, all of which feedback to affect the equilibrium value of kelp. Thus the 2D overview of d_A and i_R provides the most comprehensive visualization into what qualitative dynamics will appear across the widest breadth of kelp equilibrium values.

The inflection point i_R of kelp recruitment controls the range of equilibrium kelp values where cyclic dynamics can possibly occur. This is achieved by moving the nonlinear, sigmoidal region of the kelp recruitment R_A function across the range of equilibrium kelp values (Fig. A8). Any change in model parameters or initial conditions that moves the kelp equilibrium either below or above the sigmoidal region around i_R yields a fixed pt and the system will no longer exhibit stable limit cycles. This interplay between equilibrium values overlapping with the nonlinear region of a logistic function centered around i_R is responsible for the “L” shape (Fig. 3.3c) of cyclic dynamics. (The interplay between equilibrium values, nonlinear sigmoidal functions (such as i_R and s_R), and the qualitative dynamics that can emerge are depicted by Fig. A14).

If i_R provides the underlying nonlinear structure by which kelp stable limit cycles may emerge, then kelp mortality d_A is the parameter that controls whether or not those dynamics appear. Kelp mortality d_A determines the amount of drift created, which affects urchin grazing behavior via Q_S that is channeled through F_A and F_S , all of which feedback to affect the equilibrium values of kelp, future drift production, and therefore whether or not kelp are at an equilibrium value where it exhibits stable limit cycles. Kelp mortality d_A therefore regulates the net expression of all constituent processes and functions within this system. When kelp mortality is < 0.1 , too little drift is produced such that urchins exclusively consume kelp and restrict the system to the *Low* state (Fig. 3.3a,c,d). Kelp mortality $0.1 < d_A < 0.2$ produces sufficient drift to elicit the *High* state, and $0.2 < d_A < 0.4$ is the region where kelp recruitment dynamics enable stable limit cycles. Once $d_A > 0.4$, kelp mortality is depressed below the sigmoidal region of R_A and the system passes a critical point and the *High* state exhibits a fixed points. Note, however, that decreasing i_R while simultaneously increasing d_A keeps the sigmoidal region of R_A positioned such that it tracks the decrease in the equilibrium value of kelp brought about by increasing d_A , and this produces the

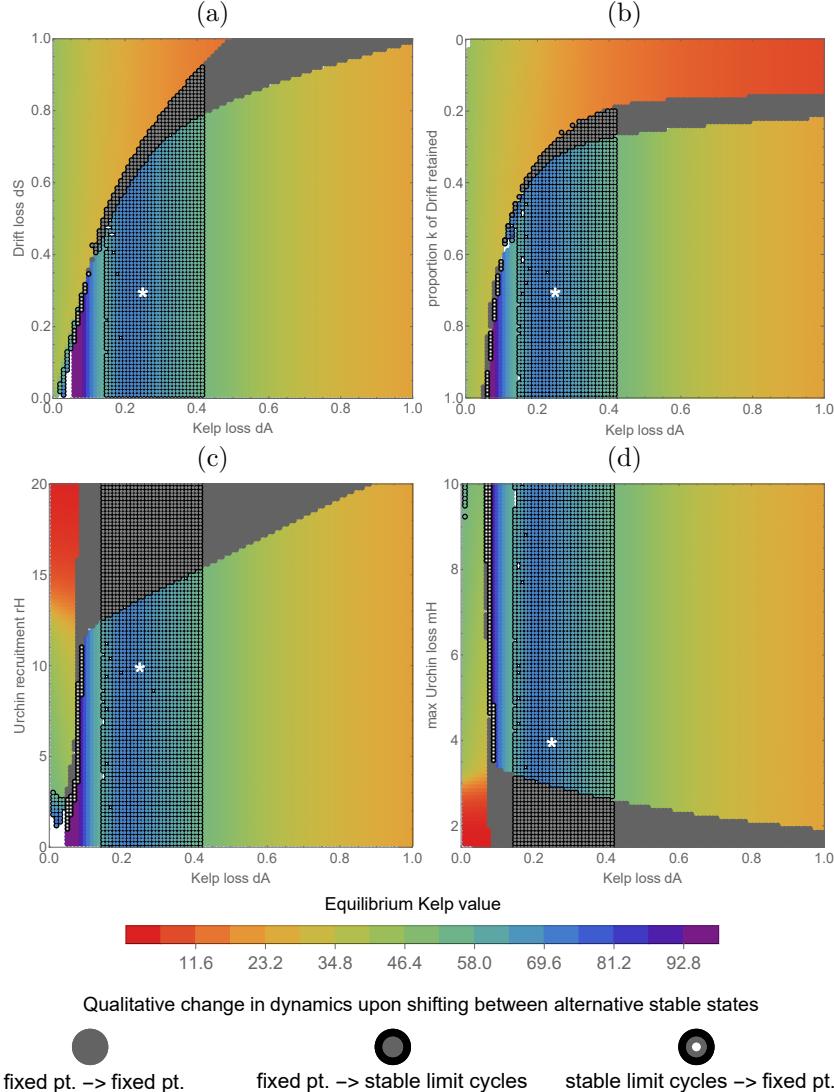


FIGURE 3.4: System dynamics controlled by kelp mortality d_A , where the 1D range of kelp dynamics that emerge as kelp mortality varies (Fig. 3.3a) are visible in 2D parameter space when kelp mortality d_A is analyzed with: (a) drift mortality d_S , (b) proportion k_S of drift retained, (c) urchin recruitment r_H , (d) and max urchin loss m_H . Alternative stable states appear along the border between where not enough kelp is being lost (i.e., not enough drift is being produced) to produce the urchin switch in consumption. Drift mortality d_S and the proportion of drift retained k_S have nonlinear effects upon the values of parameter space exhibiting alternative stable states, whereas r_H and m_H impact the region of alternative stable state space in a linear, step-wise fashion.

“L” shaped region of cyclic dynamics (Fig. 3.3c). In biological terms, as the rate of kelp mortality increases and the abundance of kelp required to produce stable limit cycles likewise decreases, the equilibrium values of kelp where cycles appear track progressively lower, hence the “L”.

3.5.3 Urchin switching between resources controls shifts between the two attractors

The capacity for urchins to switch between resources controls the existence of the *High* state, as well as the emergence of alternative stable states. The *High* state only appears when the slope s_Q is high enough that switching between the two resources is discontinuous. This is verifiable by setting $s_Q = 0$, such that $Q \rightarrow 1$ and all urchins default to exclusively consuming kelp (Fig. 3.5b). Thus the existence of the *High* state, along with the capacity to switch between the *Low* and *High* states, is dependent upon the capacity for urchins to switch between the two resources. The existence of the *Low* state is likewise dependent upon urchin dynamics. Urchins can be effectively suppressed by setting urchin recruitment to a low values (e.g., $r_H = 0.1$), which essentially destroys the *Low* fixed point (Fig. 3.5d), whereupon kelp cycle effectively independent of urchin grazing activity.

The dynamic transition between the *Low* and *High* state is dependent upon urchins rapidly consuming kelp relative to drift. Specifically, the maximum feeding rate upon kelp h_A needs to be low ($h_A < 0.3$) for the switch between resources to be discontinuous (Fig. 3.6c). This is evidenced by the narrow band of parameter space at low values of h_A where alternative stable states can appear, largely irrespective of drift mortality d_S , except at exceptionally large values of d_S . In contrast, drift mortality d_S and drift handling time have a proportionally greater area of parameter space occupied by the *Low* state (Fig. 3.6d). Our model thereby demonstrates the importance of empirically understanding in natural systems how the feeding rate upon drift relates to the rate of drift export.

3.6 Discussion

3.6.1 Summary of discussion

This discussion is organized around three points. (1) Kelp loss—either via urchin consumption or non-consumptive related kelp mortality—is necessary for kelp to cycle. (2) The relative and combined effects of drift consumed by urchins and lost to other (non-consumptive) sources highlight future experimentation and ecological measurements. (3) The equilibrium value of drift—and therefore the processes of drift production, retention, and loss—all feedback to affect urchin grazing behavior, the kelp equilibrium, and thereby whether the system exhibits alternative stable states. The first point delves into the mechanics of the model, its constituent processes, and how they

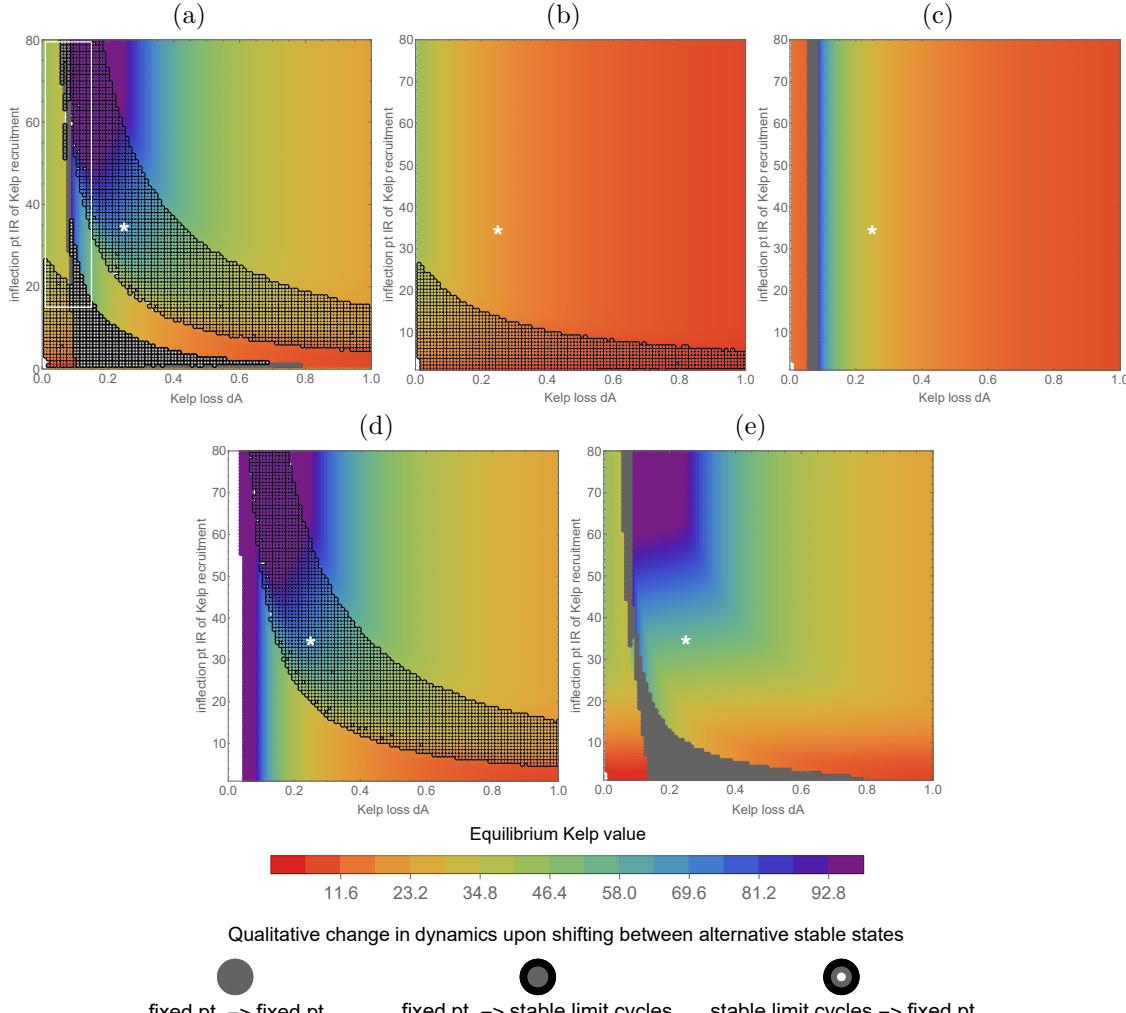


FIGURE 3.5: (a) Kelp mortality d_A and the inflection point i_R of kelp recruitment provide an overview of system dynamics, especially once certain processes are effectively disabled by setting them to certain values, including: (b) slope $s_Q = 0$ for the proportion of urchins grazing kelp Q_S , which defaults $Q = 1$, and all urchins graze exclusively upon kelp. This in essence removes the capacity of urchins to switch resources, and accordingly the *High* state is obliterated. (c) Slope $s_R = 0$ for kelp recruitment within R_A , which defaults $R = m_R$, the maximum kelp recruitment. This removes the capacity for kelp to exhibit limit cycles, though both the *Low* and *High* attractors remain intact. As kelp no longer exhibit recruitment dynamics, i_R no longer affects either the equilibrium values or qualitative dynamics. (d) Urchins are effectively minimized from the system by setting urchin recruitment $r_H = 0.1$, such that there is approximately no kelp or drift consumed due to grazer activity. The *Low* state disappears, though relatively low kelp equilibrium values can be achieved through high kelp mortality. Notably, the lower region of cyclic dynamics seen in (a,b) are now absent, demonstrating how the interaction of kelp recruitment R_A and urchin grazing produced that lower band of limit cycles. (e) Setting τ to 0 removes the capacity for kelp to cycle, though density-dependent kelp recruitment dynamics still operate to produce the “L” shaped bend in the bordering between the *Low* and *High* states. Note the individual effects of disabling the slope s_R of kelp recruitment (c) and the temporal lag τ (e), and that both parameters are necessary for kelp to exhibit limit cycles.

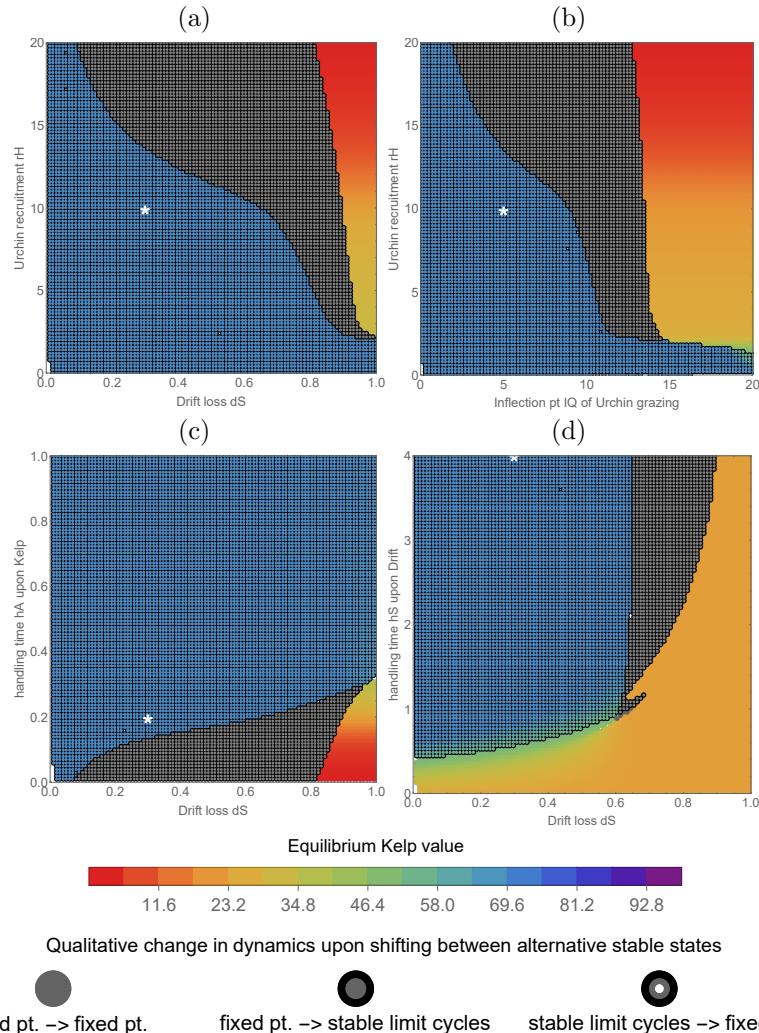


FIGURE 3.6: Urchin grazing dynamics and drift mortality. (a): Drift mortality d_S and urchin recruitment r_H exhibit a tiered structure for the *High* state (also shared by (b)) where increasing urchin recruitment r_H switches between having a large vs small effect on the area of the parameter space in which the *Low* vs *High* attractors exists. Most of the *Low* parameter space exhibits the alternative *High* state, with the exception of very high levels of drift mortality. (b): Inflection point i_Q for the proportion of urchins grazing upon kelp vs urchin recruitment r_H also exhibits the tiered region of the state. However once the amount of drift i_Q required for urchins to switch it increases past 10, the *Low* state predominates as all urchins consume kelp. (c): Drift mortality d_S versus the maximum feeding rate h_A upon kelp illustrates that rapid kelp consumption rates (i.e., $h_A < 0.3$) enable the existence of the *Low* state. (d): Drift mortality d_S versus the maximum feeding rate h_S upon drift. Similar to h_A , low values of h_S result in the *Low* state, but this is because rapidly consuming (depleting) drift forces urchin to switch to kelp.

interact to produce the observed dynamics (Fig. 3.7). The later two points contain biologically interpretable predictions relevant for future empirical research.

Two additional points in the Appendices examine unexpected regions of parameter space. Doing so helps disentangle how the mechanics of the model operate to produce the observed dynamics. These later two points are “fully in the weeds”, hence their placement in the Appendices. (4) The border between the *Low* and *High* states represents an underlying shift in the relative strength and expression of biological processes. The manner in which process shifts along that border reverses as the minimum amount of kelp necessary to inhibit recruitment changes (Appendix A2.2). (5) A biologically unexpected combination of rapid kelp consumption and kelp recruitment produces periodic dynamics along certain regions of the *Low* state (Appendix A2.3). This region represents a novel prediction as yet undocumented in the field.

3.6.2 Kelp removal necessary for cyclic dynamics

The necessity of kelp removal—either via urchin consumption or kelp mortality d_A is illustrated by an unexpected region of cyclic dynamics within 2D parameter space. Note the protruding region, or “tongue” of cyclic dynamics that emerge while at the *Low* state (Fig. 3.7e). Removing the capacity for urchins to switch resources via $s_Q = 0$ removes the tongue, while the lower region of cyclic kelp dynamics remain (Fig. 3.5c). Simulations verified that limit cycles within this tongue are produced by a combination of kelp recruitment dynamics *and* the process of urchins switching between kelp and drift. This region (the tongue) is unique because the oscillating kelp equilibrium (when exhibiting limit cycles) tracks the equilibrium values where urchins switch between kelp and drift. Thus, as kelp cycle, urchins switch back and forth, and the two processes together produce cyclic dynamics at the *Low* state. Suppressing either kelp recruitment (via slope $s_R = 0$, Fig. 3.5c) or urchin switching (via slope $s_Q = 0$, Fig. 3.5b) eliminates cyclic dynamics along the tongue, emphasizing the necessity of both processes to produce the observed limit cycles.

Increasing the initial conditions of drift causes all urchins to consistently (and exclusively) consume drift within this region, and the aforementioned combination of processes and resulting cyclic dynamics cease. However, and despite kelp experiencing no grazing pressure once at the *High* state, the system does not produce cycles (Fig. 3.7e, and also see d,f). This is because insufficient kelp is being lost (kelp mortality is too low), and the kelp equilibrium has exceeded the range by which i_R and R_A enable the density-dependence that produces cyclic dynamics (i.e., there are too many kelp relative to the density at which kelp recruitment dynamics occur). Reducing the kelp

equilibrium value (e.g., by increasing kelp mortality d_A) recovers cyclic dynamics. This is the same interplay between the capacity to exhibit cycles i_R and kelp mortality d_A that produced the “L” shape in Fig. 3.3c,d). This seemingly odd protrusion therefore demonstrates an intuitive biological conclusion: kelp loss—either consumptive or intrinsically generated via density-dependent processes (or both, in the case of Fig. 3.7e)—is necessary for kelp to exhibit stable limit cycles.

3.6.3 Relative rates of drift consumption h_S and removal d_S

Examining the maximum grazing rate upon drift h_S versus drift mortality d_S reveals another unexpected protrusion. As with the previously discussed “tongue”, this protrusion occurs at the border of a shift in the expression of two non-linear processes (Fig. 3.6d). To the left of the protrusion, it is possible for urchins to switch between resources depending upon the drift consumption rate. To the right of the protrusion, as drift mortality d_S increases, the rate of drift loss reduces the density of drift. Once at (and to the right of) the border where the protrusion occurs, insufficient drift is present to enable the behavioral switch. This is because the equilibrium value of drift has dropped below the nonlinear, sigmoidal region of Q_S that enables switching. Biologically, the rate of drift removal exceeded the minimum necessary for urchins to switch away from kelp and to drift. At these high levels of d_S , even lower maximum grazing rates upon drift do not increase drift density sufficiently for urchins to switch. Thus instead of enabling switching, Q_S expresses a fixed value (i.e., $Q_S \rightarrow 1$) and kelp consumption predominates yielding the *Low* state. However, parts of this *Low* state exhibit the alternative *High* state upon increasing the initial conditions of drift.

