Research

Resilience, Social-Ecological Rules, and Environmental Variability in a Two-Species Artisanal Fishery

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ABSTRACT. Social-ecological resilience is an increasingly central paradigm for understanding sustainable resource management. In this study, we aimed to better understand the effect of environmental variability on the resilience of fishery systems, and the important role that social institutions and biophysical constraints play. To explore these issues, we built a dynamic model of the pen shell fishery of the indigenous Seri people in the Gulf of California, Mexico. This model included the dynamics of the two dominant species in the fishery (*Atrina tuberculosa* and *Pinna rugosa*), several institutional rules that the Seri use, and a number of ecological constraints, including key stochastic variables derived from empirical data. We found that modeling with multiple species, rather than the standard one-species model, uncovered more of the resilience that is present in the system. We also found that it is the combination of several social-ecological rules working in conjunction with the endogenous environmental variability that helps ensure the resilience of the system.

Key Words: *artisanal fisheries; common-pool resources; environmental variability; Gulf of California, Mexico; multi-species; resilience; social-ecological systems; stochasticity; system dynamics*

INTRODUCTION

Sustaining small-scale fisheries is of vital importance to the livelihood of many fishing communities across the world (Berkes et al. 2001, Béné 2006). How to achieve this, however, is unresolved because most of what we know about fisheries comes from industrialized country's experiences, which often do not apply to small-scale fishing settings in developing countries (Pauly 2006). One of the more striking differences is the multi-species character of artisanal fisheries; artisanal fishers are apt at switching harvested species depending on a suite of social-ecological conditions, an adaptive strategy that is linked to the apparent resilience of artisanal fisheries (Cinner et al. 2012). Also, the compliance to regulations suited to the specific socioeconomic and ecological contexts of each fishery is important (McClanahan et al. 2011).

Resilience is the amount of disturbance or change a system can sustain without shifting from one system state to another (Walker et al. 2004). The concept is non-normative; therefore, the shift may be to a more or less desirable state, however defined. When studying the resilience of social-ecological systems (SESs), it is often not only the resilience of the natural resource stocks that is in question but also that of the institutions that govern these resources (Cashore and Howlett 2007, Young 2010). Other resilience studies of marine coastal resources have explored sustainable small-scale fisheries as related to path dependence and transformation in governance (Gelcich et al. 2010), co-management and attributes of success (Gutiérrez et al. 2011), and mismatches between industrial fishery management and the biological and socioeconomic context of invertebrate artisanal fisheries (Freire and García-Allut 2000, Defeo and Castilla 2005).

Previous works have observed that a system may be forced over a threshold into an alternate state that may be reached simply by the slow degradation of the system (Scheffer et al. 2001, Güneralp and Barlas 2003). Detecting the gradual erosion of resilience is critical to assessing the vulnerability of a community or ecosystem to variability in the environment (Scheffer et al. 2001), but detection can be challenging and requires systematic investigation of the interactions among its various components. Moreover, while shocks and stressors are critical to pushing a system close to a threshold, it may often be natural stochastic variations that push it over the edge. Environmental variability is ubiquitous in the natural world and can play a critical role in the dynamics of SESs (Ludwig et al. 1993). Stochasticity becomes central, then, to our understanding of when and why shifts in system states occur (Beisner et al. 2003).

The area around the Infiernillo Channel, between the Sonora mainland and Tiburon Island on the Gulf of California, Mexico, is a protected homeland area for the Seri people, or Comcáac people (Fig. 1). In their artisanal fishery, the Seri harvest pen shells, or Callos de Hacha, large sessile bivalve mollusks that live buried in the sand on the seafloor (Moreno et al. 2005). Over the years, the Infiernillo Channel has remained home to the most abundant pen shell beds in the region, while the neighboring Mexican fishery of Kino Viejo just south of the channel has been dramatically depleted (Basurto et al. 2012). Extensive fieldwork and case studies have indicated that the local institutions that the Seri have created to govern their common pool resources play a key role in their success (Basurto 2005, 2006).

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Fig. 1. Map of the study area—Seri fishing grounds.
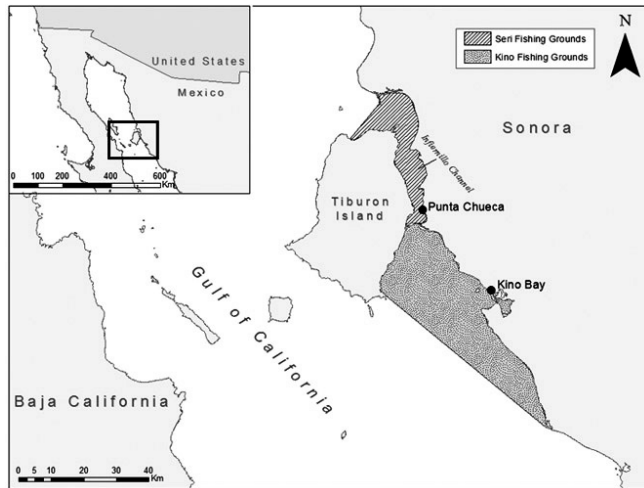
Bueno and Basurto (2009) developed a deterministic dynamic model to study the resilience of the pen shell fishery of the Seri. Their study demonstrated the role of very small, incremental endogenous changes in the relationship between ecological and socio-cultural variables in facilitating the collapse of a seemingly resilient system. We explore several major elements of the system that have not been previously examined, including its two-species character, using an expanded model. The model incorporates both stochastic elements and several social-ecological rules; we study how their dynamic interactions affect the resilience of the system. The social-ecological rules are the institutional rules and ecological constraints that collectively govern harvesting patterns in the fishery. Our objective is to systematically analyze the potential role of (1) interactions between institutional rules and biophysical settings, and (2) dynamic environmental variability on the resilience of an SES, using an experimental design framework.

Our study has two main hypotheses. First is that including both species in the model will more accurately capture the inherent resilience of the system—as Seri fishers shift their harvest between the two species according to their social-ecological rules. Second is that incorporating environmental variability into the model will increase the range of possible outcomes and degrade the system's resilience, on average, as the increased variability will increase the system's chances of crossing over a threshold into collapse. We conducted a series of simulation experiments to test these hypotheses, each with different combinations of stochastic variables, institutional rules, and biophysical constraints. Our results, which affirm our first hypothesis but refute the second, can inform studies on management of two-species artisanal fisheries.

METHODS

Building a dynamic model of the Seri social-ecological system

The Seri fishery includes two major species—*Atrina tuberculosa* (*At*) and *Pinna rugosa* (*Pr*) (Basurto 2006). *At* is smaller and sells for a much higher price because it is only sold fresh, while *Pr* is often sold frozen. Incorporating the immature and mature population dynamics of both species and Seri institutional rules provided a richer and more complete representation of the system structure in relation to its resilience properties than would a more conventional single-species model (Shelton and Mangel 2011). A causal loop diagram presents the major feedback structures of the modeled system (Fig. 2). The time horizon of the simulations was 100 years; the time step was one week (0.02 years), small enough to capture the finer grain of decision-making by the fishers as well as the population dynamics of the species (Ford 1999). The model was built using the Vensim software, produced by Ventana Systems, Inc. The parameter values and assumptions in the model were based on data and information collected from the field over the past decade by X. Basurto, and from peer-reviewed literature (Appendix 1). The full list of equations and a copy of the model are provided in Appendices 2 and 3, respectively.

Population growth, driven by two positive, or reinforcing, feedback loops (R1a and R1b), is moderated by two negative, or balancing, feedback loops (B2a and B2b), where an increase in population causes a shrinking of the resources available to the species, which results in fewer young pen shells surviving, and thus a slowing of the population growth (Fig. 2). The carrying capacity of each species was estimated by extrapolating the total number of pen shells found in one sample area to the total area and applying the average 2:1 ratio of *Pr* to *At* (based on field data collected by X. Basurto for three time periods: 2000–2001, 2004–2006, and 2009–2012). This nonetheless remained a first-order approximation because there were not sufficient data on habitat and physiological characteristics of the two species to produce more reliable estimates (Pineda 2000). The survival function for newly recruited individuals was a smooth curve based on the Beverton-Holt equation used to model fish populations, wherein recruitment was based primarily on the population of mature, reproducing individuals (Ricker 1975) (Fig. 3A).

Seri social-ecological rules

The Seri rely on several institutional rules in managing their fishery; in addition, the fishery is subject to certain ecological constraints imposed by its biophysical setting. We labeled these rules and constraints, which collectively govern harvesting patterns in the fishery, as social-ecological rules. We present the social-ecological rules as they are explicitly represented in the model. Social-ecological rules are not a representation of how the Seri think of institutional constraints

