

Tegula spp. Indirectly Stabilize *Macrocystis pyrifera* Kelp Forest Systems by Increasing Drift Kelp

Gabriel Gabbert, Natalie Rossi, Vinicius Souza, Elsie Herman, Gavin Houghton, Pete Raimondi, and Mark Carr

Introduction:

What creates stable state resistance in ecological communities? Stable state resistance is commonly thought to be attributed to the presence of a keystone species (Estes et al. 1978), however, the intratrophic herbivory effects studied here could provide an alternate dynamic. The alternative stable-state theory suggests that changes in ecosystem conditions can result in shifts in an ecosystem's population, or composition (Beisner et al. 2003). For example, the reintroduction of wolves in Yellowstone National Park demonstrates strong top-down effects, where wolf predation on elk populations allows for plants, such as willows, to reflourish (Ripple and Beschta 2005). The theory of trophic cascades suggests that in ecosystems each trophic level in a food web is either directly or indirectly connected, and keystone predators affect its ecosystem in a disproportionate manner (Brett & Goldman 1996). Stable state changes can be influenced by many different abiotic and biotic perturbations (Ebeling et al. 1985, Harvell et al. 2019, Estes et al. 1978). Factors such as toxicity (Heide et al. 2010) and spatial competition (Buenau et al. 2007) are also shown to play a role in shifting alternative stable states. These shifts in states are typically abrupt and result in drastic shifts in multiple trophic levels.

Giant kelp (*Macrocystis pyrifera*) forests are temperate marine ecosystems and are an ideal place to research varying stable states because of their well documented propensity to switch to an alternate stable state, the urchin barren (Filbee-Dexter, 2015). Kelp forests are nutrient dense due to the periodic influx of nutrient-enriched water along the central coast via upwelling (Mansergh and Zehr 2014). The amount of nutrient input into this system is comparable to a rainforest. Kelp forests and urchin barrens are great examples of alternative stable states (Ebeling et al. 1985). Alternative stable states are typically caused by a drastic change between a foundation species and major consumer. However, stable states can be alternated by abiotic forces as well. It has been shown that severe storms such as one that occurred in Southern California can switch alternative stable states of a kelp forest into an urchin barren and then back again into a kelp forest (Ebeling et al. 1985). This example shows that it typically takes a large energy disturbance to change from one stable state to another. However, with more instability in our ecosystems these changes could become a more likely occurrence. The most common cause of kelp forest stable state change is herbivorous decimation of giant kelp by purple urchin (*Strongylocentrotus purpuratus*) (Filbee-Dexter, 2015). In a healthy kelp forest state, urchins typically stay hidden in crevices from predators such as sea otters (*Enhydra lutris*) and sunflower star (*Pycnopodia helianthoides*), consuming detached drift giant kelp (Britton-Simmons, 2009). Another herbivore spatially associated with giant kelp are *Tegula spp.* (referred hereafter as turban snails) (Riedman et al. 1981). Turban snails have radula used for scraping small layers of algal blades, and show a strong preference for giant kelp (Watanabe et al. 1984). However, the association of drift algae with turban snails, and subsequently their potential role in maintaining stable states has never been studied.

In this study, we aimed to shed light on turban snails influence on stable state resistance in kelp forest communities. We conducted SCUBA surveys on giant kelp plants (*Macrocystis pyrifera*), turban snails (*Tegula spp.*), and purple urchins (*Strongylocentrotus purpuratus*).

Turban snail abundance and kelp individual size were measured to determine if larger plants inhabit more turban snails. Additionally, we attempted to quantify abundance of drift kelp around each surveyed plant. The count and crevice habitat association of purple urchins in relation to proximity to the survey plant was assessed. Comparing drift-snail relations with urchin-crevice spatial associations will provide insight on the resistance of urchin barren stable state change. Specifically, we ask:

- 1) Are larger plants able to support a higher density of turban snails?
- 2) Do higher snail densities result in larger drift abundance?
- 3) In relation to distance to the plant, does higher kelp drift abundance result in more urchin crevice habitat association?
- 4) Does greater turban snail abundance influence urchin crevice association?

These questions will aid our understanding of the mechanisms behind a kelp forest's resistance to stable state changes.