In biological terms, when rates of drift mortality outpace the maximum consumption rate of urchins relative to rates of drift production and retention, a pulse of drift algae may divert urchin consumption away from kelp, allowing it to recover and restore the original processes of kelp growth, senescence, and drift production. In the absence such a drift pulse, increasing rates of drift mortality must be balanced by less urchin consumption (or increased drift production). This can be achieved through fewer urchins, or a lower maximum drift grazing rate. The latter of which is represented by $\frac{1}{h_S} < \frac{1}{h_A}$, reflecting inactive grazing by urchins hiding in cracks and crevices. This grazing rate difference also represents empirical observations of urchins: when actively foraging while forming a barren, urchins consume the base of a kelp individual (near the holdfast), such that the kelp is detached from the seafloor. This may preclude further consumption by those precipitating urchins as the kelp individual is often removed due to water motion. Future experimentation could evaluate maximum consumption rates both for urchins from a barren and from a kelp forest (the former

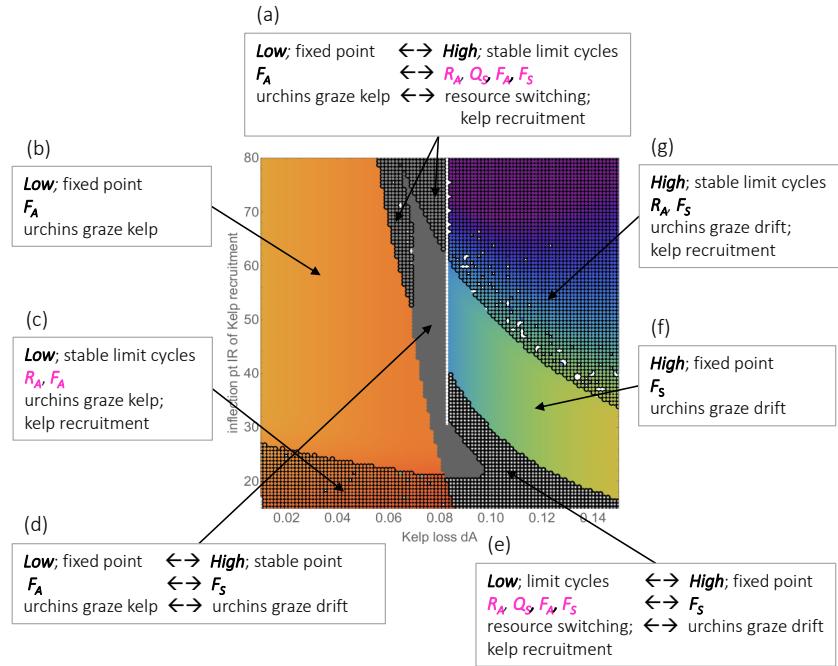


FIGURE 3.7: Region specific information including system state *Low* or *High*, the qualitative dynamic “fixed point” versus “stable limit cycles”, the predominant function being expressed: i.e., density-dependent kelp recruitment R_A , switching between resources Q_S , and realized kelp and drift mortality, F_A and F_S , respectively, and text summarizing the specific functions and/or processes affecting the system in each region (e.g., urchins graze kelp, or resource switching); black arrows denote the presence of alternative stable states and the concordant underlying shift in state, qualitative dynamics, and the net-expression of functions (see (a), (d), & (e)); having multiple functions in pink represent a combined or interactive effect where disabling (via certain parameter values) *any one* of the functions listed shifts (in all three cases) the expression of stable limit cycles to a fixed point (see (a), (c), (e)); (a) is biologically intuitive as a fixed point “urchin barren” where urchins graze kelp, and this region shifts—upon a pulse of drift—to a “forested” state exhibiting limit cycles and where urchins switch back and forth between resources; (b) is a persistent and stable (i.e. resistant to the effects of drift) “urchin barren”; (c) warrants extreme biological skepticism given that the limit cycles present are generated from the combined effects of a high rate of kelp consumption *and* density-dependent kelp dynamics (both processes are not concurrently observed in natural systems); (d) a pulse of drift shifts this borderline region from an urchin-dominated (i.e. consuming kelp) fixed point to a forested fixed point where all urchins consume drift—too little kelp is being lost (as with (e) & (f)) to elicit limit cycles; (e) also warrants biological skepticism (see (c)), but this region is highly informative regarding the mechanics of the model; this region exhibits the reverse switch in process (relative to (a)) upon shifting to the alternative stable state; (f) an intermediary region where urchins consume drift yet not enough kelp is being lost to produce limit cycles via density-dependent kelp recruitment; (g) a forested state where all urchins consume kelp and kelp exhibit limit cycles; as with (a), this region is highly relevant given observed biology.

evaluated in *Chapter 4*). These predictions also echo findings from *Chapter 2* where high densities of inactive urchins were found to coexist with kelp (Fig. 2.4), suggesting two distinct maximum

consumption rates for urchins when feeding in a forest versus an urchin barren.

It is worth reiterating that at extremely high levels of drift mortality, there is no grazing rate low enough or initial condition of drift high enough to switch urchins away from consuming kelp. In other words, if drift removal/consumption exceeds drift production, urchins will always (exclusively) consume kelp, precluding the emergence of the *High* state. These mathematical predictions emphasize the need to evaluate rates of drift production, retention, drift consumption by urchins, and urchin-independent drift removal.

3.6.4 Influence of drift on grazer behavior and system dynamics

Drift affects urchin grazing behavior which provides feedback to the kelp equilibrium and subsequent capacity to produce additional drift. The equilibrium density of drift directly controls the proportion of urchins grazing upon kelp via Q_S . The placement of i_Q determines sensitivity of the behavioral switch to drift. Thus the biological processes that control the equilibrium values of drift—kelp mortality d_A , the proportion of kelp mortality k_S that becomes drift, and drift mortality d_S —feedback to determine the steady state of kelp and system dynamics as a whole. Systematically varying these parameters alters dynamics in a manner consistent with *a prior* predictions. For example, increasing drift retention enables the *High* kelp state, and increasing drift removal (low k_S or high d_S) shifts the system to the *Low* kelp state (Fig. 3.4a,b).

The proportion k_S of kelp removed that becomes drift will be a useful parameter to consider further in the future. For example, if considered in a spatially explicit context, k_S could be a function of certain habitat characteristics that modify local rates of drift algae retention. As the realized effect of k_S is a function of kelp availability and thus kelp mortality, k_S also represents the retention of locally produced drift. k_S may thus also be interpreted as small spatial scale ($10m$) variation in environmental heterogeneity associated with varying rates of drift retention. That is, k_S could be a function of the complexity of the seafloor, such that low-complexity locations retain relatively little drift, while high-complexity substrates retain a greater proportion of drift (*Chapter 2*).

Drift mortality d_S (independent of grazer activity) is a function drift density (not kelp), and thus represents broader-scale processes that all drift are subject to. For example, drift decay due to microbial decomposition, or a stochastic process simulating large-wave events that removes drift. Future models could specify drift mortality d_S following a large-wave event, where the realized effects of d_S are conditional upon local variation in substrate complexity k_S . Given the

rich spatiotemporal dynamics exhibited by kelp forest populations, the processes of drift creation, retention, and loss may be useful for future kelp-forest metapopulation models.

3.7 Conclusions

We evaluated how the processes of kelp recruitment, drift creation, retention, and loss, and urchin grazing activity that switches between the two resources as a function of drift availability, all interact to affect system dynamics. Our model reproduces empirically observed dynamics such as a fixed point when urchins are grazing kelp and stable limit cycles when kelp are abundant and urchins are grazing drift. These results suggest that if urchins prefer to consume drift as our model assumes, then the processes structuring drift production, retention, and loss could have cascading effects on community stability. Future work could expand upon this model—particularly in the metapopulation context—to further explore how drift creation, transport, and retention affect spatiotemporal dynamics in kelp-forest ecosystems.

3.8 Acknowledgments

The College of Science, Oregon State University Unix High Performance Cluster greatly expedited all analyses.

4 Kelp consumption controlled by the availability of drift algae

4.1 Abstract

Understanding how positive and negative feedback processes change in strength to stabilize community states is essential for managing complex ecosystems that exhibit multistability. Temperate kelp forests exhibit abrupt shifts between alternative stable states where community structure is dominated by macrophytes or an urchin barren state where herbivory inhibits kelp recovery. Forefront to urchin barren formation is an inferred urchin behavioral switch, where, when drift algae is depleted or removed, formerly sedentary urchins leave cracks and crevices to actively move across the benthos and graze upon live kelp. We used a subtidal experiment to assess how the densities of drift algae and live kelp modified rates of urchin consumption upon those two resources. We used a one-consumer (purple urchins) two-resource (drift algae and live kelp) functional response design to obtain a temporal sequence of three observations, where resources were “restocked” up to their original initial conditions twice (after the initial stocking). We fit a system of ordinary differential equations to this three-period sequence and used urchin “gut fullness” as a latent variable to model how cumulative consumption within and across the three-period sequence affected rates of consumption. We demonstrate that urchins exhibit a strong preference for drift over live kelp and rank switching from kelp to drift as total biomass available increased. Moreover, whereas drift consumption increased with the density of drift available, kelp consumption was independent of kelp available, and instead was controlled by the biomass of available drift.

4.2 Introduction

Managing systems that exhibit alternative stable states requires not only understanding the drivers of abrupt ecological shifts, but also the manner in which the strength of feedback processes stabilize alternative community structures (Thomas 1981; Scheffer, Carpenter, et al. 2001a; Schröder et al. 2005; Leemput et al. 2016). Temperate kelp forests are renowned for their capacity to exhibit shifts between a diverse and productive community of macroalgae (i.e., macrophytes in the Order Fucales and Laminariales, henceforth, kelp, for brevity), and one dominated by encrusting coralline algae, where sea urchin herbivory maintains a deforested state known as an urchin barren (Paine et al. 1969; Laurence 1975; Mann 1977; Filbee-Dexter and Scheibling 2014b). Kelp are susceptible to disturbance or stress from the highly dynamic nearshore subtidal environment:

large wave events, changing nutrient availability, variable water temperature, and herbivorous consumption all have the capacity to either directly remove existing growth or inhibit younger stages (Dayton, Tegner, Parnell, et al. 1992; Steneck, Graham, et al. 2002; Reed, Rassweiler, et al. 2011). Recovery from such disturbances is supported through the production of massive quantities of spores (in the case of Giant kelp *Macrocystis pyrifera*), which disperse tens of meters to a few kilometers, enabling recolonization of adjacent and distant patches (Santelices 1990; Schiel et al. 2006; Cavanaugh, Kendall, et al. 2013; Castorani et al. 2015).

However, when the spatial extent of kelp loss is widespread (i.e., the scale of loss exceeds the typical scale of dispersal, but see Kinlan et al. 2003; Thiel et al. 2006; Hawes et al. 2017), or when kelp removal and/or inhibition persists through time, the strength of feedback processes that stabilize kelp forests can be degraded, and other processes may strengthen to stabilize the barren state (Filbee-Dexter and Scheibling 2014b; Ling, Kriegisch, et al. 2019; McPherson et al. 2021). For example, a large-wave event may locally remove live kelp and drift algae—the detached form of macroalgae also known as kelp detritus—which is believed to prompt urchins to actively move across the benthos and graze upon live kelp, providing stabilizing feedback that perpetuates the barren state and inhibits kelp recovery (Harrold and Reed 1985a). Once an urchin barren establishes and encrusting algae coverage expands, a chemical cue produced by coralline algae induces urchin larval settlement, providing additional stabilizing feedback for the barren state via increased local urchin recruitment (Pearce et al. 1990; Taniguchi et al. 1994; Hernández et al. 2010). Thus, even though urchins in the barren state are starving and exhibit poor gonad conditions (Thompson 1983; Dodge et al. 2012), local reproductive output and sources of adult urchin mortality from regulatory processes such as predation and disease are decoupled from local rates of urchin replenishment via dispersal (Uthicke et al. 2009; Karataev et al. 2020). Understanding and countering these stabilizing urchin barren processes—particularly at the local scale—is essential when considering kelp-forest restoration such as outplanting or urchin culls (Campbell et al. 2014; Morris and Blamey 2018).

4.2.1 Drift enables meta-ecosystem functioning and modifies sea urchin behavior

A suite of processes that stabilize kelp forests and provide meta-ecosystem functioning via spatial subsidies are those involved in autochthonous drift algae production, allochthonous drift transport to adjacent reefs, and subsequent drift retention (Polis et al. 1997; Marczak et al. 2007;

Figurski 2010b). Kelp forests are incredibly productive ecosystems, and typically only a small fraction of the standing stock of live kelp is directly consumed by herbivores (Mann 1973; Schiel et al. 2015). Once removed via senescence, large wave events, or herbivores (who sometimes release kelp fronds by chewing through stipes near the holdfast), macrophytes including kelp become drift. Drift can be transported kilometers (Harrold and Lisin 1989; Kirkman et al. 1997) up onto rocky and sandy shores (Romana 2003) and to adjacent subtidal habitat (Kim 1992) providing food for benthic invertebrates (Yorke et al. 2009) and other ecological functions (McCormick et al. 2008; Duggins et al. 2016; Lowe et al. 2020).

As alluded to above, it has been inferred that drift can modify urchin movement and grazing behavior. The processes of drift production, transport, and local retention may thereby affect kelp forest resilience. It is generally understood that urchins are known to exhibit a behavioral switch: when drift—either locally produced or delivered from elsewhere (Vanderklift and Wernberg 2008; Britton-Simmons et al. 2009; Kelly et al. 2012; Filbee-Dexter and Scheibling 2014a)—is sufficiently abundant, urchins largely remain hidden in cracks and crevices where they graze upon drift. Only when drift is removed do urchins leave shelter, actively roam, and graze upon live kelp (Harrold and Reed 1985a; Filbee-Dexter and Scheibling 2014b). In southeast Australia, experimental work has demonstrated that urchins enclosed in plots grazed upon drift instead of live kelp, and that drift can accumulate by getting caught in urchin spines (Vanderklift and Kendrick 2005). Experiments have also shown that urchins exhibit directional movement towards drift and a subsequent decrease in movement to consume the drift (Kriegisch et al. 2019).

Despite the known association between drift and urchin behavior, the functional form of the density-dependence between resource availability and grazer behavior remains undescribed. That is to say, it is unknown how much drift is necessary to elicit urchins away from actively grazing kelp, nor do we have a model for this density-dependent relationship. Further, while an urchin “preference” for drift has been observed, this preference—defined as the proportion of resource i consumed exceeds the proportion of resource i available (Baudrot et al. 2016)—has not formally been evaluated. Nor has switching between alternative resources been formally evaluated (Abrams 1987; Baudrot et al. 2016), where the proportion of resource i consumed changes given proportional availability (positive and negative switching), or where the proportion of resource i consumed changes as the total biomass of the alternative resources increases (rank switching).

Here we present a subtidal experiment to characterize the density-dependent effects of two alternative urchin resources upon relative rates of consumption. This was a one-consumer (purple

urchins, *Strongylocentrotus purpuratus*) two-resource (drift and kelp) functional response experiment (Colton 1987). Functional responses are widely used to characterize feeding rates as they describe how the number or biomass of resources consumed per consumer changes with resource density (Holling 1966; Jeschke et al. 2002). The functional response approach using varying densities of two resources allowed us evaluate urchin resource preference and switching—including positive, negative, and rank switching—between drift and kelp.

4.3 Methods

4.3.1 Field site and experimental cage array

The experiment was conducted offshore of Hopkins Marine Station in Monterey, California, over the summer of 2019. We affixed an array of 20 cages onto the seafloor at depths of 4 – 6m in the center of a large, sandy stretch between two rocky reefs ($36^{\circ}37'12''N$, $121^{\circ}54'07''W$). The cages were comprised of a single 7.62m length of steel rebar bent into a square 1 x 1 x 0.4m frame (Fig. 4.1a,b). Two layers of mesh—both stitched to the rebar frame—enveloped our cages. The first was a netting that provided structure and siding, the second was a layer of fiberglass window-screening that prevented transit of particulate matter either in or out of the cages. This second and outer layer was essential for maintaining treatments levels within the cages. (See Fig. A15 and Appendix A3.1 for cage assembly and array deployment). Eight paving stones (each 20lbs) were placed into four stacks of two within each cage. These stones acted as “rocky reef” and provided habitat for urchins to hide among—particularly in the “plus sign” shaped crevice in between the four stacks (Fig. 4.1c,d).

Each cage contained 20 4 – 5cm purple urchins haphazardly collected by hand from urchin barrens to the north-west of Hopkins. Following collection, urchins were placed in mesh goodie bags suspended in the water prior to their introduction to the cages. Once within the cages, urchins were allowed to habituate to their environment for 24hrs. During this 24hrs, we provided abundant drift for them to consume to standardize their gut fullness (Griffen 2021).

Drift comprised adult blades of Giant kelp that were clipped, weighed, and gently rolled into a goodie bag for transport to the cages within three hours of collection. Drift was dispersed within the cage, with water motion invariably pushing it off the paving stones and onto the floor of the cage. Kelp were young sporophytes (< 1m) that were gently removed from the substrate with their holdfast intact. Kelp holdfasts were fixed in place atop the paving stones via wire threaded through

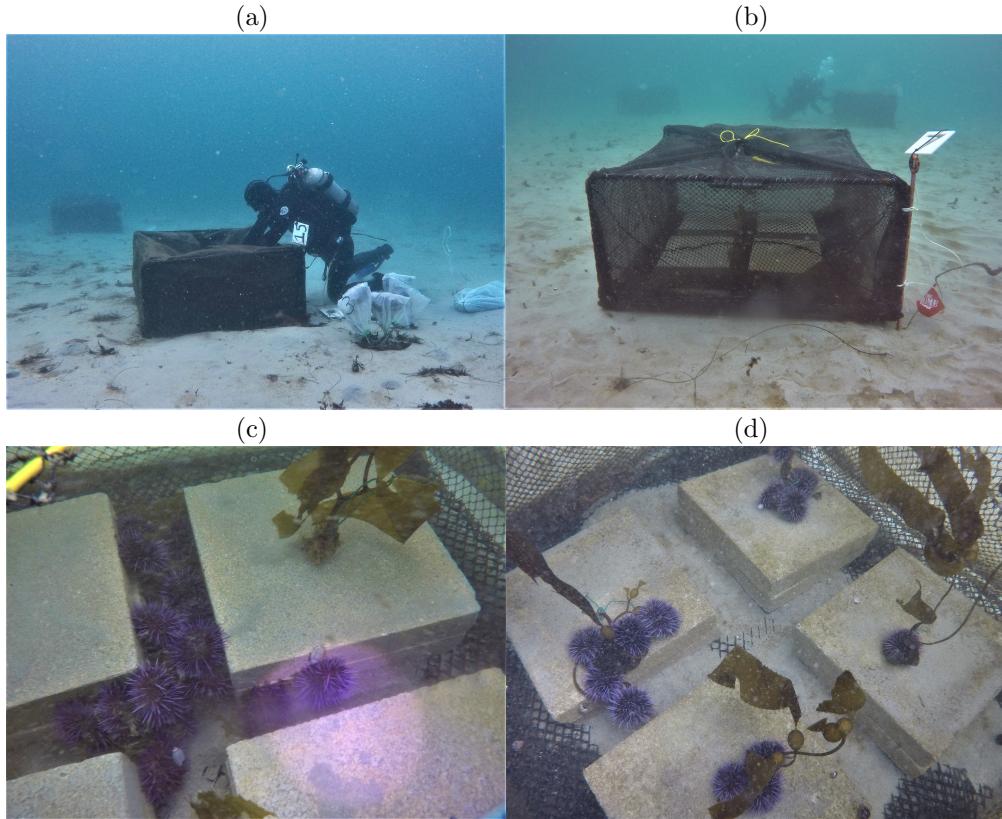


FIGURE 4.1: (a) A diver accesses the interior of a cage through doors in both the screening and netting in the top, center of the cage. (b) A deployed cage with the four stacks of two paving stones visible through the “double-hull” of screening and netting. (c) Urchins hidden in the “plus sign” crevice structure formed by the paving stone stacks in a cage with abundant drift. (d) A treatment with no drift, and all urchins are roaming and grazing upon kelp affixed atop the paving stones.

holes pre-drilled in the paving stones, replicating the typical location of growth atop rocky reef.

This experiment was not intended to test a consumptive preference in terms of nutrients or composition of the two resources per se; both our kelp and drift were from the same species. Rather, our design associated resources with a behavioral choice and subsequent location within the cage: urchins could either hide on the cage floor where they were likely to find drift on the cage floor, or actively move throughout the cage interior—including atop the paving stones—where they would find kelp.