Fig. 2. Causal loop diagram showing the feedback loops and key variables in the model. Each arrow has a positive sign (+) or negative sign (–), which signifies whether an increase in the variable at the root of the arrow creates an increase or decrease in the variable at the terminus of the arrow. The variables that were altered in our experiments are italicized, with the stochastic variables also underlined. Variables in the lower half of the figure with < > around them correspond to the identically named variables in the top half; they are repeated to enhance readability. Pr refers to *Pinna rugosa*, At refers to *Atrina tuberculosa*, and CDH refers to Callos de Hacha, or the entire pen shell population, including both species. R: positive, or reinforcing, feedback loop; B: negative, or balancing, feedback loop.
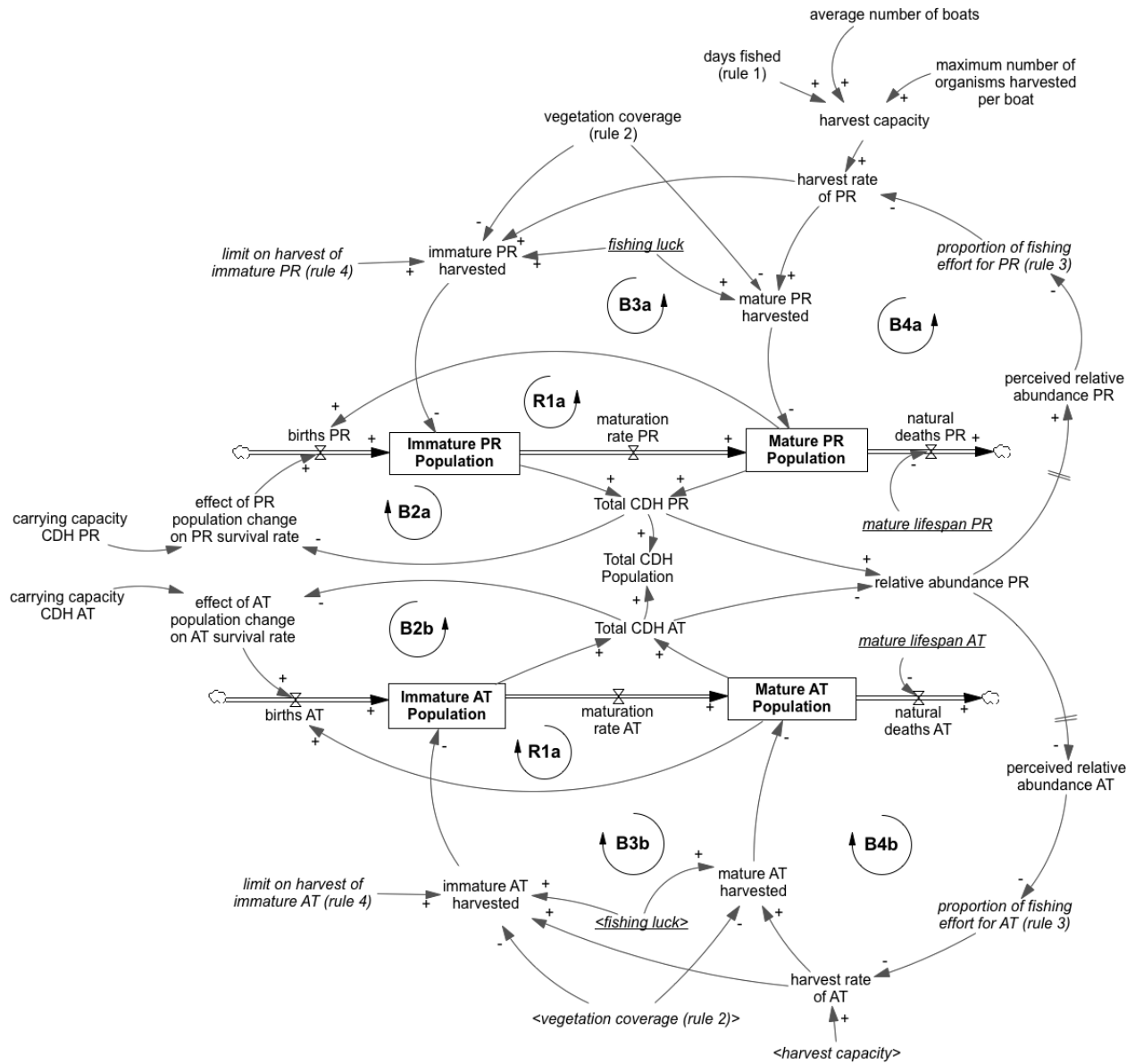
Fig. 3. (A) The survival function for newly recruited individuals is a smooth curve based on the Beverton-Holt equation used to model fish populations, wherein recruitment is based primarily on the population of mature, reproducing individuals. This curve shows survival of newly recruited individuals compared to the total pen shell population in the model. (B) Type III functional response curve that drives the foraging behavior of the fishers in switching their relative effort between the two pen shell species. CDH refers to Callos de Hacha, or the entire pen shell population, including both species *Atrina tuberculosa* and *Pinna rugosa*.
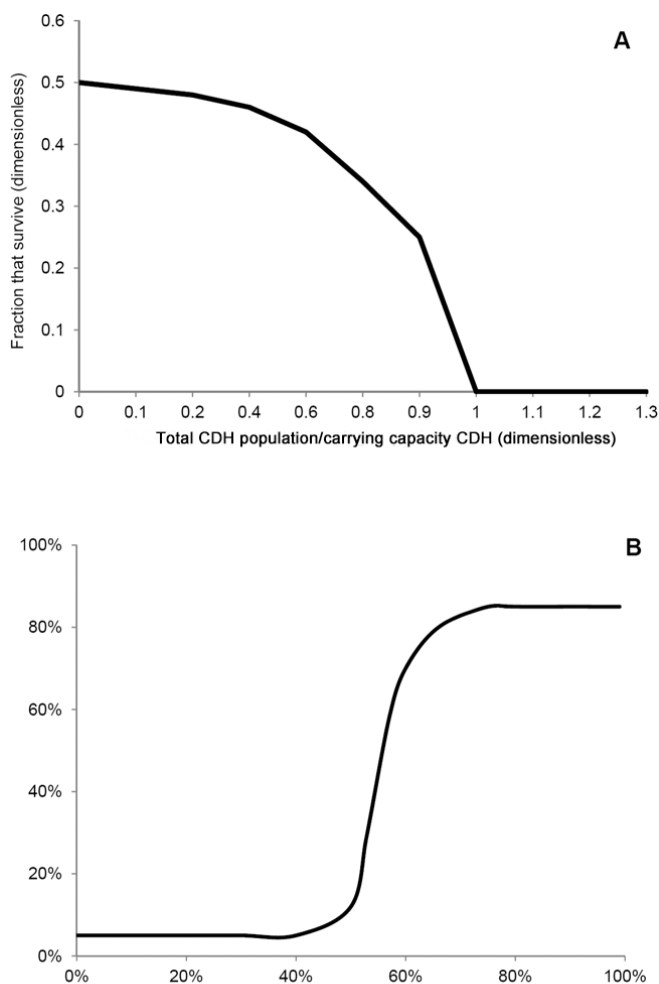
they design and articulate to outsiders. Rather, these rules represent the authors' translation and interpretation of how key institutional and ecological constraints may affect the dynamics of the social-ecological system in question:

1. a rule governing the number of days spent harvesting pen shells each year;

2. a set of rules governing areas that are off-limits;

3. a rule governing the allocation of harvest effort between the two species;

4. a set of rules governing the harvest of immature individuals;

5. a set of rules governing outsider fishing boats in the territory and how those outsiders operate while in the fishery.

Rule 1 was set to 50%, or half the days of the year (it could be increased or decreased to compensate for environmental shocks, as was examined in Bueno and Basurto 2009). Rule 2 represents the rules that render certain areas off-limits for commercial harvesting, and includes both ecological constraints, such as seagrass beds, which are difficult and hazardous areas in which to gather pen shells, and social rules that reserve sandbars for subsistence fishing, mainly by women, elders, children, and adults without access to diving gear. When eelgrass (*Zostera marina*) is present in the channel, the pen shell beds are covered and therefore out of reach for harvesting (Basurto 2008). The limits on harvesting within seagrass beds were implemented in the model through a mechanism that reduces the harvest by a percentage equal to that of the area covered by eelgrass during the eight months of each year. The limits on harvesting from sandbars were implemented by considering the sandbars to be permanently outside the spatial coverage of the model (Bueno and Basurto 2009).

Rule 3 involves the balancing feedback loops B3a, B3b, B4a, and B4b in Fig. 2. Seri fishers report that they can, and do, distinguish between the two species on the seafloor and allocate their harvesting effort between the two according to their relative abundance. While we hypothesized that this method helps keep both populations from collapsing, we do not assert that the Seri do this out of altruism or long-term decision-making. There is a higher financial gain per unit effort for harvesting *At*. *At* can only be sold fresh, and thus commands a much higher price than *Pr*, which is often sold frozen. Seri fishers would thus preferentially target *At* for harvesting if it is sufficiently abundant. When *At* is much less abundant, fishers either target the two species equally or even preferentially harvest *Pr* because it is more beneficial to harvest *Pr* rather than seek scarce *At*. We represented this strategy as a functional form similar to Holling's Type III functional response curve. Our formulation of this rule was similar to other optimal foraging theory (OFT) models that assume a forager aims to maximize short-term gains, whether in energy (for animals and subsistence hunters/fishers) or revenue (for commercial artisanal fishers) (Stephens and Krebs 1986, Aswani 1998). Because fishers switch between only two species, the same OFT curve drives harvesting effort for both species (Fig. 3B). As relevant data become available, additional factors could be incorporated into this formulation,

such as monetary units, or net effort expended in terms of kilocalories (Aswani 1998, Béné and Tewfik 2001).

Unlike some artisanal fisheries, the Seri do not have explicit rules that forbid the harvesting of immature individuals; nonetheless, empirical data indicate that immature individuals generally make up less than 30% of the catch. Rule 4 represents the combination of factors that keep immature harvests at this level or below, including both the Seri preference for harvesting, and ease of locating, larger individuals of either species. Due to its slower growth rate, we hypothesized that *Pr* would be less resilient in our model, absent of countervailing forces. So, as a scenario analysis, we also studied the effect on the system of modifying Rule 4 to specifically ban harvesting of any immature *Pr*.

The Seri regulate how many outsider boats are allowed in their territory (Rule 5). A Seri fisherman must ride on each outsider boat to ensure it follows the community's rules. The Seri fisherman actively participates in the harvest and reaps a share of the catch, which is customarily determined to be equally distributed among all crew members and the boat owner. The increase in number of boats is one of the main stressors on the fishery, and it is to this increase in harvest pressure that we tested the resilience of our modeled system. Experiments wherein institutional rules 3 and 4 were "turned off" represented cases in which all the new boats were outsiders' boats.

