Evidence of market-driven size-selective fishing and the mediating effects of biological and institutional factors

Sheila M. W. Reddy,[1,2,7] Allison Wentz,[3,8] Octavio Aburto-Oropeza,[4] Martin Maxey,[3] Sriniketh Nagavarapu,[5] and Heather M. Leslie[6]

[1]*Sustainability Science, The Nature Conservancy, 334 Blackwell St., Suite 300, Durham, North Carolina 27701-2394 USA*
[2]*Environmental Change Initiative, Brown University, Box 1951, Providence, Rhode Island 02912 USA*
[3]*Department of Applied Math, Brown University, 37 Manning Street, Providence, Rhode Island 02912 USA*
[4]*Scripps Institution of Oceanography, University of California–San Diego, La Jolla, California 92093 USA*
[5]*Department of Economics and Center for Environmental Studies, Brown University, Box B, Providence, Rhode Island 02912 USA*
[6]*Department of Ecology and Evolutionary Biology and Center for Environmental Studies, Brown University, Box 1943, Providence, Rhode Island 02912 USA*

Abstract. Market demand is often ignored or assumed to lead uniformly to the decline of resources. Yet little is known about how market demand influences natural resources in particular contexts, or the mediating effects of biological or institutional factors. Here, we investigate this problem by examining the Pacific red snapper (*Lutjanus peru*) fishery around La Paz, Mexico, where medium or "plate-sized" fish are sold to restaurants at a premium price. If higher demand for plate-sized fish increases the relative abundance of the smallest (recruit size class) and largest (most fecund) fish, this may be a market mechanism to increase stocks and fishermen's revenues. We tested this hypothesis by estimating the effect of prices on the distribution of catch across size classes using daily records of prices and catch. We linked predictions from this economic choice model to a staged-based model of the fishery to estimate the effects on the stock and revenues from harvest. We found that the supply of plate-sized fish increased by 6%, while the supply of large fish decreased by 4% as a result of a 13% price premium for plate-sized fish. This market-driven size selection increased revenues (14%) but decreased total fish biomass (−3%). However, when market-driven size selection was combined with limited institutional constraints, both fish biomass (28%) and fishermen's revenue (22%) increased. These results show that the direction and magnitude of the effects of market demand on biological populations and human behavior can depend on both biological attributes and institutional constraints. Fisheries management may capitalize on these conditional effects by implementing size-based regulations when economic and institutional incentives will enhance compliance, as in the case we describe here, or by creating compliance enhancing conditions for existing regulations.

Key words: coupled natural and human systems model; coupled social-ecological systems; ecosystem services; fishing; human behavior; life history traits; population modeling; selective harvest; size selection.

Introduction

Demand for fisheries products, tourism opportunities, and other ecosystem services have contributed substantially to ecosystem change in coastal and marine systems (e.g., Lotze et al. 2006, Swartz et al. 2010, Buckley 2011). Nonetheless, investigations of human impacts in marine systems, and even of fisheries-related impacts specifically, often ignore market demand entirely or simply consider it to be an exogenous factor leading directly and uniformly to greater pressure on fisheries (as reviewed in Millar 1992). However, evidence from a variety of systems suggests that ecological, economic,

and institutional processes can dictate the strength of the relationship between market demand and ecosystem health, and even whether growing demand reduces or increases ecosystem health (Renwick and Archibald 1998, Armsworth et al. 2006, Kuminoff et al. 2008, Ebeling and Yasué 2009). For example, Foster and Rosenzweig (2003) suggest that the presence of strong property rights over forest-lands in isolated Indian villages may have caused growing demand for wood products to actually induce greater forest growth (see also Brewer et al. [2009] and Tissot et al. [2010] for reef fish/market interactions from the tropics). In contrast, Armsworth and colleagues (2006) show that the ecological value of land may determine whether market feedbacks from purchasing land for nature conservation undermine conservation efforts. Here, we build on this literature by investigating how market demand drives selective harvest, how both ecological and institutional

factors mediate the effects of market demand, and the implications for populations and revenues.

Selective harvesting (where exploitation favors a particular species, stock, body size, sex, season, or geographic location) is common, particularly for marine species (Fenberg and Roy 2008, Darimont et al. 2009, Zhou et al. 2010). Across species, selective harvest of large species, especially predators, has changed community structure and trophic interactions in a variety of ecosystems (Simenstad et al. 1978, Jennings and Kaiser 1998, Darimont et al. 2009). Within species, individual traits, demographics, and the ecology of diverse taxa have been affected by harvest that targets specific size classes, stages, or sexes (Darimont et al. 2009). Size-selective harvest, where large species or individuals of a species are preferentially caught, has been especially important in shaping fish populations and fisheries (as reviewed in Zhou et al. 2010). It has led to the loss of large individuals and taxa globally (e.g., Pauly et al. 1998, Myers and Worm 2003) and in some cases led to demographic or evolutionary changes in fish populations that may have negative consequences for fisheries yields (Conover and Munch 2002, Olsen et al. 2009, Shackell et al. 2010).

Most work on the drivers of size-selective fish harvest has focused on the interaction between fishing technology and fish biology and how regulations may mediate this interaction. Fishing gear, such as hook and line, select for large species or individuals (Millar 1992). These large species and individuals tend to be from upper trophic levels and have slow growth rates and low fecundity, which exacerbate the effects of fishing (Jennings et al. 1999). The correspondence between size, trophic level, and vulnerability has been implicated as the cause of the phenomenon of fishing down the food chain, which refers to sequentially fishing from upper trophic-level species to lower trophic-level species (Pauly et al. 1998). Similarly, size-selective fishing has led to dramatic changes in the median size of individuals within populations (Friedlander and DeMartini 2002, Dulvy et al. 2004, McClenachan 2009, Olsen et al. 2009).

Size-based regulations that protect key size classes or life stages, such as juveniles that are needed to recruit to the population and large adults that are disproportionately fecund, are a widely used fishing strategy (Berkeley et al. 2004, Zhou et al. 2010). Minimum length limits became popular in the 1960s and 1970s after theoretical results by Ricker (1945) and Saila and Horton (1957) suggested higher stocks and harvests could be achieved by protecting small, fast-growing fish (Wilde 1997). Minimum length limits are thought to produce the most benefits for fish populations with low recruitment rates and natural mortality, moderate to high growth rates, and high fishing mortality (Novinger 1984). Less commonly used are slot limits, which either protect fish within a given length range or fish both below a minimum length and above a maximum length (Anderson 1974, Kennedy and Sutton 2007). Slot limits that protect both small and large fish may produce higher steady state yields for slow-growing fish populations with high natural mortality at the age of first sexual maturity (Reed 1980). However, regulations alone may be difficult to enforce and not flexible enough to take advantages of the dynamic synergies between species life histories and the economic incentives created by market demand.

Market demand for fisheries products has the potential to influence the size distribution of the catch, and thus, population abundance, harvest, and revenue, through economic incentives rather than regulations. For instance, Sethi et al. (2010) argue that profits are a better predictor of the sequence of fisheries development than trophic group or size, in contrast to Pauly et al.'s (1998) fishing down the food chain hypothesis. Similarly, differences in profits associated with different size classes of fish may be a good predictor of the size distribution of the fish catch. High prices associated with high demand for certain size classes may make it worthwhile for fishermen to focus their effort on that size class. One example of a particular size class with a price premium are so-called "plate-sized" fish that are served whole in restaurants, especially in tourism areas. In this case, demand from the tourism market may have similar effects on catch distributions as a slot-limit regulation; but, with no enforcement requirements and greater revenues from both high value target size classes and non-target size classes that would have to be discarded under a slot limit.

Whether higher market demand has positive effects on the fish population and fishermen's profits will depend, in part, on the biology of the fish populations, fishermen's behavior, and institutional constraints (e.g., practices that enhance selectivity or entry into the fishery). For example, if increased demand for plate-sized fish results in more plate-sized fish being caught without significantly increasing catch overall, higher market demand may have positive impacts on the fish population and fishermen's revenues because mortality of the smallest (recruit size class) and largest (most fecund) individuals is reduced and plate-sized fish can be sold at a premium. To test these hypotheses, we empirically examine how biological and institutional processes mediate the effect of higher market demand on the Pacific red snapper (or huachinango; *Lutjanus peru*) fishery near La Paz, Mexico. Our results show how biology and institutions may determine both the direction and magnitude of the influence of higher market demand on a fishery. These results are significant in Mexico and globally where governments are turning to local institutions to improve resource management and markets for specialized products are on the rise.

METHODS

We developed a five-stage analysis using logbook data containing three fishing cooperatives' daily purchases from 2007–2009 in and around La Paz (collected by O.

Fig. 1. The location of three fishing cooperatives and the tourism market of La Paz, Baja California Sur, Mexico.

Aburto-Oropeza and colleagues) and information on the biology of *L. peru* (Fig. 1). First, we examined the differences in prices associated with the different size classes and relative influence of the market. Given the location of the fishing cooperatives and time period covered by the logbooks, these data provide significant geographic and temporal variation in fishermen's connections to markets. Second, once we established the price differences across size classes, we estimated the effect of these price differences on the supply of different size classes of fish. Third, in order to simulate the effect of market-driven size-selective fishing on the fish population and fishermen's revenues, we developed a stage-based model of the fish population with harvest using parameter estimates from the literature. Fourth, we explored how institutional constraints could further mediate the interaction between market demand and size-selective fishing. Fifth, we evaluated the effect of market-driven size-selective fishing if we assume that by-catch of this species is unreported. Finally, we examined the robustness of the outcomes of interactions between market drivers, biology, and institutional constraints to important assumptions of our integrated model.

