Biography of Juan Carlos Castilla

Chile boasts almost 4,500 kilometers of shoreline with hundreds of unique species, an exclusive ecology seen nowhere else. Along with distinct families of shellfish, marine worms, and tunicates, humans manipulate and dominate the environment. Before the last two decades, researchers had not investigated the impact of human activity on the Chilean coastline. However, in 1985, Juan Carlos Castilla published a pioneering article based on a study where humans were excluded from a small segment of the shore (1–3). His findings formed the basis for conservation practices and environmental laws, leading to important changes in the Chilean fishing industry.

Castilla's original human exclusion research is still bearing fruit two decades later. Additionally, his body of more than 180 published articles on this experiment and others has earned him a prestigious Fulbright Scholarship (1988), awards from the Third World Academy of Sciences (1996) and the Pew Fellowship in Marine Conservation (1996), and a Presidential Chair in Science (1997). In 2003, he was elected a foreign associate of the National Academy of Sciences. His Inaugural Article (4), published in this issue of PNAS, investigates why a nonindigenous marine species is limited to a small stretch of the Chilean coastline and exists nowhere else in the country. This research contributes to a better understanding of the ecological impacts of nonindigenous marine species on rocky intertidal systems.

Communicating with Invertebrates

After taking a class with a particularly good chemistry teacher in high school, Castilla decided to major in chemistry at Pontificia Universidad Catolica in Santiago. However, midway through his undergraduate career, Castilla found inspiration in another teacher, a marine biology professor named Patricio Sanchez. Sanchez, a medical doctor who had branched into evolution and marine biology later in life, sensed Castilla's enthusiasm and invited him to join a cohort of other students performing research outside class. "From one minute to the next, that work really inspired me," Castilla said.

For the next four summers, Sanchez and several of his top students, including Castilla, canvassed Chile's rocky seashores to study various marine fauna. Sanchez delegated the study of each particular organism to individual students. "He said, 'Somebody's going to do the algae, somebody's going to do the crustaceans, somebody's going to do the mollusks. I got the polychaetes," said Castilla, referring to a group of soft-bodied marine worms.

Juan Carlos Castilla

Through his work with Sanchez's team, Castilla soon became an expert in polychaete taxonomy, describing two new species in the course of his research (5). He seriously considered extending these polychaete studies into a career. However, 2 years after graduating with a degree in chemistry, a major his college required him to keep despite his growing interest in marine biology, Castilla turned his attention away from polychaetes to pursue higher education outside Chile. With financial assistance from UNESCO and British Council scholarships, he decided to study at the University College of North Wales in Bangor, United Kingdom, based on the extraordinary fame of its top marine biology professor, Dennis Crisp. "Crisp was one of the biggest names in marine biology at the time," Castilla said.

In 1967, Castilla enrolled in a master's program in marine biology with Crisp as his mentor. Despite some early difficulties learning English, Castilla excelled in his work. His success prompted Crisp to offer Castilla the opportunity to go directly into a Ph.D. program without finishing his master's, which Castilla eagerly accepted. Although Crisp's area of expertise was barnacle physiology, he supported Castilla in following his own interest, invertebrate behavior. Having had a lifelong curiosity about predators and carnivores, Castilla chose the starfish *Asterias rubens* as his biological model. "I was eager to ask questions to the animals: What do they eat? How do they respond to food conditioning? What about olfactory stimulus, light, or pressure? Everything was interesting to me," he said.

To test the effects of various stimuli on starfish behavior, Castilla placed the animals in a Y-maze filled with sea water and waited for them to follow one arm or the other. The work could often be extremely tedious. "Starfishes move very slowly, and I'd wait sometimes for hours for them to choose between arms A and B," he said. Nonetheless, Castilla was able to develop a rapport with his subjects, conscientiously documenting starfish behavior in response to water currents, light, prey, and other stimuli. "I thought I was able to communicate to them, ask them questions, and they were able to give me answers. It sounds crazy, but it was communication between myself and these invertebrates," he said. Castilla published his conclusions in more than six articles (6–11), graduating with his doctorate in 1970.