Incorporating stochasticity into the dynamic model
Three key parameters in the model were given stochastic analogues to represent either environmental variability—in the case of variables "lifespan of *At*" and "lifespan of *Pr*"—or variability that relates to drivers of environmental forcing and the social subsystem, in the case of variable "fishing luck." Thus, in our study, environmental variability refers to dynamic demographic variation in recruitment, death, and harvest rates in response to weather, disease, competition, predation, or other factors not captured by the model. The stochasticity dealt with in this model was in some ways different from the stochasticity often studied in resilience science. Usually, stochasticity is used to refer to shocks coming from outside the system, which represents exogenous and hard-to-predict risks. The mature lifetime variables, on the other hand, are endogenous to the system. In the real world, environmental variability is highly correlated over time (e.g., while a very hot day can be followed by a very cold day, it is more likely to be followed by another hot day). Thus, we modeled all three stochastic variables so that the successive values of a variable over time were, while following a random pattern, partly conditioned on the values of that variable in the preceding time points. It is as if the random variability in these variables had inertia, or memory, in which the next value was not independent of the last, as in a traditional random normal Gaussian distribution, but depended on history (Sterman 2000:

917). This type of random process is called pink noise or 1/f noise (Halley 1996).

The literature suggests that *At* and *Pr*, which differ greatly in size, may also differ in lifespan (Baqueiro and Castagna 1988). *At* and related species grow rapidly and reach sexual maturation at 1 year of age (Bueno and Basurto 2009). The genus *Atrina* reaches sexual maturity at ~10 cm in shell length (Ahumada-Sempoal et al. 2002), which suggests that the *At* harvested in the channel had a chance to reproduce at least once before harvesting, as most of them (70.2%, *n* = 3261) measured at least twice the minimum size for sexual maturity (average size = 20.8 cm, SD = 2.53) (based on field data collected by this study for three time periods: 2000–2001, 2004–2006, and 2009–2012). Literature on the lifespan of species similar to *P. rugosa*, e.g., *Spondylus calcifer* and *Pinna nobilis*, suggests that they can reach an age ranging from 12 to 20 years and take 2.5 to 4 years to mature (Vicente et al. 1980, Siletic and Peharda 2003, Cudney-Bueno and Rowell 2008). Thus, in the model, mature lifespans of *At* and *Pr* were normally distributed with a mean of, respectively, 9 years (SD = 2) and 12 years (SD = 3) and time to mature of 1 year and 2 years, respectively, to capture the differences between the species. Because a new cohort of individuals is born each year, the correlation time for both species was set as 1 year.

Fishing luck captures influences on harvest success such as weather conditions, malfunctioning equipment, skill and experience of the crew, or turbidity of the water affecting the divers' harvesting efficiency. Fishing teams tend to choose minimum-risk strategies depending on environmental conditions such as seasonal weather, but that does not guarantee every fishing outing will be a success. We assumed that fishing luck was normally distributed (mean = 1, SD = 0.4) based on the recorded daily variation in harvests collected by X. Basurto and colleagues in 2000, 2001, and 2009. While many factors influence fishing luck, seasonal weather patterns are crucial and more likely to be correlated over time than are some of the other drivers of fishing luck; therefore, the correlation interval of the random variability in fishing luck was 0.25 years.

Validation testing
Prior to conducting our experiments, we built confidence in the model by using several validation tests to ensure an adequate representation of the SES for the purposes of our study. The validation process was a gradual one, dispersed throughout the methodology, beginning with model conceptualization and continuing through experimentation (Barlas 1996). Our model was not expected to provide "point" predictions but rather to capture the broad dynamic patterns of the system (behavioral validation) for the correct reasons (structural validation). Therefore, the structural validity of the model was as important as its behavioral validity. We divided the formal validation work into two phases, following an

established procedure in systems modeling (Barlas 1996). In structural validation tests, we assessed the logical validity of model equations by evaluating them individually and by testing their behavior under extreme conditions. With behavior validation tests, we evaluated the patterns of key variables generated by the model against the available data. The comparison between model-generated values and observed values allowed us to evaluate if the model was an adequate representation of the real-world system. The results of some of these comparisons are discussed in the *Results* section.

Across many disciplines, it has become recognized that expert knowledge is an important and critical component of dynamic-modeling studies (Balci 1994, Lutz and Samir 2010). Therefore, in addition to these empirical tests, one of the co-authors (X. Basurto) contributed his expert knowledge on the Seri fishery extensively during the model building and validation processes.

Hypotheses testing
To test our hypotheses, we compared model runs with deterministic and stochastic lifetime and "fishing luck" variables, and with and without social-ecological rules governing relative foraging effort (Rule 3) and the harvest of immature individuals (Rule 4), for a total of 16 scenarios. The base case was fully deterministic and assumed there were no social-ecological rules in force that distinguished between the two species. In half the scenarios, lifetime was made deterministic by setting *At* lifetime's mean value of 9 years as constant, and *Pr* lifetime's mean value of 12 as constant, and in the other half of the scenarios, lifetime was a stochastic function, as previously described. Fishing luck could be either a stochastic function or an identity function of 1. Rule 3 was active when the fishers varied harvest effort between *At* and *Pr* according to the OFT function from Figure 3B, or was "off" when the relative abundance of the species was not considered. The eight experiments where Rule 4 was active constituted a scenario test where fishers did not harvest immature *Pr*. Each experiment consisted of 10 replications to better capture the breadth of random variability. For each of the 16 experiment scenarios, we conducted two tests—one to test resilience to collapse, and one to test the system's ability to recover from a near-collapsed state (referred to as the "collapse experiments" and the "recovery experiments," respectively).

To test the system's resilience to collapse, we let the system operate with 15 boats, then increased the number of boats at Year 5 and kept it constant for the remaining 95 years (the starting point of 15 boats was consistent with the field data collected by this study during 2000–2001, 2004–2006, and 2009–2012). We ran a multivariate sensitivity analysis for each experiment with 10 replications, and varied the number of additional boats between 0 and 50 to represent the change in fishing pressure. Collapse was defined as the overall pen shell population falling below 10% of carrying capacity in
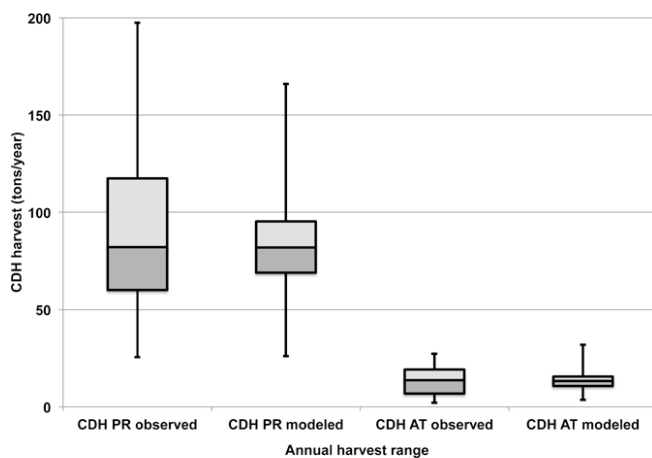
more than 2/3 of the runs for that level of fishing pressure. In order to capture the range of variability, we also recorded the "range" for each collapse experiment—the difference between the number of boats required to cause the overall pen shell population to fall below 10% of carrying capacity in at least one replication and the number of boats required to cause the overall pen shell population to fall below 10% of carrying capacity in each of the 10 runs.

To look at the system's ability to bounce back, we ran a second set of experiments. In each experiment, we increased the number of boats in Year 5 from 15 to a number sufficient to engender eventual collapse, and then 30 years later, we brought the fishing effort back down to 15 boats—representing a scenario in which, for instance, the Seri decide to no longer allow outside fishers into their channel. Because of the wide variation in the critical level of fishing effort across the experiments, one single elevated fishing effort level could not be chosen to engender collapse in all the experiments. To compare like items, we separated the 16 experiments into four groups depending on which social-ecological rules were active or not, and identified the average threshold level, and then ran all four recovery experiments for that set with the same number of boats. Recovery was defined as the first stretch of more than 5 years where the total pen shell population equaled or exceeded the level it was at prior to the increase in fishing pressure in Year 5. As with the collapse experiments, each experiment consisted of 10 replications.

RESULTS
Prior to running any experiments, we compared model results with real-world data for validation purposes. The most detailed observed data were from daily harvests of the two species (by weight). Data collected by X. Basurto in 2000, 2001, and 2009 suggested that the daily harvest of an individual Seri boat crew is, on average, 27 kg of *Pr* and 7 kg of *At*, that there are, on average, 15 Seri boat crews harvesting on any given day, and that crews harvest, on average, 50% of the days in each year. Extrapolating daily harvests into a yearly harvest, with the average fleet of 15 boats fishing 50% of the year, yielded an average (median) yearly harvest of 82 tons of *Pr* and 14 tons of *At*. Our model predicted that a fleet of 15 boats operating in conditions similar to experiment #8 would harvest, on average (median), about 82 tons of *Pr* and 13 tons of *At* each year. Experiment #8, with both stochastic rules and the OFT effort switching rule but with no limitation on harvesting of immature pen shells, most closely resembled the real-world conditions of the Seri fishery during the time period for the observed data. The 75th and 25th percentiles and maximum and minimum (nonoutlier) values of the extrapolated observed harvest yield were also very similar to the model results. The observed and modeled probability distributions are shown in Fig. 4.

Fig. 4. Validation of the pen shell harvest in tons per year. Pr refers to *Pinna rugosa*, At refers to *Atrina tuberculosa*, and CDH refers to Callos de Hacha, or the entire pen shell population. The two box plots on the left show the maximum, 75th percentile, median, 25th percentile, and minimum harvest values (excluding outliers) as extrapolated from the observed harvest data. The box plots at right show the distribution for harvest tonnage as calculated by the model over a 100-year period under conditions similar to experiment #8 (the experiment with the most realistic base conditions).

Fig. 5. (A) Four examples of model runs showing the collapse trajectory of the total Callos de Hacha (CDH), or pen shell, population in different experiments. (B) Five example runs showing the collapse-and-recovery of the total CDH population in different experiments. Note that experiments #1 and #4 do not ever fully recover: this is because the *Pinna rugosa* (*Pr*) population has collapsed, as shown in Fig. 5C. (C) Four example runs showing the collapse-and-recovery of the *Pr* population in different experiments. The presence of either institutional Rule 3, the optimal foraging theory effort switching rule (experiment #5), or the institutional rule for limiting the harvesting of immature *Pr* (experiment #12) is sufficient to prevent collapse of *Pr*. CDH refers to Callos de Hacha, or pen shell, including either *Atrina tuberculosa* or *Pr*.