Methods:

Study System

Site description

We conducted our study on the west coast of the United States, in central California at Hopkins Marine Station in Monterey Bay (36.6203 N, 121.9042 W). The station is located in Lovers Point State Marine Reserve; therefore the study system is legally protected against fishing and development. This subtidal ecosystem is a rocky reef kelp forest, dominated by giant kelp (*Macrocystis pyrifera*). The benthos is incredibly variable, dominated by granite boulders with patches of sandy bottom. The water temperature remains around mid 50-60°F (10-15°C) year round, remaining cool due to the local nutrient rich coastal upwelling. The excess nutrients allow for giant kelp forests to be incredibly species rich. We conducted this study throughout the month of November, 2019. During the majority of the month, coastal upwelling and storms were at a lull and waters are relatively calm. The last week of the month was hit with a minor storm, producing a swell of about 1.5-2 meters in height. This swell resulted in intermediate amounts of surge, causing minor disturbance to the forest.

Species description

In this study, we surveyed giant kelp (*Macrocystis pyrifera*), purple urchin (*Strongylocentrotus purpuratus*), and turban snail species (*Tegula spp.*). Giant kelp is considered a foundation species, providing habitat and food for all the species in the system. It is found globally, in cold temperate waters where upwelling is present (Castro and Huber. 2010). The species is among the fastest growing plants in the world, growing up to 27 cm per day (Abbott and Hollenberg 1982). Without the presence of this extremely productive species, the whole community will collapse, including all of the species it provides habitat to. The turban snails in our study consist of three different species, *Tegula brunnea*, *Tegula pulligo*, and *Tegula montereyi*, all ranging on the north eastern coast of the Pacific, primarily in California (Jensen et

al 2018). Aside from sea urchins, turban snails are the main grazers of kelp (Vásquez and Buschmann. 1997) (Watanabe 1984). The purple urchin is the primary grazer on giant kelp. Its distribution is along the eastern edge of the Pacific Ocean, extending as far north to Canada and as far south as Mexico (Castro and Huber. 2010). These urchins typically feed on drift kelp but will actively graze living kelp when drift abundances are inadequate (Ebeling et. al 1985). The consumption of living kelp can cause catastrophic changes in these systems, as the loss of large kelps results in an ecosystem change referred to as “barrens.”

Study Design and Sampling

Hypotheses

1) There is a monotonic positive relationship between turban snail density and stipe density.

A free form regression analysis with line of best fit will be used to test this hypothesis. A positive monotonic relationship will support this hypothesis.

2) Drift abundance is positively associated with turban snail abundance.

A poisson distribution will be used to test this hypothesis and a chi squared effects test with a value of ≤ 0.05 will support this hypothesis.

3) There is an inverse relationship between proximity to kelp plant holdfasts and urchin crevice habitat association.

We will use a generalized linear model to test the relationship between location and urchin crevice association and again separately for urchin non-crevice association. A chi squared effects test with a value of ≤ 0.05 will support this hypothesis.

4) There is a positive relationship between urchins in crevices and turban snail abundance.

A linear regression analysis and students t-test will be used to test this relationship. A positive monotonic relationship and a p-value of ≤ 0.05 will support this hypothesis.

We used a survey approach on SCUBA at depths of ~ 10-12 meters. We chose 16 giant kelp plants to focus on for the duration of our study, all of which varied in size. The plants were chosen in a block format with 4 plants per block, totalling to 4 blocks. The locations of all the blocks were on the perimeter of the reef. Block one was located on the north perimeter of the reef and illustrated as the red box, block two on the north west section and the green box, block three on the south west section and the blue box, and block four on the south and the orange box (Figure 1). We conducted the same surveys for every plant on every dive.

For each plant, the number of stipes were counted. We then gently tugged on one stipe, pulling the whole stipe down while counting the number of turban snails on the single stipe. The number of stipes per plant and number of turban snails per stipe will produce a snail density per plant. We then counted the number of purple urchins inside the plant's holdfast and on top of the plant's holdfast. A 50 by 50 centimeter quadrat was placed at random at the base of the holdfast. Within the quadrat we counted the number of purple urchins hidden in crevices and the number

of urchins out on the reef. The quadrat was then flipped twice and the same variables surveyed, producing a 0.5 by 1.5 meter area from the holdfast out. The abundance of drift around the kelp plant was assessed observationally and categorized as small, medium, and large. No threshold for drift density was established between the divers, and abundance was determined by the individual.