To assess the density-dependence of grazing behavior upon drift, we used eight different target levels of drift ranging 30 – 300g wet-weight. Although an experiment also assessing the density-dependence of grazing behavior upon kelp would have been ideal, a full-factorial design with eight levels for each of the two resources would require $8^2 = 64$ cages, which was not logically feasible. Instead we used two levels of kelp: low kelp treatments with a single plant (targeting 25 – 120g),

and high kelp with four plants (targeting 100 – 300g), where a singular “plant” refers to a kelp individual. We refer to these two treatments as Low and High, respectively. Thus we had eight Low treatments, eight High treatments, and one cage each for drift control (no kelp treatment), a low control (one plant, no drift treatment), a high control (four plants, no drift treatment), and an urchin control cage with no resource treatments (for a concurrent urchin behavioral study not presented here).

In order to evaluate the temporal dynamics of grazing behavior and increase our inferential power, we followed these 16 focal treatments and four controls through time across three time periods, sampling and restocking resources at: $t = 44\text{hrs}$ (the end of period 1 and beginning of period 2); $t = 89\text{hrs}$ (the end of period 2 and beginning of period 3); and $t = 134\text{hrs}$ (the end of period 3 whereupon we sampled a third and final time without restocking).

When restocking a cage, we targeted its approximate original initial resource densities, tolerating a small amount of variation (within 10% of the original density). Urchins were not replaced between time periods. Four independent trials of this three-period experiment were completed over the course of the summer. New urchins from the barrens were used for each of the four independent trials, with treatments re-randomized across the cage-array to control for cage-specific effects. Five observations were dropped due to logistical error in field observation. Thus with four replicates of the 16 focal treatments we had 59 treatments (59 independent cages) that were followed across the three-period sequence for a total of 177 data points.

4.3.2 System of drift and kelp remaining, and urchin fullness through time

We anticipated that rates of resource consumption would change across the three-period sequence, but we did not expect any such change would reflect a biological change in urchin “parameter values” over time. That is to say, given the short time scale and confined space of our experiment, the *capacity* for urchins to “encounter” or “handle” prey was not anticipated to change. Rather, if consumption indeed varied across the three-period sequence, we wanted that change to be an emergent dynamic of the model, not a temporally dependent change in parameter values. We therefore modeled rates of change for drift remaining ($\frac{dS}{dt}$), kelp remaining ($\frac{dA}{dt}$), and the fullness of urchin “guts” ($\frac{dF}{dt}$) as

$$\begin{aligned}
\frac{dS}{dt} &= -aS * \left(1 - \frac{1}{1 + \frac{S^q}{A}}\right) * \left(1 - \frac{F}{v}\right) \\
\frac{dA}{dt} &= -aA * \left(\frac{1}{1 + \frac{S^q}{A}}\right) * \left(1 - \frac{F}{v}\right) \\
\frac{dF}{dt} &= \left(aS * \left(1 - \frac{1}{1 + \frac{S^q}{A}}\right) * \left(1 - \frac{F}{v}\right) + aA * \left(\frac{1}{1 + \frac{S^q}{A}}\right) * \left(1 - \frac{F}{v}\right)\right) - pF.
\end{aligned} \tag{4.1}$$

Fitting this model to the observed drift loss data provided time-invariant estimates of our parameters, where consumption through time is a function of the increasing “fullness” of urchin guts. Urchin gut fullness was not measured. Instead, gut fullness F was used as a latent variable to model how cumulative drift and kelp consumption decreases grazing activity over time. The rates of drift and kelp encounter encapsulated by a we assumed to be the same, with total consumption decreasing as a function of gut fullness, approaching 0 as F approaches v , the maximum volume of the gut.

The logistic expressions $\frac{1}{1 + \frac{S[t]^q}{A[t]}}$ and $1 - \frac{1}{1 + \frac{S[t]^q}{A[t]}}$ express urchin’s resource preference via parameter q . $q = 1$ equates to drift and kelp consumption proportional to their relative availability (i.e., no preference). $q < 1$ equates to kelp being disproportionately consumed relative to its availability; $q > 1$ equates to drift being disproportionately consumed relative to its availability. Parameter p specifies the rate at which gut fullness declines (“gut clearance”) in proportion ($-pF$) to the state of gut fullness.

4.3.3 Model fitting and parameter estimation via Stan

We used a Bayesian approach to fit our model to the data using the Stan and the Runge-Kutta method of integration. We used *cmdstan* (version 0.4.0) to access *Stan* (Stan Development Team 2019) via the *cmdstanr* package for *R* (version 4.0.4, R Core Team 2017). The initial conditions of kelp $A[0]$ and drift $S[0]$ used in Stan were the supplied experimental values for the first treatment and subsequent two restocking events. Gut fullness initial conditions for the start of period 1 ($t = 0$), denoted $F_1[0]$, was set to 0. The value of gut fullness at the end of period 1 was used as the initial condition of period 2. Likewise, the gut fullness at the end of period 2 was used as the initial condition of period 3. Thus, while our fitting accounted for the restocking of kelp and drift at the beginning of each period, gut fullness changed in a cumulative fashion across the three-period sequence.

TABLE 4.1: Parameters and model constituents with priors, reparameterizations, and models.

parameter	interpretation	prior
a	encounter rate	$a \sim \text{exponential}(0.1)$
q	resource preference	$q \sim \text{normal}(1, 10)$
v	max gut volume	$v \sim \text{normal}(60, 15)$
p	gut clearance	$p \sim \text{exponential}(0.1)$
σ	error	$\sigma \sim \text{exponential}(0.1)$
constituent	interpretation	model
α	reparameterized shape	$\alpha = \frac{R^2}{\sigma^2}$
β	reparameterized scale	$\beta = \frac{1}{R^2}$
R	likelihood; observed drift consumed	$R \sim \text{gamma}(\alpha, \beta)$

As wet-weight values of drift and kelp are continuous instead of discrete, and as all observed values of drift consumed R are necessarily ≥ 0 , we used a *gamma* likelihood to describe the data. The gamma’s mean depends on both the mean and the variance (i.e., the scale parameter affects the mean). Where possible, conjugate priors were selected (Table. 4.1). Four parallel chains were sampled with 5,000 warmup and 10,000 sampling iterations per chain. All data and code used in this manuscript are available at https://github.com/zhrandell/Functional_Response_Experiment.

4.4 Results

4.4.1 Experimental data

Urchins in treatments with abundant drift settled into the base of the cage—either in the “plus” or between the cage siding and perimeter of the paving stones to consume drift (Fig. 4.1 *c*). Active urchin movement was extremely rare in treatments where drift was abundant. In contrast, when drift was scarce, urchins actively moved up onto all interior surfaces of the cage, including atop the paving stones, whereupon we observed: (1) grazing just above the holdfast which detached the plant (sometimes rendering it unreachable), (2) urchins climbing up into the fronds and blades to graze, (3) urchins pinning kelp stipes onto the paving stones to graze, and (4) pulling kelp into the “plus” to graze (Fig. 4.1 *c*).

Drift consumption within the $1 * 1m$ cages increased with drift availability. Drift approximately saturated at 70, 55, and 25g consumed by the end of periods 1, 2, & 3, respectively, per 20 urchins. However, the higher levels of drift treatments in period 3 did not appear to exhibit typical asymptotic saturation, and instead appeared to exhibit an overall decline in consumption at all densities of drift (Fig. 4.2 row 1). Kelp consumption appeared unrelated to kelp availability (Fig. 4.2 row 3) and was instead dependent upon the availability of drift (Fig. 4.2 row 2).

Urchins exhibited a preference to consume drift, disproportionately consuming it relative to the proportion of available drift (Fig. 4.3a). Neither positive or negative switching between drift and kelp was observed (Fig. 4.3a). Urchins did exhibit rank switching—from kelp to drift—as the total biomass of resources (i.e., drift + kelp) increased. This rank switch occurred at approximately 100g of total biomass available (Fig. 4.3b), corresponding to approximately 40g of wet-weight drift alone (Fig. 4.3c).

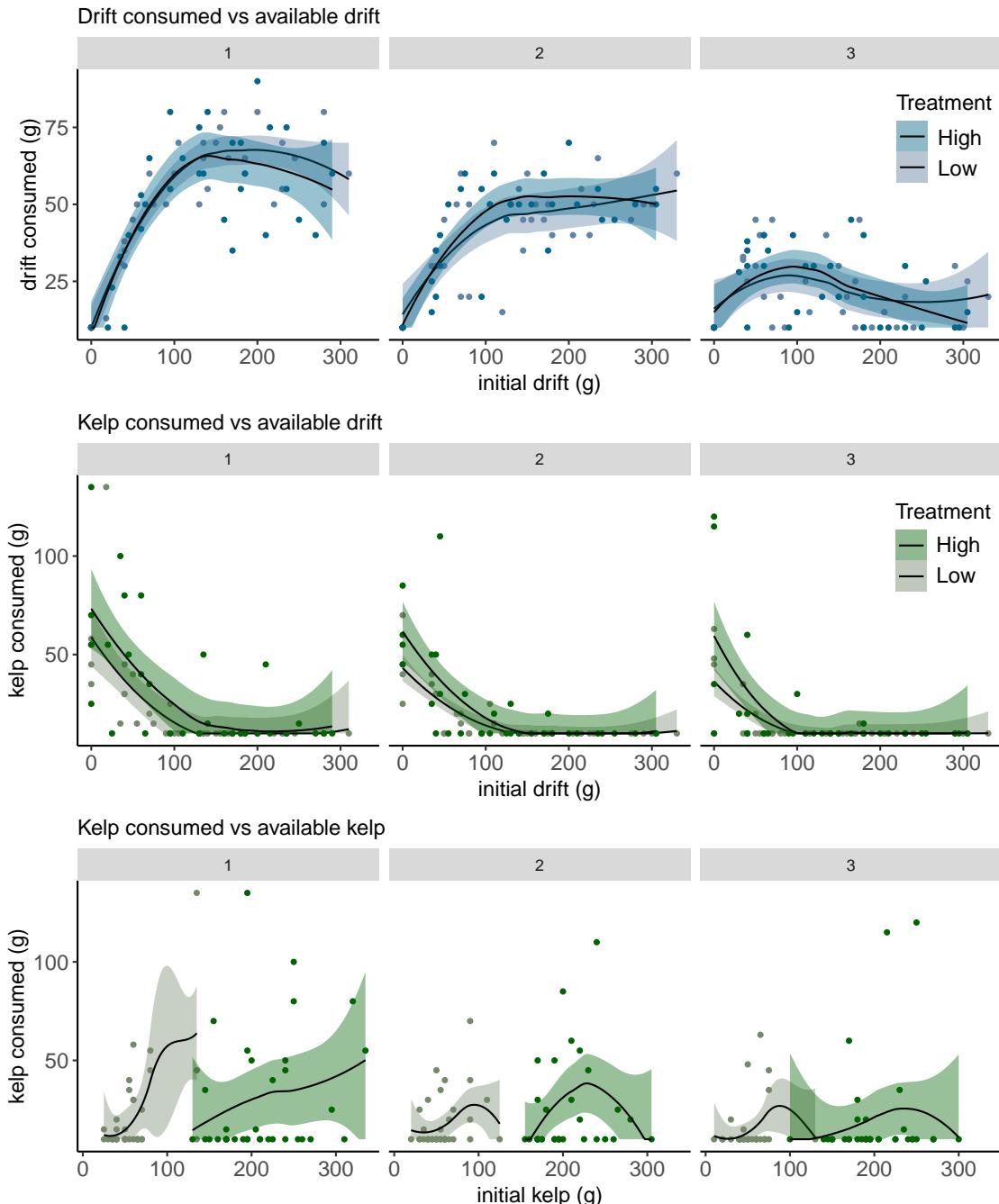


FIGURE 4.2: (row 1): Drift consumed vs drift available across the three-period sequence (labeled columns). Note the temporal decline (across columns) in drift consumption, including period 3's decline in consumption at high resource levels. Black lines across all rows and columns loess-smoothed (span=1) via `geom_smooth` in ggplot2 (Wickham 2016b), with shaded 95% confidence intervals. The Low (one kelp plant) and High (four kelp plants) treatments are visualized separately to illustrate the lack of difference in terms of resource loss between the two. (row 2): Kelp consumed vs drift available, where most kelp consumption occurs when drift is scarce (when drift is approximately < 100g). (row 3): There is no relationship between kelp availability and kelp consumption, emphasizing how kelp consumption is controlled by the availability of drift.

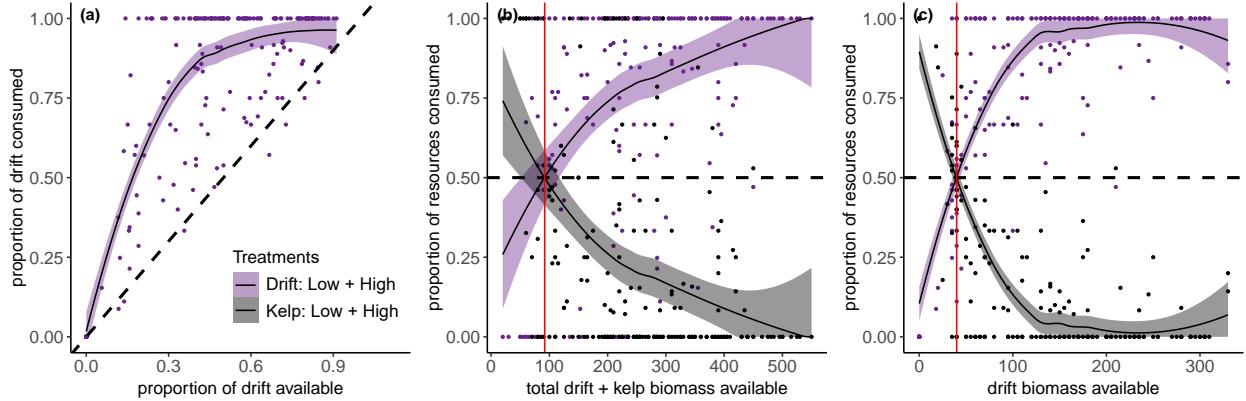


FIGURE 4.3: (a) Preference for drift exhibited as proportion consumed consistently exceeded the proportion of drift available. The dashed line represents hypothetical 1:1 consumption strictly proportional to resource availability. No positive or negative switching is observed. (b) Rank switching exhibited as urchins proportionally consume kelp when total resource availability is low ($< 100g$), and switch to drift (red vertical line) once sufficient ($> 100g$) total biomass is present. (c) Is the same figure as (b) except *only* available drift (and not kelp + drift) is plotted on the x-axis, indicating approximately 40g of wet-weight drift biomass is required for urchins to switch to drift. Colors differ here relative to Fig. 4.2 to emphasize that Low and High treatments are grouped together, visualizing all drift (purple) and kelp (black) loss.

4.4.2 Model fitting and simulation overview

Fitting Eqn. 4.1 to the experimental measurements of drift consumed R returned well-mixed chains (Fig. A16), approximately normal posteriors (Fig. 4.4), and no divergent transitions or other sampling issues (Fig. A17). Based on median parameter values (Fig. 4.4): urchins exhibited a baseline encounter rate of $a = 0.06$, a strong preference for drift with $q = 22.8$. Maximum gut volume was estimated at $v = 39.42$ with a gut-clearance rate of $p = 0.02$. Overall variance across the three-period sequence was estimated at $\sigma = 16.34$.

Simulating with these parameter values returned a time series of drift remaining, kelp remaining, and gut fullness across the three-period sequence that conformed well to the experimental time-series: (1) drift consumption increased with higher drift availability and kelp consumption controlled by the availability of drift (Fig. 4.5 rows 1, 2); (2) a preference to consume drift (Fig. 4.6 a); (3) rank switching from kelp to drift (Fig. 4.6b), (4) and dependency of switching upon the availability of drift alone (Fig. 4.6c). The switch in proportional consumption between resources as a function of drift alone was particularly consistent between the observed (40g) and simulated data (50g) (Figs. 4.3c vs. 4.6c).

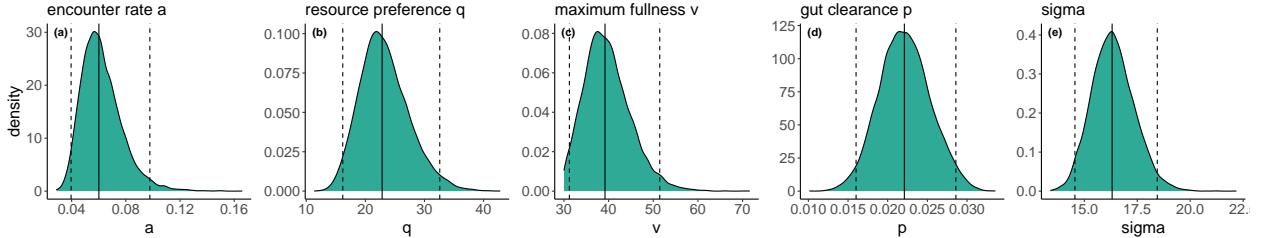


FIGURE 4.4: Posterior parameter distributions from fitting Eqn. 4.1 to observed drift loss R ; dashed lines are the 95% Credible Interval (CI) using (0.025, 0.975) quantile. The solid line delineates the median. (a) a : median = 0.06, CI: (0.039, 0.097); (b) q : median = 22.83, CI: (16.17, 32.58); (c) v : median = 39.19, CI: (31.21, 51.45); (d) p : median = 0.022, CI: (0.016, 0.028); (e) σ : median = 16.31, CI: (14.55, 18.44). See Fig. A17 to evaluate covariation between parameters and between chains. And see Fig. A16 for the trace plots of the sampling procedure that generated these posteriors.

The model also described kelp consumed by the end of each period, particularly the lack of difference between the Low and High treatments (Fig. 4.5 rows 1 & 2, Fig. 4.2 rows 1 & 2). That is to say, both the observed and simulated data point towards the unimportance of kelp availability upon kelp *and* drift consumption and that both are controlled by the availability of drift.

The inferred dynamics of gut fullness across the three periods behavior as generally predicted. Specifically, assuming the initial conditions of kelp increase at $A[0] = 30$ to $A[0] = 400$, as representative of the Low and High treatments, fullness increases through time and between the Low and High simulated treatments. However, unexpected predictions were also made. That is to say, these simulations also suggested sub-optimal foraging behavior, where, as the availability of drift “increases”, urchins preferentially consume drift instead of kelp even when the biomass of kelp available exceeds that of drift. Urchin preference for drift thereby results in a decline in total consumption relative to urchins at lower levels of drift. This sub-optimal foraging manifests as a “dip” in gut fullness as initial conditions of drift increase and was most pronounced in the Low treatments (Fig. 4.6d-f).

That said, the model did not accurately fit all aspects of the experimental data. Specifically, while the model exhibited a decline in drift consumption between periods 1 and 2 which aligned well with observed data (Fig. 4.5 a,b, vs. Fig. 4.2 a,b), it suggests no apparent decline in drift consumption between periods 2 and 3, in contrast to our experimental observations (Fig. 4.5 b,c, vs. Fig. 4.2 b,c). We return to this discrepancy in the *Discussion*.