In the first set of experiments on the collapse threshold, there appeared to be four distinct cohorts of experiments, depending on which social-ecological rules were in place (Table 1). In the base-case scenario (experiment #1), it took 23 boats to overharvest the system to the point of collapse; this did not change with the addition of either one of the stochastic rules (experiments #2 and #3), and with both stochastic rules active, a collapse threshold of 24 boats resulted (experiment #4). As expected, the system was most resilient with all social-ecological rules in place. With both rules in place (experiments #13–#16), it took 50–52 boats to collapse the fishery; with only Rule 3 in place (experiments #5–#8), it took 40–42 boats; and with only Rule 4 in place (experiments #9–#12), it took 26–27 boats. Several sample runs illustrating collapse scenarios in different experiments are shown in Fig. 5A.

The recovery experiments likewise sorted into the four cohorts based on the institutional rules (Table 2). With both institutional rules active, the system recovered in 5.6–13 years (average recovery of 10.3–12.4 years). When the fishers took into account the relative abundance of the species (Rule 3), but did not limit the harvest of immature *Pr*, the system recovered in 18.2–29.0 years (average recovery of 19.2–22.6
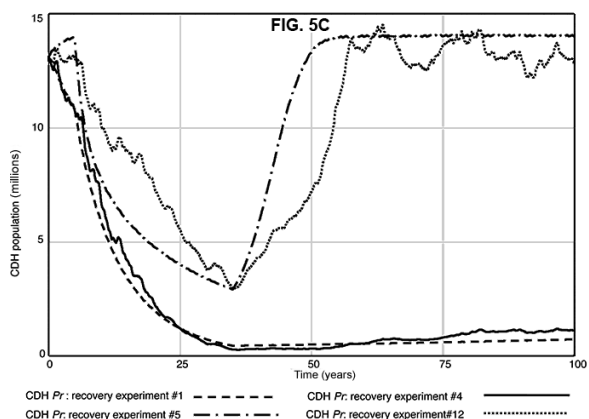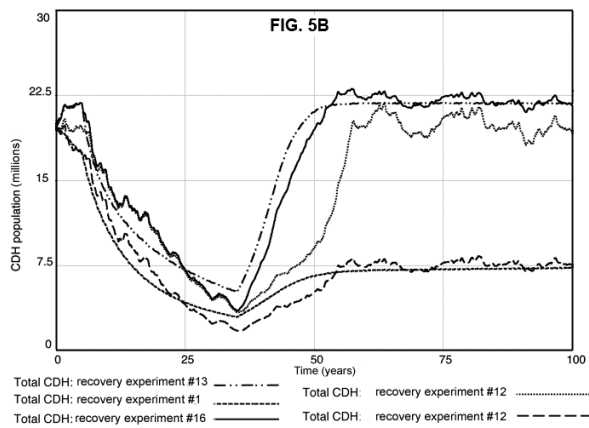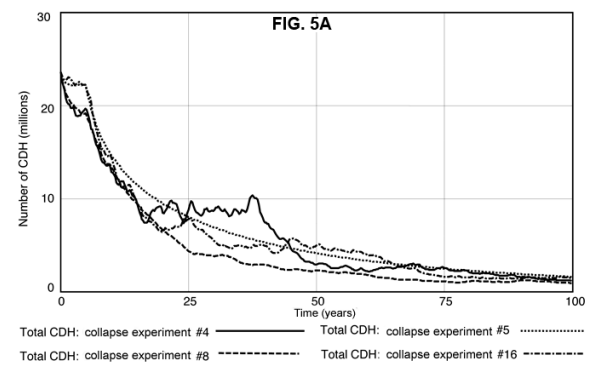
Table 1. Collapse experiments, sorted by collapse threshold. The letter x indicates which stochastic variables and/or institutional rules are active in each experiment. Range represents the difference between the number of boats needed to trigger collapse in one stochastic run and the number of boats needed to trigger collapse in every stochastic run.

Exp. no.	Stochastic adult lifetime	Stochastic fishing luck	Rule 3: Seri optimal foraging theory rule	Rule 4: Seri *Pinna rugosa* immature harvest rule	No. of boats to collapse	Range (boats)	Range (%)
14	x		x	x	52	3	6%
16	x	x	x	x	52	4	8%
15		x	x	x	51	3	6%
13			x	x	50	0	0%
6	x		x		42	1	2%
8	x	x	x		42	3	7%
7		x	x		41	1	2%
5			x		40	0	0%
10	x			x	27	2	7%
12	x	x		x	27	2	7%
9				x	26	0	0%
11		x		x	26	1	4%
4	x	x			24	2	8%
1					23	0	0%
2	x				23	1	4%
3		x			23	1	4%

Table 2. Recovery experiments, sorted by average recovery period. The letter x indicates which stochastic variables and/or institutional rules are active in each experiment. Range is the difference between the fastest and slowest recovery time.

Exp. no.	Stochastic adult lifetime	Stochastic fishing luck	Rule 3: Seri optimal foraging theory rule	Rule 4: Seri *Pinna rugosa* immature harvest rule	Maximum no. of boats	Fastest recovery (years)	Average recovery (years)	Slowest recovery (years)	Range (years)	Range (%)
16	x	x	x	x	52	5.6	10.3	14.9	9.3	90%
14	x		x	x	52	6.3	10.4	15.5	9.2	88%
13			x	x	52	12.1	12.1	12.1	0.0	0%
15		x	x	x	52	10.2	12.4	13.0	2.8	23%
5			x		41	18.2	18.2	18.2	0.0	0%
8	x	x	x		41	10.3	19.2	28.8	18.4	96%
6	x		x		41	10.6	22.4	26.4	15.8	71%
7		x	x		41	14.4	22.6	29.9	15.5	69%
10	x			x	27	20.4	37.3	53.1	32.7	88%
9				x	27	44.6	44.6	44.6	0.0	0%
11		x		x	27	24.6	48.4	53.5	28.9	60%
12	x	x		x	27	12.6	53.2	61.5	48.9	92%
1					23	N/A	N/A	N/A	N/A	N/A
2	x				23	N/A	N/A	N/A	N/A	N/A
3		x			23	N/A	N/A	N/A	N/A	N/A
4	x	x			23	N/A	N/A	N/A	N/A	N/A

years). With only a rule to limit harvesting of immature *Pr* active, the system recovered in 20.3–61.5 years (average recovery of 27.2–53.2 years). Five different experiment runs are displayed in Figure 5B.

Something very different happened in experiments #1–#4, when neither institutional rule was in force. Without either rule to lower the relative fishing pressure on *Pr*, the *Pr* population, as a result of its longer maturation times, was not sufficiently resilient to recover from the near-collapsed state it reached by year 30, and only the *At* population recovered. However, because *At* was limited by its own carrying capacity, lower than that of *Pr*, the total pen shell population never climbed to the level it was at prior to the increase in fishing pressure (Fig. 5B). Therefore, we recorded results of N/A for recovery experiments #1–#4. Either institutional rule was sufficient to keep *Pr* from collapsing (Fig. 5C).

The stochastic variables did make a small difference in the range of collapse thresholds (Table 3). Because higher collapse thresholds had larger numerical ranges, the range was best measured as a percentage of the average number of boats needed to cause collapse. Again, there were four distinct cohorts. By including stochastic fishing luck while keeping average lifespan deterministic (experiments #3, #7, #11, #15), results ranged 2–6%. When stochastic lifespans were included for both species without any variation for fishing luck (experiments #2, #6, #10, #14), results ranged 4–17%. When both stochastic variables were included (experiments #4, #8, #12, #16), results ranged 7–8%.

The effect of stochasticity was best shown by the range of recovery times for each of the recovery experiments, measured as a percentage of the average recovery time (Table 4). The results were clearly grouped by stochastic rules. Experiments with both stochastic factors had recovery periods that ranged 90–96%; experiments with stochasticity only in lifetime had recovery periods that varied by 7–88%; and experiments with stochasticity only in fishing luck had recovery periods that varied by 23–69%.

DISCUSSION

It is important to be specific about what exactly is being examined ("resilience of what") and against what specific impacts that system's resilience is measured ("resilience to what") (Scheffer et al. 2001). We expressly looked at the Seri community's social-ecological rules as factors that help maintain or degrade resilience; thus, it is the resilience of the Seri pen shell fishery to overfishing that is the subject of this paper. By drawing a larger system boundary around the system, we treated the fishing pressure as an endogenous attribute of the system rather than an exogenous factor of the sort more commonly studied in resilience research (Guttal and Jayaprakash 2007).

Our first hypothesis was that disaggregating the system into two species and incorporating social-ecological rules the Seri use to shift their harvest between the two species would better capture the resilience of the actual system. Our results affirm this hypothesis. By shifting fishing pressure from one species to another, the Seri maintain the fishery longer with more fishers and larger harvests. Compared to the scenarios wherein fishing pressure was applied regardless of species, the experiments where social-ecological rules limited harvesting of immature *Pr* (Rule 4) were, on average, able to withstand three more boats before collapsing, or 12% more than the 23–24 boat baseline; experiments with fishing effort that varied between the two species according to the foraging response curve (Rule 3) were able to withstand an average of 17 extra boats before collapse (75% increase); and experiments with both rules were able to withstand 27–29 extra boats (~120% increase). Furthermore, comparing all runs with social-ecological rules to their counterparts, we found that adding the rules decreased the number of years it takes the system to recover from near-collapse, to as little as 5–13 years.