Study system

Fishery.—*Lutjanus peru* is relatively slow growing and is among the longest lived species in the Lutjanid family (with a lifespan exceeding 30 years [Rocha-Olivares 1998]). These fish constitute a substantial and increasing fraction of commercial finfish landings (34% or 598 Mg [1 Mg = 1 metric ton]) and revenue (46% or >US$1 million) in the region around La Paz (Diaz Uribe et al.

2004, Erisman et al. 2010). However, fishing mortality around La Paz is still relatively low compared to other regions in Mexico (Diaz Uribe et al. 2004). This fishery is a day-boat fishery using small boats, called *pangas*, and is managed by a permit system. Permits can be owned by cooperatives or independent fishermen, operating individually or as firms, called *permisionarios* (Cisneros-Mata 2010). Permits allow for the sale of fish on the market. Cooperative leaders typically arrange contracts for the sale of a certain quantity of fish at particular prices. Cooperatives may announce or negotiate the price that they will buy fish for from their members as a fraction of the market price. *Permisionarios* may act similarly but with limited to no negotiation on the buying price for fishermen. Fishing is typically done by fishing teams of two to three fishermen who are members of a cooperative, sell to *permisionarios*, or are *permisionarios* themselves. Fishing boats may be owned by members of a fishing team or by the cooperative.

In the tourist zone around La Paz, medium or plate-sized red snapper are the preferred fish for restaurants and hotels (Erisman et al. 2010) and are sold at a premium price compared to smaller and larger sized fish. Plate-sized fish are typically between 20 and 35 cm in length (O. Aburto-Oropeza and S. M. Walsh, *personal observations*), which corresponds to the size of small adults (Cruz-Romero et al. 1996). When selling fish, fishermen distinguish plate-sized fish from small fish (<20 cm) and large fish (>35 cm; O. Aburto-Oropeza and S. M. Walsh, *personal observations*). Fishermen use hook and line to catch *L. peru* and "free the size that does not pay" (S. M. Walsh, *personal observation*). Interviews with fishermen indicate that they are able to be very selective in fishing particular sizes by their choice of hook, location, and depth (L. Sievanen and S. M. Walsh, *personal observations*; Fig. 2). Harvest of small adults may have less of an impact on the fish population than fishing juveniles and large adults, given that large adults produce disproportionately more offspring (Berkeley et al. 2004), and newly mature adult and juvenile mortality already is significant (Ralston 1987). These aspects of fish biology motivated the management of fisheries using slot limits, where only medium size adults are fished, and has been shown to increase stocks and yields for fish with certain biological attributes (Reed 1980). The relatively slow growth and low fishing mortality of *L. peru* around La Paz suggests that its stock could increase due to a market-driven or regulatory slot limit.

Institutional context.—Fisheries in Mexico are governed by a set of reasonable laws, which include size limits for some fisheries. However, the government agency CONAPESCA, which is responsible for enforcing fisheries regulations, has limited resources (Cinti et al. 2010). In this low-enforcement-capacity setting, higher market demand combined with local institutional constraints could help incentivize compliance with size limits, when they exist; or create a non-regulatory

mechanism to promote better fishing practices. Although, with few exceptions, cooperatives no longer retain exclusive rights to particular species, cooperatives operating under permit regimes still appear to have significant influence on resource use (CONAPESCA 2010a; S. M. Walsh et al., *personal observations*) and could play an important role in mediating the effects of higher market demand.

Increased tourism demand for plate-sized fish only would be beneficial if it does not induce large supply responses by fishermen and if fishermen selectively harvest plate-sized fish and decrease their harvest of non-plate-sized fish. Fishing cooperatives may be able to control fishing effort in a way that is consistent with these two conditions. Moreover, effective monitoring and collective action by cooperative members could limit entrance of new fishermen (Ostrom 1990, Wilson et al. 2007, Basurto and Coleman 2010), who may be attracted by the increase in fish prices. All these solutions depend on the cooperative wielding enough influence; if there are a large number of non-cooperative members in the fishery, it is less likely these conditions will hold.

Interviews with cooperative leaders indicate that they are able to influence the fishing practices of their members and, to some extent, control entry in the fishery. Around La Paz, cooperative leaders report that size selection is common practice for their members. Cooperatives may use a variety of mechanisms to encourage or constraint fishing practices, including passing on a proportion of the market price premium to their members, making lower payments for non-plate-sized fish, limiting purchases of other size classes, mandating the use of certain hook-and-line technology or fishing in certain habitats, sharing knowledge of the ecological and economic benefits of selective harvest, and promoting social norms that define good fishermen as those that protect small and large fish. In addition, cooperatives may limit entry by actively patrolling fishing areas, not taking new members, and not purchasing from non-members. However, without rights to particular species or areas, cooperatives are limited in their ability to control entry.

Integrated model

Given this understanding of the fishery and institutional context, we developed an integrated bioeconomic model of the fishery. The fishing cooperative logbook data enabled us to empirically estimate reduced form versions of an economic choice model that characterizes fishermen's decisions to fish particular types of fish. We linked these fish catch supply (i.e., harvest) functions estimated with the logbook data to a stage-based model of the *L. peru* population. Given that no fisheries independent data were available for *L. peru*, we used published parameter estimates from the literature for the stage-based population model of *L. peru*. Together, we used these integrated models to examine the effect of the

FIG. 2. Fishermen select for plate-sized fish by using #8 and #9 hooks (indicated by the black arrows). Photo credit: Leila Sievanen.

price premium for plate-sized fish on the distribution of the catch and the consequences for the fish stock and fishermen's revenues. We also explored other unobserved harvest scenarios representing effects of institutional constraints (e.g., incentives or best practices for selectivity from fishing cooperatives) and unreported by-catch (i.e., unreported sales or discards of non-target size classes) of this species.

Economic choice model.—We tested the effect of variation in market demand across size-classes on size-selective fishing by estimating a linearized economic choice model of fishermen's supply decisions using detailed daily logbook data from three cooperatives, from 2007 to 2009. We assumed that fishermen choose whether to fish *L. peru* or another species and which size class of *L. peru* to fish, based on the profits obtained from fishing. The choice is a two-stage process. First, fishermen determine the maximum profits that can be obtained from targeting a particular fish given his production function for that fish and an optimal choice of inputs. The maximum profits from targeting fish type i can be denoted $p_i(p, r, n, C)$, where p is a vector of product prices for the size classes of *L. peru* and fish other than *L. peru*, r is a vector of input prices, C indicates a set of institutional constraints, and n is a vector indicating the relative abundance of each size class of *L. peru* or fish other than *L. peru*. Second, the fishermen chooses to target fish type i if $p_i(p, r, n, C) > p_k(p, r, n, C)$ for all $k \neq i$. Note that the entire vector of product prices appears in each expression. Fishermen

SHEILA M. W. REDDY ET AL.

TABLE 1. Descriptive statistics of monthly aggregate catch, number of fishing teams, and price by other species or size class of *Lutjanus peru* for all cooperatives combined (2007–2009).

Variables	N	Mean	SD	Minimum	Maximum
Catch (kg/month)					
All *L. peru*	28 224	20.4	268.8	0	12 008
Other species	7 056	65.0	508.7	0	12 008
Small *L. peru*	7 056	7.5	109.2	0	3539
Medium *L. peru*	7 056	8.2	124.1	0	4291
Large *L. peru*	7 056	0.8	15.3	0	557
No. teams per coop per month					
All *L. peru*	432	1.8	4.5	0	32
Other species	108	5.2	7.5	0	32
Small *L. peru*	108	0.9	1.9	0	9
Medium *L. peru*	108	0.8	1.8	0	10
Large *L. peru*	108	0.2	0.7	0	4
Price (MXN$/kg)					
Other species	7 056	33.4	14.4	10	121
Small *L. peru*	7 056	37.8	2.4	30	43
Medium *L. peru*	7 056	52.1	2.1	33	55
Large *L. peru*	7 056	37.1	1.2	32	42

Note: Prices are in 2010 pesos.

target types of fish by choosing different technology (e.g., size of hook) or fishing location, which will be reflected in the input prices; however, "targeting" a particular type of fish i does not mean that other size classes of *L. peru* or other species are not caught in the process. Cooperative logbook data shows that 44% of days fishing teams report catching *L. peru* and in only 6% of days do teams only catch one size class of *L. peru*. The most common catch combination is small and medium *L. peru* and other species (15%), followed by small *L. peru* and other species (10%), and by medium *L. peru* and other species (6%). If there is by-catch of *L. peru*, it can be sold for a rate that depends on the market price for that by-catch. Of course, if institutional constraints penalize the selling of non-plate-sized fish, this will be reflected in the profit functions.