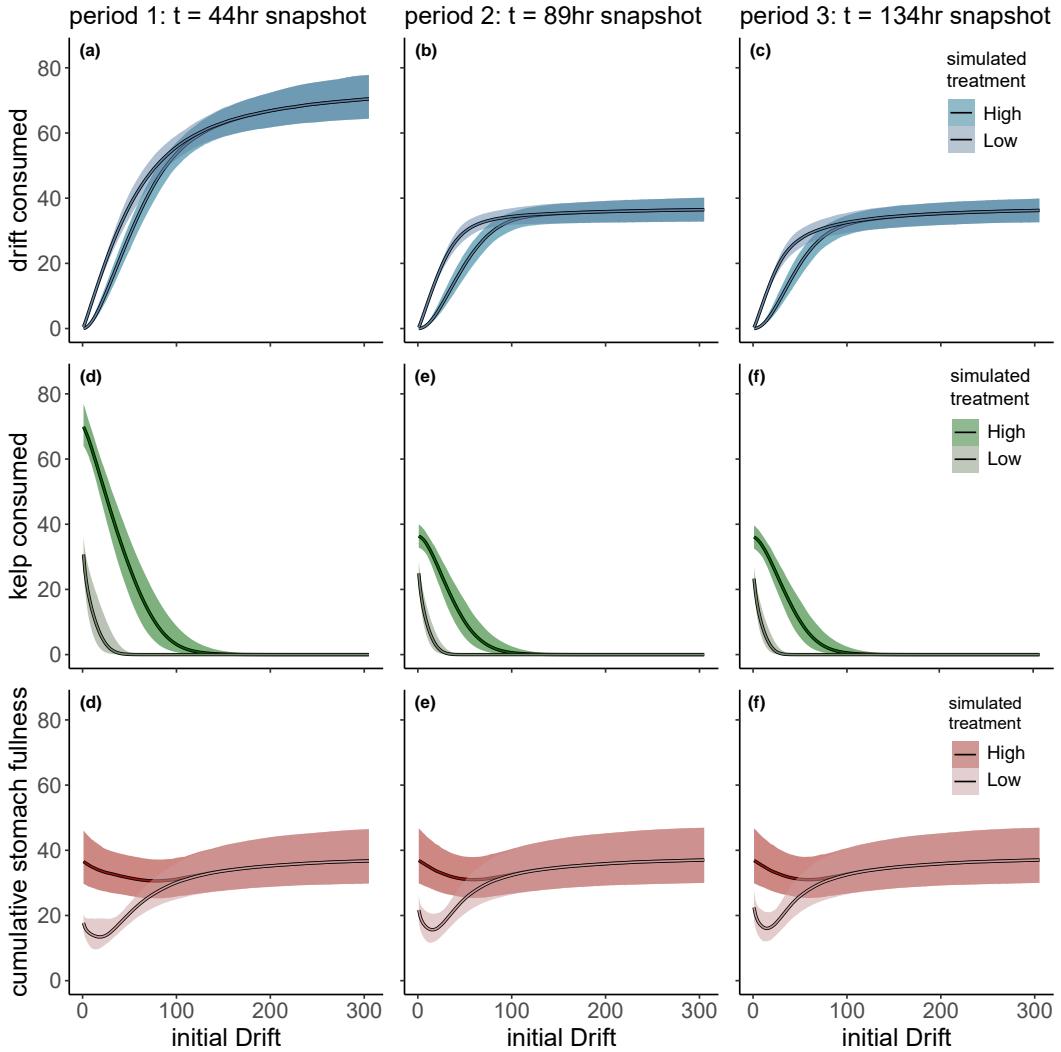


FIGURE 4.5: State values converted into (row 1) drift consumed and (row 2) kelp consumed within each respective period (periods 1 – 3 are columns 1 – 3). (row 3) cumulative gut fullness across the three-period sequence i.e. across the columns. We simulated drift initial conditions $S[0]$ as a sequence (length = 200) from 30 – 300g. we simulated two levels of kelp initial conditions: $A[0] = 30$, representing a “Low kelp” treatment (lighter shading across all panes), and $A[0] = 400$, representing a “High kelp” treatment (darker shading across all panes). Every 10th set of parameter values comprising our posteriors were used to simulate Eqn. 4.1, and the shaded bands are the 95% Credible Intervals from the simulations. The solid blue, green, and red lines (outlined in black) are the median values of the simulated data. Period 1 is well represented by the simulated data, as is period 2, which exhibits a decline in consumption relative to period 1 (contrast to Fig. 4.2 a,b for drift consumed, and d,e for kelp consumed). However period 3 does not exhibit a continued decline, as is found in the observational data (Fig. 4.2c). Note the “decline” in gut fullness at low initial conditions of drift—this is sub-optimal foraging behavior, as the strong preference exhibited by urchins (Fig. 4.6) results in less net-consumption than otherwise possible.

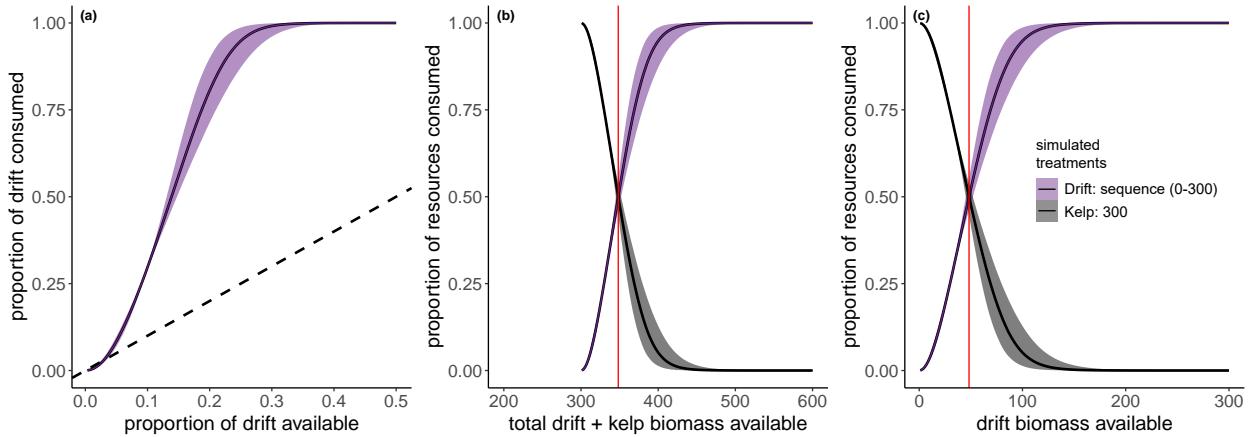


FIGURE 4.6: Simulated data used to visualize (a) resource preference, (b) rank switching, and (c) switching dependent upon only available drift. Contrast these simulated results to the experimentally observed preference, rank switch, and drift-dependent switch data visualized in Fig. 4.3a-c. Initial conditions used to simulate these data differ from those of Fig. 4.5: drift initial conditions $S[0]$ were a sequence from (0 – 300) with a length of 200. Initial conditions of kelp $A[0]$ were held fixed at 300, i.e., a sequence of (300 – 300) with a length of 200. This evaluated switching behavior when drift was \leq kelp. Fullness initial conditions were treated the same as previously described—as were all other aspects of the simulation procedure (described in the caption of Fig. 4.5). Drift loss, kelp loss, gut fullness for this system are visualized by Fig. A18. The solid lines are the median simulated value, and the shading around the lines are 95% Credible Intervals of the simulated data. (a) urchins once again exhibit preference for drift. (b) rank switching is observed and the switch point (red line) is at 350g of total biomass (kelp and drift). This contrasts with the observed rank switch results in Fig. 4.3b, but the “high” biomass required for the rank switch is a product of the large amount of kelp available in *all* treatments of these simulated data, i.e. $A[0] = 300$. (c) Visualizes the relationship between drift biomass *only* upon the proportional switch in consumption. 50g of drift biomass is required for the switch, closely aligned to the 40g experimentally observed (Fig. 4.3c).

4.5 Discussion

4.5.1 Summary of discussion

Urchins exhibited a preference to consume drift over kelp, and a rank switch in proportional consumption from kelp to drift as total biomass increased. Fitting Eqn. 4.1 to experimental observations of drift loss R emphasized urchin’s preference to consume drift over kelp via the preference parameter $q = 22.83$ (CI: 16.17, 32.58). Furthermore, treating urchin gut fullness in Eqn. 4.1 as a latent variable enabled a temporal decline in consumption across the three-period sequence, approximating the decline observed in the experimental data.

The *Discussion* (points 1-3) and *Conclusion* (point 4) are structured around the following points. (1) we believe that the observed preference to consume drift over kelp reflects a behavioral preference for urchins to remain hidden in cracks and crevices, and not a nutritional difference between the two resources. We also address the possibility that our 24hr feeding may have influenced drift preference. (2) We discuss the temporal component of our consumption measurements. We also consider how an additional experiment could gain insight into the “other direction” of shift, i.e., future work could address how much (how little) drift would be required to *elicit* active grazing from well-fed and gravid “kelp-forest” urchins. (3) we contextualize Eqn. 4.1 within the functional response models. We also consider why the simulated data from Eqn. 4.1 model does not capture the continuous decline in consumption depicted in the experimental data. (4) we conclude by considering how drift could potentially be used as a means to modify urchin consumption. This includes a brief consideration of two serious logistical caveats, along with two potential workarounds.

4.5.2 Urchin preference for drift is a function of behavior

Urchins from an urchin barren rapidly switched to drift and avoided live kelp. We believe this preference has little to do with the composition or nutrient profile of the two resources—especially given that both were the same species (though different ages). Instead, we believe this preference for drift reflects an urchin behavioral preference to “hunker down”, i.e. to cease movement and become inactive, particularly within cracks, crevices, and other habitat features that provide some measure of protection. If sufficient drift is available, urchin opt to hide, graze the drift, and—crucially—ignore kelp.

We cannot rule out the possibility that providing a large supply of drift, once, (essentially *ab libitum*) over a 24hr period prior to the initiation of the experiment influenced their preference

for drift. We do not believe this to be the case however, given that treatments with low levels of drift were associated with rapid and substantial losses of kelp. The intent of this 24hr feeding was to standardize the hunger level of urchins as much as possible, while also habituating urchins to the cage following collection (Griffen 2021). Thus while we do not believe the 24hr feeding affected resource preference, it may have influenced overall consumption, particularly at high treatment densities.

4.5.3 Temporal dynamics and directionality of the behavioral shift

This experiment revealed a switch to consume drift instead of kelp for urchins from an urchin barren. It is worth noting that well-fed, healthy (gravid) urchins from a kelp forest may exhibit a very different switching pattern. That is to say, our experiment cannot speak to the “other direction” of the urchin-behavioral shift, going from a fed, gravid kelp-forest urchin to an actively grazing urchin barren urchin. A future experiment could ask: how little drift—and for how long—is necessary to *elicit* active consumption of live kelp? We speculate the switch to active grazing will take longer than we observed. It is also likely that the duration could in-part be a function of previous sensory cues of urchin predators, thus repeating this experiment in locations with and without urchin predators could provide further insight regarding the mechanism.

4.5.4 Novelty and limitations of model

The three-period sequence and resource restocking structure of our experiment required a non-traditional model-fitting approach. Ordinary differential equations have been used in the functional response literature to model prey depletion through time (Novak 2010; Rosenbaum et al. 2018), but our study expanded this approach by explicitly modeling the two restocking events at the beginning of period 2 and 3. These restocking events dynamically perturb in time what would otherwise be an uninterrupted decline in resources remaining. In doing so, we increase the information available to estimate our parameters relative to the initial conditions, and gain added insight into overall temporal dynamics across the three-period sequence. Likewise, our use of gut fullness as a latent variable expanded upon existing functional response methods, specifically those surrounding satiation and hunger level (Gause 1934; Ivlev 1961). Most recently, Jeschke et al. 2002 developed the Steady-State Satiation (SSS) equation, which incorporated handling and digesting prey as distinct components, and where satiation (or hunger level) is determined by ingestion and digestion. As stated in the name, this model assumes that hunger level is at steady state. Our model considers

hunger level as a function of cumulative ingestion akin to the SSS, but differs by explicitly assuming hunger level is *not* at steady state. Once restocking events cease and given sufficient time, urchins in our model eventually deplete all resources, their guts empty, and all state variables and their rates of change approach 0. It is thus the approach *towards* steady state—the process of “filling a gut”—that scales hunger-level and thereby rates of consumption.

Our model does not perfectly reproduce all patterns of our experimental data, particularly the gradual decline in consumption between period 2 and 3 (contrast Fig. 4.2 *b,c* and Fig. 4.5 *b,c*). We verified that future hypothetical additional restocking events would not produce any substantial declines in consumption beyond those present in periods 1-3. This suggests the simulated period 3 dynamics are nearing steady-state. However, as we do not believe our experimental data are at steady-state—and we anticipate consumption would decline further with additional restocking events—it is likely our model is incorrect or incomplete regarding the characterization of maximum gut volume, clearance (i.e. digestion), and/or the manner in which gut fullness depresses grazing activity. For example, drift consumption was experimentally observed to saturate within each period (Fig. 4.2 *a-c*), *and* overall consumption declined across the three-period sequence. Within our model however, saturation is brought about as the gut fills and approaches v . We slow the approach to v with gut-clearance pF , and this mechanism does allow continued consumption. However, our experimental data clearly have urchins saturating within period 1 (and 2 and 3) of the experiment, and thus our gut fullness is *forced* (given the structural formulation of our model) to approach v within the first period. Because the gut is required to fill within period 1, the vast majority of the “potential” approach towards v that could otherwise enable a more gradual decline in consumption is instead spent in period 1. We therefore do not see much decline in consumption past period 2, and instead we see continued consumption facilitated by gut clearance.

Nonetheless, we contend that the purpose of modeling gut fullness is not to “predict” or reproduce the entirety of the data (Shmueli 2010). Rather, our objectives were to test whether our biological intuition regarding the increasing fullness of a starving urchin from an barren urchin could be used as a mechanism to scale consumption across our three-period sequence, and whether a preference parameter could be estimated from the data. From the perspective of these objectives our model succeeded, and in doing so we functionally characterized the density-dependence of urchin preference and switching.

4.6 Potential conservation application

The results of this experiment suggests it may be possible to mitigate kelp consumption from actively foraging urchins by modifying drift availability. That is to say, it may be possible to “calm down” actively foraging urchins or temporarily divert urchins away from live kelp in contexts of kelp forest conservation efforts that are currently contending with urchin barrens (Watanuki et al. 2010; Morris, Hale, et al. 2020; Gleason et al. 2021). That said, subsidizing drift has significant challenges. First, the practicalities of sourcing or creating macrophyte drift from natural reefs or aquaculture might be impractical, and removing drift from one reef (or removing live kelp to “create” drift) would deprive those source locations from the associated benefits of drift and kelp. Urchins are omnivores however, and it is possible to entice actively foraging urchins with non-macrophyte resources, such as fish byproducts, as illustrated by a Norwegian fishery (Sivertsen et al. 2008). It may also be possible to use agricultural by-products of fruit, vegetable, and grain to attract urchins. Second, even if a resource proves effective and its supply is abundant, there are significant logistical limitations to the spatial extent across which resources can be applied. Such large spatial subsidies would also be difficult to maintain in the long-term. We therefore suggest that artificial drift subsidies should not be considered a large scale “fix” for urchin barrens, but rather a short-term strategy to modify urchin behavior when at a critical juncture. For example, given the patchy metapopulation dynamics that characterize species such as Giant kelp, the preservation of small, remnant hot spots of kelp growth surrounded by an urchin barren may be paramount for future recovery. Such remnant locations could perhaps be buffered with a “firewall” of drift subsidies to stave off kelp consumption long enough for urchin removal or decline. Likewise, kelp outplanting efforts could be enhanced by providing alternative resources such that any urchins present are attracted, buying time for the out-planted kelp to establish. Despite the logistical challenges and associated spatiotemporal limitations, drift subsidies ought to be considered an option in the kelp-forest conservationist toolkit.

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5 Concluding remarks

5.1 Overview

This dissertation evaluated grazer-resource interactions from three distinct perspectives and methodologies. I: (1) evaluated empirical patterns of kelp-forest community dynamics and inferred a variable that controls kelp-forest stability landscapes and the velocities by which systems transit across them; (2) used a model to investigate key aspects of the mechanism by which this variable influenced dynamics to show that alternative stable states and other qualitative dynamics can emerge as inferred; and (3) experimentally evaluated a focal assumption from that model with a subtidal caging experiment.

Chapter 2 utilized multivariate analyses and principals from potential analysis and stochastic dynamical systems theory to quantify velocities of community shift across a stability landscape. I demonstrate how substrate complexity determines not only three distinct states of community structure, but also the velocities with which communities respond to perturbations. My hypotheses for how substrate complexity modified urchin behavior formed the hypotheses tested in *Chapters 3 and 4*.

Chapter 3 used computational methods to analyze a system of delayed-differential equations. Via *1D* and *2D* bifurcation analysis, I explored if and how an assumption regarding urchin preference and processes such as drift production, retention, and loss, affected the capacity of kelp forests to exhibit (1) discontinuous movement between alternative stable states, and (2) qualitative shifts in dynamical behavior, such as the emergence of stable limit cycles versus a fixed point. All of these results were dependent upon the untested assumption that urchins preferred to consume drift over kelp.

Chapter 4 tested this assumption with a one-consumer (urchins) two-resource (drift and kelp) functional response experiment. The experiment showed that (1) urchins exhibit a preference for drift, (2) the consumption of kelp is controlled by the availability of drift, and (3) urchins exhibit a rank switch from kelp to drift as drift abundance increases. I fit an ordinary differential equation (ODE) model to our experimental data and estimated posterior distributions for parameters including resource preference q . In creating this ODE model I demonstrated a novel, non-equilibrium method of accounting for decreasing consumption as a function of increasing gut fullness.

Here I will motivate a few final points that merit further consideration down the road.

5.2 Concluding *Chapter 2*

5.2.1 The association between substrate complexity and kelp-forest dynamics

Many questions remain regarding the relationship between substrate complexity and kelp-forest stability. Foremost is the question, where else does this pattern emerge? It may be that San Nicolas Island is unique such that the convergence of warm water (eliciting urchin disease), large wave events (kelp/drift removal), and high predator diversity (CA sheephead, sea stars, spiny lobsters, and sea otters) is present no where else. It is likely that high-latitude kelp forests may not exhibit similar patterns with substrate complexity, as those locations are structured by strong species interactions. There may also be other variables that modify stabilizing processes and urchin behavior other than substrate complexity, and the emergence of these variables may associate with broader biogeographical patterns.

Another issue regarding evaluation of the relationship between substrate complexity and kelp-forest stability is the lack of (widespread) fine-scale side-scan sonar acoustic imagery. $2m$ grain side-scan sonar data exist for SNI. However, a $2m$ cell contains 20% of a $10 \times 2m$ benthic transect, which equates to five data points per each SNI benthic swath transect (hence why I measured rugosity with a magnetic surveyor's wheel). While this $2m$ grain imagery was not suited to the $10 \times 2m$ transect questions I wanted to ask in *Chapter 2*, future work could use this imagery to expand upon other aspects of the SNI subtidal data. In particular, the fish data—collected along $50 \times 4m$ transects—would be well-suited for analysis in conjunction with the acoustic imagery. It would be interesting to evaluate whether changes in fish community structure and composition tracked or not (i.e. synchronous, lagged, or no relationship) the invertebrate and kelp state dynamics described in *Chapter 2*.

5.2.2 Future methods

Emerging technology has great potential to ease current logistical and financial hurdles preventing widespread collection of side-scan sonar imagery. For example, a recent study in the Florida National Marine Sanctuaries used an Autonomous Underwater Vehicle (AUV) in shallow water to gather photographic and acoustic imagery (Brown, Lawrence, et al. 2019). Essentially, AUVs are a torpedo with advanced sensors such as side-scan sonar, as well as “traditional” sensors such as cameras. AUVs do not have a tether like Remotely Operated Vehicles (ROVs), and instead follow pre-programmed paths along the benthos. Such vehicles could “mow the lawn”, running reciprocal transects back-to-back along the benthos, collecting acoustic and photographic imagery all along

the way. There is likely much potential (Hamel et al. 2020) in combining acoustic imagery from such automated technologies with photos concurrently gathered by the AUV. As SCUBA divers are fundamentally limited by how much gas they can carry in a SCUBA tank, among other logistical limitations, AUVs and small ROVs (Buscher et al. 2020) may well open up new spatial scales (or at the very least, a larger spatial extent) of benthic ecology, especially if those unmanned tools are incorporated into long-term monitoring programs. The potential payoff for this approach expands exponentially when one considers an Artificial Intelligence approach towards analyzing what will admittedly be an overwhelming amount of imagery for an observer to manually annotate. In particular, supervised classification—once algorithms are properly trained—has great potential to maximize our inference from benthic imagery (Brown, Smith, et al. 2011; Salman et al. 2016; Sarwar et al. 2020). Algorithms such as those associated with CoralNet are already leading the charge in this domain for shallow, warm water benthic systems (Williams et al. 2019; Raphael et al. 2020), and kelp forest ecology needs to catch up.

5.3 Concluding *Chapter 3*

5.3.1 Species interactions via function output and steady state

Owing to the numerical methods used, I was able to extract “realized” values of functions when the system is at steady-state, such as kelp recruitment R_A and the proportion of urchins grazing kelp Q_S . That is, I extracted these values at each point in parameter space that was tested via 1D or 2D bifurcation analysis. We could then combine state values and output from functions to calculate interaction strengths across 1D or 2D parameter space. An example combining numerical function output and state values is the interaction strength:

$$\begin{aligned} I_A &= \frac{Q_A * F_A * H}{A}, \\ I_S &= \frac{Q_S * F_S * H}{S}. \end{aligned} \tag{5.1}$$

Here, I_A is interaction strength upon kelp, i.e., realized kelp consumed by urchins. Q_A is the proportion of urchins grazing kelp, F_A is potential kelp consumed by urchins, H is the state value of urchins, and A is the state value of kelp. The numerator is the realized amount of kelp consumed given the number of urchins in the system, and dividing by the denominator yields a per-capita metric of interaction strength. (likewise for I_S , Q_S , and S for the interaction strength of drift

consumed by urchins). In essence, Eqn. 5.3.1 allows us to evaluate how kelp and drift consumed by urchins varies with respect to the state values of kelp and drift. I can then calculate how these interaction strengths change throughout *1D* or *2D* parameter space.