The results also show the importance of different management strategies for different species. In our model, *Pr*'s longer maturation time and larger immature harvest made it more susceptible than *At* to fishing pressure. In the absence of any management strategy to correct for it, the population of *Pr* is susceptible to an early collapse. However, by either limiting their harvest of immature *Pr* directly (Rule 4) or shifting their relative fishing effort (Rule 3), the Seri can give immature *Pr* a greater chance of growing to maturity. More importantly, our results show that a carpet ban on immature harvesting, as was modeled in our scenario test with Rule 4, is not needed to prevent either species' collapse, so long as the fishers pay attention to the relative proportion of the two species, and adjust accordingly. Indeed, paying attention to the relative abundance of the two species is a much more effective strategy than a targeted ban on immature harvests. More field studies of *Pr* and *At* would be needed to verify that *Pr* is actually less resilient than *At* in their natural habitat in the absence of Seri rules.

Our second hypothesis was that introducing environmental variability would increase the range of possible outcomes but might also reduce the resilience of the system, on average, by making it more likely that a critical threshold would be crossed. Our findings show that stochasticity does result in an increased range of possible outcomes. The findings also show that stochasticity can marginally increase the resilience of the system. Contrary to our original hypothesis, the experiments show that the stochasticity in the mature lifespan actually increases the resilience of the system, as measured by the amount of fishing pressure it can sustain, but only by one to three additional boats before collapse (only 3–6%), as compared to the deterministic case. However, the pattern is consistent enough that it cannot be dismissed as noise. In the

Table 3. Collapse experiments, sorted by the range of collapse thresholds in different runs (as percent of collapse threshold). The letter x indicates which stochastic variables and/or institutional rules are active in each experiment. Range represents the difference between the number of boats needed to trigger collapse in one stochastic run and the number of boats needed to trigger collapse in every stochastic run.

Exp. no.	Stochastic adult lifetime	Stochastic fishing luck	Rule 3: Seri optimal foraging theory rule	Rule 4: Seri *Pinna rugosa* immature harvest rule	No. of boats to collapse	Range (boats)	Range (%)
4	x	x			24	2	8%
16	x	x	x	x	52	4	8%
12	x	x		x	27	2	7%
8	x	x	x		42	3	7%
10	x			x	27	2	7%
14	x		x	x	52	3	6%
15		x	x	x	51	3	6%
2	x				23	1	4%
3		x			23	1	4%
11		x		x	26	1	4%
7		x	x		41	1	2%
6	x		x		42	1	2%
13			x	x	50	0	0%
5			x		40	0	0%
9				x	26	0	0%
1					23	0	0%

Table 4. Recovery experiments, sorted by range between fastest and slowest recovery in different runs (as percent of recovery period). The letter x indicates which stochastic variables and/or institutional rules are active in each experiment. Range is the difference between the fastest and slowest recovery time.

Exp. no.	Stochastic adult lifetime	Stochastic fishing luck	Rule 3: Seri optimal foraging theory rule	Rule 4: Seri *Pinna rugosa* immature harvest rule	Maximum no. of boats	Fastest recovery (years)	Average recovery (years)	Slowest recovery (years)	Range (years)	Range (%)
8	x	x	x		41	10.3	19.2	28.8	18.4	96%
12	x	x		x	27	12.6	53.2	61.5	48.9	92%
16	x	x	x	x	52	5.6	10.3	14.9	9.3	90%
14	x		x	x	52	6.3	10.4	15.5	9.2	88%
10	x			x	27	20.4	37.3	53.1	32.7	88%
6	x		x		41	10.6	22.4	26.4	15.8	71%
7		x	x		41	14.4	22.6	29.9	15.5	69%
11		x		x	27	24.6	48.4	53.5	28.9	60%
15		x	x	x	52	10.2	12.4	13.0	2.8	23%
13			x	x	52	12.1	12.1	12.1	0.0	0%
5			x		41	18.2	18.2	18.2	0.0	0%
9				x	27	44.6	44.6	44.6	0.0	0%
1					23	N/A	N/A	N/A	N/A	N/A
2	x				23	N/A	N/A	N/A	N/A	N/A
3		x			23	N/A	N/A	N/A	N/A	N/A
4	x	x			23	N/A	N/A	N/A	N/A	N/A

recovery experiments, the differences were more noticeable but not consistent; while the presence of stochastic variables did consistently produce faster recovery times in some runs, it also produced much longer recovery times in other runs, without any consistency in the effect on average recovery time.

The reason stochasticity increases the resilience of the modeled system is due to the dual nature of the reinforcing feedback loops for species recruitment. If the regrowth rate is positive, then the reinforcing loop operates in a growth trajectory and repopulates/sustains the species despite fishing pressure. But if the regrowth rate is negative for a sustained period of time, then the loop enters a collapse trajectory with each year's population being smaller than the last. In a deterministic model, this can create a trap, whereby the population is doomed to die out in the area being covered. However, when mature lifespan is stochastic, there are quite a few time periods where the regrowth rate is not only positive but quite high, as opposed to the deterministic scenario where the regrowth rate, depending on the harvest pressure, ends up being negative or only slightly positive. This finding is consistent with previous studies, which have drawn clear links between natural variability in growth rates and resilience (Ives 1995, Holling and Meffe 1996).

Our systematic analysis affirms that local communities can effectively govern common-pool resources, so long as access is controlled and rules are enforced (Cinti et al. 2010, Cinner 2011). The accord among the Seri social-ecological rules is critical to maintaining a resilient system even in the presence of environmental variability. These rules, rather than aiming to eliminate the variability in the system for the sake of maximizing harvest efficiency, actually protect the system from outside interference and enforce adaptive harvesting that respects the inherent variability in the system.

Our model left out several key areas for future studies. We did not attempt to directly incorporate how fluctuations in sale price affect relative fishing effort. The price data cited in Moreno et al. (2005) and that we collected for three time periods—2000–2001, 2004–2006, and 2009–2012—show that the price range is US$16–20 for *A. tuberculosa* and US$5–6 for *P. rugosa*, which suggests that the price structure is inelastic to supply and demand. The persistent price differential between the two species does impact fishing decisions, and this effect is incorporated into our model via Rule 3, which shifts effort between the two species along an OFT function. The Seri do choose either to allow outside fishers into the channel or to expel them. However, we do not model this fifth institutional rule in our model because it is driven by many complex factors exogenous to our model, such as the success of other Seri enterprises, financial transfers, and the changing demand of outside fishers to enter the channel, which is in turn driven by their local economies. In addition,

more extensive experiments with wider ranges of stochasticity scenarios could also be conducted. The utility of a spatially explicit model representation should also be explored.

CONCLUSION

No one element, but the particular combination of different social-ecological rules and their interaction with the inherent environmental variability of the system, enables the resilience of the Seri artisanal fishery. This is in line with the view that multi-pronged approaches rather than simplistic policy prescriptions are needed in the management of complex systems. Small-scale fisheries or artisanal fisheries are for the most part multi-specific, but the management schemes are often designed as if they were mono-specific. We show that incorporating the variability in the system and the dynamics of each species of concern into the modeling effort can lead towards devising management and policy schemes that more comprehensively take into account factors that ensure a more sustainable future for these fisheries.

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LITERATURE CITED

Ahumada-Sempoal, M. A., S. J. Serrano-Guzmán, and N. Ruiz-García. 2002. Abundancia, estructura poblacional y crecimiento de *Atrina maura* (Bivalvia: Pinnidae) en una laguna costera tropical del Pacífico mexicano. *Revista de Biología Tropical* 50:1091–1100.

Aswani, S. 1998. The use of optimal foraging theory to assess the fishing strategies of Pacific Island artisanal fishers: a

methodological review. Pages 19–26 *in* SPC Traditional Marine Resource Management and Knowledge Information Bulletin.

Balci, O. 1994. Validation, verification, and testing techniques throughout the life cycle of a simulation study. *Annals of Operations Research* 53(1):121–173. http://dx.doi.org/http://dx.doi.org/10.1007/BF02136828

Baqueiro, E., and M. Castagna. 1988. Fishery and culture of selected bivalves in Mexico: past, present and future. *Journal of Shellfish Research* 7(3):433–443.

Barlas, Y. 1996. Formal aspects of model validity and validation in system dynamics. *System Dynamics Review* 12:183–210. http://dx.doi.org/10.1002/(SICI)1099-1727(199623)12:3<183::AID-SDR103>3.0.CO;2-4

Basurto, X. 2005. How locally designed access and use controls can prevent the tragedy of the commons in a Mexican small-scale fishing community. *Society & Natural Resources* 18:643–659. http://dx.doi.org/10.1080/08941920590959631

Basurto, X. 2006. Commercial diving and the Callo de Hacha fishery in Seri territory. *Journal of the Southwest* 48:189–209.

Basurto, X. 2008. Biological and ecological mechanisms supporting marine self-governance: the Seri callo de hacha fishery in Mexico. *Ecology and Society* 13(2): 20. [online] URL: http://www.ecologyandsociety.org/vol13/iss2/art20/

Basurto, X., A. Cinti, L. Bourillón, M. Rojo, J. Torre, and A. H. Weaver. 2012. The emergence of access controls in small-scale fishing commons: a comparative analysis of individual licenses and common property-rights in two Mexican communities. *Human Ecology* 40(4):597–609. http://dx.doi.org/http://dx.doi.org/10.1007/s10745-012-9508-1

Beisner, B. E., D. T. Haydon, and K. Cuddington. 2003. Alternative stable states in ecology. *Frontiers in Ecology and Environment* 1:376–382. http://dx.doi.org/10.1890/1540-9295(2003)001[0376:ASSIE]2.0.CO;2

Béné, C. 2006. *Small-scale fisheries: assessing their contribution to rural livelihoods in developing countries*. Food and Agriculture Organization of the United Nations, Rome, Italy.

Béné, C., and A. Tewfik. 2001. Fishing effort allocation and fisherman's decision making process in a multi-species small-scale fishery: analysis of the conch and lobster fishery in Turks and Caicos Islands. *Human Ecology* 29:157–186. http://dx.doi.org/10.1023/A:1011059830170

Berkes, F., R. Mahon, P. McConney, R. Pollnac, and R. Pomeroy. 2001. *Managing small-scale fisheries: alternative directions and methods*. International Development Research Centre, Ottawa, Ontario, Canada.