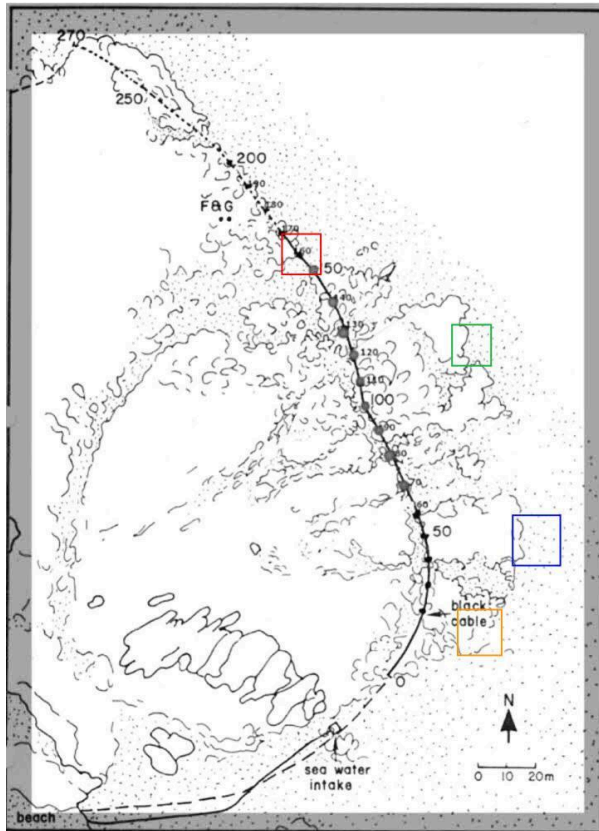


Figure 1: Image of Hopkins permanent transect in relation to the four blocks. From top to bottom; block 1 (red), 2 (green), 3 (blue), and 4 (orange).

Results:

We fail to reject all hypotheses of turban snail-urchin interactions (Figures 2, 3, 4, & 5). Our results indicate that larger plants are able to support higher snail densities which in turn are associated with larger kelp drift abundances. The combination of greater turban snail and drift kelp results in greater urchin crevice habitat association, particularly at a distance of 0.5 meter from the holdfast (Figure 5). All other distances (in holdfast, 0 m, and 1 m) yielded no significant results and therefore were not included.

1) There is a positive relationship between turban snail density and stipe density.

We fail to reject the hypothesis that there is a positive relationship between turban snail density and stipe density (Figure 2, $p < 0.0001$)

2) Drift abundance is positively associated with greater turban snail abundance.

We fail to reject the hypothesis that drift abundance is positively associated with greater

turban snail abundance (Figure 3, $p < 0.0001$).

3) *There is an inverse relationship between proximity to kelp plant holdfasts and urchin crevice habitat association.*

We fail to reject the hypothesis that there is an inverse relationship between proximity to kelp plant holdfasts and urchin crevice habitat association (Figure 4, $\text{ChiSq} = 0.0004$).

4) *There is a positive relationship between turban snail abundance and urchin crevice association.*

We fail to reject the hypothesis that there is a positive relationship between turban snail abundance and urchin crevice association (Figure 5, $p = 0.0384$).