The choice of which fish to target leads to supply functions for each fishing team. These functions can be aggregated over time and linearized to get models of fish supply that can be estimated with standard regression techniques. Fishermen's aggregated monthly supply of each size class of *L. peru* and all other species are estimated by the following equation:

$$\ln(q_i) = b_0 + b_1 \ln(p_o) + b_2 \ln(p_g) + b_3 \ln(p_m) + T + C + e$$

where q_i is the quantity of fish of type i supplied [the two economically relevant size classes of *L. peru* (m is medium or plate-sized and g is non-plate-sized) and all other species (o)], the price of these types of fish, month fixed effects (T), and cooperative fixed effects (C).The prices of non-plate-sized fish (small and large fish) were grouped because we found that these prices were statistically indistinguishable. This specification is further validated by the fact that results from models where the price of small and large fish price enters separately

are extremely similar to results from this model specification (see Appendix A: Table A1). Direct information on the price of inputs (r) is not available; however, differences in input prices are captured in part by the buying prices from the cooperative (p) because cooperatives typically pay fishermen after subtracting out the cost of fuel, which may vary due to different travel distances or fishing times associated with different types of fish. It should be noted that interviews with fishermen suggest that the differences in costs are relatively small (L. Sievanen and S. M. Walsh, *personal observations*). Month and cooperative fixed effects capture temporal and spatial variation in the abundance of the fish (n). Cooperative fixed effects also capture differences in fishing ability that may be common to fishermen in the cooperative because of shared ecological knowledge or capital. Institutional constraints that the cooperative exerts, for instance, on fishing certain size classes also will be captured by this variable. We were unable to control for unobserved heterogeneity across fishermen because the data represent a very unbalanced panel (i.e., not all fishermen are observed in all time periods); however, cooperative fixed effects likely capture the most important differences across fishermen.

These models of supply were estimated using the daily logbook data (2007–2009) from three cooperatives around La Paz (Table 1; see Appendix A [Table A1] for descriptive statistics by cooperative). The logbook data are the cooperatives' records of each fishing team's daily catches (kg) and the price paid by the cooperative (peso/kg) by fish type. Given that this is a day-boat fishery, the daily catch of a fishing team represents a single fishing trip. The logbook data identified the catches by species and, for some species including *L. peru*, by size class. In the logbook data, fishermen distinguish between the three size classes of *L. peru*,

chico (<20 cm), *mediano* or *orden* (20–35 cm), and *grande* (>35 cm; O. Aburto-Oropeza and S. M. Walsh, *personal observations*). The catch of the three size classes of *L. peru* and all other species combined was aggregated by month for each fishing team or sub-cooperative group. The price associated with these catch records was taken as the average price the fishing team or group received over the time period. If a fishing team or group did not fish a particular type of fish during a given month, the price the fishermen would have observed was assumed to be the average of the price received by other fishermen in the same cooperative for that type of fish in that month. In some cases, it was necessary to match prices by averaging across the year or the entire data set for a given cooperative. In total, the database contained 7056 observations of monthly catches by fishing teams or groups for the three size classes of *L. peru* and all other species combined.

The results of our regression analysis show how changes in prices affected the aggregate monthly catch for a given fishing team but do not provide information on whether the total number of fishing teams in the fishery changes with prices. In order to examine the effect of prices on the number of fishing teams, we estimated a Poisson regression model with the same predictor variables as above, using the total number of fishing teams reporting catch to a given cooperative in a given month.

Stage-based fishery model.—To estimate the effects of market-driven size-selective fishing as well as the role of institutional constraints on the fish stock and fishermen's revenues, we simulated the effects of fishing using a stage-based nonlinear matrix population model of the *L. peru* fishery. We first developed an age-based model of *L. peru* because age-specific demographic information was available for *L. peru* and related snappers. However, in order to couple this model with results from the economic choice model, we reduced the age model to stages that correspond to the size classes recognized in the market (see Appendix B). This process resulted in the following matrix model:

$$\begin{pmatrix} n_1 \\ n_2 \\ n_3 \end{pmatrix}(t+1) = \begin{pmatrix} P_1 & l_1 F_2 & l_1 F_3 \\ G_1 & P_2 & 0 \\ 0 & G_2 & P_3 \end{pmatrix} \begin{pmatrix} n_1 \\ n_2 \\ n_3 \end{pmatrix}(t)$$

where l_1 is pre-recruit survival, P_i is the probability of staying in the same stage, and G_i is the probability of surviving and growing to the next stage. Our models employ a compensatory Beverton and Holt function that determines pre-recruit survival based on total egg density, M. Pre-recruit survival is given by $l_1 = a/(b + M)$ where $M = \sum_{i=1}^{S} F_i n_i$ and F_i is the fecundity of stage i, n_i is the population size in stage i, and S is the maximum stage. The parameter a represents the maximum number of recruits in the population and b is the number of eggs needed to produce $a/2$ recruits. An egg-recruitment relationship was chosen over stock-recruitment because adults and pre-recruits of this

species inhabit separate habitats (Parrish 1987, Rocha-Olivares 1998, Saucedo-Lozano et al. 1998). Therefore, we assume that pre-recruit mortality is affected by egg density (e.g., through starvation or vulnerability to predators), rather than by the adult stock (e.g., via cannibalism).

Parameter values were derived from previously published data on *L. peru* and related species. Diaz Uribe et al. (2004) provides estimates of the parameters for the Beverton and Holt function for *L. peru*. The function was presented in terms of total population size N, so we scaled the parameters in order to use them in a Beverton and Holt function in terms of total egg production M. In addition, we scaled the parameters to account for only females because the model in Diaz Uribe et al. (2004) quantified both males and females. The resulting parameter values were a = 5.94×10^5 individuals and b = 5.29×10^9 eggs. Weighted averages of age-specific parameter values from the age-based model were used in the stage-based model, assuming that the in-stage age distributions are the same as the age distributions that result from the age-based model (see Appendix B).

At equilibrium in the absence of harvest, the vast majority of individuals (94%) are in the first two stages; however, 67% of the biomass was in the third, largest stage. We estimated the proportional sensitivity, or elasticity, of the output variables to the parameters (see Appendix B). Total biomass and total egg production were more sensitive to the survival of the large-sized fish than to those fish in the two smaller classes. Total population, however, was less sensitive to all survival parameters than total biomass and total egg production. Total biomass, population, and egg production also were more sensitive to the fecundity of large-sized fish, as opposed to medium-sized fish. The output variables were also more sensitive to the Beverton and Holt parameter a, which bounds the number of recruits to the population and thus the population size, than to the parameter b.

The results of the economic choice model were incorporated into the stage-based model of *L. peru* such that harvest was a function of the prices for the three stages of *L. peru*. Harvest was assumed to be proportional and defined as $H_t = a \times \sum_{i=1}^{S} b_i(t)$ where a is the proportion of the total biomass harvested and b_i is the biomass in stage i. Harvest may be distributed differently across the stages, hence, stage specific harvest is $h_i(t) = k_i[(100 + E_{h_i;p_m}Dp_m + E_{h_i;p_g}Dp_g + C)/100]H(t)$, where is k_i the proportion of total harvest taken from stage I and $\sum_{i=1}^{S} k_i = 1$. For simplicity, these stage-specific harvest equations are represented differently than the equations we used to statistically estimate harvest above. The elasticity of the stage-specific harvest with respect to the price of plate-sized fish ($E_{h_i;p_m}$) and with respect to the generic, non-size specific price ($E_{h_i;p_m}$) was estimated by the economic choice model. The elasticities were multiplied by the percentage change in

SHEILA M. W. REDDY ET AL.

the plate-sized fish price (p_m) and the generic, non-size-specific price of fish (p_g), which allowed harvests to change based on observed price differences and fishermen's responses to those price differences. The institutional constraints (C) on the percentage change in selectivity represent changes in harvest according to controls exerted by fishing cooperatives and are reasonable assumptions based on interviews with cooperatives members and leaders (L. Sievanen and S. M. Walsh, *personal observations*). These assumptions are necessary because we were unable to separate the effect of a given cooperative from its location, which may also affect the stock.

These harvest equations generate stage-specific harvest in terms of biomass, but the population model is in terms of individuals. Harvest in terms of individuals is $u_i(t) = h_i(t)/W_i$, where W_i is the average per capita biomass in stage i. In order to calculate the population in the next year as a result of fishing, we subtract $u_i(t)$ from the population vector, $n(t)$. We assume that harvesting takes place directly after the breeding season, such that total egg production is still defined as $M = \sum_{i=1}^{S} F_i n_i(t)$.

Harvest scenarios

We compared four different harvest scenarios that represent changes in harvest as a result of changes in the price of fish and institutional constraints on size-selective fishing. Prior to running these scenarios, we simulated 20% total harvest for 20 years so that the modeled fish population represented a fished population similar to that in the vicinity of contemporary La Paz. The distribution (k) of the catch across the size classes (20% small, 40% plate-sized, 40% large) was based on the equilibrium population structure and catch size distributions in lightly fished places (Gaines et al. 2010). For the four harvest scenarios of interest, we then simulated a 30% total harvest for seven years. The total harvest level was chosen to represent recent increases in catch of *L. peru* (Erisman et al. 2010). The initial distribution (k) of the catch across size classes for all four scenarios was based on the observed distribution of catch away from the tourism market (40% small fish, 60% plate-size fish, 0% large fish; see Appendix A: Fig. A1). However, given that no catch of large *L. peru* away from the tourism market were reported in the database, we assumed that 10% of the harvest was in the large size class based on other length-frequency distribution data in the area and reduced the proportion of the catch in the plate-size fish category to 50% (Rocha-Olivares 1998). This is a reasonable assumption because large-sized *L. peru* likely were caught away from the tourism market but not observed in the catch records because of the smaller number of observations or the greater number of fish that were reported without a size designation. The simulation duration (7 years) was chosen to be long enough so that newly born fish progressed through all the size stages, but short enough

that it was reasonable to assume that prices were not responding to changes in catch. In fact, we found that prices for plate-sized fish decreased over the study period and the prices for other sizes of fish did not change. In both the initial population run-down phase and the simulation of the four scenarios of interest, total harvest levels (20% and 30%) were set at levels that were judged to be sustainable in the short run based on studies of marine protected area design for fisheries (see, for example, Gaines et al. (2010), from empirical and model-based estimates of sustainable harvest derived from no-take marine reserve effects).