This could be especially helpful to see how various parameters affects species interactions in proximity to the switch in grazing behavior. This is because the behavioral switch is determined less by a change in urchin density per say, and rather a change in the mode of grazing. Visualizing interaction strengths that rely upon density alone would not encompass the behavioral shift. Furthermore, calculating interaction strength that include numerical function output would provide insight into the underlying processes structuring the system when, as in Fig. 3.7, the kelp equilibrium at two different regions exhibits the same value, yet via radically different processes (e.g., high urchin grazing upon kelp versus high kelp mortality due to non-grazing processes).

For example, Fig. 5.1 *a,b* visualizes Eqn. 5.3.1 calculated across a range of values for urchin recruitment r_H . In contrast, Fig. 5.1 *c,d* visualizes the same values, but with the urchin state variable H on the x-axis. These results indicate how the *same* density (abundance) of urchins can associate with two very different modes of grazing—all of which is dependent upon the relative rate of urchin recruitment. Reworded, rates of drift and kelp consumption are predicted to depend upon the rate of urchin replenishment—not just the abundance of urchins.

5.4 Concluding *Chapter 4*

5.4.1 Future experiments evaluating drift

Many questions remain regarding the switch in urchin behavior experimentally captured with our experiment. As articulated in *Chapter 4*, there are multiple ways in which to expand upon these findings.

It would be worthwhile to repeat the experiment but with urchins sourced from a kelp forest to test what levels of drift are required to *elicit* active grazing upon kelp. It is possible kelp-forest urchins would be too difficult to extract from the substrate, as they were for us. In this case, then it might be worth repeating the experiment with urchin barren urchins and (1) continue the restocking events for longer periods of time to evaluate when consumption equilibrates, then (2) fatten-up urchins for a sufficient period of time such that they are essentially “kelp-forest” urchins (this will need to be evaluated by examining gonad status), and then (3) repeat our experimental treatments. This experiment, while no doubt a significant time investment, would provide invaluable insight

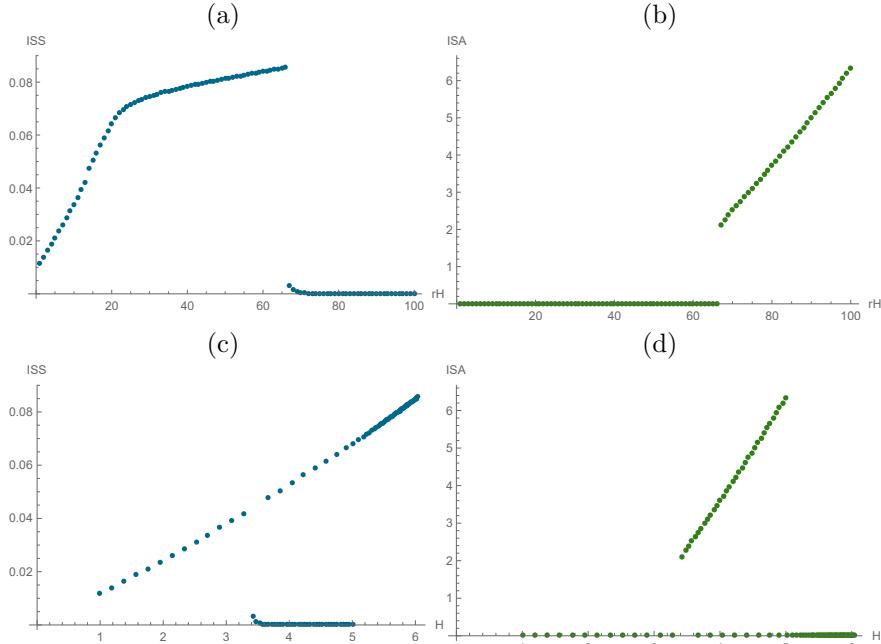


FIGURE 5.1: (a) consumption of drift (blue dots), seen to increase as urchin recruitment increases (along the x-axis), until the rate exceeds a critical point and all urchins switch to consume kelp, whereupon the loss of drift declines to 0; (b) consumption of kelp (green dots) is 0, as all urchins graze drift, until the rate of urchin recruitment exceeds a critical point, whereupon kelp consumption increases linearly with the increasing rate of urchin recruitment. (c) Drift consumption with the steady state value of urchins on the x-axis. Two modes of grazing are visible for a range (3.5-5) of urchins, with the rate of recruitment being the driver of the two modes. (d) Kelp consumption with the steady state value of urchins on the x-axis, again demonstrating the two modes of grazing dependent upon the rate of urchin recruitment.

into the other direction of shift, which is more pertinent to avoiding the formation of barrens than the restoration of kelp forests.

Finally, in closing *Chapter 4*, I motivated the potential for using drift as a short-term strategic tool to modify urchin behavior. Practically speaking, what needs to happen first is the effects of drift need to be assessed at a larger scale. In particular, it would immensely useful to apply “treatments” of sustained drift application *and* removal within both forested and urchin barren states. An obvious issue is: how to retain drift along the benthos? It is likely that some sort of netting could be constructed, such as a “pillowcase”, where netting is wide enough for urchins to consume the drift therein, but not too wide such that the drift sifts out and is removed by water motion. Such a two-by-two factorial design would provide valuable insight into the community effects of drift (and its absence). And such an effort would go a long ways towards evaluating the practicality (or lack-thereof) of using drift as a temporary action to modify urchin behavior.

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APPENDICES

A1 Chapter 2 Appendix

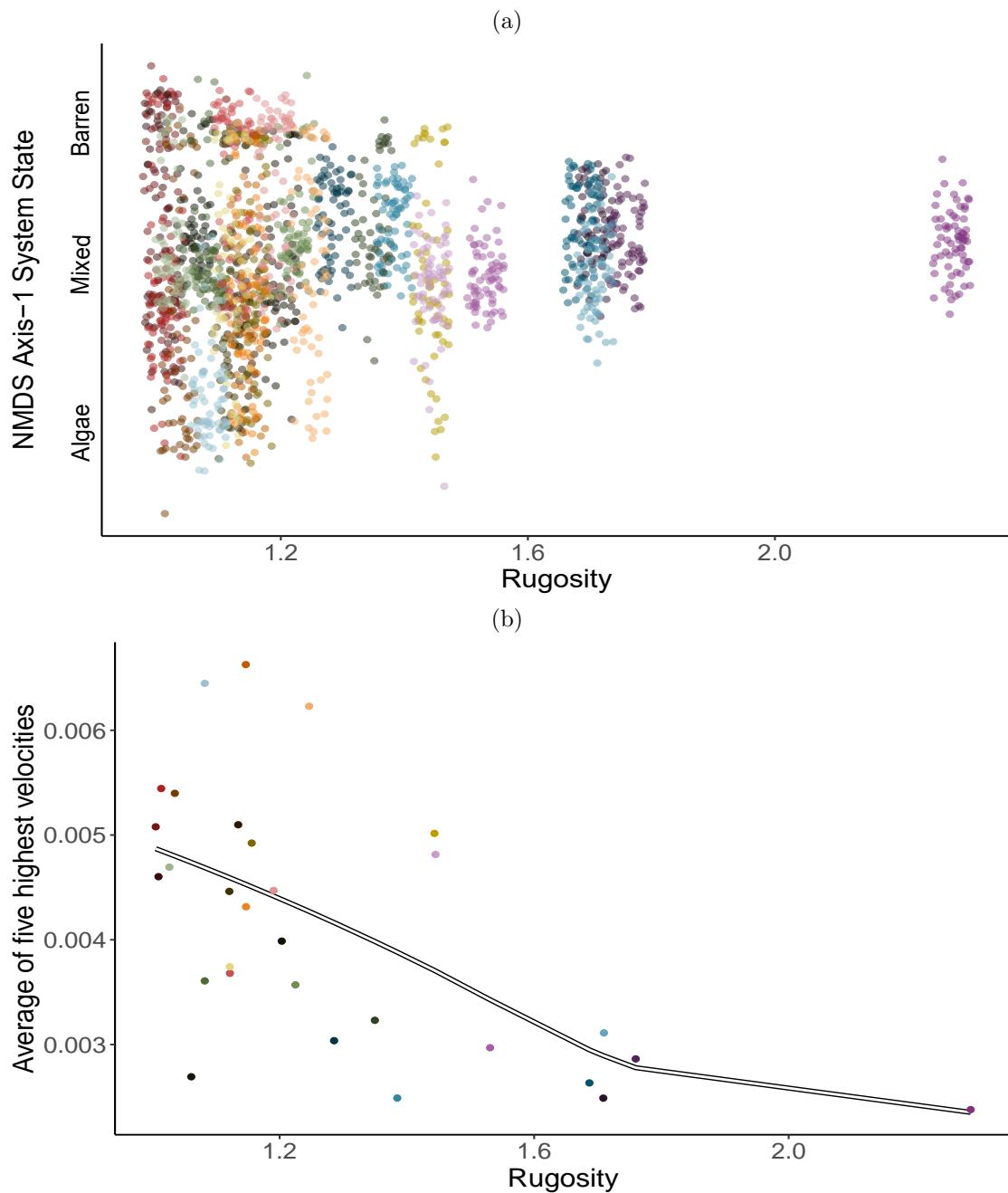


FIGURE A1: (a) System state (*NMDS Axis-1 System State* from Fig. 2.2a-f) and rugosity, evidence that rugosity predicts community state. Points are jittered horizontally by 0.3 in *ggplot2* (Wickham 2016a). (b) Points are the average of the five highest velocity movements per transect plotted against transect rugosity, demonstrating that the velocity of community shift decreases with increasing rugosity. The white line is loess-smoothed with a span of 1.

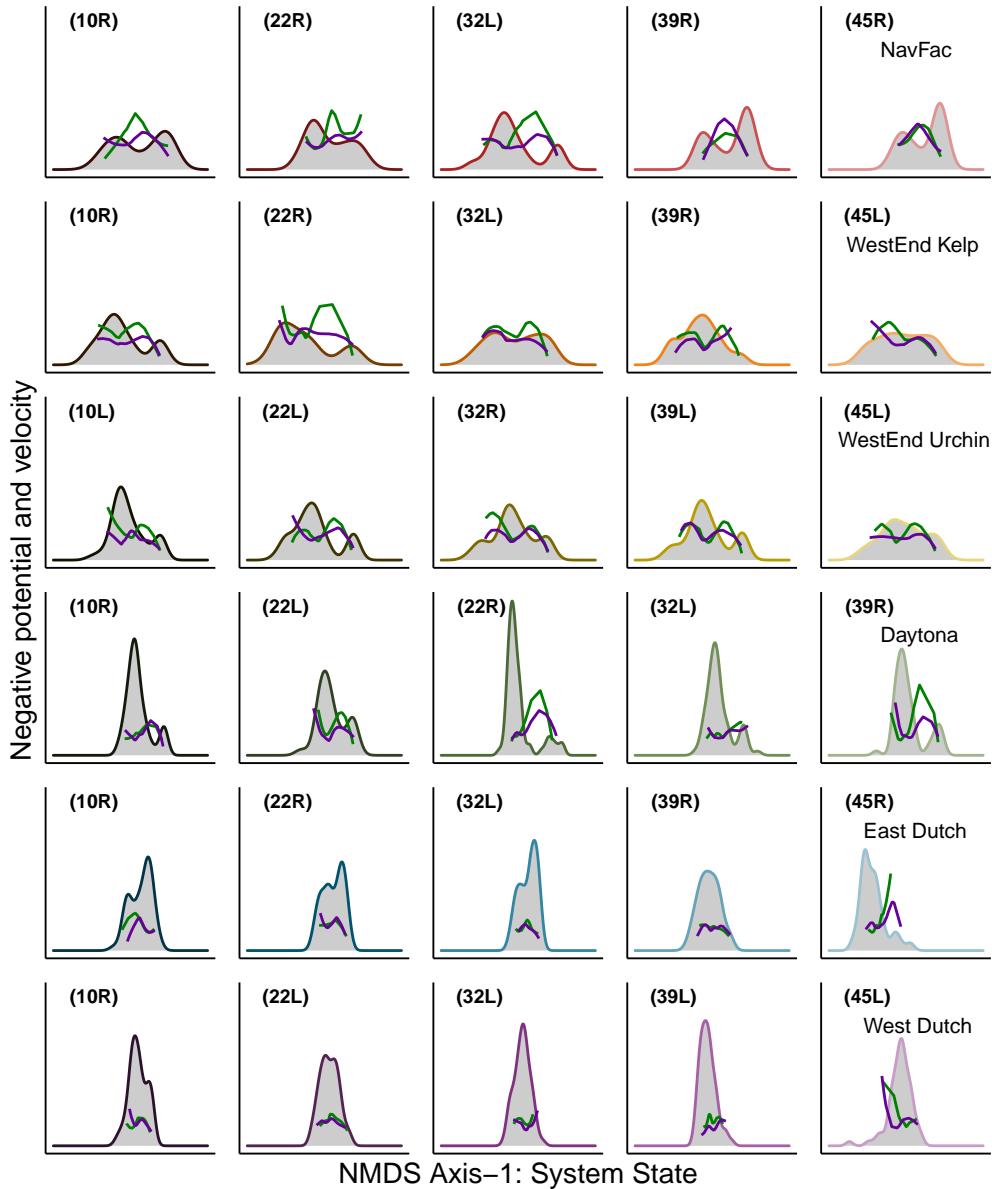


FIGURE A2: Negative potential landscapes and directional velocities of community shift for all 30 transects evidence that movements towards the urchin barren state (purple loess-smoothed lines) and towards the algal-only state (green loess-smoothed lines) exhibit low within-state velocities and high between-state velocities.

TABLE A1: Evidence for multi-modality as assessed using Gaussian mixture models fit to individual transects.

Site	Transect	n	Clusters	Mixing Probabilities	Means	Variances
NavFac	10R	65	3	0.49; 0.19; 0.30	-0.32; 0.46; 0.78	0.048; 0.02; 0.004
NavFac	22R	66	2	0.58; 0.41	-0.22; 0.54	0.035; 0.551
NavFac	32L	67	2	0.82; 0.17	-0.29; 0.81	0.08; 0.001
NavFac	39R	67	3	0.27; 0.19; 0.53	-0.22; 0.13; 0.72	0.003; 0.02; 0.005
NavFac	45R	67	2	0.48; 0.51	0.003; 0.70	0.047; 0.005
W.E. Kelp	10R	64	2	0.81; 0.18	-0.35; 0.62	0.08; 0.0005
W.E. Kelp	22R	64	2	0.78; 0.21	-0.65; 0.54	0.089; 0.014
W.E. Kelp	32L	64	3	0.53; 0.24; 0.21	-0.49; 0.23; 0.62	0.07; 0.01; 0.0003
W.E. Kelp	39R	64	1	1	-0.23	0.16
W.E. Kelp	45L	64	2	0.83; 0.16	-0.2; 0.64	0.17; 0.0004
W.E. Urchin	10L	64	2	0.57; 0.31; 0.10	-0.04; -0.22; 0.64	0.11; 0.009; 0.00008
W.E. Urchin	22L	64	2	0.81; 0.18	-0.37; 0.59	0.07; 0.003
W.E. Urchin	32R	64	2	0.9; 0.1	-0.18; 0.61	0.15; 0.0003
W.E. Urchin	39L	64	2	0.83; 0.16	-0.24; 0.63	0.108; 0.0008
W.E. Urchin	45L	64	2	0.83; 0.16	-0.17; 0.62	0.14; 0.0002
Daytona	10R	66	2	0.87; 0.13	0.08; 0.68	0.02; 0.001
Daytona	22L	58	2	0.79; 0.2	0.03; 0.59	0.03; 0.002
Daytona	22R	66	2	0.86; 0.13	-0.09; 0.71	0.01; 0.01
Daytona	32L	66	2	0.84; 0.15	0.05; 0.66	0.02; 0.01
Daytona	39L	60	3	0.13; 0.55; 0.30	-0.2; -0.04; 0.3	0.0001; 0.009; 0.14
East Dutch	10R	68	2	0.42; 0.57	-0.003; 0.37	0.02; 0.01
East Dutch	22R	68	4	0.27; 0.18; 0.07; 0.47	-0.1; 0.08; 0.19; 0.37	0.004; 0.0005; 0.00002; 0.004
East Dutch	32L	68	2	0.41; 0.58	0.018; 0.33	0.011; 0.0059
East Dutch	39R	68	1	1	-0.06	0.046
East Dutch	45R	68	2	0.87; 0.12	-0.7; -0.15	0.02; 0.02
West Dutch	10R	69	1	1	0.15	0.03
West Dutch	22L	69	1	1	0.1	0.03
West Dutch	32L	69	1	1	0.08	0.02
West Dutch	39L	69	1	1	-0.09	0.025
West Dutch	45L	69	2	0.10; 0.89	-0.54; -0.08	0.12; 0.02

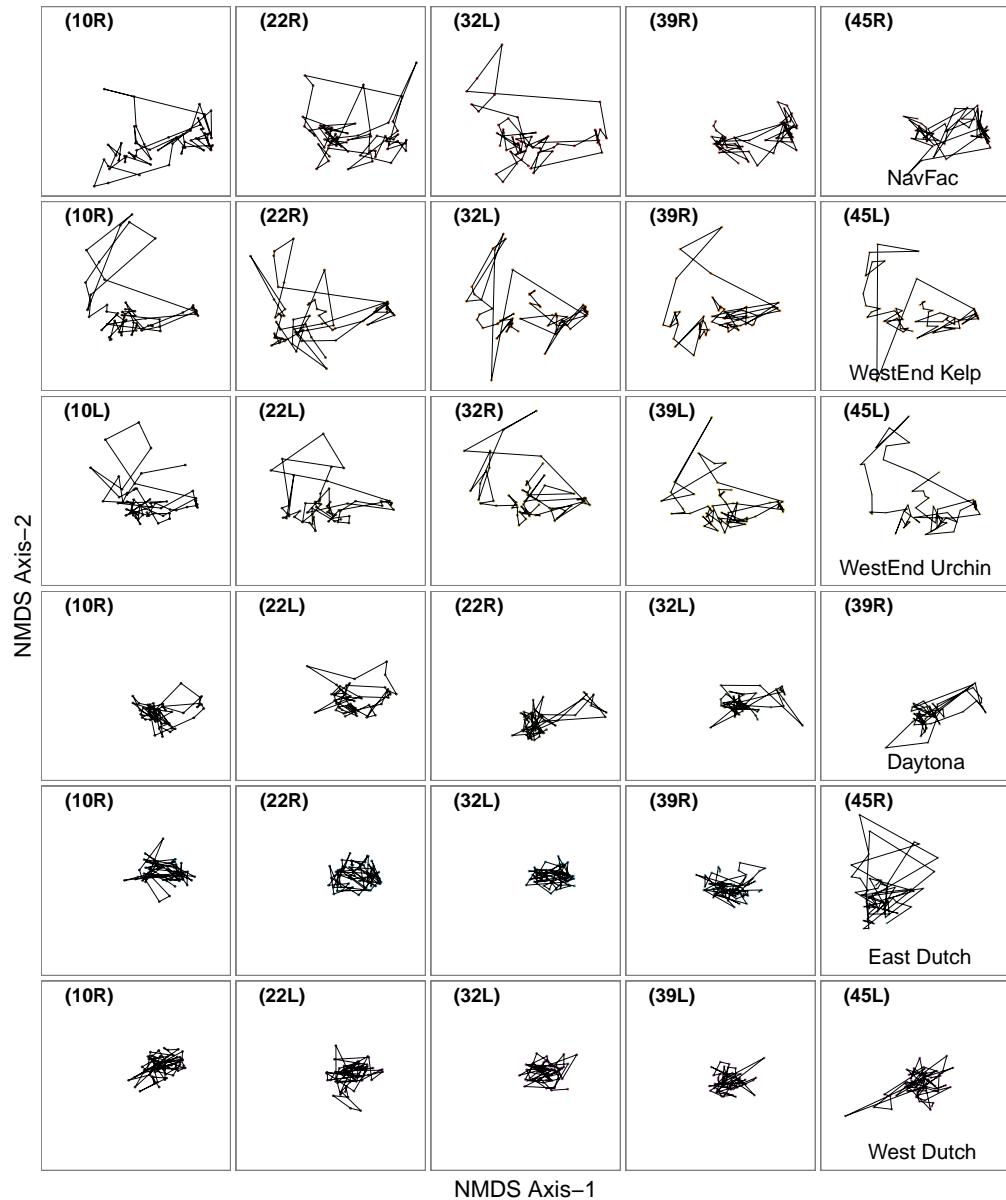


FIGURE A3: Trajectories through two-dimensional species-space for all 30 transects. Substrate rugosity increases by row across sites. Note the extending periods of fluctuating community structure at both WestEnd sites which we interpret as long-term transients through an algal-only state, and that transects exhibiting high-velocity kelp fluctuations do not associate with substrate complexity along Axis-2.