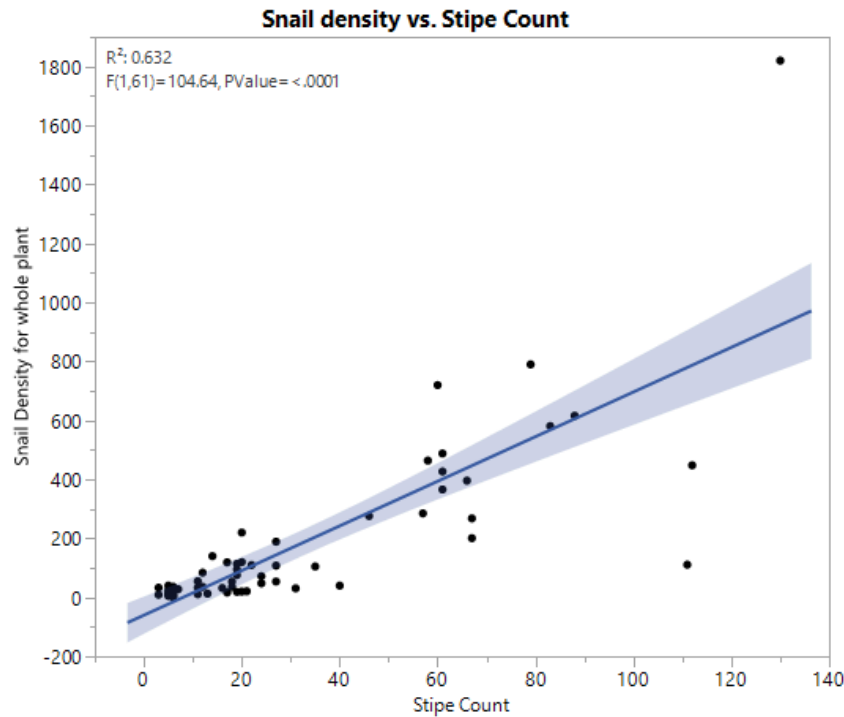


Figure 2: The linear relationship between turban snail abundance and stipe count. Larger plants with more stipes support larger snail abundances ($R^2 = 0.632$).

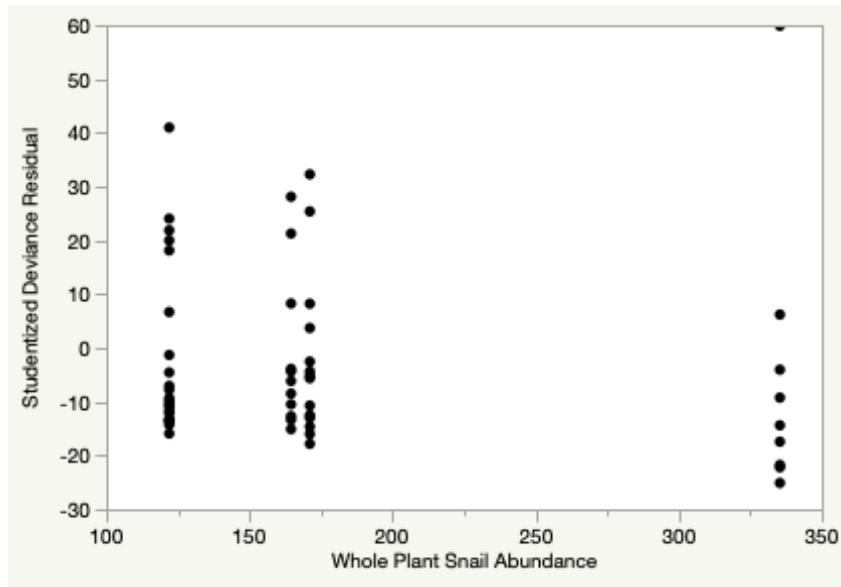


Figure 3: Kelp drift abundance in relation to snail abundance. Drift abundance (small, medium, large) increases as tegula abundance increases. Each dot represents an observation of kelp drift abundance.

Effect Tests			
Source	DF	ChiSquare	Prob>ChiSq
Kelp drift density(sm/m/L)	3	1532.4311	<.0001*

Table 1: Effects test of the kelp drift density poisson distribution yielding a chi squared value of <0.0001.