In scenario a, the "status quo" harvest scenario, the distribution of the catch is the same as the catch distribution we observed away from the tourism market (i.e., 40% small fish, 50% medium fish, 10% large fish). We represent this by setting the change in the price of medium or plate-sized fish and the change in the generic, non-size specific price to zero (i.e., no price premium). In scenario b, the "market-driven" harvest scenario, the change in the price of plate-sized fish is the percentage difference in this price that we observed near and far from the tourism center (13%; i.e., a price premium exists). There is no change in the generic, non-size specific price of fish. In scenario c, the "market-driven + institutional constraints" scenario, we assume that there are the same price changes as in scenario b (i.e., there is a price premium for plate-sized fish and no change in the generic price), but that cooperatives may increase selectivity for plate-sized fish 5% above and beyond the increases caused by higher market demand. We chose a 5% increase so that it would be similar to the level of increased selectivity caused by the market (i.e., 6%). We assumed cooperatives also encouraged decreased selectivity for small and large fish. The decreases in catch of these size classes are at such levels that the gain in revenues from enhanced selectivity of plate-sized fish is offset by decreased catches of small and large fish. In scenario d, the "market-driven + by-catch" scenario, again we assume the same changes in prices as in scenario b (the "market-driven" scenario), but we also assume that there is unobserved by-catch of small and large *L. peru*. We represent this unobserved by-catch by setting the elasticity of the catch of both small and large fish with respect to the price of plate-sized fish to the elasticity of plate-sized fish with respect to its own price (i.e., $E_{h_s;p_g} = E_{h_m;p_m} = E_{h_l;p_g} = 0.454$). This representation simply assumes that as the catch of plate-sized fish increases with price, the catch of small and large fish also increase by the same percentage with respect to the changes in the price of plate-sized fish.

We also considered how the results of these four harvest scenarios are affected by three additional drivers of change in this social-ecological system: (1) variation in the initial condition of the population; (2) additional fishermen entering the market; and (3) a non-size-specific increase in demand for *L. peru*. We considered the effect of the initial condition of the population by
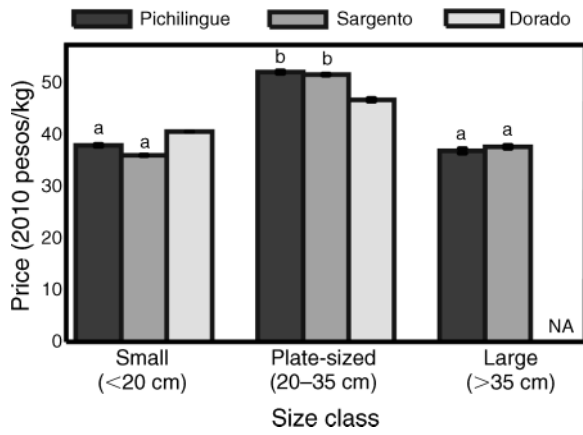
Fig. 3. The mean price of *Lutjanus peru* by size class and fishing cooperative. Pichilingue, Sargento, and Dorado are located at increasing distances away from the markets of La Paz. The mean price is significantly different across size classes ($F_{2,7} = 19.26$, $P < 0.0001$), cooperatives ($F_{2,7} = 0.03$, $P < 0.05$), and certain size classes at a cooperative ($F_{3,7} = 2.28$, $P < 0.0001$; two-way ANOVA). Error bars are $\pm$SD, and the same lowercase letters above bars indicate means that are not significantly different as determined by Tukey's HSD post hoc tests ($P > 0.05$).

increasing the harvest in the run-down phase to 30% and increasing the initial harvest in the simulation of the four harvest scenarios to 40%. To determine whether new fishermen were entering the market in response to changes in fish price, we estimated the number of unique fishing teams fishing a given size class of *L. peru* or other species at a particular cooperative in a given month using a Poisson regression model. The predictor variables were the same as in the models of fish catch. The resulting price elasticities were incorporated into the harvest equations in the stage-based model. In this case, institutional constraints were assumed to reduce new entrants by 50%, as well as enhance selectivity by 5%. Lastly, we considered that there may be an increase in the generic, non-size-specific price of *L. peru* of similar

magnitude to the price premium for plate-sized fish (e.g., 15%).

Confidence intervals for the outcome variables were constructed through Monte Carlo simulation methods. Values for the parameters were either drawn 1000 times from a normal distribution defined by the estimated mean and standard deviation of the parameter or from a uniform distribution when there was no estimate of the error in the parameter. When parameter values were drawn from uniform distributions, they were drawn from values $\pm 20\%$ of the parameter value reported in the literature.

RESULTS

Based on the empirical data on daily catches, we find that the price of medium or plate-sized fish is as much as 13% greater near the main market in La Paz (Pichilingue, 53 ± 3 MXN\$/kg [mean $\pm$ SD]; Sargento, 52 ± 2 MXN\$/kg) than away from this market (Dorado, 47 ± 3 MXN\$/kg; Fig. 3). The average price of plate-sized fish across all cooperatives is also greater than the average prices of small or large fish. In contrast, the average prices of small and large fish across all cooperatives are not different (Fig. 3).

Increases in the price of plate-sized fish are associated with increases in the supply of plate-sized fish and decreases in the supply of large fish and other species, but are not associated with changes in the supply of small fish (Table 2). The monthly supply of plate-sized fish increases 0.43% (SE = 0.26, $P < 0.10$) for every 1% increase in its own price. This same increase in the price of plate-sized fish also results in a 0.33% (SE = 0.14, $P < 0.05$) decrease in the monthly supply of large fish and a 1.1% decrease in the supply of other species (SE = 0.64, $P < 0.10$). The increases in the supply of plate-sized fish that are associated with increases in the price of plate-sized fish are in addition to the increase in supply that result when the generic, non-size-specific price of *L. peru* increases (0.72%, SE = 0.25, $P < 0.01$). Given the difference in the price of plate-sized fish near and far from the market (13%), higher levels of market demand

TABLE 2. Regression results for models estimating monthly catch for all species other than *L. peru* and for each size class of *L. peru*.

Predictors	Other species	L. peru Small	L. peru Medium	L. peru Large
Price of other species	0.103* (0.060)	0.020 (0.024)	0.070*** (0.024)	−0.029** (0.013)
Price of medium *L. peru*	−1.126* (0.644)	0.177 (0.256)	0.426* (0.255)	−0.334** (0.135)
Price of non-medium *L. peru*	0.934 (0.625)	0.382 (0.250)	0.723*** (0.249)	0.534*** (0.132)
Pichilingue	−1.521*** (0.184)	0.418*** (0.073)	0.707*** (0.073)	0.100** (0.039)
Sargento	1.384*** (0.231)	1.629*** (0.092)	1.179*** (0.092)	1.058***(0.048)
Constant	2.448 (2.135)	−1.711** (0.851)	3.293*** (0.848)	−0.611 (0.448)

Notes: Values are coefficient estimates and standard errors (in parentheses) of the predictor variables. Monthly catch (kg/month) and prices were log-transformed for the analysis. The price of non-medium *L. peru* is the average price of small and large fish (the prices of large and small fish were not significantly different [$P > 0.05$]. It is meant to represent the generic non-size-specific price. Pichilingue and Sargento are fishing cooperatives. All models included fixed effects. There were 7056 observations (see *Methods: Integrated model: Economic choice model*). R^2 = 0.075, 0.153, 0.150, and 0.126 for other species, and small, medium, and large *L. peru*, respectively.

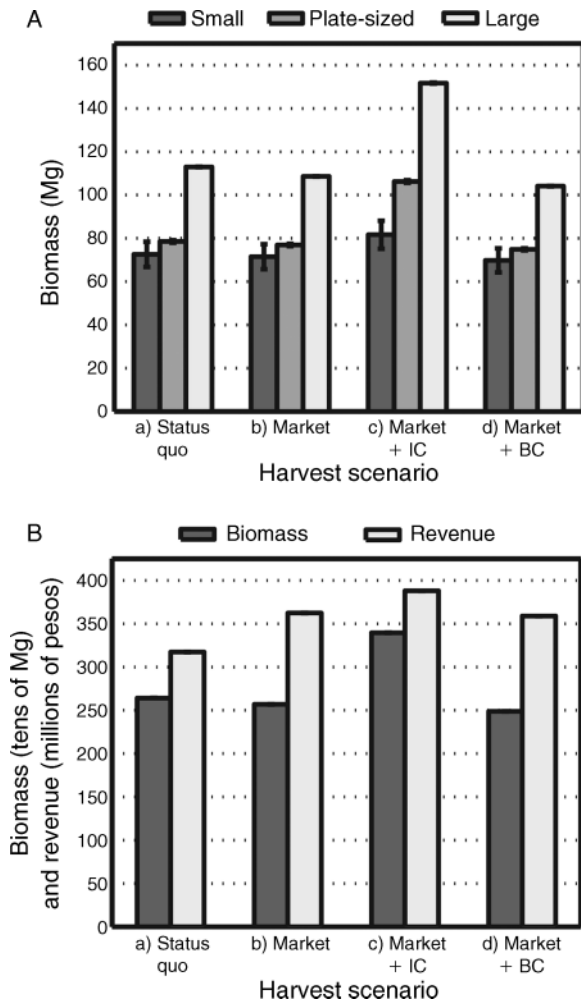   * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Fig. 4. Market effects acting on catch per trip: (A) biomass of *L. peru* by size class and harvest scenario; (B) biomass and revenue of *L. peru*. The harvest scenario are defined as (a) the status quo away from the market in La Paz, (b) market-driven size selection, (c) market-driven size selection plus institutional constraints (IC), and (d) market-driven size selection plus by-catch (BC). Error bars are 95% confidence intervals.

may have resulted in at least a 6% (price difference × price elasticity = 13% × 0.43) increase in the overall supply of plate-sized fish and a 4% (price difference × price elasticity = 13% × 0.33) decrease in the supply of large fish.