A1.1 Environmental variables overview

To assess whether potentially confounding environmental variables were associated with substrate complexity and kelp-forest dynamics, we analyzed 21 years of daily satellite-derived chlorophyll *a* data (2000-2021), 4 years of water temperature measurements (2015-2019), and 11 months of wave height measurements (2015-2016) taken at our sites and around San Nicolas Island. The chlorophyll *a* data were obtained from NASA's MODIS-Terra satellite (NASA Goddard Space Flight Center 2018 Reprocessing. NASA OB.DAAC, Greenbelt, MD, USA) from which we considered measurements taken from within 3km buffers around our sites (Fig. A4a). (Because of their sub-3km proximity, we combined Dutch Harbor and Daytona and subsequently refer to regions rather than sites for the chlorophyll *a* data). Temperature and wave height were measured *in situ* using sensors deployed at four sites—NavFac, WestEnd, Dutch Harbor, and Daytona—that encompass the entirety of kelp-forest dynamics we observed at SNI (Fig. A4a).

We visually assessed these data by plotting: (1) the time series for temperature and wave height; (2) kernel density plots for chlorophyll *a*, temperature, and wave height; and (3) inverse empirical cumulative distributions (eCDFs)—depicting the probability of observing measurements of equal or greater magnitude than a given magnitude—for chlorophyll, temperature, and wave height. We also used nonparametric two-sample Kolmogorov-Smirnov (KS) tests (Massey 1951) to quantitatively compare the distributions of each variable among all pairs of regions/sites (Fig. A2).

Our inferences are summarized as follows (with additional context and details below): Chlorophyll *a* (Fig. A4b,c) and temperature (Fig. A5b,c) exhibited little to no biologically meaningful differences between sites. By contrast, NavFac and the two WestEnd sites located to the north and northwest of SNI experienced greater wave heights than did the sites located to the south and southeast of SNI. Large wave events are known to perturb kelp forests and thereby elicit shifts in state from kelp forests to urchin barrens (Reed, Rassweiler, et al. 2011). However, variation in wave height is a less parsimonious explanation than substrate complexity for the dynamics we observed around SNI because we also observed state shifts at the site with the lowest mean and maximum measured wave heights (i.e. Daytona).

TABLE A2: Results of two-way Kolmogorov-Smirnov tests applied to each pair of regions (for chlorophyll *a*) and sites (for temperature and wave height). The reported *D* statistic takes a value of 0 for identical distributions and a value of 1 for disparate distributions.

	Chlorophyll	Temperature	Wave Height
North & SouthWest	0.067	-	-
North & SouthEast	0.073	-	-
SouthWest & SouthEast	0.128	-	-
NavFac & EastDutch	-	0.110	0.128
NavFac & WestEnd	-	0.070	0.421
NavFac & Daytona	-	0.044	0.153
WestEnd & EastDutch	-	0.058	0.495
WestEnd & Daytona	-	0.043	0.530
Daytona & EastDutch	-	0.071	0.137

A1.2 Chlorophyll *a*

Concentrations of chlorophyll *a* can be indicative of the extent to which cold, nutrient rich waters reach the surface to promote not only planktonic but also benthic algal growth. We used 3km wide bands around sites (“regions”) to investigate whether chlorophyll varied systematically among our sites. We were unable to reliably investigate site-specific differences due to the proximity of Daytona and the two Dutch Harbor sites (Fig. A4*a*) relative to the 1km grain size of the chlorophyll data. That said, the three measured regions encompass the oceanographic and bathymetric features around each site that could affect nutrient delivery.

Sea surface imagery was obtained by NASA’s MODIS Terra satellite (Esaias et al. 1998) and processed into chlorophyll *a* (mg/m^3). We analyzed *Level 2* data which are not aggregated spatially or temporally but instead contain daily observations, removing *NA*’s caused by cloud cover. Data were retrieved for each day between 24 February 2000 and 11 June 2021. We rarefied measurements across the regions by randomly subsampling measurements from the North ($n = 11,465$) and SouthEast ($n = 20,981$) regions to the sample size of the region with the lowest number of raster cells containing non-*NA* chlorophyll data (SouthWest $n = 10,262$).

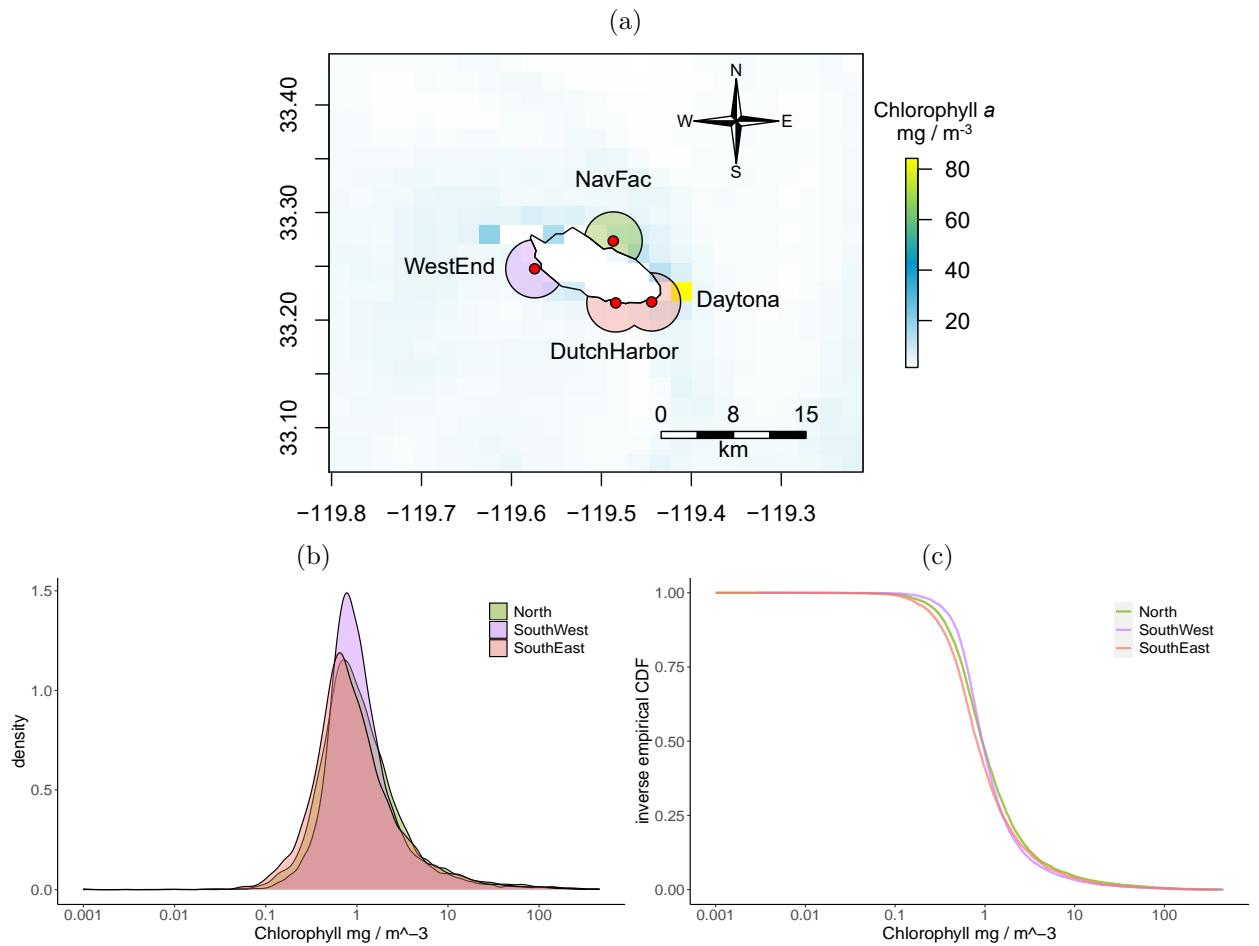


FIGURE A4: (a) A single day of chlorophyll *a* concentrations (mg/m^3) overlaid on a map of SNI with 3km buffer regions around the sites. The red dots indicate the locations where temperature and wave height sensors were deployed. (b) Kernel densities and (c) eCDFs of chlorophyll *a* concentrations by region.

A1.3 Water Temperature

Four Hobo temperature sensors were deployed at 10-14m depth at four of the six sites (Fig. A4a), recording temperature once every hour. We restricted our analyses to the time-period when all four sensors were concurrently deployed, from November 11th 2015 to October 2nd 2019 ($n = 33,766$ observations per site; $n = 135,064$ total observations).

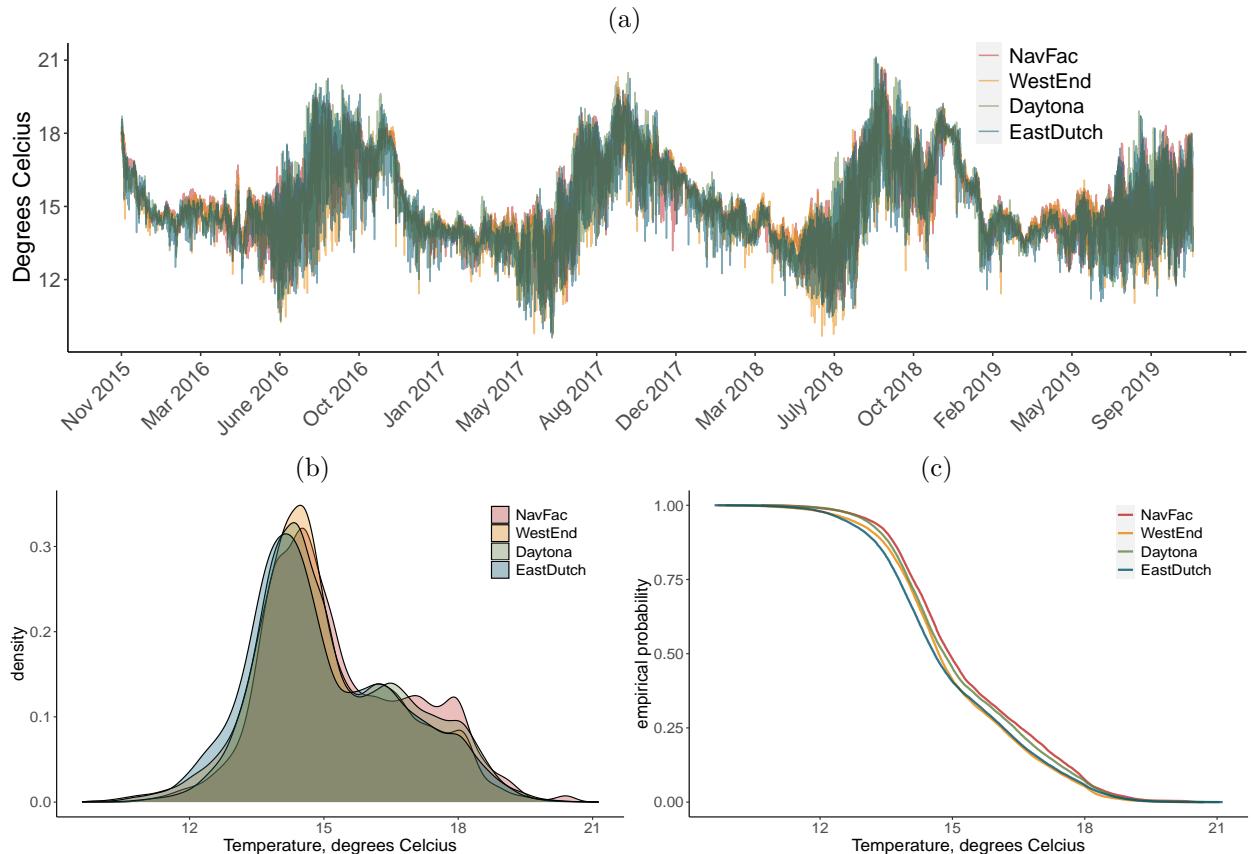


FIGURE A5: (a) Time series (b) kernal densities, and (c) inverse eCDFs of hourly temperatures by site.

A1.4 Wave height

A pressure sensor was deployed at each of the same four sites where temperature sensors were deployed (10-14m depth). Measurements were calibrated to estimate wave-height (in meters). We analyzed $n = 12,453$ sample points for each of the four sites from the period of 11 Nov 2015 - 25 Sep 2016 when all four sensors were deployed (Lafferty et al. 2018).

During this period, WestEnd and NavFac experienced pronounced large wave events that the other two sites do not (Fig. A6b). Further, WestEnd did not experience the same calm conditions experienced by the other sites (Fig. A6c). Nonetheless, in addition to observing shifts in community state at the high wave height sites (at the two WestEnd sites and at NavFac), we also observed community shifts at Daytona, the site that exhibited the lowest range of wave heights (Fig. A6c). We thus conclude that while large wave events are undoubtedly an important source of disturbance and a key proximate mechanism capable of eliciting shifts from kelp forests to urchin barrens, differences among sites in wave energy are not a more parsimonious (nor “upstream”) explanation than substrate complexity for the dynamics we observed around SNI.

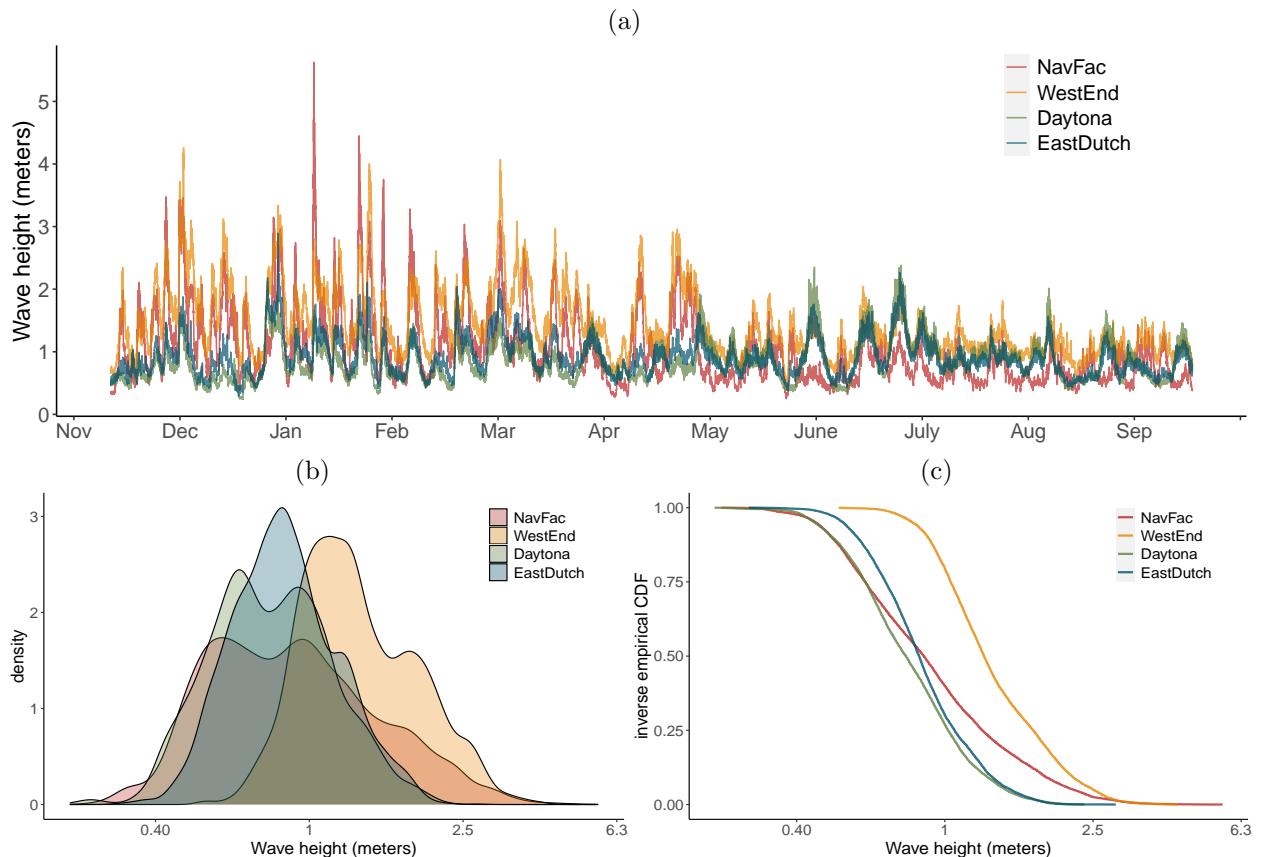


FIGURE A6: (a) Time series, (b) kernal densities, and (c) inverse eCDFs of wave heights by site.

A1.5 California sheephead

California sheephead (*Semicossyphus pulcher*) are capable of regulating urchin density and behavior (Cowen 1983; Hamilton et al. 2015; Eisaguirre et al. 2020). Sheephead were surveyed concurrent with the benthic surveys of the main text along five $50 \times 4m$ benthic and midwater transects (Kenner, Estes, et al. 2013; Kenner and Tinker 2018). Their abundances were highest at the two high substrate complexity sites, but were also high at Daytona, a low-complexity site (Figs. A7, 2.2p, (Kenner, Estes, et al. 2013)). The high abundance of sheephead at Daytona was likely due to nearby high-complexity habitat with which they preferentially associate (Cowen 1983). The bimodality of Daytona's kelp-forest community states (Fig. 2.2d,j, 2.3d, A2 row 4, A3q-u) suggests that its sheephead abundances are insufficient to preclude shifts in community state, despite urchins being susceptible to predation along Daytona's relatively low-complexity substrate. Sheephead abundances alone are therefore not a more parsimonious (nor "upstream") explanation than substrate complexity for the dynamics we observed around SNI.

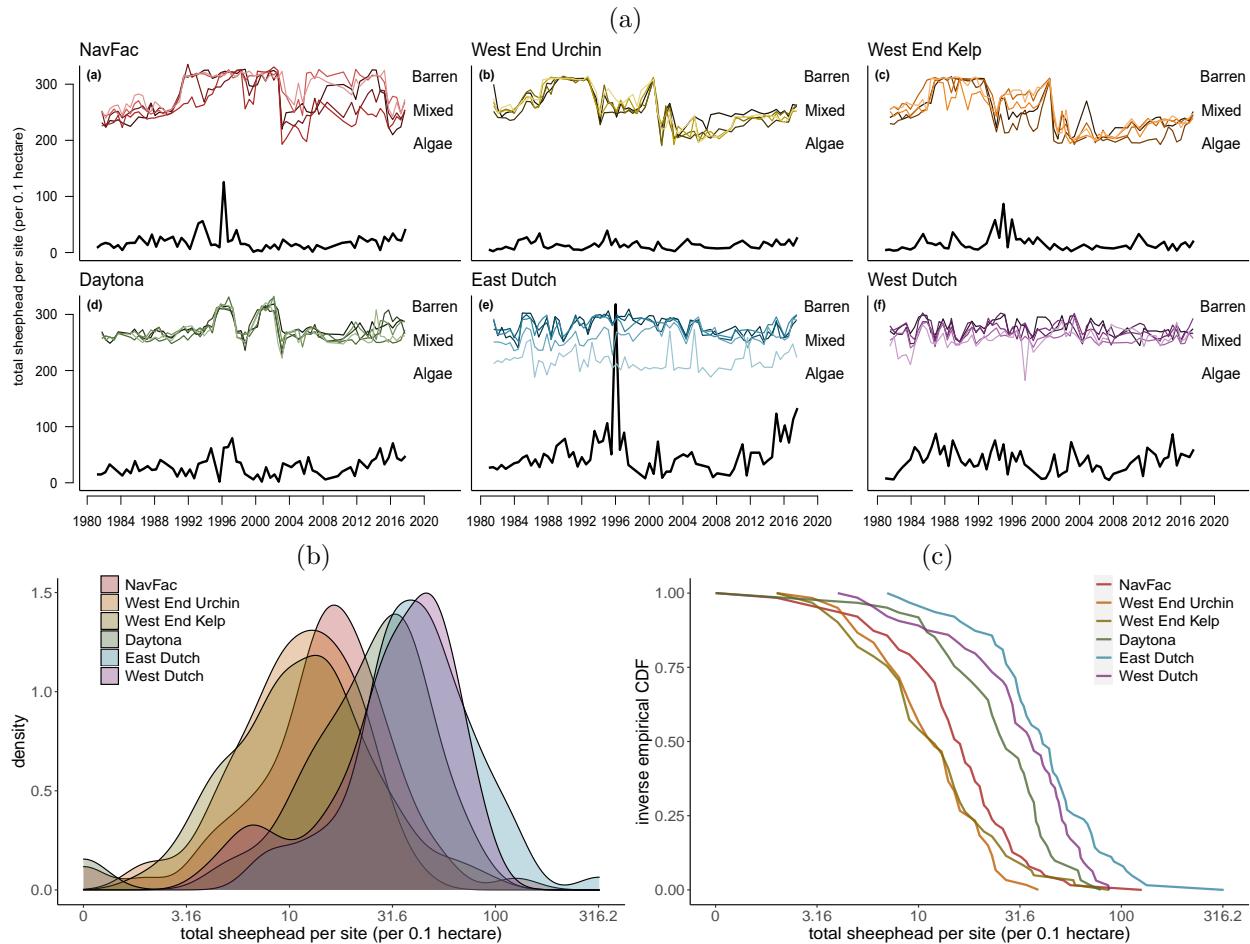


FIGURE A7: (a) Site-total sheephead abundance visualized as time-series (black line, with the transect-specific dynamics of community state from Fig. 2.3: *NMDS Axis-1: System State* superimposed), and as (b) kernel densities, and (c) inverse eCDFs.