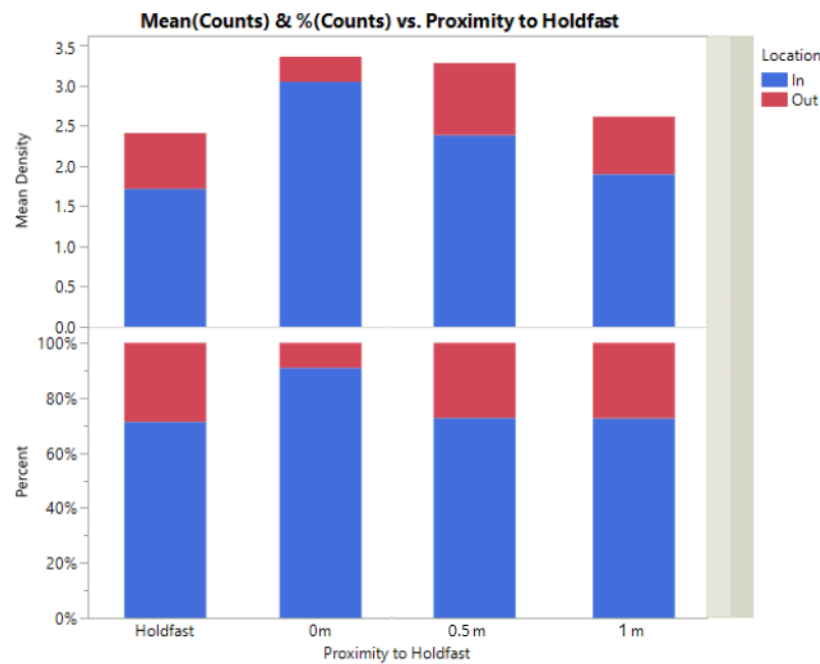


Figure 4: Mean counts and percent counts of urchins and their distance from the holdfast. Fewer urchins are associated in crevices as the proximity to the holdfast decreases. This same relationship exists between the mean density of urchins and the percent of urchins.

	Location[0m]	Location[0.5m]	Location[1m]
Location[0m]			
Location[0.5m]	0.095238491		
Location[1m]	0.000513361	0.07000314	
Location[Holdfast]	0.707647698	0.04107904	0.000120138

Table 2: Significance values of the relationship between proximity to holdfast and urchin-crevice habitat association. Each p-value compares means between individual locations.

Effect Tests			
Source	DF	ChiSquare	Prob>ChiSq
Location	3	18.324258	0.0004*

Table 3: Chi squared value of the effects test between the crevice associated proximity means. There was a significant effect of proximity location on crevice associated urchin count (Chi Square = 10.55, DF 3, p=0.0144).

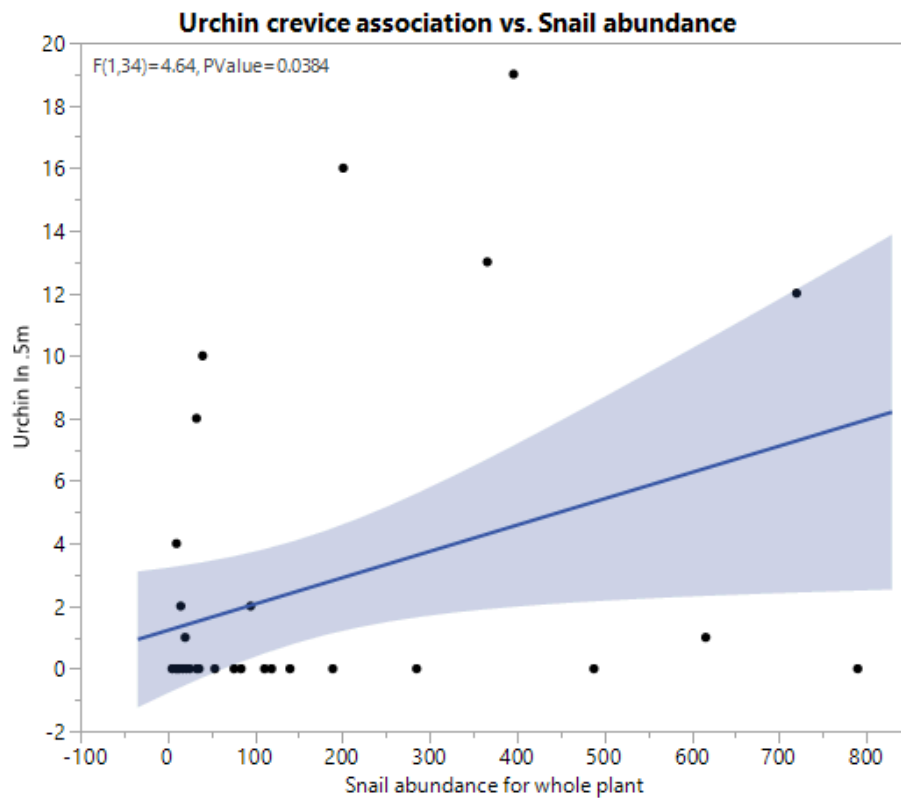


Figure 5: Monotonic positive relationship between snail abundance and crevice associated urchins. Urchins here are measured at 0.5 meters away from the surveyed plant. As the abundance of snails increases, the number of urchins located in crevices increases.

