Galapagos study identifies keystone predator in a complex food web

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Despite popular metaphors and cartoons depicting straightforward "food chains," ecologists such as Brown University Professor Jon Witman typically doubt that they'll see predators in diverse tropical ecosystems have meaningful impacts on species even just two links down the line. But after six years of meticulous experimentation and observation off the coast of the famed Galápagos Islands, Witman and two colleagues

have amassed direct evidence that just such an important "trophic cascade" is happening there.

The researchers report in the journal *PLOS ONE* that two species of triggerfish are overcoming consistent pestering by sharks, sea lions and especially hogfish to gobble up enough pencil urchins to reduce the urchins' consumption of algae. Determining such interactions matters, Witman and his co-authors wrote, because while it is clear that humans disrupt the normal functioning of tropical ecosystems across the world, it is often unclear exactly how. Understanding when and how trophic cascades occur, and who is involved, is the only way to prevent or fix such problems.

"As human exploitation is depleting large predators in the ocean, there is a growing appreciation that many predators have important indirect effects on species lower in the food web," wrote Witman and co-authors Franz Smith of Brown and Mark Novak of Oregon State University.

In the Galápagos, which remain relatively untouched, the new study provides a clear example of a mid-level predator that's proving crucial to the coastal ecosystems' vitality.

"Triggerfish are 'keystone' predators in the subtidal food web, capable of controlling the abundance of pencil urchins and in turn, the abundance of algae," Witman said. "Triggerfish warrant special protection because of their strong effects on ecosystem function."

Chewing on pencils

Not content to simply watch the ecosystem or make inferences by counting the relative abundance of different species, the team devised several controlled experiments between 2007 and 2013 to prove cause-and-effect. They recorded hundreds of thousands of time-lapse

photographs to document the results.

One way they experimentally untangled the food web was to tether different urchins to rocks at various sites, making them readily available prey to encourage predatory action for observation. These experiments showed the researchers which predators ate the urchins and what kind of urchins the predators preferred. The results were clear: Two species of triggerfish, blunthead and finescale, did all the urchin eating, and they had a very clear preference for large pencil urchins. Smaller pencil urchins and especially green urchins escaped unscathed.

Green urchins were so undesirable that when researchers tethered them side-by-side with a pencil urchin, the fish would almost always eat the pencil urchin. Although in one particular moment that proved to be a double exception, a hogfish carried off a green urchin.

Meanwhile, the researchers saw some of the challenges that triggerfish face in scrounging a meal. Nearly half the time, hogfish would harass the triggerfish, circling them and trying to steal the urchins the triggerfish started eating. When they couldn't take the urchins outright, the hogfish would scavenge the leftovers.

In a second set of experiments, the scientists confined urchins a little differently. They built rings of fencing next to enclosable cages on the undersea rocks. They let a full year go by to ensure a healthy growth of algae inside. Then they populated the cages, and some of the open-but-fenced pens with urchins. In the pens, urchins could graze on the algae but they were vulnerable to predators. In the enclosed cages, they could dine in peace. Some of the pens were left empty of urchins as experimental controls.

"This experiment was truly novel as it was open to the full suite of fish, sharks, sea lions and more interacting with the triggerfish feeding on sea

urchins," Witman said. "We were able to do this because we filmed the whole experiment at one-second intervals in time lapse—that's how we discovered the interactions between hogfish and triggerfish, sea lions and sharks with triggerfish and so on."

In the experiment, triggerfish again made quick work of the penned urchins. They ate 21 out of 24 urchins in less than three hours. Just three urchins survived the night (other experiments showed that triggerfish hunt by day, and freely behaving urchins, apparently realizing this, tend to come out in the late evening). By the next morning the surviving urchins were triggerfish breakfast.

The urchins were gone so fast that they couldn't manage to make any real impact on the algae. Meanwhile in the cages, the urchins could eat algae. An experimental population of pencil urchins ate about 10 percent of their algae over a span of eight days.

The difference in urchin predation combined with the difference in algae grazing provided "experimental evidence of a three-level consumptive trophic cascade from triggerfish to pencil urchins to benthic algae," the researchers wrote.

The empty pens, meanwhile, served to show that left completely alone, the algae remained in tact and thriving so whatever algae was gone in the cages was gone because of the urchins.

As in the tethered experiments, the triggerfish did not find life easy. Not only did hogfish continue to harass them, but so did the occasional shark (four different species showed up on camera) and, somewhat more commonly, hungry sea lions. One sea lion even realized it could lie in wait near the cages and pens to ambush triggerfish and hogfish.

These top-predator interactions with the lower predators turned out to

significantly slow down—but not stop—triggerfish predation of urchins, the researchers found both through observation and mathematical modeling led by Novak.

"If these preliminary results are borne out by further study, they suggest that the behaviors of mesopredators (fish) and top predators (sea lions and sharks) can play a role in maintaining a healthy, productive marine ecosystem in the Galápagos because they will indirectly regulate the rate of removal of algae by pencil urchins," Witman said.

They have to endure a lot of harassment, but triggerfish have what it takes to accomplish a rare ecological feat: they manage to execute a trophic cascade in a rich, tropical environment.

"With 16 species of sea urchin predators known in the Galápagos subtidal, only two species, blunthead and finescale triggerfish, preyed on large pencil urchins to the extent that they precipitated a trophic cascade," the authors wrote. "Consequently, blunthead and finescale triggerfish are key consumers in the Galápagos subtidal ecosystem, ecologically important for indirect, positive effects on the abundance of benthic algae."

More information: Jon D. Witman et al, Experimental demonstration of a trophic cascade in the Galápagos rocky subtidal: Effects of consumer identity and behavior, *PLOS ONE* (2017). DOI: 10.1371/journal.pone.0175705

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