Bueno, N., and X. Basurto. 2009. Resilience and collapse of artisanal fisheries: a system dynamics analysis of a shellfish fishery in the Gulf of California, Mexico. *Sustainability Science* 4:139–149. http://dx.doi.org/10.1007/s11625-009-0087-z

Cashore, B., and M. Howlett. 2007. Punctuating which equilibrium? Understanding thermostatic policy dynamics in Pacific Northwest forestry. *American Journal of Political Science* 51(3):532–551. http://dx.doi.org/10.1111/j.1540-5907.2007.00266.x

Cinner, J. E. 2011. Social-ecological traps in reef fisheries. *Global Environmental Change* 21:835–839. http://dx.doi.org/10.1016/j.gloenvcha.2011.04.012

Cinner, J. E., T. R. McClanahan, N. A. J. Graham, T. M. Daw, J. Maina, S. M. Stead, A. Wamukota, K. Brown, and O. Bodin. 2012. Vulnerability of coastal communities to key impacts of climate change on coral reef fisheries. *Global Environmental Change* 22:12–20. http://dx.doi.org/10.1016/j.gloenvcha.2011.09.018

Cinti, A., W. Shaw, and J. Torre. 2010. Insights from the users to improve fisheries performance: fishers' knowledge and attitudes on fisheries policies in Bahía de Kino, Gulf of California, Mexico. *Marine Policy* 34:1322–1334. http://dx.doi.org/10.1016/j.marpol.2010.06.005

Cudney-Bueno, J. R., and K. Rowell. 2008. Establishing a baseline for management of the rock scallop *Spondylus calcifer* (Carpenter 1857): growth and reproduction in the Upper Gulf of California, Mexico. *Journal of Shellfish Research* 27:625–632. http://dx.doi.org/10.2983/0730-8000(2008)27[625:EABFMO]2.0.CO;2

Defeo, O., and J. C. Castilla. 2005. More than one bag for the world fishery crisis and keys for co-management successes in selected artisanal Latin American shellfisheries. *Reviews in Fish Biology and Fisheries* 15:265–283. http://dx.doi.org/10.1007/s11160-005-4865-0

Ford, A. 1999. *Modeling the environment: an introduction to system dynamics modeling of environmental systems*. Island Press, Washington, D.C., USA.

Freire, J., and A. García-Allut. 2000. Socioeconomic and biological causes of management failures in European artisanal fisheries: the case of Galicia (NW Spain). *Marine Policy* 24:375–384. http://dx.doi.org/10.1016/S0308-597X(00)00013-0

Gelcich, S., T. P. Hughes, P. Olsson, C. Folke, O. Defeo, M. Fernández, S. Foale, L. H. Gunderson, C. Rodríguez-Sickert, M. Scheffer, R. S. Steneck, and J. C. Castilla. 2010. Navigating transformations in governance of Chilean marine coastal resources. *Proceedings of the National Academy of Sciences of the United States of America* 107(39):16794–16799. http://dx.doi.org/10.1073/pnas.1012021107

Güneralp, B., and Y. Barlas. 2003. Dynamic modelling of a shallow freshwater lake for ecological and economic sustainability. *Ecological Modelling* 167:115–138. http://dx.doi.org/10.1016/S0304-3800(03)00172-8

Gutiérrez, N. L., R. Hilborn, and O. Defeo. 2011. Leadership, social capital and incentives promote successful fisheries. *Nature* 470:386–389. http://dx.doi.org/10.1038/nature09689

Guttal, V., and C. Jayaprakash. 2007. Impact of noise on bistable ecological systems. *Ecological Modelling* 201:420–428. http://dx.doi.org/10.1016/j.ecolmodel.2006.10.005

Halley, J. M. 1996. Ecology, evolution and 1/f-noise. *Trends in Ecology & Evolution* 11:33–37. http://dx.doi.org/http://dx.doi.org/10.1016/0169-5347(96)81067-6

Holling, C. S., and G. K. Meffe. 1996. Command and control and the pathology of natural resource management. *Conservation Biology* 10:328–337. http://dx.doi.org/10.1046/j.1523-1739.1996.10020328.x

Ives, A. R. 1995. Measuring resilience in stochastic systems. *Ecological Monographs* 65:217–233. http://dx.doi.org/10.2307/2937138

Ludwig, D., R. Hilborn, and C. Walters. 1993. Uncertainty, resource exploitation, and conservation: lessons from history. *Science* 260:17–36. http://dx.doi.org/10.1126/science.260.5104.17

Lutz, W., and K. C. Samir. 2010. Dimensions of global population projections: what do we know about future population trends and structures? *Philosophical Transactions of the Royal Society B: Biological Sciences* 365(1554):2779–2791. http://dx.doi.org/http://dx.doi.org/10.1098/rstb.2010.0133

McClanahan, T. R., N. A. J. Graham, M. A. MacNeil, N. A. Muthiga, J. E. Cinner, J. H. Bruggemann, and S. K. Wilson. 2011. Critical thresholds and tangible targets for ecosystem-based management of coral reef fisheries. *Proceedings of the National Academy of Sciences of the United States of America* 108:17230–17233. http://dx.doi.org/10.1073/pnas.1106861108

Moreno, C., J. Torre, L. Bourillón, M. Durazo, A. H. Weaver, R. Barraza, and R. Castro. 2005. Estudio y evaluación de la pesquería de callo de hacha (*Atrina tuberculosa*) en la Región de Bahía de Kino, Sonora y Recomendaciones para su Manejo. Page 27. Reporte interno.

Pauly, D. 2006. Major trends in small-scale marine fisheries, with emphasis on developing countries, and some implications for the social sciences. *Maritime Studies (MAST)* 4:7–22.

Pineda, J. 2000. Linking larval settlement to larval transport: assumptions, potentials and pitfalls. *Oceanography of the Eastern Pacific* 1:84–105.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. *Bulletin of the Fisheries Research Board of Canada* 191:1–382.

Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. *Nature* 413:591–596. http://dx.doi.org/10.1038/35098000

Shelton, A. O., and M. Mangel. 2011. Fluctuations of fish populations and the magnifying effects of fishing. *Proceedings of the National Academy of Sciences of the United States of America* 108:7075–7080. http://dx.doi.org/10.1073/pnas.1100334108

Siletic, T., and M. Peharda. 2003. Population study of the fan shell Pinna nobilis L. in Malo and Veliko Jezero of the Mljet National Park (Adriatic Sea). *Scientia Marina* 67(1):91–98.

Stephens, D. W., and J. R. Krebs. 1986. *Foraging theory*. Princeton University Press, Princeton, New Jersey, USA.

Sterman, J. D. 2000. *Business dynamics: systems thinking and modeling for a complex world*. Irwin/McGraw-Hill, Boston, Massachusetts, U.S.A.

Torre-Cosío, J., L. Bourillón-Moreno, A. Meking-López, and P. Ramírez-García. 2003. Distributional patterns of an annual eelgrass, *Zostera marina*, population in the Gulf of California. *Gulf of Mexico Science* 21:136.

Vicente, N., J. Moreteau, and P. Escoubet. 1980. Etude de l'evolution d'une population de Pinna nobilis L. (mollusque eulamellibranche) au large de l_anse de la Palud (Parc National sous-marin de Port-Cros). *Travaux Scientifiques du Parc national de Port-Cros* 6:39–68.

Walker, B., C. S. Holling, S. R. Carpenter, and A. Kinzig. 2004. Resilience, adaptability and transformability in social–ecological systems. *Ecology and Society* 9(2): 5. [online] URL: http://www.ecologyandsociety.org/vol9/iss2/art5/

Young, O. R. 2010. Institutional dynamics: resilience, vulnerability, and adaptation in environmental and resource regimes. *Global Environmental Change* 20:378–385. http://dx.doi.org/10.1016/j.gloenvcha.2009.10.001

Appendix 1:
Parameter estimates used in the model, with brief explanations, estimates, and citations.

Parameter Name	Attribute of System	Estimate	Units	Citation and/or Description
Algae	Percentage of seafloor covered by algae when algae are in season (during 1/3 of year).	0.06	Dimensionless	Torre-Cosio et al. 2003; Basurto 2008 cited in Bueno and Basurto 2009: 143
Fecundity Rate	This variable represents the number of individuals (baby mollusks) produced by a female mollusk over her lifetime.	20	Dimensionless	Bueno & Basurto 2009; 144
Average organism per person per day	Number of organisms caught per fisher per day.	0.54	Thousand mollusks/person/day	Bueno & Basurto 2009; 144
Average Seri Boats	Average number of Seri boats at start of model run, changed at year 5 for scenario testing.	15	boats/year	Basurto personal counts in two multi-year periods: 1998-2001 and 2009-2012
Average number of organisms caught per boat per day	Average number of organisms caught per boat per day.	2.16	Thousand mollusks/boat/day	Bueno & Basurto 2009
Carrying Capacity At	Carrying Capacity for A. tuburculosa; is 1/3 of the 24,500 carrying capacity for CDH from the Bueno and Basurto model.	8,167	Thousand mollusks	Bueno and Basurto 2009; 144
Carrying capacity Pr	Carrying Capacity for A. tuburculosa; is 2/3 of the 24,500 carrying capacity for CDH from the Bueno and Basurto model.	16,333	Thousand mollusks	Bueno and Basurto 2009; 144
default fisher delay	Delay in fishers' response to changes to relative abundance.	1/12 (=1 month)	year	Interviews to key informants and Basurto personal observations in two multi-year periods: 1998-2001 and 2009-2012.