Discussion:

Our results were consistent with our hypotheses. A higher abundance of turban snails is associated with larger plants that have more stipes (Fig. 2, $p < 0.0001$). This is expected due to larger plants having a greater surface area to support turban snails, reducing intraspecific competition for food and space (Reidman et al. 1981). In addition, our results indicate that snail abundance is directly proportional to kelp drift abundance (Fig. 3, Table 1, $p < 0.0001$). This supports our assumptions that as snails graze on giant kelp, they leave the blades and stipes of a plant fragile. These fragile pieces will break off and produce drift, indicating that snails facilitate the production of kelp drift. Thirdly, in relation to urchin crevice association, more urchins were found in crevices near the holdfast (Figure 4). Drift is most likely to fall from upper stories, where wave action is high, to the benthic community directly proximate to the kelp holdfast. The density of drift, and thus of urchins in crevices, is most likely to resemble a chi squared distribution. Lastly, a significant positive relationship between snail abundance and urchins in cracks 0.5 meters from the holdfast was found (Fig. 5, p value = 0.0384). This behavior is consistent with healthy, well fed urchins found in kelp dominated reefs (Harrold & Reed 1985). The habitat associations found among sampled urchins suggest that the drift kelp produced by turban snails is sufficient to keep urchins from actively grazing. Since sub-surface grazing is unlikely to disperse drift kelp far from the holdfast, our results support the association of drift algae with turban snails and therefore urchin grazing. This study was unique in that it addressed the relationship between urchins and kelp but focused on another set of grazing species, turban snails, as a mediator in this dynamic. Our hypotheses were generated under the assumption that as turban snails graze on kelp blades in the upper canopy, they release drift kelp that settle below. Purple urchins are known to settle in cracks and crevices and feed on drift algae, not posing any immediate threat to giant kelp as long as there is sufficient drift algae available (Harrold and Reed 1985). Ultimately, we presumed that the abundance of turban snails is directly aligned with the abundance of drift kelp. Consequently, urchins would exist in cracks and crevices in proximity to holdfasts rather than exposed on the reef grazing giant kelp directly due to the drift kelp available. Therefore, turban snails indirectly cause the normal behavior of purple urchins, which can indirectly benefit giant kelp (Fig. 6). A high abundance of snails could potentially keep urchins satisfied in their cracks, saving giant kelp from being overgrazed.

These findings led us to make predictions regarding the intratrophic herbivory relationship between urchins, snails, and kelp. Using hypothetical data, we generated a model that predicts how the abundances of turban snails will impact the abundances of purple urchins. A low density of snails (A) can support a low urchin density, a medium density of snails (B) can support a medium urchin density, and a high density of snails (C) can support a high urchin density without a stable state change. The density of snails and their alignment with kelp drift abundance might potentially counteract the negative interaction strength between urchins and kelp (Fig. 8).

Our results allow us to explore how some grazer species contribute to kelp forest resistance to stable state changes. The intratrophic approach is a novel way to analyze interaction strengths and alternative stable states. Although snails pose a direct negative impact on kelp via consumption, their direct correlation with kelp drift abundance supports our assumption that snail grazing mechanisms release drift kelp from the canopy. Correlation does not imply causation, however these findings lead us to believe that the phenomena of snails producing kelp drift is worthy of exploring in future studies. It is known that urchins feed on drift kelp in cracks and crevices when kelp forests are healthy, and when drift kelp is not abundant, urchins come out

