

ECOLOGY

New Model Charts Swings in Crab Populations

It's not easy being a crab. Hatched in the dead of winter, crab larvae mature at sea for 3 months before swimming to shore to settle. And once there, they not only have to compete for food, they run the risk of becoming food for other creatures—fellow crabs included.

But if you think living a crab's life sounds hard, ecologists joke, try modeling it. Crab populations are notoriously erratic, skyrocketing one year and tumbling the next. Catch figures in Eureka and Crescent City, California, for the Dungeness crab, for instance, have been known to plunge from 7 million to 130,000 kilograms in just 4 years. For decades, ecologists have wondered what forces drive these swings: Is it biology—behaviors such as competition and cannibalism, which depend on the density of crabs in a given locale? Or is it environment—random changes in water temperature, ocean currents, and other aspects of the crabs' habitat?

Now, on page 1431 of this issue, Kevin Higgins of the University of Helsinki, Alan Hastings of the University of California, Davis, and their colleagues report that the answer may well be both. With a new computer model that incorporates the effects of both biological and environmental forces on the Dungeness crab, the researchers find that biological feedbacks can amplify even small changes in the crabs' physical environment, resulting in huge swings in the population.

Scientists say that this ecological model is among the first in the field to evince the chaotic behavior often seen in complex physical systems, such as global climate. In these systems, the impact of small, random events—called noise—can be greatly amplified, leading to huge, systemwide events. "This [paper] is the best example in a natural system that this is what's going on," says Stephen Ellner, a mathematician at North Carolina State University in Raleigh. He and other researchers add that the model will help scientists understand the population dynamics of a host of animals, from pest insects such as gypsy moths to endangered butterfly species. "This work is like the tip of the iceberg; you can expect a lot to follow it," says Ellner.

Biologists have long marveled at the volatility of catch figures for the Dungeness crab, the most heavily harvested crustacean on the West Coast of the United States. Says David Hankin, a biologist at Humboldt State University in Arcata, California, "When I first came here in 1976, I thought I'd arrived in

paradise. Fishermen were literally giving away crabs. Then just a half a dozen years later, they couldn't catch a thing."

Intrigued, he and others began studying feedback mechanisms that might affect crab populations. For example, using mathematical models, they explored the link between the number of females and population size. They found that as the number of females rises, so does the number of crab eggs, which initially causes the juvenile crab population to jump. But fights over limited food and living space—as well as cannibalism—can



Tough life. Small environmental changes can lead to big drops in numbers of Dungeness crabs (above).

quickly kill off crabs, setting back the population. Because such self-regulating mechanisms are nonlinear—that is, their response to perturbations in the system isn't proportional to the size of the perturbations—these ecologists reasoned that the mechanisms alone might account for the wild fluctuations in crab numbers.

While Hankin and others were exploring biological feedback mechanisms, other ecologists were trying to understand the effects of environmental changes, such as an increase in ocean temperature, on populations. These scientists reasoned that physical perturbations—although often tiny—were more likely to account for the observed population swings because they affected a big proportion of the population at once.

In the last few years, the theoretical divide between the two camps has narrowed, with most ecologists conceding that both biology and environment are probably at work. And now the new model is providing some

supporting evidence. To build their model, the researchers first collected basic biological data on the crabs, including larval, juvenile, and adult survival rates; the age of female crabs when they first lay eggs; and how often juvenile and adult crabs eat smaller crabs. These interactions became the "deterministic skeleton" of the model.

To get at the impacts of environmental changes, the researchers worked indirectly. They entered crab population numbers for a single year into their skeletal model, let it run for several "years," and compared the model's output to actual crab-catch numbers. The pattern of population changes in the model looked nothing like the real-world fluctuations. In fact, in the absence of environmental perturbations, crab populations in the model strongly self-regulated. Environmental variance (noise) that randomly boosted or depressed the ranks of crabs had to be playing a role.

When they fed various amounts of noise into the model, the team members found that the biological feedbacks no longer had a stabilizing effect. Instead, they appeared to act like "deterministic noise amplifiers," inflating small environmental changes into huge population swings. One such change, for instance, might be a delay in a nearshore current's annual shift from its winter to summer pattern, the researchers say. While that wouldn't affect adults on land, it could wipe out a whole class of youngsters trying to get to shore, decimating the population. "It appears that even very small [environmental] shocks can excite huge population fluctuations," Higgins says.

Researchers caution that although the model offers intriguing clues about the interactions between biological feedback mechanisms and the environment, many questions remain. For example, the model doesn't incorporate the effects of specific environmental variables, such as temperature shifts. Says Peter Turchin, a physicist at the University of Connecticut, Storrs, "They've developed a sophisticated algorithm for estimating populations, and it's a valuable step forward. Now we need to go beyond this very limited model to more detailed models of [environmental] noise."

Indeed, ecologists are working on models of voles and flour beetles (*Science*, 17 January, p. 389), among other species. And crab model co-author Alan Hastings says his team may eventually try to tease apart the precise effects on crab populations of different environmental forces. "Our ultimate goal is to really understand what regulates these populations," Hastings says. "We can't do that yet."

—Kathryn S. Brown

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