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Productivity of kelp forests, sans the iconic kelp

Forest canopies provide important functions that cannot be taken up by the understory

Date:	August 2, 2021		
Source:	University of California - Santa Barbara		
Summary:	A lush canopy is a defining feature of most of the planet's forests. But canopy-forming species can be particularly vulnerable to disturbances and environmental change. So the question is: What is a forest without its trees?		
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A lush canopy is a defining feature of most of the planet's forests. But canopy-forming species can be particularly vulnerable to disturbances and environmental change. So the question is: What is a forest without its trees?

A new paper out of UC Santa Barbara's Marine Science Institute (MSI) and the University of Virginia seeks to address part of this question by looking at how the productivity of kelp forests changes when its biggest species is gone. After a 10-year removal experiment, the researchers discovered that, while smaller understory algae did take advantage of the brighter conditions, they weren't able to compensate for the lost productivity of the missing giant kelp, the largest alga in the world. The study, published in *Ecology Letters,* covers only one aspect of forest ecology; however, it reveals the fundamental importance of canopy-forming species.

A forest canopy performs many functions. It forms habitat, creates microclimates, provides food and much more. The understory can't fill all these different roles, but there is one place where it could compensate for the loss of the canopy: primary production, which is how much organic carbon plants and algae produce from sunlight during a given amount of time in a given area.

All these organisms are photosynthesizing. "In the absence of the canopy, the understory vegetation on the forest floor may soak up all the light and be just as productive," said senior author Dan Reed, a research biologist at MSI.

With a hypothesis in hand, the team devised an experiment. They would mimic the conditions created by natural disturbances, such as ocean storms and heatwaves, by clearing the canopy from patches of forest. They would then record how much light reached the forest floor and how much biomass was produced by the exposed understory. Because of how quickly giant kelp grows and dies, the researchers were able to look at many cycles of disturbance and recovery over the course of 10 years. A similar study could have taken decades or centuries in a terrestrial forest, Reed said.

Fortunately, an ideal test bed was just a few hundred meters offshore: the Santa Barbara Coastal Long Term Ecological Research Project (SBC LTER) managed by UC Santa Barbara. The site is part of the National Science Foundation's LTER Network, set up to investigate ecological processes over longer timespans.

It was important to run the study under a variety of conditions, so the team conducted their experiment at five different locations in the Santa Barbara Channel. Some were ideal for algal growth, featuring plenty of hard surfaces for the seaweed to grow and few sea urchins eager to eat it. Meanwhile, other sites had more urchins and sandy substrates, which are poor places for seaweeds.

The scientists marked off three plots per site. One would be left alone to serve as a control. The second would be cleared of giant kelp on a yearly basis, which would mimic the winter swells and storm surges that can uproot the forest canopy. The final plot would be cleared quarterly, providing the researchers with a picture of what happens when giant kelp is simply absent. This may become more common in the future as ocean conditions change.

To avoid tampering with the experiment, the team used non-destructive methods to estimate algal growth and productivity. The researchers developed these methods after half a decade making measurements and collecting samples to compare their accuracy and refine their techniques. They were able to establish relationships between biomass and measures like canopy cover or algae size for around 30 different species.

Calculating productivity from these assays required building on yet more past work. Co-authors Robert Miller and Shannon Harrer, both at MSI, had developed a bio-optical model that predicts the productivity of seaweed under a particular amount of light. By feeding this model light and biomass data from the field sites, the team calculated productivity over a given time period.

Over the course of the 10-year study, the researchers saw a gradual reduction in the productivity of the canopy and an exponential increase in the productivity of the understory algae, especially in high-quality habitats. They also saw stronger effects with more frequent canopy removal, as anticipated. That said, the boost to the understory wasn't able to fully make up for the lost canopy productivity.

When giant kelp is removed, suddenly there's plenty of light and space for understory algae to grow. The increased light should foster a flourishing forest floor that might compensate for the lost canopy. However, the data indicates that giant kelp is simply so incredibly productive that the understory algae can't possibly make up the difference, even under ideal conditions.

"This is an important finding," said Harrer. "It highlights the importance of considering site-level factors when we assess the impacts of disturbance on ecosystem function."

Even though the understory can compensate for some of the lost productivity from the canopy, it doesn't mean the fate of that productivity will be the same as before. For instance, a lot of giant kelp grown in the forest ends up washing onto beaches. "Southern California has some of the highest diversities of beach organisms in the world," Miller said, "and that's because of giant kelp, which is the most important source of beach wrack." Other seaweeds simply can't fill that role.

The team expects a similar dynamic to hold true in terrestrial forests. Decreasing the number of large trees can give rise to forests with more understory growth. And fast-growing, opportunistic species may take the place of canopy-forming giants in the new, more disturbed ecosystem.

This is the value of long-term studies, explained lead author Max Castorani, previously at MSI and now assistant professor at the University of Virginia. "These changes took time to develop, even in a really dynamic, fast-growing environment like a kelp forest," he said. "Most field studies are less than three years. If we had run our experiment for only a few years, we would have missed these dramatic changes and come to different conclusions."

The results have implications for the future as the climate continues to change. Stronger and more frequent storms, warmer water and shifts in ocean chemistry may create unfavorable conditions for giant kelp. Climate change and human activities also threaten forests on land, potentially altering ecosystem productivity and

biomass, and the complex interactions among different species.

The team stopped removing kelp from the experimental plots in 2018, but continues to monitor the sites and track how the ecosystem changes as it recovers. They plan to investigate the effects of environmental and grazing variability. A new long-term experiment will also look at competitive interactions between invertebrates and understory algae.

"Kelp forests play a vital role in coastal environments and provide many benefits to society," Castorani said. "We need long-term experiments like these to understand how future ecosystems will function in a changing ocean."

Story Source:

Materials provided by **University of California - Santa Barbara**. Original written by Harrison Tasoff. *Note: Content may be edited for style and length.*

Journal Reference:

 Max C. N. Castorani, Shannon L. Harrer, Robert J. Miller, Daniel C. Reed. Disturbance structures canopy and understory productivity along an environmental gradient. *Ecology Letters*, 2021; DOI: 10.1111/ele.13849

Cite This Page:	MLA	APA	Chicago

University of California - Santa Barbara. "Productivity of kelp forests, sans the iconic kelp: Forest canopies provide important functions that cannot be taken up by the understory." ScienceDaily. ScienceDaily, 2 August 2021. <www.sciencedaily.com/releases/2021/08/210802160651.htm>.

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