eelgrass	Percentage of seafloor covered by eelgrass when eelgrass is in season (during 2/3 of the year).	0.22	Dimensionless	Torre-Cosio 2002; Basurto 2008 cited in Bueno and Basurto 2009
Female percent	Percent of population that is female.	0.5	Dimensionless	Estimate based on fisheries counts published in Basurto (2008)
Mean FL	Mean fishing luck; drives pink noise probability distribution function for fishing luck.	1	Dimensionless	Informal interviews with expert fisher key informants by Basurto in 2000, 2001, and 2009
Standard Deviation FL	Standard Deviation for fishing luck; drives pink noise probability distribution function for fishing luck.	0.5	Dimensionless	Informal interviews with expert fisher key informants by Basurto in 2000, 2001, and 2009
Correlation Time FL	Correlation time of pink noise probability distribution function for fishing luck.	0.25 (3 months)	Year	
Initial proportion *Pr*	Percentage of CDH population composed of *Pr*.	2/3	Dimensionless	Informal interviews with expert fisher key informants by Basurto since 1998
Initial immature *At* population	Initial immature *At* population (initial ratio of immature to mature is 1:9).	789	Thousand mollusks	Informal interviews with expert fisher key informants by Basurto since 1998
Initial immature *Pr* population	Initial immature *Pr* population.	1,579	Thousand mollusks	Informal interviews with expert fisher key informants by Basurto since 1998
Initial mature *At* population	Initial mature *At* population.	7,105	Thousand mollusks	Informal interviews with expert fisher key informants by Basurto since 1998
Initial mature *Pr* population	Initial mature *Pr* population.	14,209	Thousand mollusks	Informal interviews with expert fisher key informants by Basurto since 1998
Initial *At* harvested	Starting point for the tonnage harvest of *At*; needed for delay to function.	23	Tons/year	

Initial *Pr* harvested	Starting point for the tonnage harvest of *Pr*; needed for delay to function.	14	Tons/year	
Mean *At*	Drives pink noise distribution function for mature *At* lifetime; when model in deterministic mode this becomes the adult lifespan.	9	Year	Discussed in text. See Mean *Pr*
Standard Deviation *At*	Drives pink noise distribution function for mature *At* lifetime.	2	Year	
Correlation Time *At*	Drives pink noise distribution function for mature *At* lifetime.	1	Year	
Mean *Pr*	Drives pink noise distribution function for mature *Pr* lifetime; when model in deterministic mode this becomes the adult lifespan.	12	year	Vicente et al. 1980; Siletic and Peharda 2003; Cudney-Bueno and 2008; discussed in text
Standard Deviation *Pr*	Drives pink noise distribution function for mature *Pr* lifetime.	3	Year	
Correlation Time *Pr*	Drives pink noise distribution function for mature *Pr* lifetime.	1	Year	
Number of immature *At* per kg	Used to convert immature *At* harvest numbers, measured in thousand mollusks/year, into metric tons/year.	60	Thousand mollusks/ton. (=Mollusks/kg)	Basurto 2006; 193, informal interviews with expert fisher key informants by Basurto, and catch counts conducted by Basurto in 2009
Number of immature *Pr* per kg	Used to convert immature *Pr* harvest numbers, measured in thousand mollusks/year, into metric tons/year.	40	Thousand mollusks/ton. (=Mollusks/kg)	Basurto 2006; 193, informal interviews with expert fisher key informants by Basurto, and catch counts conducted by Basurto in 2009

Number of mature *At* per kg	Used to convert mature *At* harvest numbers, measured in thousand mollusks/year, into metric tons/year.	30	Thousand mollusks/ton. (=Mollusks/kg)	Basurto 2006; 193, informal interviews with expert fisher key informants by Basurto, and catch counts conducted by Basurto in 2009
Number of mature *Pr* per kg	Used to convert mature *Pr* harvest numbers, measured in thousand mollusks/year, into metric tons/year.	20	Thousand mollusks/ton. (=Mollusks/kg)	Basurto 2006; 193, informal interviews with expert fisher key informants by Basurto, and catch counts conducted by Basurto in 2009
Number of people/boat	Crew of one boat, usually contains only one diver plus three other crewmembers.	4	people/boat	Bueno & Basurto 2009
Rule 1 days fished	Percentage of year fished.	0.5	Year	Bueno & Basurto 2009
Rule 4 *At* immature harvest	Lack of any enforced limitation on the harvesting of immature *At*.	1	Dimensionless (percentage)	Bueno & Basurto 2009
Rule 4 *Pr* immature harvest	No allowed take of immature *Pr* when active.	0 when rule 4 active; 1 otherwise	Dimensionless (percentage)	Catch counts and underwater harvesting observations in the field by Basurto in two multi-year time periods: 1998-2001 and 2009-2012.
OFT function in terms of *Pr*	Type III functional response curve for distributing fishing effort for *Pr* and *At* based on perceived proportion of *Pr* in the underwater CDH. Effort for *At* is 1 minus the output of this function.	[(0,0)-(1,1)],(0,0.05),(0.05,0.05),(0.3,0.05),(0.4,0.05),(0.5,0.12),(0.53,0.3),(0.57,0.58),(0.6,0.7),(0.66,0.8),(0.75,0.85),(1,0.85)	Dimensionless (percentage)	

Survival rate function	A smoothed Beverton-Holt equation function of the survival rate of newly born CDH based on the total CDH population / carrying capacity.	[(0,0)-(1.5,0.6)],(0,0.5),(0.1,0.49),(0.2,0.48),(0.4,0.46),(0.6,0.42),(0.8,0.34),(0.9,0.25),(0.95,0.15),(1,0),(1.5,0),(2,0)	Dimensionless	Bueno and Basurto 2009, modified
time to mature *At*	length of time for *At* to reach reproductive age.	1	year	Bueno and Basurto 2009; Basurto 2008; discussed in text
time to mature *Pr*	length of time for *Pr* to reach reproductive age.	2	year	Cudney-Bueno and Rockwell 2008 (2.5-4 years); discussed in text
Noise Seed	Noise seeds for the 10 repetitions in each experiment scenario; ensures randomness.	1,11,21,31,41,51,61,71,81,91	Dimensionless	
Time Step	Time step of model.	0.02 (=1 week)	Year	

Appendix 2: Model equations

The model was built using the Vensim software, produced by Ventana Systems, Inc. (www.vensim.com). Vensim PLE is freely available, and is required to read, modify, and run the model.

Immature PR Population= INTEG (
        births PR-maturation rate PR-immature PR harvested,initial CDH population*Initial Proportion PR*immature ratio)
thousand molluscs

Mature PR Population= INTEG (
        maturation rate PR-natural deaths PR-mature PR harvested,initial CDH population*Initial Proportion PR*(1-immature ratio))
thousand molluscs

Mature AT Population= INTEG (
        maturation rate AT-natural deaths AT-mature AT harvested,initial CDH population*(1-Initial Proportion PR)*(1-immature ratio))
thousand molluscs

Immature AT Population= INTEG (
        births AT-maturation rate AT-immature AT harvested,initial CDH population*(1-Initial Proportion PR)*immature ratio)
thousand molluscs

immature ratio = 0.1
Dmnl

stable CDH population with 15 boats=initial CDH population
thousand molluscs

population effect AT=surviving rate function (Total CDH AT/carrying capacity AT)
Dmnl

population effect PR=surviving rate function (Total CDH PR/carrying capacity PR)
Dmnl

Seri average boats=initial boats*(1-outsider boat percentage)+PULSE(5 , 100)*(more boats*(1-outsider boat percentage))
boat/Year
Average number of boats at start of model run; pulse at year 5 with more Seri boats for scenario testing

outsider average boats=initial boats*outsider boat percentage+PULSE(5 , 100)*(more boats*outsider boat percentage)
boat/Year
Number of outsider boats in fishery, with pulse at 25 years of more outsider boats

outsider boat percentage=IF THEN ELSE("Rule 3 On?", 0, 1)

final boats=15
boats/Year

"Stochastic Adult Lifetime?"=0
Dmnl

mature lifespan distribution AT=IF THEN ELSE("Stochastic Adult Lifetime?"=1, Pink Noise AT, 9)
years

more boats=final boats-initial boats

boats/Year [0,50,1]

"Rule 4 On?"=0
Dmnl

rule 4 PR immature harvest=IF THEN ELSE("Rule 4 On?"=1, 0, 1)
Dmnl
0 to turn rule on at 100%, 1 to turn rule off

fishing luck distribution=IF THEN ELSE("Stochastic Fishing Luck?"=1, Pink Noise FL, 1)
Dmnl

mature lifespan distribution PR=IF THEN ELSE("Stochastic Adult Lifetime?"=1,Pink Noise PR,12)
years

"Stochastic Fishing Luck?"=0
Dmnl

"Rule 3 On?"=0
Dmnl

boats to collapse=IF THEN ELSE((Total CDH Population/carrying capacity CDH)<0.1, (Seri average
boats+outsider average boats), 0)
boat/Year

recovery=IF THEN ELSE(Total CDH Population>stable CDH population with 15 boats,1, 0)
Dmnl

fecundity rate AT=fecundity rate PR
Dmnl

Change in Pink Noise Fec=(White Noise Fec-Pink Noise Fec)/Correlation Time Fec
Dmnl

Standard Deviation Fec=5
Year

White Noise Fec=20*(White Noise AT/9)
Year

births AT=Mature AT Population*female percent*(fecundity rate AT/mature lifespan distribution AT)*population effect AT
thousand molluscs/Year

Correlation Time Fec=1
Year

Pink Noise Fec= INTEG (Change in Pink Noise Fec,Mean Fec)
Year

fecundity rate PR=20
Dmnl

Mean Fec=20
Year

White Noise PR=12*(White Noise AT/9)
Year

White Noise FL=Mean FL+
        (((Standard Deviation FL^2)*
        ((2-(TIME STEP/Correlation Time FL)) / (TIME STEP/Correlation Time FL)))^0.5)*

RANDOM NORMAL(-Mean FL,Mean FL,0, 1, NOISE SEED)
Dmnl

Change in Pink Noise FL=(White Noise FL-Pink Noise FL)/Correlation Time FL
Dmnl/Year

Standard Deviation FL=0.5
Dmnl

Mean FL=1
Dmnl

Pink Noise FL= INTEG (Change in Pink Noise FL,Mean FL)
Dmnl

Correlation Time FL=0.25
Year

Change in Pink Noise AT=(White Noise AT-Pink Noise AT)/Correlation Time AT
Dmnl

Change in Pink Noise PR=(White Noise PR-Pink Noise PR)/Correlation Time PR
Dmnl

Mean AT=9
Year

Pink Noise AT= INTEG (Change in Pink Noise AT,Mean AT)
Year

Pink Noise PR= INTEG (Change in Pink Noise PR,Mean PR)