Using the stage-based model of the fishery, we find that this market-driven size-selective fishing may decrease the abundance of plate-sized fish and large fish, with no effect on small fish (Fig. 4A, scenario b), relative to fishing in the absence of market-driven size-selective fishing (Fig. 4A, scenario a). The decrease in the abundance of plate-sized fish is a result of direct harvest. In contrast, the decrease in large fish is not a result of direct harvest but of changes in the survival of plate-sized fish. Higher market demand for plate-sized fish had no direct effect on the catch of small fish.

In total, the change in the size structure of the population and the resulting catch under market-driven size-selective fishing resulted in a 3% decrease in the total biomass of the stock and a 14% increase in revenues (Fig. 4B, scenario b). The increase in the revenue is a result of the relative increase in the catch of plate-sized fish and the price premium for plate-sized fish. The total harvest actually decreased by less than 1%.

Our modeled harvest scenarios suggest that if institutional constraints increase the selectivity for plate-sized fish by 5% above and beyond market-driven selectivity and impose compensating decreases in the supply of small and large fish, the total biomass of the stock could increase 28% and revenue from harvest could increase 22% (Fig. 4B, scenario c). This total biomass increase is a result of increases in the abundance of both plate-sized and large fish (Fig. 4A, scenario c). The increases in revenue are due primarily to changes in the distribution of the catch and the price premium for plate-sized fish. The total harvests in these two scenarios were similar: market-driven size selection combined with institutional constraints resulted in a <0.2% decrease in harvest relative to the status quo.

Although fishermen indicate they release small and large fish, there may be unobserved by-catch (i.e., unreported sales or discards of non-target size classes) of this species. If unobserved by-catch does occur, we estimate that the losses in total biomass may be greater (6% vs. 3%) while the gains in revenue may be less (13% vs. 14%) than estimated with market-driven size selection alone (Fig. 4B, scenario d). This is a result of even greater decreases in abundance of both plate-sized and large fish under this harvest scenario (Fig. 4A, scenario d).

When we modeled the four harvest scenarios for a more heavily fished population (40% initial harvest rather than 30%), there was a lower abundance of large fish, which resulted in the heavily fished populations to have biomass more evenly distributed across the size classes (see Appendix A: Fig. A2i) than in the less heavily fished population (Fig. 4A). Under these conditions, all three market-driven harvest scenarios (including additional institutional constraints and unobserved by-catch) resulted in lower total biomass and higher revenues compared to the status quo scenario without market driven size selective fishing (see Appendix A: Fig. A2ii). Notably, for the more heavily fished population, institutional constraints were no longer sufficient to enhance both revenues *and* total biomass.

The results so far are based on analyses that only considered changes in monthly catches for each fishing team and not due to new entrants to the fishery. When we estimated the effect of prices on new entrants into the fishery (see Appendix A [Table A3] for detailed results), we found that the number of fishing teams fishing small fish increased 11% (SE = 6.1, $P < 0.10$) and the number of teams fishing large fish decreased 11% (SE = 6.1, $P < 0.10$) for every 1% increase in the price of plate-sized

TABLE 3. Summary of the effects on biomass and revenue of three harvest scenarios (compared to the status quo) that examine changes in catch and/or effort under different initial stock levels.

| | Catch per trip | | | | Catch per trip and numbers of fishermen | | | |
| | Higher initial stock | | Lower initial stock | | Higher initial stock | | Lower initial stock | |
Harvest scenario	Biomass	Revenue	Biomass	Revenue	Biomass	Revenue	Biomass	Revenue
Market driven	−	+	−	+	−	−	−	−
Market driven + institutional constraints	+	+	−	+	−	−	−	+
Market driven + by-catch	−	+	−	+	−	−	−	−

Notes: The first two columns summarize the results from Fig. 4, while the other columns summarize results described in the text and presented in supplemental figures. A "+" means that there was an increase or a positive effect on the outcome variable under the scenario; a "−" means that there was a decrease or negative effect.

fish. The number of fishing teams fishing plate-sized *L. peru* or other species was not affected by the price of plate-sized fish. However, an increase in the generic price of *L. peru* markedly increased the number of fishing teams fishing small (12%, SE = 5.7, $P < 0.05$), plate-sized (12%, SE = 5.3, $P < 0.05$), and large *L. peru* (20%, SE = 5.8, $P < 0.01$). Overall, when we incorporated the role of new entrants into our harvest equations, we found that, in the absence of institutional constraints, fish size structures shifted from being monotonically increasing with size (e.g., with the greatest biomass in the large size class) to having the lowest biomass in the plate-sized fish size class (see Fig. A3i, scenarios b and d). When institutional constraints were present, biomass of small and large fish was lower than biomass of plate-sized fish due to enhanced selectivity coupled with the large shift in harvest onto these size classes (see Fig. A3i, scenario c). In sum, total biomass was greatly reduced and the gains in revenues from market-driven size-selective fishing were eliminated under all market driven scenarios that included new entrants (see Fig. A3ii, scenario b). Even with institutional constraints that enhance selectivity of catch and limit new entrants, large decreases in biomass and small decreases in revenue occurred (see Fig. A3ii, scenarios b–d). Unsurprisingly, when we modeled changes to both the catch and the number of new entrants into the fishery due to the price premium for a more heavily fished population, we found that market-driven size-selective fishing resulted in large decreases in both biomass and revenue (see Fig. A4ii, scenario b). Under these conditions, market-driven size-selective fishing combined with institutional constraints resulted in a monotonically decreasing size structure (e.g. least biomass in large stage; see Fig. A4i, scenario c) and a lower total biomass overall compared to market-driven size-selective fishing alone. However, harvest revenues increased (see Fig. A4ii, scenario c).

Last, we found that including a change in the generic price of *L. peru* made no qualitative change in the size structure of the population, total biomass, or revenues. Moreover, the price of other size classes of *L. peru* showed no trend over time, while the price of plate-sized fish actually decreased 2% across the study period (SE = 0.001, $P < 0.001$).

DISCUSSION

Natural resource management studies and strategies typically ignore market demand or assume it has negative effects on natural resources. This approach, however, may result in missing opportunities to create win-win situations that benefit both ecological and economic objectives. Using an integrated modeling approach motivated by empirical data from the La Paz region of Mexico, we find evidence for market-driven size-selective fishing that decreases the catch of large, disproportionately fecund fish. We show how this market-driven size-selective fishing may be combined with limited institutional constraints to improve fish stocks and fishermen's revenues (Table 3).

These results contribute to the debate over whether economic growth may have positive impacts on the environment by identifying conditions where higher market demand may enhance sustainable use of resources. Understanding and enabling these conditions may be increasingly important as incomes grow and consumer demand increases. Future coupled human-natural systems research may help meet this challenge by integrating market dynamics with the dynamics of natural populations.

Market demand shifts catch distribution with impacts on the fish population and revenues

Variation in market demand not only can affect the quantity of resource harvested but also how it is harvested. Both these processes have implications for sustainability. The market-driven pattern of harvest we observed is the opposite of the pattern reported for most hook-and-line fisheries and demonstrates that fishermen's economic decisions, along with technology and biological factors, can structure fish populations. Tracing the effects of observed market-driven size-selective fishing on the size structure of an economically important fish population using a stage-based model, we found that, overall, higher market demand for plate-sized fish had a negative effect on the fish stock. Although the catch of large fish decreased, it was not sufficient to offset the decrease in the number of plate-sized fish surviving and entering the large stage. The decrease in the abundance of the large stage, in turn,

decreased overall egg production, which is most sensitive to changes in the large stage (see Appendix B).

Despite these changes in egg production, there was no change in the abundance of small fish. This may be explained by the fact that changes in egg production have limited effects on the abundance of small fish if total egg production is near the saturation level, as defined by the density dependent pre-recruit survival function we employ. This same logic implies that the negative effects of market-driven size-selective fishing may be even greater for a population with lower population-level egg densities. Although the combined consequences of market-driven size-selective fishing resulted in a lower fish stock, fishermen's revenues were higher because of changes in the size distribution of the catch and the price-premium for plate-sized fish, not because of increases in total harvest (the total harvest actually decreased).

Market demand combined with institutional constraints may result in a win-win

In contrast, our model results indicate that both fish stocks and fishermen's revenues may increase due to market-driven size-selective fishing if institutional constraints lead to even small improvements in size selection. This finding, that it is possible to increase the biomass of the stock by shifting catch toward medium or plate-sized fish without significantly changing the overall level of harvest, suggests that a slot limit type of fishery may be beneficial for the *L. peru* fishery near La Paz, given its biology and the status of the fishery (Reed 1980). How likely is it that institutional constraints together with market incentives will result in sufficient changes in size selectivity to create outcomes similar to what we have modeled? Based on interviews with fishermen, it seems that La Paz area fishing cooperatives already encourage selection against small and large fish. Fishermen report that they target plate-sized fish, not just because the price is higher, but also because it is part of the practices of their cooperative.