A1.6 Sea otters

Southern sea otters (*Enhydra lutris nereis*) were reintroduced to SNI between August 1987 and July 1990 (Rathbun et al. 2000). The population hovered around 15 adult animals between 1990 – 1998 (Rathbun et al. 2000) and only exceeded 100 individuals for the first time in 2016 (Yee et al. 2020), with the great majority of individuals occupying the northwest end of the island until recently (Rathbun et al. 2000; Yee et al. 2020). We infer that their population has been too low in abundance and their distribution around the island too spatially limited to influence the propensity for switching between kelp-forest states across our focal sites to date. Indeed, both shifts and persistent kelp-urchin coexistence were seen *prior* to sea otter translocation, and abrupt shifts continued after 1990, both in regions with and without consistent sea otter foraging activity. Nevertheless, we do not dismiss the possibility that sea otter predation contributed to the expression of the long-term transient algal-only state at the two West End sites (Fig. 2.3b,c), the formal evaluation of which is beyond the scope of this paper.

A2 Chapter 3 Appendix

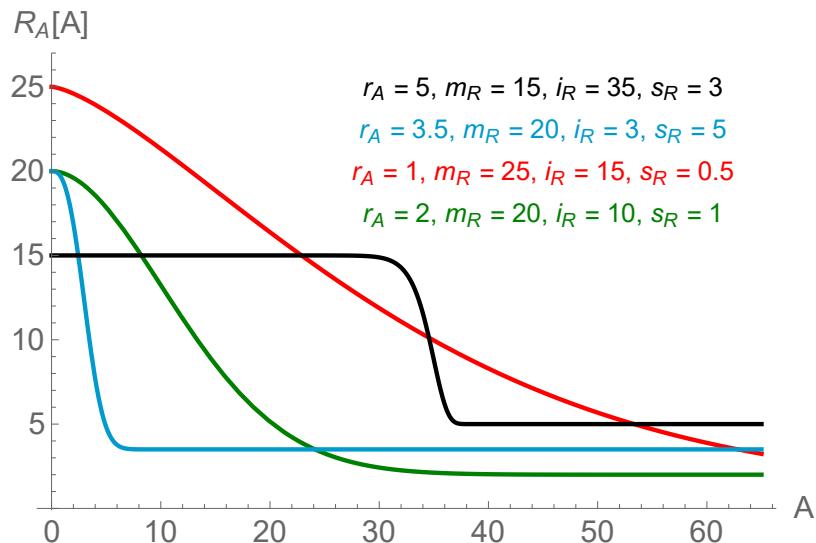


FIGURE A8: Kelp recruitment R_A with the current kelp density A on the x-axis and the associated recruitment R_A on the y-axis. Constituent parameters include max recruitment m_R , min recruitment r_R , the inflection point i_R along the x-axis, and the slope s_R around i_R . The parameter values comprising the black function were used in all subsequent numerical analyses, and the associated nonlinearity is in-part responsible for the emergence of periodic kelp dynamics. The blue function models a dramatic dropoff in recruitment at small kelp densities, i.e., strong intraspecific competition. In contrast, the red function exhibits modified min m_R and max r_R parameter values, and the low slope approximately models relatively weak intraspecific competition.

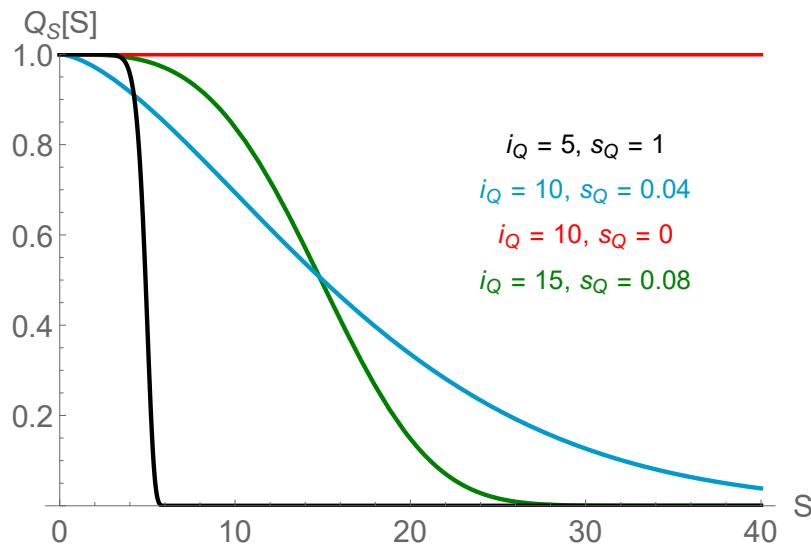


FIGURE A9: Proportion Q_S of urchins grazing upon kelp, where $(1 - Q_S)$ = the proportion of urchins grazing upon drift. i_Q is the inflection point and s_Q controls the slope around i_Q . The black function models a strong (highly nonlinear) dietary preference for drift > 5. The blue function models a gradual switch from kelp to drift as drift levels increase. the red function with slope $s_Q = 0$ models the exclusive consumption of kelp regardless of drift density. The black parameter values were retained for the baseline parameter set.

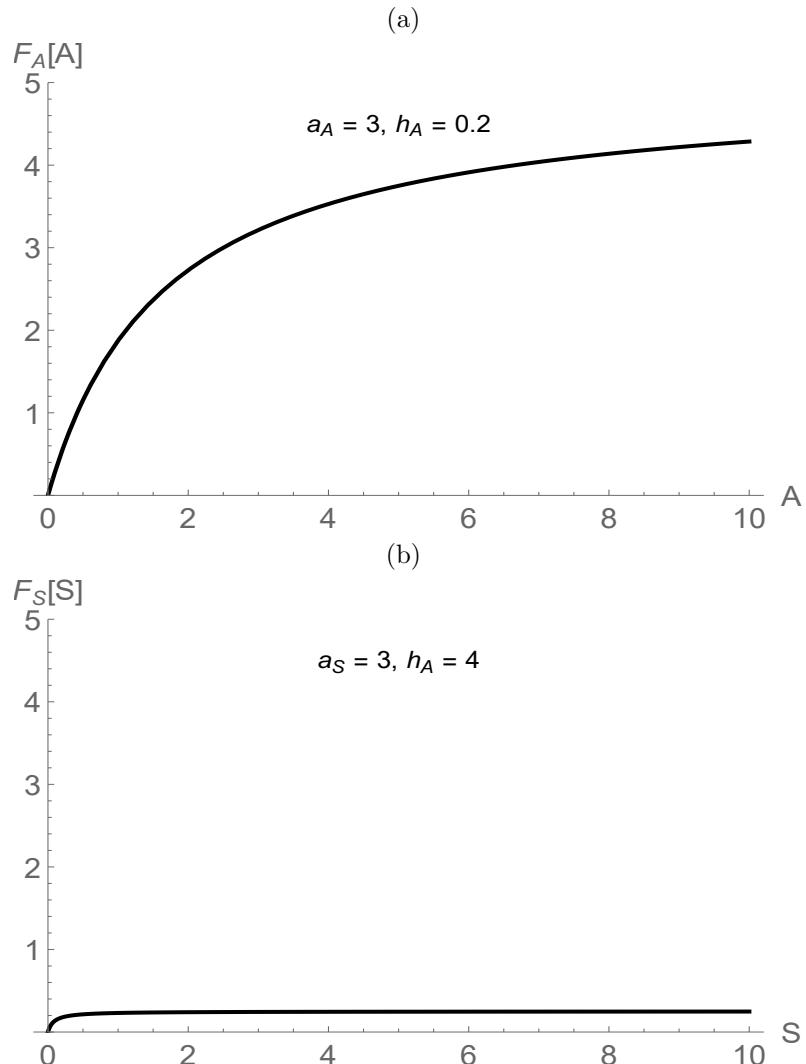


FIGURE A10: Functional forms of (a) kelp consumed F_A and (b) drift consumed F_S by urchin grazing. The slope or encounter rate parameter a_A and a_S are equal, representing equal capacity to obtain the two resources. h_A and h_S represent the handling time, or inverse maximum feeding rate.

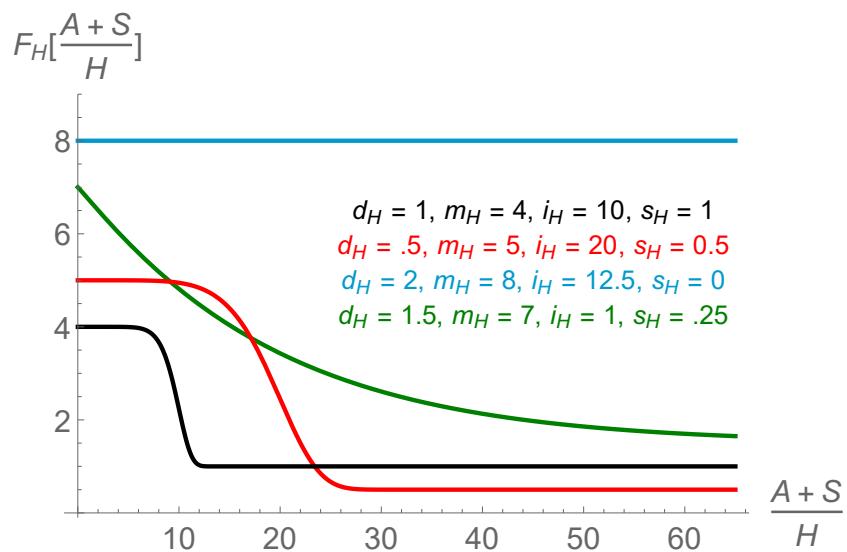


FIGURE A11: Urchin loss modeled much in the same way as kelp recruitment R_A , though where the biological interpretation represents distinct mechanisms, and the F_H is a function of $A[t]$, $S[t]$, & $H[t]$. The black parameters values represented a relatively constrained range of urchin mortality per unit time, between $d_F = 1$ and $m_F = 4$, and these values were used in all subsequent analyses.

A2.1 Constituent exponential functions b_R and c_R

This section elaborates how the two exponential functions b_R and c_R operate within kelp recruitment R_A . This applies to the urchin mortality function F_H with constituent functions c_F and b_F as well. This section also applies to the proportion of urchins grazing kelp Q_S , with the minor exception that Q_S ranges between $(0 - 1)$ and thus there are no minimum and maximum parameters. R_A is modeled with a declining logistic function (Table 3.1, Fig. A8)

$$R_A = r_A + (m_R - r_R) * e^{-c_R * A[t-\tau]^{b_R}}. \quad (\text{A2})$$

R_A is comprised of two exponential functions b_R and c_R with four parameters: maximum kelp recruitment m_R , minimum kelp recruitment r_R , the inflection point i_R along the x-axis of R_A , and the slope s_R around that inflection point. Here I unpack how these exponentials, in concert with parameters, operate to provide a large degree of customization over the final shape of the parent logistic function. The expression b_R contains four parameters: maximum kelp recruitment m_R , minimum Kelp recruitment r_R , the inflection point i_R along the x-axis of R_A , and the slope s_R around that inflection point (Table 3.2). The inflection point i_R determines the abundance of kelp necessary to inhibit kelp recruitment. b_R is calculated to satisfy the expression

$$(b_R - 1) * e^{\frac{-(b_R - 1)}{b_R}} = \frac{s_R * i_R}{m_R - r_A}. \quad (\text{A3})$$

c_R is then calculated such that

$$c_R = \frac{(b_R - 1)}{b_R * (i_R^{b_R})}. \quad (\text{A4})$$

As b_R increases, c_R decreases, and vice-versa: increasing c_R by decreasing i_R , decreases b_R . The importance of these exponential functions comes from the behavior of $e^{-c_R * A^{b_R}}$ in the parent function R_A , where A is the current abundance of kelp. The value $e^{-c_R * A^{b_R}}$ asymptotically approaches either 0 or 1. As $-c_R * A^{b_R}$ increases, e.g. through increasing b_R (accomplished by increasing r_R and m_R , or by decreasing s_R and i_R), and/or by increasing kelp abundance, $e^{-c_R * A^{b_R}} \rightarrow 0$, such that $r_R + (m_R - r_R) * 0 = r_R$. This recovers the minimum kelp recruitment r_R , anchoring our lower point along the y-axis of R_A . In contrast, as $-c_R * A^{b_R}$ decreases, either through decreasing b_R (in turn, accomplished by decreasing r_R and m_R , or by increasing s_R and i_R), and/or as kelp abundance decreases, $e^{-c_R * A^{b_R}} \rightarrow 1$. It follows that $r_R + (m_R - r_R) * 1 = m_R$, and we recover

maximum kelp recruitment m_R . Therefore, the minimum and maximum recruitment parameters directly set the upper and low y-axis bounds of R_A . The specific shape of the function between these bounds is controlled by the other two parameters, with the location of the sigmoidal function's inflection point along the x-axis set by i_R , and the slope around that inflection point is controlled by s_R . Crucially, these two parameters control the approximate range of Kelp equilibrium values at which R_A 's nonlinear sigmoidal region overlaps. s_R and i_R thereby in-part control the capacity for nonlinear kelp dynamics to potentially manifest.

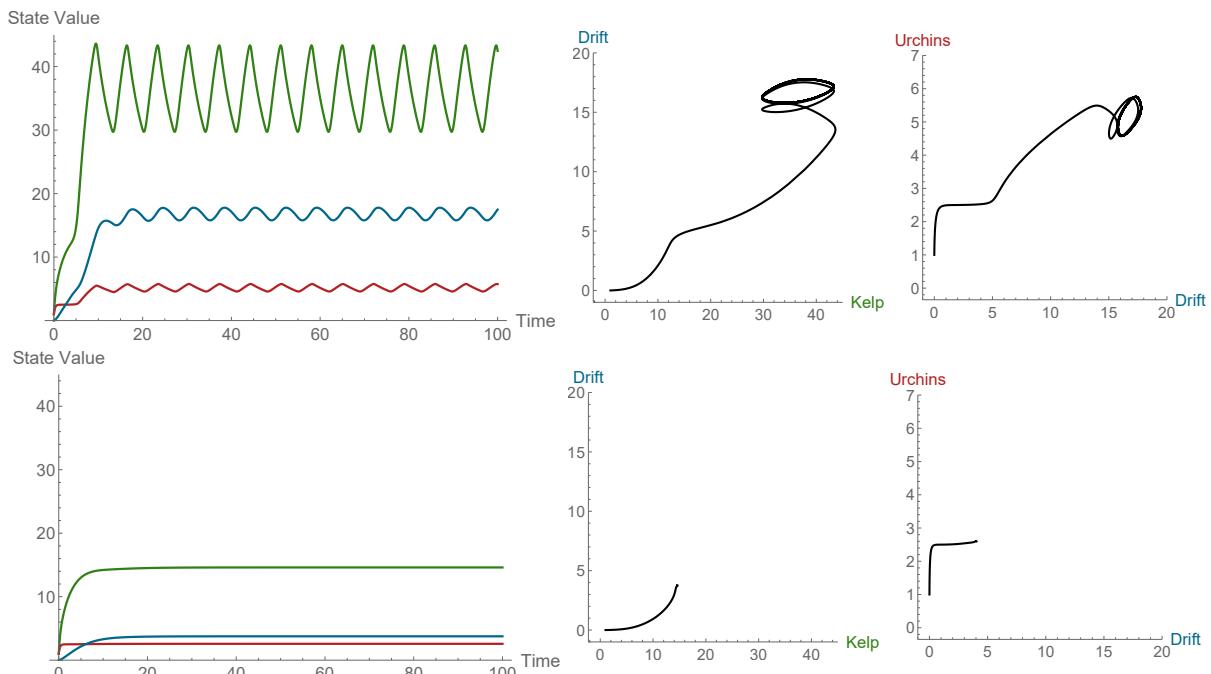


FIGURE A12: System dynamics through time and phase space with **Kelp**, **Drift**, and **Urchins** all exhibiting stable limit cycles around the *High* periodic attractor in row 1. Row 2 depicts the *Low* state fixed point where $\frac{dA}{dt}$, $\frac{dS}{dt}$, $\frac{dH}{dt}$ all $\rightarrow 0$ as the system is solved through time. Two different parameter values were used to visually illustrate how the *High* state often exhibits stable limit cycles, whereas the *Low* state often exhibits a fixed point.

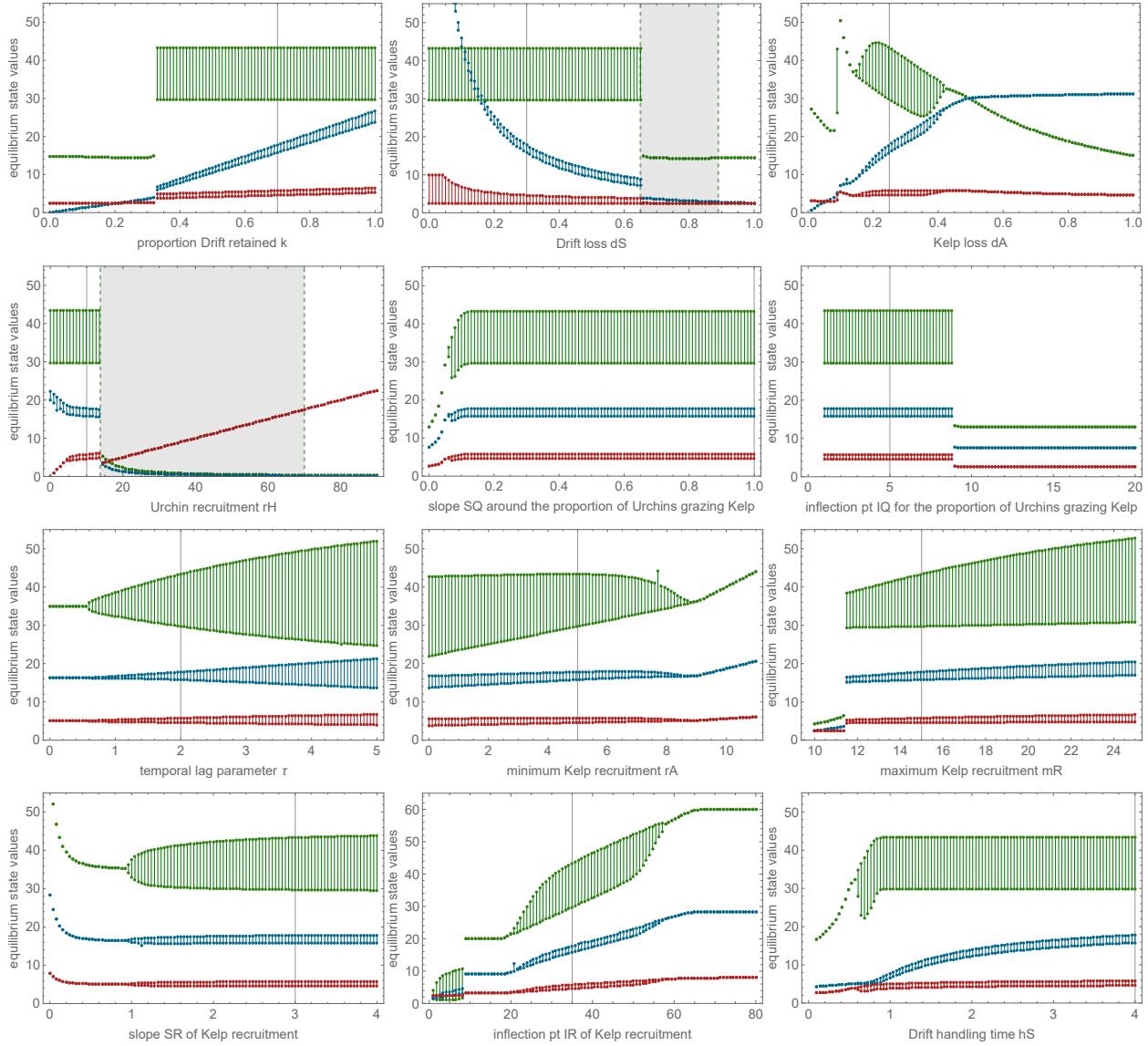


FIGURE A13: *1D* bifurcation plots of parameter space and the associated system behavior for **Kelp**, **Drift**, and **Urchin** state variables at equilibrium. Periodic dynamics are represented by two points connected with a vertical line, whereas a “dot” through parameter space denotes a fixed point equilibrium. The vertical gray line in each subplot marks that parameter’s value used for all other analyses, i.e., the “baseline” value. Alternative stable states are visualized for r_H and d_S only.