Crazy for Locos

After finishing his doctoral degree, Castilla returned to Chile and began teaching zoology at his undergraduate alma mater, Pontificia Universidad Catolica. Eager to begin research, but confined to the inland city of Santiago, Castilla imported sea water from the coast and started his own salt-water aquarium in a 6-m^2 laboratory. He was uninterested in continuing his work with starfishes and sought a new biological model to study marine invertebrate behavior. "I'm a believer that selection of the right biological model is critical in science," Castilla said. After months of searching, he found the perfect model in

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This is a Biography of a recently elected member of the National Academy of Sciences to accompany the member's Inaugural Article on page 8517.

a carnivorous mollusk unique to Chile called *Concholepas concholepas*.

Commonly called "locos," *Concholepas* is frequently collected by local fisherman and forms the basis of several traditional Chilean dishes. "I thought this species had tremendous potential from the behavioral, ecological, and also the fisheries' point of view," said Castilla. "I thought it would be a good subject for a wonderful combination of basic research and trying to transfer that basic research to real life, which is the life of the fishers."

After studying spawning, circadian rhythms, and other behavior in *Concholepas* and marine predators for 3 years (12, 13), Castilla traveled to Duke University's marine laboratory in Beaufort, NC, for a 6-month postdoctoral fellowship under the mentorship of ecologist John Sutherland. Here, Castilla gained a strong appreciation for marine ecology and for Sutherland's work. "Sutherland is the most wonderful marine ecologist I've met so far. I became in love with ecology," he said. Before returning to Chile, Castilla made plans to visit the west coast of the United States and meet Robert T. Paine, a well known marine ecologist who studied starfish in rocky intertidal zones. Castilla flew into San Diego and took a 2-week trip up the coast on a Greyhound bus. When he finally arrived in Seattle around midnight, Paine was waiting for him in the bus station. "We became extremely good friends from that moment," Castilla said. Over the course of a week, Castilla and Paine discussed several aspects of marine ecology, including the prospect of comparing the west coast of the United States with Chile's seashore.

Paine had made a name for himself in marine ecology by developing the concept of keystone species: that particular species are crucial to the makeup of an environment such that if the species disappears, the environment drastically changes. On his return to Chile, Castilla wondered whether he had found his own keystone species in *Concholepas* (14). He recruited a cohort of graduate students, much like Patricio Sanchez had recruited him years ago, and Castilla's team began exploring Chile's coast in the rocky intertidal and subtidal zones. He and his students immediately noticed that the ecology of shores frequented by humans was markedly different from more remote areas. For instance, "in isolated areas, there were lots of *Concholepas*. Around fishing coves where people live, there were none. Why was the ecology so different?" he wondered.

At that moment, "I decided to do the biggest experiment of my life," he said. Castilla reasoned that the only way to test humans' impact on coastal systems and determine whether *Concholepas* was indeed a keystone species was to fence off a section of shoreline to exclude people; in essence, to start one of Chile's first marine coastal research stations. It took him 5 years to raise funds from the university and get a research grant from the International Development Research Center in Canada before he could establish a research station in Las Cruces, central Chile. Unwilling to wait for government approval or permits, he and his students illegally fenced off 1 km of coastline inside the research station in 1982. Castilla eventually obtained a legal permit after explaining the merits of his research to the Chilean authorities.

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After 2 years of excluding humans, Castilla's team started searching for any changes that might have taken place within the research station. Not surprisingly, the first transformation the researchers noticed was an extremely large increase in *Concholepas*; the population within the research station had grown close to 10 times as large as the population outside (15). However, with further probing, Castilla's group found a wealth of other differences. With the growth of carnivorous *Concholepas*, populations of the mussel species *Perumytilus purpuratus*, frequently consumed by *Concholepas*, had drastically decreased. Because these mussels are a "bio-engineer species," meaning that their shells create habitats for other organisms, 60 to 70 other species that relied on the mussels also had disappeared. "It seems contradictory to popular thinking, but in the rocky intertidal zone there was actually more diversity outside the station than inside," Castilla said.