Cooperatives are most likely to benefit from such catch restrictions if they have legal or de facto property rights. In Mexico, fishing *L. peru* is controlled by a permit system but there are no exclusive area rights and little official enforcement of permits (Cisneros-Mata 2010; L. Sievanen, S. M. Walsh, S. Nagavarapu, and H. Leslie, *unpublished data*). However, there is some evidence that fishing cooperatives may make efforts to exclude others from fishing without permits or in their unofficial territories (S. M. Walsh, *personal observation*). Unfortunately, we are unable investigate the existence or influence of these practices empirically with our data set. If cooperatives can exert significant institutional constraints related to selective fishing, the price premium on plate-sized fish may enhance compliance with the constraints by offsetting some of the potential costs associated with more selective fishing. Through co-management, state or federal fisheries managers could create new size-based regulations that reflect such informal institutional constraints on size-selective fishing and take advantage of enabling biological and economic conditions. Together, these efforts would likely increase compliance, reducing enforcement costs of regulations and management effectiveness (Jentoft et al. 1998, Jentoft 2000). However, it should be noted that regulations that eliminate the sale of non-target size classes could reduce revenues to fishermen, relative to revenues under market-drive size selection, even if price premiums for target species were unchanged.

However, when overall fishing effort was high (40% vs. 30%), we found that modest institutional constraints combined with market-driven size-selective fishing did not improve fish biomass, although there were improvements in revenues. When the larger size-classes were already greatly depleted due to high levels of fishing, shifts in the size-distribution of the catch were not sufficient to improve the fishery in the short time frame of our analysis. The effects of shifts in the size distribution of the catch also may be overwhelmed by the effect of higher levels of total harvest, as total biomass (as well as total population size and egg production) is more sensitive to total harvest than to harvest in a particular stage. Thus, the beneficial effects of the price premium for plate-sized fish may be undermined if the higher price attracts more fishermen to enter the fishery and increases total harvest.

Our empirical results suggest that new fishermen may in fact be entering the fishery around La Paz; however, given that we are only observing three cooperatives over a relatively short time period (relative to the reporting of some fishing teams) and that there is some reporting by groups larger than individual fishing teams, we cannot be certain. Others have reported dramatic and rapid shifts in fishing effort due to "roving bandits" that respond to the demands of the global fisheries markets by moving into and depleting unprotected fisheries (Berkes et al. 2006). Although the price premium for plate-sized fish may have attracted some new fishermen, it does not appear to have resulted in this sort of phenomenon. This could be due to fishing cooperatives exerting some constraints on fishermen's access and movement, although the extent of their control is unclear (L. Sievanen, H. Leslie, S. M. Walsh, and S. Nagavarapu, *unpublished data*). Taken together, these results emphasize the important role that institutions such as fishing cooperatives could play in both enhancing selectivity and limiting entry in order for higher market demand to contribute to positive ecological and economic outcomes.

Environmental impacts of economic development depend on social-ecological conditions

Considerable research has focused on when and how such local institutions are successful, but little work has explicitly addressed how they mediate market demand. Our research advances this latter theme and contributes

to the ongoing debate about if and how increased economic growth (and associated growth of markets) results in improved environmental conditions. This phenomenon has been observed for forest resources (e.g., Foster and Rosenzweig 2003) as well as for other common pool resources (e.g., air and water quality [Grossman and Krueger 1995]), but rarely for fisheries (see however, Cinner et al. 2009). There are two key competing hypotheses that may explain how economic growth leads to improvements in environmental conditions. The "Environmental Kuznets Curve" hypothesis posits that economic growth and incomes will result in increased demand for environmental amenities and decreases in pollution or increases in the conservation of resources (Grossman and Krueger 1993). Alternatively, increases in demand for products from renewable resources leads to expansion of the resource in order to increase production of these products (Foster and Rosenzweig 2003). Our results lend support for Foster and Rosenzweig's hypothesis. In contrast to Foster and Rosenzweig, who show that property rights are a necessary condition for this hypothesis, we suggest that institutional constraints on harvest can lead to improvements in environmental conditions even in the absence of formal property rights.

However, recent studies showing how overfishing has caused losses in fish catch and revenues suggest that, in general, higher market demand is not leading to improvements in ecological and economic outcomes for fisheries (FAO and the World Bank 2009, Hesselgrave et al. 2011, Srinivasan et al. 2012). These global trends, like our work, are consistent with the thesis that higher market demand will only lead to sustainable resource exploitation if effort is limited, whether through formal or informal mechanisms. Both in the La Paz area and others parts of Mexico, however, few fisheries currently limit entry and effort (Cinti et al. 2010, Cisneros-Mata 2010). However, we know from previous studies that fisheries with private property rights or strong management, that includes effort controls, have been less likely to collapse or are more likely to be rebuilding (Costello et al. 2008, Worm et al. 2009, Srinivasan et al. 2012). Yet, global trade has undermined these successes (Srinivasan et al. 2012) by creating a disconnect between local depletion and prices faced by consumers.

Trends in fisheries and other systems (Armsworth et al. 2006) suggest that the spatial and temporal nature of market dynamics are a critical area for future coupled ecological-economic studies on sustainable resource use. Here, we limited our analysis to a time frame in which it was reasonable to assume that market-driven changes in fish harvest would not generate subsequent changes in prices. A more complete dynamic analysis could reveal that increases in the supply of plate-sized fish reduces prices and erodes the market driver for size-selective fishing. However, this seems unlikely because changes in the fishery we studied may not impact the price of plate-sized fish, which are also sold in regional and export markets. Even if local changes in supply impacted the price, it seems more likely that the sale of surplus plate-sized fish would simply reduce the average price *L. peru* and the price premium for plate-sized fish would be maintained. Regardless, the complex market dynamics we have documented, and the further analyses these patterns hint at, suggest that the argument that strong coupling between humans and resources is needed to ensure sustainability may need to be elaborated further.

Consumer preferences may have widespread and variable consequences

Just as increases in the total demand for seafood has had widespread (although variable and mostly negative) effects on fisheries, demand for specialized seafood products may also impact fisheries, particularly through selective fishing. Here we present evidence for how a somewhat specialized group of consumers, tourists and restaurant goers, has driven selective fishing in the La Paz region of Mexico. However, arguably common cultural preferences or even less common cultural preferences may have global consequences. For example, at one time cod was the major source of protein for Western Europe (Kurlansky 1998). Once North Atlantic cod stocks collapsed, the demand for firm, white fish led to the development of Alaskan Pollock and then to farmed African tilapia and Vietnamese tra (Greenburg 2010). Similarly, Asian demand for products like sea cucumbers and shark fins has led to global impacts to these species (Vianna et al. 2012). In addition to demand for particular species or species with similar qualities, demand for particular sexes, stages, or sizes of species is also important. For example, gravid female mud crabs are in high demand in Southeast Asian restaurants while soft-shell crabs, or molting crabs, garner high prices in sushi restaurants worldwide or as a traditional, seasonal cuisine in restaurants in the eastern United States and Italy (Famularo 2003, Bureau of Agricultural Research 2008, Kipfer 2011).

Size, in particular, has long been recognized as an important determinant of fish demand and price; however, typically prices for fish are higher for larger fish than smaller fish (Gates 1974). The typical trends in fish prices with size would be expected to result in the same patterns of size-selective fishing as hook-and-line fishing technology: larger fish are selected more often (Jennings et al. 1999). In contrast, demand for plate-sized fish may lead to trends in selectivity that run counter to technology-driven trends in selectivity, as we observed here. Although the effects of technologically driven size selection have been widely reported, the effects of market-driven size-selective fishing have been largely overlooked. Examining these effects provide important, general insights for fisheries management and policy and specifically address the potentially growing demand for plate-sized fish. Large singular portions that are served in the center of the plate (like

plate-sized fish) may indicate "value, quality, or opulence" to consumers and demand for these products are expected to grow with increasing incomes and demand for seafood (FAO 2010, Tlusty et al. 2011). Already, various wild-caught and farmed snappers and seabasses, among other species, are reportedly sold for higher prices when they are "plate-sized" in Australia and other parts of the world (Rimmer 2006, Sydney Fish Market 2012; S. M. Walsh, *personal observation*). In the La Paz region, we have observed that plate-sized cabrilla are also sold at a price premium, but we did not have sufficient data to model the implications of this trend.

Future research needs

By focusing on how biology and institutional constraints influence both the direction and magnitude of the effect of variation in market demand on an exploited fish population, we provide a model of how integrated analyses of ecological and economic data can be leveraged to assess key dynamics within a coupled social-ecological marine system (McLeod and Leslie 2009, Collins et al. 2011, Schlüter et al. 2012). These interconnections between micro human decisions and natural population dynamics may be especially important in developing countries where people are directly and highly dependent on wild populations and there is low governance capacity (e.g., Allison and Ellis 2001, Schlüter et al. 2012). Future research could build on this modeling framework to compare market and institutionally driven size-selective fishing to alternative management strategies (e.g., pure effort controls, marine reserves, or by-catch reduction in other fisheries) or to consider additional mechanisms beyond fecundity and survivorship by which size-selective fishing alters fish populations (e.g., temporal variability in recruitment, survivorship of larvae spawned from different size classes).