of their cracks to feed on giant kelp directly, resulting in urchin barrens (Harrold and Reed 1985). Turban snails present a unique solution to urchin barrens by mediating the relationship between urchins and kelp by providing the resource that ensures that a stable state change will not occur. Perturbations causing changes in alternative stable states can impact ecosystems significantly, making it so that it could be difficult for the system to restabilize at the healthier stable state. The idea that alternative stable states may exist in communities has been a dominant theme in ecology since the 1960's (Beisner et al. 2003). Kelp forests, which are susceptible to being driven out of their healthy stable state via disturbances like intensive top-down control, have been analyzed for this phenomenon for decades. Interaction strengths of various scales can determine a species' role in a community that faces stable state changes. The interaction strength between purple urchins and giant kelp is very strong (Estes et al. 1998). Unnatural grazing behavior enacted by purple urchins can deplete entire forests, and recovery is only possible with the introduction of a disturbance. Urchin barrens are characterized by low primary productivity and low food-web complexity, and often are considered a collapsed version of a healthy kelp forest (Filbee-Dexter and Scheibling 2014).

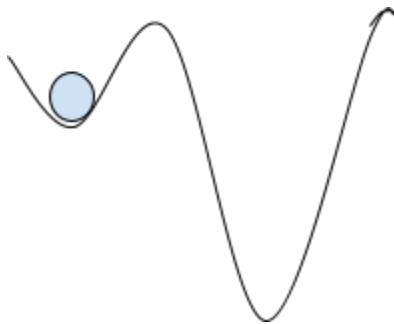


Figure 6: Alternative stable states - In this diagram, the ball exists in the smaller cup that is a healthy kelp forest. A small perturbation that causes an increase in urchin abundance can bring the ball over the hump into another stable state that is harder to recover from, an urchin barren.

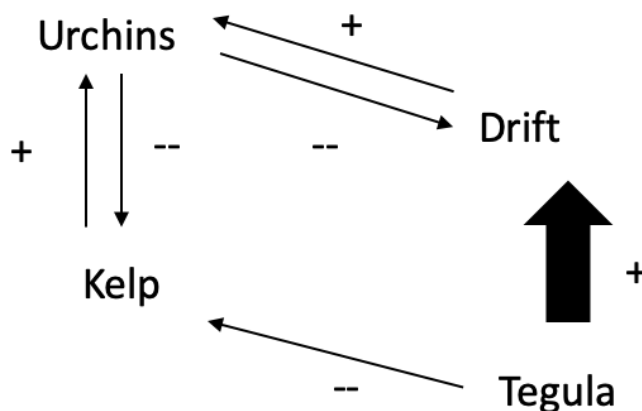


Figure 7: An intratrophic herbivory interaction with the implementation of drift demonstrates an indirect positive impact of *Tegula spp.* on urchins.

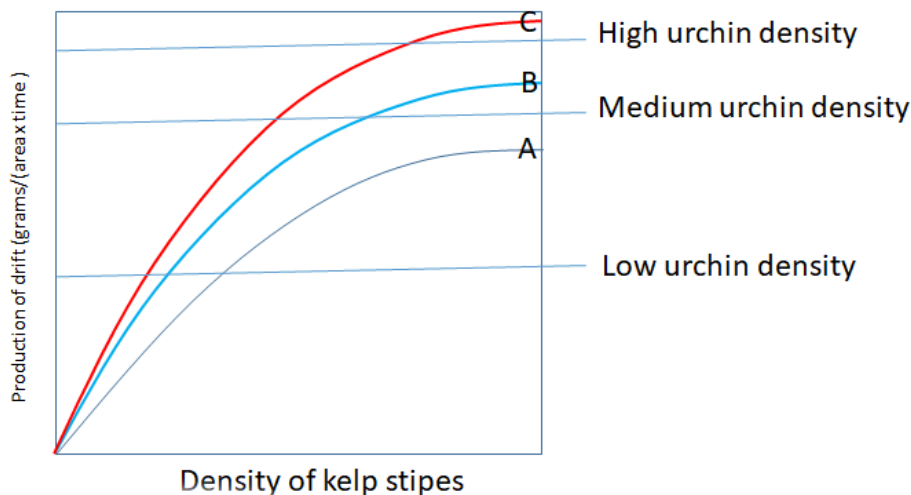


Figure 8: This model addresses how snail abundance (A grey, B blue, C red) can sustain kelp forest resistance to stable state change enacted by urchin density. High snail abundance (C) can support high urchin density, intermediate snail abundance (B) can support medium urchin density, and minimal snail abundance (A) can support low urchin density. There is a linear relationship between number of stipes and abundance of snails, resulting in these logarithmic curves (A,B,C). As a higher density of stipes supports higher abundances of snails, urchin populations are controlled.