Comanagement Is Good Management

Castilla and his students learned so much within the first few years of running the Las Cruces station that he decided to continue the experiment, and it has remained in place for 22 years. During that time, his team has been able to document specific events, such as the changes brought about by a 1985 earthquake (16), as well as several ongoing trends (2, 17–20). Ecological theory predicted that as time passed, numbers of predatory dominant species would rise and then eventually fall as resources were consumed within the environment. "That's exactly what happened," said Castilla. Over the years, his team has recorded populations of *Concholepas*, sea urchins, and keyhole limpets as they crescendo, peak, and fall (15, 21). "The important thing is to know these trends over a long time, particularly if you want to give good fishing or management advice to people. If you know the rate that the populations increase, when they peak, and when they start to descend, you can give advice on when is the right time for extracting resources," he said.

With that idea in mind, Castilla decided to shift his focus from basic to applied science. "Las Cruces is an academic experiment. What about doing an experiment in the real world with fishers?" he said. In 1988, he reached an agreement with the Chilean government to implement a practice known as "comanagement" on a 4-km section of seashore near the fishing cove Caleta Quintay. Shores in Chile then were considered "open access," meaning that anyone could extract seafood from the sea, leading to resource overexploitation (22). However, in the area Castilla's group had designated for comanagement, only members of a particular small-scale fishery association were allowed to extract resources. Thus, fewer shellfish were collected, and extraction was restricted to certain times of the year. "We convinced fishers that this was like a savings account in a bank. They would be saving resources, but they would not be able to depend all year round on that account. It was not difficult to convince them; they knew what would happen, and they had waited years and years for this action to be taken."

The experiment, which involved 3 years of data collection (15, 23–25), was a success: the shore flourished with conservation measures in place, and the fishers also were satisfied with adequate resource extractions. With his positive data set in hand, Castilla and other scientists lobbied the Chilean government to enact comanagement procedures more broadly. Today, more than a decade after his initial comanagement experiment ended, 185 areas with exclusive territorial user rights for fisheries are currently comanaged under Chilean law.

An Unusual Settlement

While continuing his studies on comanagement and his ongoing work at Las Cruces, Castilla has collected many other interests along the Chilean shoreline. For example, in his Inaugural Article (4), he investigates why a particular nonindigenous tunicate settlement exists only within a 60- to 70-km patch of Chile's Bay of Antofagasta (4, 26, 27) and is not more widely dispersed along the coast. In his early research with Patricio Sanchez, Castilla had noticed the tunicate species *Pyura praeputialis* distributed exclusively along 60–70 km of coast. The crusty tunicates form a large lump in the otherwise smooth bay, with a ridge so firm Castilla and his classmates could walk on it.

The only other site known to harbor this species is along 2,000–2,500 km of Australian coastline. Previously, researchers had theorized that the two tunicate settlements were relics of Gondwana, when continents in the southern hemisphere were joined together; thus, the two tunicate populations separated when the continents became disjointed. However, by performing genetic testing, Castilla demonstrated in 2002 that the Chilean tunicates probably arrived to the Bay of Antofagasta relatively recently as an invasive species (28).

In his Inaugural Article (4), Castilla and his colleagues experimentally manipulated *Pyura* to determine whether the tunicate could survive in various places inside and outside the Bay of Antofagasta, as well as how the species competed with native mussel populations. Because the tunicates grew well in several different locations, Castilla's group concluded that ocean currents or *Pyura*'s brief larval dispersal period restricted the species to its particular location. The tunicates successfully outcompeted native mussels, suggesting that inside the mid-rocky shore of the Bay of Antofagasta, *Pyura* replaced native mussels after its arrival, sometime within the past several hundred years. The team's findings create a plausible model to explain how and why the tunicates have come to dominate a portion of the Bay.

Besides this research, Castilla also is actively studying linkages between the ocean's water column and the rocky intertidal and benthic subtidal zones, for example, how marine larvae rely on the column for transport from one zone to another (29–31). Additionally, he has been heavily involved for almost 30 years in urging the establishment of protected marine parks (3, 32), an initiative to which he says the Chilean government finally is starting to yield. He is an active member of the Center for Advance Studies in Ecology and Biodiversity at the Pontificia Universidad Catolica, and he takes pride in the 12 Ph.D. students and scores of Chilean and Latin American scientists he has trained over the years. Although he plans to retire within the next few years, Castilla says that he will continue to remain active in many of these pursuits. "It's been a wonderful scientific life. I've been able to move in many different directions, but always keeping basic science and ecology in the middle of my heart," he said.

Christen Brownlee, *Science Writer*

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