Our coupled model represented key behaviors in both the economic and ecological system; however, the lack of fisheries independent data on *L. peru* and limitations of the fishing cooperative data necessitated simulation modeling of the fish population and simplified albeit representative harvest scenarios. Future assessments of coupled social-ecological system dynamics and policy outcomes may continue to be impeded, unless we as a community are able to design or identify real or natural experiments and collect matching, long-term social, economic, and ecological data (Walters 1986, Ferraro and Pattanayak 2006, Schlüter et al. 2012). In addition, by design, here we focused on short-term, deterministic dynamics. Future analyses that consider longer-term ecological and social feedbacks, especially of changes in biomass on supply and prices as well as stochastic shocks to recruitment, survivorship, and costs of fishing may reveal important new information about this fishery and other coupled systems (Walker et al. 2002, Tallis and Kareiva 2006, Schlüter et al. 2012).

These trends also have important implications for research in fisheries ecology and management, which has increasingly been focused on selective harvesting in recent decades (Zhou et al. 2010). In particular, researchers argue that protecting large and old fish is critical to successful management (Longhurst 2002, Francis 2003, Berkeley et al. 2004). Berkeley and colleagues assert that, in theory, large, old fish could be protected by greatly reducing effort, imposing slot limits, or creating marine reserves, but conclude that marine reserves are the only viable option because reducing effort greatly would not be economically viable and mortality of by-catch in slot limit fisheries is too high. Although they overlooked the potential importance of economic incentives for compliance with slot limits, concerns over by-catch are clearly important. Here we considered the possibility that unobserved by-catch of small and large individuals is occurring and found that, indeed, this would lead to greater losses in fish biomass and reduced revenues, although these changes were not large. However, both by-catch and institutional constraints mediate the success of market-driven size-selective fishing. Interestingly, some authors have recently advocated for "balanced harvest," in contrast to selective fishing, where fishing effort is spread across sizes, stages, stocks, species, etc. (Zhou et al. 2010, Garcia et al. 2012). By shifting technologically driven selectivity away from large individuals, the market-driven size-selective fishing we observed actually resulted in more balanced harvests by counter-acting the technologically driven selection for large fish.

CONCLUSIONS AND POLICY IMPLICATIONS

Worldwide, increasing market demand, combined with the largely open access status of fisheries and global trade, has led to great losses in fish catch and revenues through overcapacity in fisheries and the side-effects of selection for large fish (Pauly et al. 1998, FAO and the World Bank 2009, Hesselgrave et al. 2011, Srinivasan et al. 2012). In theory, market demand should provide an incentive to ensure the sustainable supply of a resource if property rights are strong and profits from resource extraction cannot be more profitably invested elsewhere. When property rights are assigned to individuals or groups, fishermen are given incentives to make decisions that consider the impacts on their future catch. As a result, increased market demand can lead to higher prices and profits for fishermen without leading to overfishing. However, these types of regulatory markets may not be successful in developing countries where there is low enforcement capacity and/or individual or even group property rights are not culturally appropriate.

Here, we identify conditions where high market demand for medium-sized fish may lead to improvements in both the fish population and fishermen's revenues. These conditions do not require implementation of property rights, but rather other institutional

mechanisms, such as those already used by some fishing cooperatives in Mexico and elsewhere, that relate to how, when, and where fishermen fish.

In the La Paz area of Mexico, market-driven size-selective fishing only resulted in improvements in both the fish population and revenues if we assumed that fishing cooperatives could encourage modest enhancements in selectivity for medium-sized fish with compensating decreases in the selection of small and large fish, and that the price premium did not attract new fishermen or cooperatives could exclude new entrants. Moreover, these results depended on aspects of the biology and the status of the *L. peru* fishery. Fishing practices that select for large fish (who disproportionately contribute to sustaining fish populations into the future) has had major impacts on fish populations (Jennings et al. 1999). Here we show that for low or moderately exploited fish populations characterized by slow growth and high natural mortality in young adults, the size-selective fishing that shifts harvest away from large fish may be beneficial to the fish population structure and growth. Our projections for improvements in fish biomass and fishermen's revenues under market and institutionally- driven selective fishing scenarios support the claim that maintaining fish population structure (specifically by protecting older, larger fishes) is just as critical as managing overall fisheries effort (Berkeley et al. 2004).

Aligning economic incentives with conservation is a key strategy for sustainable fisheries management (Beddington et al. 2007). These findings suggest there may be opportunities to design regulations and/or enhance informal fishing rules or practices that complement market-driven fishing decisions. Fisheries with similar conditions as the *L. peru* fishery may benefit from new slot limit type size-regulations and/or increased capacity for local fishing cooperatives to encourage size-selection and limit entry. Under certain conditions, as we explore above, high market demand can provide an incentive for fishermen to comply with such rules and regulations. One challenge, however, would be that regulations could reduce revenues by eliminating the sale of non-target size classes. Fisheries managers could build capacity as well as the incentives for fishing cooperatives to enforce these type of rules by establishing/supporting local monitoring groups and property rights (e.g., by expanding or reinstating exclusive rights and area-based concessions for cooperatives) (CONAPESCA 2010*b*). Fisheries managers also could complement these efforts by developing other regulations when market and local institutional mechanisms are insufficient, e.g., for overfished or wide-ranging populations. A key assumption underlying this strategy is that fishermen are able to successfully select for medium-sized fish without significant by-catch and mortality of large or small fish. In order for market-driven size-selective fishing to have a positive impact, it will be critical to validate this assumption and also control by-catch by other fisheries (e.g., for *L peru*, by the shrimp fishery (Rocha-Olivares 1998)).

We have identified a novel approach for sustainable resource use that not only addresses but takes advantage of increasing market demand for seafood and the growing tourism sector both worldwide and around La Paz, Mexico, where the catch of *L. peru* has increased 100-fold increase since the 1950s (Erisman et al. 2010). Given these trends and our results, it appears that there is a critical policy window to capitalize on the potential synergies between market demand and local institutional norms that we have documented by piloting a hybrid market-regulatory slot-limit fishery for this highly valued species.

LITERATURE CITED

Allison, E. H., and F. Ellis. 2001. The livelihoods approach and management of small-scale fisheries. Marine Policy 25:377–388.

Anderson, R. O. 1974. Influence of mortality rate on production and potential sustained harvest of largemouth bass populations. Pages 18–28 *in* J. L. Fink, editor. Symposium on overharvest and management of largemouth bass in small impoundments. Special Publication 3. North Central Division, American Fisheries Society, Bethesda, Maryland, USA.

Armsworth, P. R., G. C. Daily, P. Kareiva, and J. N. Sanchirico. 2006. Land market feedbacks can undermine biodiversity conservation. Proceedings of the National Academy of Sciences USA 103:5403–5408.

Basurto, X., and E. Coleman. 2010. Institutional and ecological interplay for successful self-governance of community-based fisheries. Ecological Economics 69:1094–1103.

Beddington, J. R., D. J. Agnew, and C. W. Clark. 2007. Current problems in the management of marine fisheries. Science 316:1713–1716.

Berkeley, S. A., M. A. Hixon, R. J. Larson, and M. S. Love. 2004. Fisheries sustainability via protection of age structure and spatial distribution of fish populations. Fisheries 29:23–32.

Berkes, F., et al. 2006. Globalization, roving bandits, and marine resources. Science 311:1557–1558.

Brewer, T. D., J. E. Cinner, A. Green, J. M. Pandolfi. 2009. Thresholds and multiple scale interaction of environment, resource use, and market proximity on reef fishery resources in the Solomon Islands. Biological Conservation 142:1797–1807.

Buckley, R. 2011. Tourism and environment. Annual Review of Environment and Resources 36:397–416.

Bureau of Agricultural Research. 2008. Mudcrab. AGFISH-TECH Portal, Quezon City, Philippines.

Cinner, J. E., T. R. McClanahan, T. M. Daw, N. A. J. Graham, J. Maina, S. K. Wilson, and T. P. Hughes. 2009. Linking social and ecological systems to sustain coral reef fisheries. Current Biology 19:206–212.

Cinti, A., W. Shaw, R. Cudney-Bueno, and M. Rojo. 2010. The unintended consequences of formal fisheries policies: social disparities and resource overuse in a major fishing community in the Gulf of California, Mexico. Marine Policy 34:328–339.

Cisneros-Mata, M. 2010. The importance of fisheries in the Gulf of California and ecosystem-based sustainable co-management for conservation. Pages 119–134 in R. C. Brusca, editor. The Gulf of California. Biodiversity and conservation. University of Arizona Press, Tucson, Arizona, USA.

Collins, S. L., et al. 2011. An integrated conceptual framework for long-term social-ecological research. Frontiers in Ecology and the Environment 9:351–357.

CONAPESCA. 2010a. Permisos, concesiones y authorizaciones. CONAPESCA, DF, Mexico. http://www.conapesca.sagarpa.gob.mx/wb/cona/cona_permisos_concesiones_y_autorizaciones

CONAPESCA. 2010b. Programa nacional de inspeccion y vigilancia. Comision Nacional de Acuacultura y Pesca, Mazatlan, Sinaloa, Mexico.

Conover, D. O., and S. B. Munch. 2002. Sustaining fisheries yields over evolutionary time scales. Science 297:94–96.

Costello, C., S. D. Gaines, and J. Lynham. 2008. Can catch shares prevent fisheries collapse? Science 321:1678–1681.