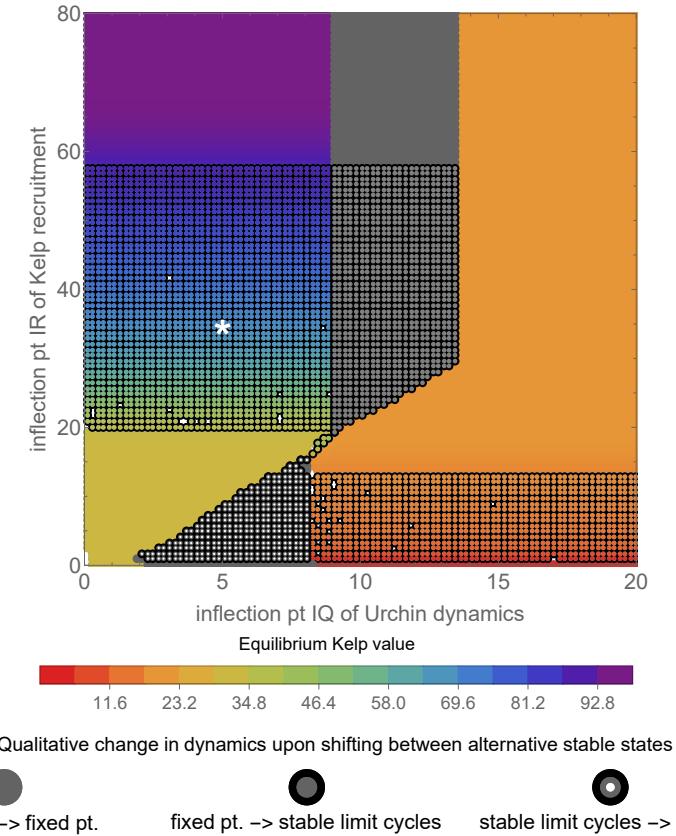


FIGURE A14: The rather complex geometry exhibited by this figure contains useful information regarding the core mechanics of the model. This figure depicts the interplay between the equilibrium value of kelp and the effects of moving the inflection point i_Q of the proportion of urchins grazing kelp, and the inflection point i_R of the abundance of kelp required to suppress kelp recruitment.

A2.2 Opposite shift in process when switching between alternative stable states

As noted in section 3.6.1, *Kelp removal necessary for cyclic dynamics*, the “tongue” or protrusion of cyclic dynamics results from the combination of kelp recruitment dynamics and urchins switching between resources (subsection 3.6.2). This combination of processes producing limit cycles disappears when shifting to the *High* alternative state, where urchins graze drift and the system exhibits a fixed point. The reverse switch in process upon shifting from the *Low* to the alternative *High* state takes place for the upper protrusion that manifests at high values of i_R (Fig. 3.7a versus e). Here, the *Low* is maintained through urchins grazing kelp. When the system shifts to the alternative *High* state, the aforementioned combination of kelp recruitment and urchin switching between the two resources producing cyclic dynamics. Note that urchins do not switch from kelp and to drift upon shifting to the *High* state in (Fig. 3.7a). Rather, urchins are switching back and forth as kelp cycle at the *High* state.

We thus have a biologically unexpected conclusion: depending upon the density of kelp required to inhibit recruits (i.e., the value of i_R) relative to the equilibrium kelp density, increasing the initial conditions of drift can elicit two distinct ways in which the underlying processes affecting the system change:

1. When the abundance of kelp necessary to inhibit future growth manifests at relatively low kelp equilibrium values (i.e., i_R is low, Fig. 3.7e): kelp exhibit recruitment dynamics and urchins switch between resources enabling limit cycles at the *Low* state. Shifting to the alternative *High* state removes the entirety of the combined kelp recruitment and urchin switching interaction, such that all urchins graze drift and the system exhibits a fixed point.
2. The reverse is true when the abundance of kelp required to inhibit recruits is high (i.e. i_R is high, Fig. 3.7a). Here the *Low* state is a fixed point and all urchins graze upon drift and too few kelp are present to exhibit recruitment dynamics. Shifting to the alternative *High* state yields the interaction between kelp recruitment dynamics and urchin switching to produce stable limit cycles.

A2.3 Non-switching processes produce limit cycles

A slightly different combination of processes is responsible for the region of cyclic dynamics when the abundance of kelp necessary to inhibit kelp recruitment is low (i.e., low values of i_R , Fig. 3.5b, & Fig. 3.7c). Here, removing the capacity for urchins to exhibit switching does not

obliterate the emergence of cycles (Fig. 3.5*b*). Simulations indicate that these cycles are a product of the interaction between kelp recruitment and kelp consumed by urchins. This contrasts with other regions exhibiting alternative stable states previously discussed (subsections 3.6.2, & A2.2) because urchins are not switching. That is the say, the combination of processes producing cyclic dynamics at this low-kelp equilibrium region is exclusively kelp recruitment, and kelp consumed by urchins. Furthermore it is the rapid maximum consumption rate upon kelp that in-part enable these dynamics; setting $h_A > 0.6$ collapses the periodic attractor to a fixed point. This is one of the relatively rare instances that the relative ratio of h_A and h_S is less important than the absolute numerical value of h_A , given that all urchins are grazing kelp (i.e., $Q_S = 1$), and thus h_S and drift loss to urchins F_S are not invoked. This part of parameter space provides predictions that have not yet been discovered in nature. That is to say, if rates of kelp recruitment, growth, and turnover were exceptionally rapid, our model predicts such a forest could exhibit limit cycles as urchin consumption of kelp in-part facilitates kelp recruitment dynamics via reductions in kelp density that enable kelp recruitment.

A3 Chapter 4 Appendix

A3.1 Subtidal cage assembly and deployment

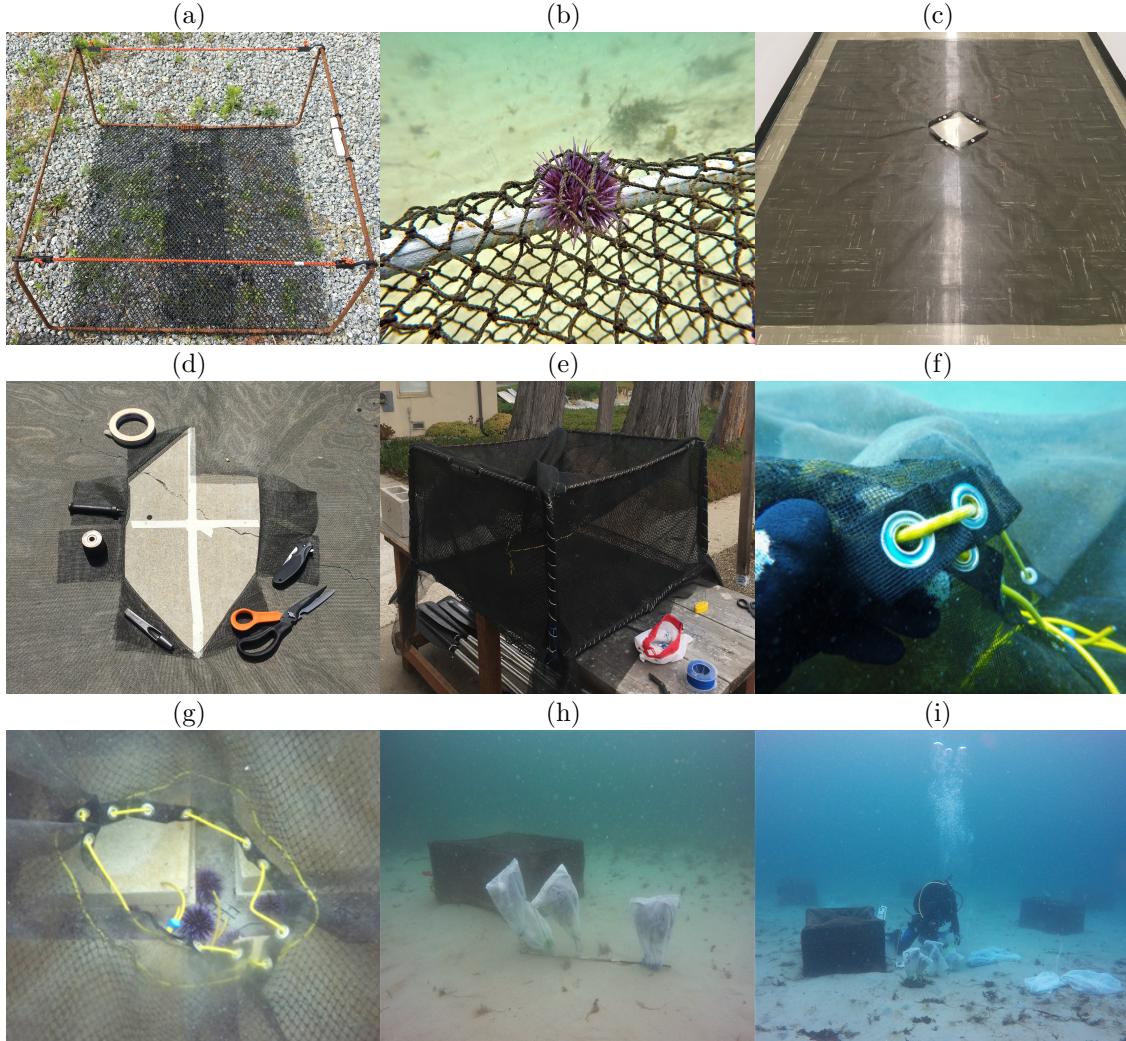


FIGURE A15: (a) Rebar frame, vexar floor, and flexible bungee struts. (b) Knotted nylon netting as the interior layer of all encompassing siding. (c) Sheet of fiberglass window screen and prototype “door”. (d) Grommet installation to create a door through the screen. (e) Both the net and the screen were stitched to the rebar frame for maximum security and support. (f) Grommet door frame with twine that cinched the door closed. (g) Double-door access point through the top of the cage. (h) 1m lengths of rebar with labels attachments were used to organize treatment deployments/retrievals. (i) Cage array layed out in a grid with 5m spacing.

The subtidal cages were comprised of a single 20' length of rebar manually bent into a $1 * 1 * 0.4m$ frame (Fig. A15a) using a vice. Hard plastic Vexar comprised the floor of the cage. Knotted nylon netting (mesh size 2cm) was stitched around the entirety of the cage (Fig. A15b). This netting comprised the entirety of the cage siding in year 1 (summer 2018). Unfortunately, the

2cm netting openings allowed numerous small pieces of drift (e.g., *Phyllospadix* spp.) to enter the cages, rendering our precise treatments of varying resource densities moot. We addressed this issue summer 2019 by retaining the netting, but adding an additional layer: the cages were completely enveloped in fiberglass window screening, and like the netting, this screening was stitched onto the rebar frame (Fig. A15c,e). A “door” was installed in the screening with aluminum grommets, allowing the screening to be cinched shut with paracord (Fig. A15c,d,f,g). This “double-hull” of netting and screening prevented particulate exchange ($> 5\text{mm}$), allowing strict control over resource density within the cages. The screening likely decreased light availability within the cages (unmeasured), but given the relatively short temporal scale of our experimental trials, this was deemed acceptable. Furthermore, water motion was likewise attenuated, though as drift visibly sifted about on the cage bottom with the surge, whatever degree of water attenuation present was again deemed acceptable. Both screening and netting “doors” overlapped together on the top center of the cage, allowing divers to quickly and easily access the entirety of the cage (Fig. 4.1a). This easy access was essential for meticulously collecting all fragments of drift following experimental trials. A single 1m Earth anchor was augured into the sand and lashed to the rebar frame along one corner. Additional cage support was provided by the four stacks of two paving stones, each weighing 20lbs. The cages were spaced 5m apart in a rectangular grid, with four rows of five cages. 1m lengths of rebar with labeled attachment points were used organize treatment application and removal, with a length of rebar for each cage array row. These cages worked exceptionally well and would be suited for other small-scale subtidal experiments where the cage contents are to remain relatively isolated while still allowing water movement.

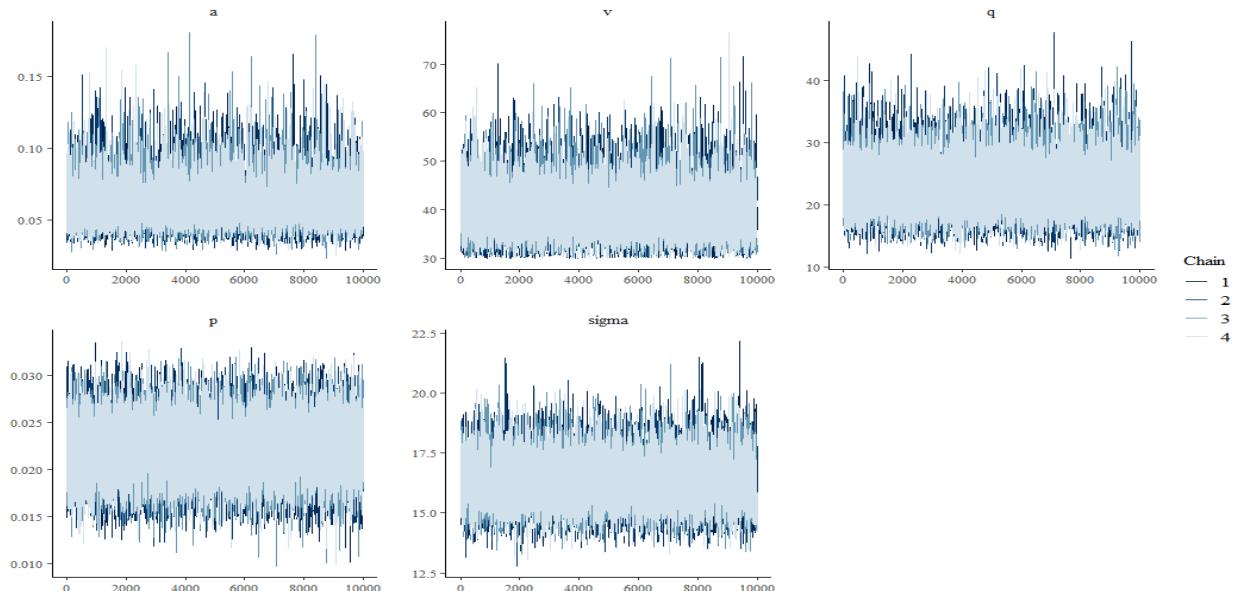


FIGURE A16: The four chains navigating parameter space (y-axis) across the 10,000 sampling iterations (x-axis) following 5,000 warmup iterations that are not shown here. Our chains are well-mixed (completely overlapping), indicating the parameter space sampled is appropriate and that—given our priors—no other regions of parameter space fit our data as well or better. This figure was generated using the *bayesplot* package to interface with *Stan* fit objects in *R*.

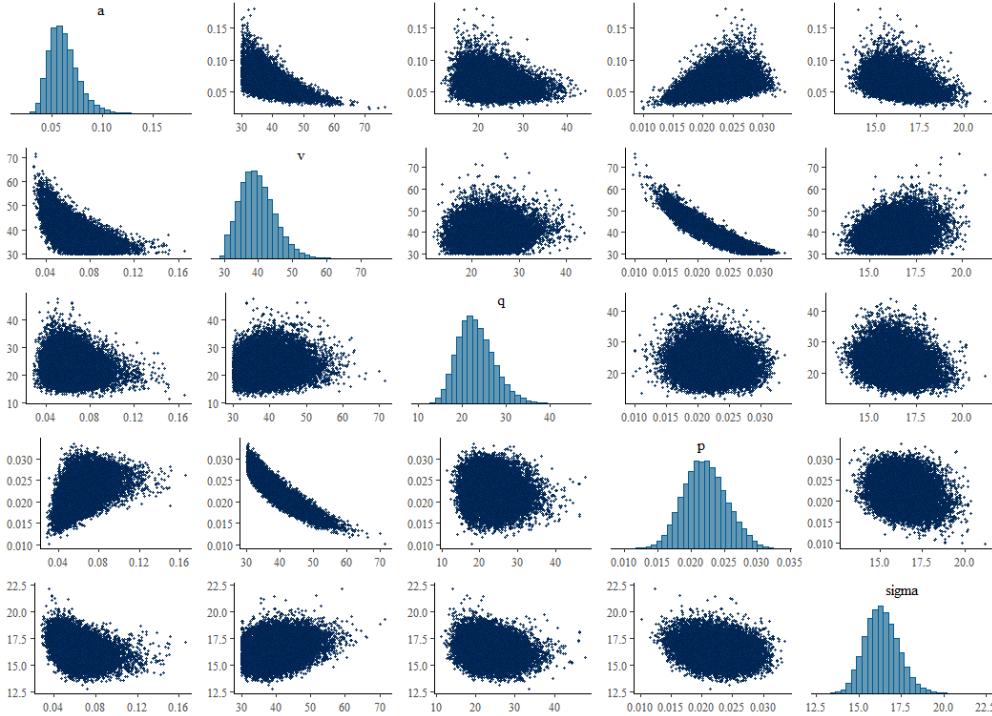


FIGURE A17: Histogram posteriors for the five fitted parameters along with pairwise scatter plots to visually assess any colinearity or sampling abnormalities (the latter of which would manifest as red dots—none are present). The pairwise scatter plots above and below the diagonal are from different chains in order to evaluate between-chain concordance. Covariation is present between maximum fullness *v* and gut clearance *p*—given our model formulation, this is not a surprise nor a concern, as increased gut clearance instantaneously allows more feeding, which would raise the equilibrium value of *F* as more resources would be consumed. Lower values of *v* “compensate” for this increased feeding by reducing maximum volume of the gut, thus balancing the instantaneous effects of higher rates of clearance. This figure was generated using the *bayesplot* package to interface with *Stan* fit objects in *R*.

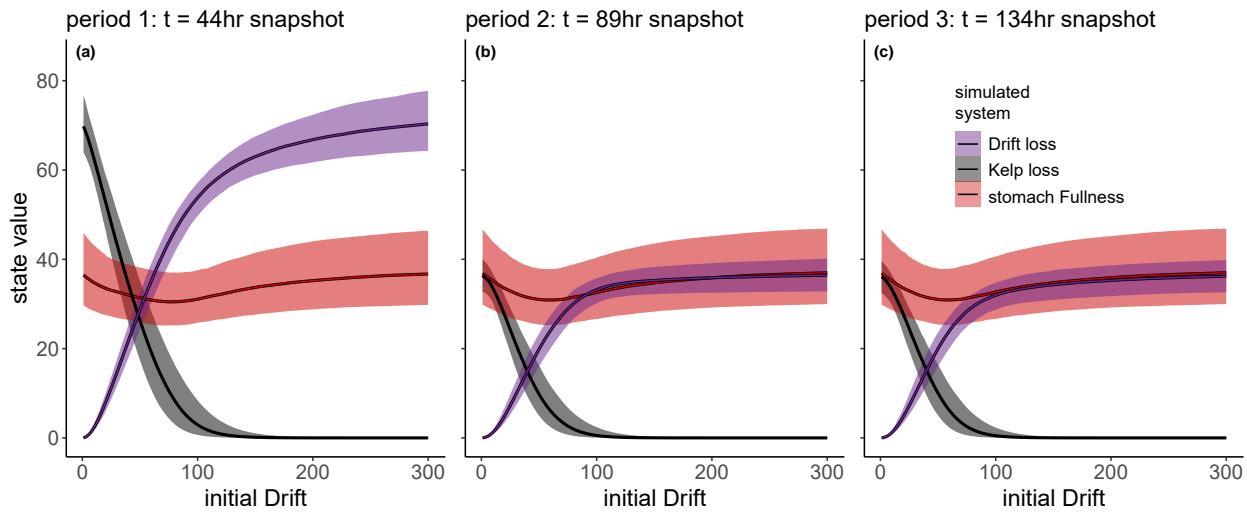


FIGURE A18: The simulated system used to visualize simulated preference, rank switch, and drift-dependent switching visualized in Fig. 4.6. This figure is analogous to Fig. 4.5, but with the three rows combined to contrast the dynamics of all three state variables across the three-period sequence. The only methodological divergence between this figure and Fig. 4.5 is that the initial conditions of kelp $A[0]$ were all set to 300, as described in Fig. 4.6.