Year

White Noise AT=Mean AT+
    (((Standard Deviation AT^2)*
    ((2-(TIME STEP/Correlation Time AT)) / (TIME STEP/Correlation Time AT)))^0.5)*
    RANDOM NORMAL(-Mean AT,Mean AT+40,0, 1, NOISE SEED)
Year

natural deaths PR=Mature PR Population / mature lifespan distribution PR
thousand molluscs/Year

Correlation Time AT=1
Year

Correlation Time PR=1
Year

regrowth and density=regrowth rate CDH/"Total CDH Population/Carrying Capacity"
Dmnl

Standard Deviation PR=3
Year

Standard Deviation AT=2
Year

Mean PR=12
Year

rule 3 proportion of fishing effort for AT=1-OFT function in terms of PR(perceived relative abundance PR)

Dmnl

rule 3 proportion of fishing effort for PR=OFT function in terms of PR(perceived relative abundance PR)
Dmnl

to market=total CDH harvested in tons per year
tons/Year

Seri Harvet Rate=Seri harvest rate of AT+Seri harvest rate of PR
thousand molluscs/Year

total CDH harvested in tons per year= INTEG (annual total CDH harvested in tons-to market, 66)
tons/Year

Seri harvest rate of PR=Seri harvest capacity*rule 3 proportion of fishing effort for PR
thousand molluscs/Year

Seri harvest rate of AT=Seri harvest capacity*rule 3 proportion of fishing effort for AT
thousand molluscs/Year

immature PR harvested=((outsider harvest rate of PR+Seri harvest rate of PR)*fishing luck distribution*immature PR density*(1-rule 2 Percentage of Seagrass Coverage))*rule 4 PR immature harvest
thousand molluscs/Year

regrowth rate AT=births AT - natural deaths AT - mature AT harvested
thousand molluscs/Year

regrowth rate PR=births PR-natural deaths PR-mature PR harvested
thousand molluscs/Year

regrowth rate CDH=(births PR+births AT)-(natural deaths PR+natural deaths AT)-(mature AT harvested+mature PR harvested)
thousand molluscs/Year

births PR=Mature PR Population*female percent*(fecundity rate PR/mature lifespan distribution PR)*population effect PR
thousand molluscs/Year

mature AT density=Mature AT Population/carrying capacity CDH
Dmnl

mature PR density=Mature PR Population/carrying capacity CDH
Dmnl

OFT function in terms of PR(
        [(0,0)-
(1,1)],(0,0.05),(0.05,0.05),(0.3,0.05),(0.4,0.05),(0.5,0.12),(0.53,0.3),(0.57,0.58),(0.6,0.7),(0.66,0.8),(0.75,0.85),(1,0.85))
Dmnl

total immature CDH=Immature AT Population+Immature PR Population
thousand molluscs

Total CDH AT=Immature AT Population+Mature AT Population
thousand molluscs

maturation rate AT=Immature AT Population/time to mature AT
thousand molluscs/Year

immature AT density=Immature AT Population/carrying capacity CDH

Dmnl

NOISE SEED=10
Dmnl [0,1000]

immature PR density=Immature PR Population/carrying capacity CDH
Dmnl

time to mature AT=1
Year

mature PR harvested=(outsider harvest rate of PR+Seri harvest rate of PR)*fishing luck
distribution*mature PR density*(1-rule 2 Percentage of Seagrass Coverage)
thousand molluscs/Year

immature AT harvested=((outsider harvest rate of AT+Seri harvest rate of AT)*immature AT
density*fishing luck distribution*(1-rule 2 Percentage of Seagrass Coverage))*rule 4 AT immature
harvest
thousand molluscs/Year

mature AT harvested=(outsider harvest rate of AT+Seri harvest rate of AT)*fishing luck
distribution*mature AT density*(1-rule 2 Percentage of Seagrass Coverage)
thousand molluscs/Year

initial boats=15
boats/Year [0,80,1]

outsider fishing effort=Seri fishing effort
Year

initial AT harvested=23

tons/Year

tons PR harvested per year=DELAY1I(((immature PR harvested/number of immature PR per kg)+(mature PR harvested/number of mature PR per kg)), default delay, initial PR harvested)
tons/Year

tons AT harvested per year=DELAY1I(((immature AT harvested/number of immature AT per kg)+(mature AT harvested/number of mature AT per kg)), default delay, initial AT harvested)
tons/Year

initial PR harvested=14
tons/Year

Outsider harvest capacity=(outsider fishing effort*days per year*number of organisms caught per boat per day*outsider average boats)
thousand molluscs/Year

outsider harvest rate of AT=Outsider harvest capacity
thousand molluscs/Year

outsider harvest rate of PR=Outsider harvest capacity
thousand molluscs/Year

thousand PR harvested per year=mature PR harvested + immature PR harvested
thousand molluscs/Year

thousand AT harvested per year=immature AT harvested + mature AT harvested
thousand molluscs/Year

perceived relative abundance PR=SMOOTH(relative abundance PR,default delay)
Dmnl

default delay=1/12
Year

proportion immature in current AT harvest=IF THEN ELSE(thousand AT harvested per year>0,immature AT harvested/thousand AT harvested per year,0)
Dmnl

proportion immature in current PR harvest=IF THEN ELSE(thousand PR harvested per year>0,immature PR harvested/thousand PR harvested per year,0)
Dmnl

initial CDH population=23683
thousand molluscs

time to mature PR=2
Year

maturation rate PR=Immature PR Population/time to mature PR
thousand molluscs/Year

rule 1 days fished=1*Seri fishing effort
years

total mature CDH=Mature AT Population+Mature PR Population
thousand molluscs

annual total CDH harvested in tons=tons AT harvested per year+tons PR harvested per year
tons/Year

proportion AT of harvest=IF THEN ELSE(annual total CDH harvested in tons>0, tons AT harvested per year/annual total CDH harvested in tons, 0)

Dmnl

proportion of PR of harvest=IF THEN ELSE(annual total CDH harvested in tons>0, tons PR harvested per year/annual total CDH harvested in tons, 0)

Dmnl

natural deaths AT=Mature AT Population / mature lifespan distribution AT

thousand molluscs/Year

Seri harvest capacity=(rule 1 days fished*days per year*number of organisms caught per boat per day*Seri average boats)

thousand molluscs/Year

Maximum annual harvest for all Seri boats in the fishery.

actual proportion PR in current harvest=IF THEN ELSE((thousand AT harvested per year+thousand PR harvested per year)>0, thousand PR harvested per year/(thousand PR harvested per year+thousand AT harvested per year), 0)

Dmnl

relative abundance AT=1-relative abundance PR

Dmnl

Total CDH Population=Total CDH AT + Total CDH PR

thousand molluscs

Total CDH PR=Immature PR Population+Mature PR Population

thousand molluscs

days per year=365

days/Year

relative abundance PR=Total CDH PR/Total CDH Population
Dmnl

"Total CDH Population/Carrying Capacity"=Total CDH Population/carrying capacity CDH
Dmnl

Initial Proportion PR=2/3
Dmnl
Anecdotal evidence from Basurto (unpublished) suggests a PR:AT ratio of 2:1.

number of mature PR per kg=20
thousand molluscs/tons

number of immature PR per kg=RANDOM NORMAL (1,2,1.75,0.2,0)*number of mature PR per kg
thousand molluscs/tons

surviving rate function(
        [(0,0)-
(1.5,0.6)],(0,0.5),(0.1,0.49),(0.2,0.48),(0.4,0.46),(0.6,0.42),(0.8,0.34),(0.9,0.25),(0.95,0.15),(1,0),(1.5,
0),(2,0))
Dmnl

algae=0.06+0.06*PULSE(10, duration) *-decrease in seagrass
Dmnl
Percentage of seafloor covered by algae when algae is in season.

decrease in seagrass=0
Dmnl [0,1,0.25]

duration=200
years

number of organisms caught per boat per day=2.16
thousand molluscs/boat/day

"number of people/boat"=4
person/boat
Crew of one boat. Default in Seri community is 4; one diver plus three other crew members.

"Average organism per person/day"=0.54
thousand molluscs/person/day

number of mature AT per kg=30
thousand molluscs/tons

number of immature AT per kg=RANDOM NORMAL (0,2,1.75,0.2,0)*30
thousand molluscs/tons

rule 4 AT immature harvest=1
Dmnl
0 to turn rule on, 1 to turn rule off. There is no rule preventing the catch of immatures, but for the most part, divers catch very little numbers of immatures because they cannot see them! With no feedbacks or forcing rules, the percentage of immatures caught is equal to their percentage in the overal population, which varies between 20% and 30%. This seems about right; 30% is an upper bound.

Seri fishing effort=0.5
Year

eelgrass=0.22+0.22*PULSE(10, duration)*-decrease in seagrass

Dmnl

percentage of seafloor covered by eelgrass when eelgrass is in season. Commercial Seri fishers do not fish in the eelgrass.

rule 2 Percentage of Seagrass Coverage=PULSE TRAIN(0, 0.67, 1 , 1000)*eelgrass+PULSE TRAIN(0.67 , 0.33 , 1 ,1000)*algae

Dmnl

Field research by Torre-Cosio (2002) and Basurto (2008) reported that, during roughly 8 months of the year, the eelgrass Zostera marina covers 22% of the Infiernillo Channel's sea bottom, and in the remaining months of the year, the algae Caulerpa spp. covers about 6%.

female percent=0.5

Dmnl

carrying capacity CDH=24500

thousand molluscs

carrying capacity AT= carrying capacity CDH*(1-Initial proportion PR)

thousand molluscs

carrying capacity PR= carrying capacity CDH*Initial proportion PR

thousand molluscs

FINAL TIME = 100

Year

INITIAL TIME = 0

Year

TIME STEP = 0.02

Year

Appendix 3. Model

Please click here to download file 'appendix3.mdl'.