Works Cited:

- Abbott I. A. and G. J. Hollenberg 1982. Marine algae of California. Stanford Univ. Pr.
- Beisner, B., D. Haydon, and K. Cuddington. 2003. Alternative stable states in ecology. *Frontiers in Ecology and the Environment*, 1.
- Brett, M. T., & C. R. Goldman. (1996). A meta-analysis of the freshwater trophic cascade. *Proceedings of the National Academy of Sciences*, 93:15.
- Britton-Simmons, K. H., Foley, G. and Okamoto, D. (2009) 'Spatial subsidy in the subtidal zone: Utilization of drift algae by a deep subtidal sea urchin', *Aquatic Biology*, 5(3), pp. 233–243. doi: 10.3354/ab00154.
- Buenau, K., A. Rassweiler, & R. Nisbet. 2007. The effects of landscape structure on space competition and alternative stable states. *Ecology*, 88:12.
- Castro, P. and M. E. Huber. 2010. Marine Biology. McGraw Hill. 8: 214
- Ebeling, A. W., D. R. Laur and R. J. Rowley. 1985. Severe storm disturbances and reversal of community structure in a southern California kelp forest. *Marine Biology*. 84.
- Estes J., N. S. S. and J. F. P. 1978 'Sea Otter Predation and Community Organization in the Western Aleutian Islands , Alaska', *Ecological Society of America*, 59(4), pp. 822–833.

- Estes, J. A. "Killer Whale Predation on Sea Otters Linking Oceanic and Nearshore Ecosystems." *Science*, vol. 282, no. 5388, 1998, pp. 473–476., doi:10.1126/science.282.5388.473.
- Filbee-Dexter, K. and Scheibling, R. E. 2014 'Sea urchin barrens as alternative stable states of collapsed kelp ecosystems', *Marine Ecology Progress Series*, 495, pp. 1–25. doi: 10.3354/meps10573.
- Harrold, Christopher, and Daniel C. Reed. 1985 "Food Availability, Sea Urchin Grazing, and Kelp Forest Community Structure." *Ecology*, vol. 66, no. 4, 1985, pp. 1160–1169., doi:10.2307/1939168.
- Harvell, C. D. *et al.*, 2019 'Disease epidemic and a marine heat wave are associated with the continental-scale collapse of a pivotal predator (*Pycnopodia helianthoides*)', *Science Advances*, 5(1), pp. 1–9. doi: 10.1126/sciadv.aau7042.
- Jensen, GC., Gotshall DW., and Flores Miller RE. 2018. Beneath Pacific Tides: subtidal invertebrates of the West Coast. Mola Marine, Bremerton, WA. 296 pp.
- Mansergh, S., and J. P. Zehr. 2014. *Vibrio* diversity and dynamics in the Monterey Bay upwelling region. *Frontiers in Microbiology*. 5.
- Riedman, M., Hines A., and Pearse, J. 1981. "Spatial segregation of four species of turban snails (Gastropoda:Tegula) in central California." *The Veliger*. 24 (2):97–102.
- Ripple, W. J. and R. L. Beschta 2005. WILLOW THICKETS PROTECT YOUNG ASPEN FROM ELK BROWSING AFTER WOLF REINTRODUCTION. *Western North American Naturalist*. 65:118-122
- Vásquez, J. and A. H. Buschmann. 1997. Herbivore-kelp interactions in Chilean subtidal communities: a review. *Revista Chilena de Historia Natural*. 70: 41–52.
- Van der Heide, T., E. Van Nes, M. Van Katwijk, M. Scheffer, A. Hendriks, & A. Smolders. 2010. Alternative stable states driven by density-dependent toxicity. *Ecosystems*, 13:6.
- Watanabe, J. M. "Food Preference, Food Quality and Diets of Three Herbivorous Gastropods (Trochidae: Tegula) in a Temperate Kelp Forest Habitat." *Oecologia*, vol. 62, no. 1, 1984, pp. 47–52., doi:10.1007/bf00377371.