Cruz-Romero, M., E. A. Chávez, E. Espino, and A. García. 1996. Assessment of a snapper complex (Lutjanus spp.) of the eastern tropical Pacific. Pages 324–330 in F. J. L. M. Arreguín-Sánchez, M. C. Balgos, and D. Pauly, editors. Biology, fisheries and culture of tropical groupers and snappers. ICLARM Conference Proceedings 48. International Centre for Living and Aquatic Resource Management, Makati City, Philippines

Darimont, C. T., S. M. Carlson, M. T. Kinnison, P. C. Paquet, T. E. Reimchen, and C. C. Wilmers. 2009. Human predators outpace other agents of trait change in the wild. Proceedings of the National Academy of Sciences USA 106:952–954.

Diaz Uribe, J., E. Chavez, and J. Garay. 2004. Evaluacion de la pesqueria del huachinango (Lutjanus peru) en el suroeste del Golfo de California. Ciencias Marinas 30:561–574.

Dulvy, N. K., N. V. Polunin, A. C. Mill, and N. A. Graham. 2004. Size structural change in lightly exploited coral reef fish communities: evidence for weak indirect effects. Canadian Journal of Fisheries and Aquatic Sciences 61:466–475.

Ebeling, J., and M. Yasué. 2009. The effectiveness of market-based conservation in the tropics: forest certification in Ecuador and Bolivia. Journal of Environmental Management 90:1145–1153.

Erisman, B., I. Mascarenas, G. Paredes, Y. S. d. Mitcheson, O. Aburto-Oropeza, and P. Hastings. 2010. Seasonal, annual, and long-term trends in commercial fisheries for aggregating reef fishes in the Gulf of California, Mexico. Fisheries Research 106:279–288.

Famularo, J. 2003. A cook's tour of Italy: more than 300 authentic recipes from the regions of Italy. Berkeley Publishing Group, New York, New York, USA.

FAO. 2010. The state of world fisheries and aquaculture. Food and Agriculture Organization of the United Nations, Rome, Italy.

FAO and the World Bank. 2009. Sunken billions: the economic justification for fisheries reform. World Bank, Washington, D.C., USA.

Fenberg, P. B., and K. Roy. 2008. Ecological and evolutionary consequences of size-selective harvesting: how much do we know? Molecular Ecology 17:209–220.

Ferraro, P. J., and S. K. Pattanayak. 2006. Money for nothing? A call for empirical evaluation of biodiversity conservation investments. PLoS Biology 4:e105.

Foster, A. D., and M. R. Rosenzweig. 2003. Economic growth and the rise of forests. Quarterly Journal of Economics 118:601–637.

Francis, R. 2003. A web of small intentions. Fisheries 28:20–23.

Friedlander, A., and E. DeMartini. 2002. Contrast in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian islands: the effects of fishing down apex predators. Marine Ecology Progress Series 230:253–264.

Gaines, S. D., C. White, M. H. Carr, and S. R. Palumbi. 2010. Designing marine reserve networks for both conservation and fisheries management. Proceedings of the National Academy of Sciences USA 107:18286–18293.

Garcia, S. M., et al. 2012. Reconsidering the consequences of selective fisheries. Science 335:1045–1047.

Gates, J. M. 1974. Demand price, fish size and the price of fish. Canadian Journal of Agricultural Economics 22:1–12.

Greenburg, P. 2010. Four fish: the future of the last wild food. Penguin Press, New York, New York, USA.

Grossman, G. M., and A. B. Krueger. 1993. Environmental impacts of the North American Free Trade Agreement. Pages 13–56 in P. Garber, editor. The U.S–Mexico Free Trade Agreement. MIT Press, Cambridge, Massachusetts, USA.

Grossman, G. M., and A. B. Krueger. 1995. Economic growth and the environment. Quarterly Journal of Economics 353–377.

Hesselgrave, T., S. Kruse, and K. A. Sheeran. 2011. The hidden cost of overfishing to commercial fishermen: a 2009 snapshot of lost revenues. A report to The Pew Charitable Trusts. Ecotrust, Portland, Oregon, USA.

Jennings, S., S. P. R. Greenstreet, and J. D. Reynolds. 1999. Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. Journal of Animal Ecology 68:617–627.

Jennings, S., and M. Kaiser. 1998. The effects of fishing on marine ecosystems. Pages 201–352 in J. Blaxter, A. Southward, and P. Tyler, editors. Advances in marine biology. Academic Press, San Diego, California, USA.

Jentoft, S. 2000. The community: a missing link of fisheries management. Marine Policy 24:53–59.

Jentoft, S., B. J. McCay, and D. C. Wilson. 1998. Social theory and fisheries co-management. Marine Policy 22:423–436.

Kennedy, A. J., and T. M. Sutton. 2007. Effects of harvest and length limits on shovelnose sturgeon in the upper Wabash River, Indiana. Journal of Applied Ichthyology 23:465–475.

Kipfer, B. 2011. The culinarian: a kitchen desk reference. John Wiley, Hoboken, New Jersey, USA.

Kuminoff, N. V., D. J. Bosch, D. Kauffman, J. C. Pope, and K. Stephenson. 2008. The growing supply of ecolabeled seafood: an economic perspective. Sustainable Development Law and Policy 9:25–28, 70–71.

Kurlansky, M. 1998. Cod: a biography of the fish that changed the world. Penguin Books, New York, New York, USA.

Longhurst, A. 2002. Murphy's law revisited: longevity as a factor in recruitment to fish populations. Fisheries Research 56:125–131.

Lotze, H. K., H. S. Lenihan, B. J. Bourque, R. H. Bradbury, R. G. Cooke, M. C. Kay, S. M. Kidwell, M. X. Kirby, C. H. Peterson, and J. B. C. Jackson. 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. Science 312:1806–1809.

Market, S. F. 2012. Species information: snapper. SFM, Sydney, Australia.

McClenachan, L. 2009. Documenting loss of large trophy fish from the Florida Keys with historical photographs. Conservation Biology 23:636–643.

McLeod, K. L., and H. M. Leslie, editors. 2009. Ecosystem-based management for the oceans. Island Press, Washington, D.C., USA.

Millar, R. 1992. Estimating the size-selectivity of fishing gear by conditioning on total catch. Journal of American Statistical Association 87:962–968.

Myers, R. A., and B. Worm. 2003. Rapid worldwide depletion of predatory fish communities. Nature 423:280–283.

Novinger, G. 1984. Observations on the use of size limits for black basses in large impoundments. Fisheries 9:2–6.

Olsen, E. M., S. M. Carlson, J. Gj sæter, and N. C. Stenseth. 2009. Nine decades of decreasing phenotypic variability in Atlantic cod. Ecology Letters 12:622–631.

Ostrom, E. 1990. Governing the commons: the evolution of institutions for collective action. Cambridge University Press, Cambridge, UK.

Parrish, J. D. 1987. The trophic biology of snappers and groupers. Pages 405–464 in J. J. Polovina and S. Ralston, editors. Tropical snappers and groupers: biology and fisheries management. Westview Press, Boulder, Colorado, USA.

Pauly, D., V. Christensen, J. Dalsgaard, R. Froese, and F. J. Torres. 1998. Fishing down marine food webs. Science 279:860–863.

Ralston, S. 1987. Mortality rates of snappers and groupers. Pages 375–404 in J. J. Polovina and S. Ralston, editors. Tropical snappers and groupers: biology and fisheries management. Westview Press, Boulder, Colorado, USA.

Reed, W. 1980. Age specific harvesting in a nonlinear population model. Biometrics 36:579–593.

Renwick, M. E., and S. O. Archibald. 1998. Demand side management policies for residential water use: who bears the conservation burden? Land Economics 74:343–359.

Ricker, W. 1945. A method of estimating minimum size limits for obtaining maximum yield. Copeia 1945:84–94.

Rimmer, M. A. 2006. Cultured aquatic species information programme. Lates calcarifer. FAO Fisheries and Aquaculture Department, Rome, Italy.

Rocha-Olivares, A. 1998. Age, growth, mortality, and population characteristics of the Pacific red snapper, Lutjanus peru, off the southeast coast of Baja California, Mexico. Fishery Bulletin 96:562–574.

Saila, S., and D. Horton. 1957. Fisheries investigation and management of Rhode Island lakes and ponds. Rhode Island Department of Agriculture and Conservation, Division of Fish and Game, Providence, Rhode Island, USA.

Saucedo-Lozano, M., E. Godínez-Domínguez, R. García-Quevedo-Machaín, and G. González-Sansón. 1998. Distribution and density of juveniles of Lutjanus peru (Nichols and Murphy, 1922) (Pisces: Lutjanidae) on the coast of Jalisco and Colima, Mexico. Ciencias Marinas 24:409–423.

Schlüter, M., et al. 2012. New horizons for managing the environment: a review of coupled social-ecological systems modeling. Natural Resource Modeling 25:219–272.

Sethi, S. A., T. A. Branch, and R. Watson. 2010. Global fishery development patterns are driven by profit but not trophic level. Proceedings of the National Academy of Sciences USA 107:12163–12167.

Shackell, N. L., K. T. Frank, J. A. D. Fisher, B. Petrie, and W. C. Leggett. 2010. Decline in top predator body size and changing climate alter trophic structure in an oceanic ecosystem. Proceedings of the Royal Society B 277:1353–1360.

Simenstad, C. A., J. A. Estes, and K. W. Kenyon. 1978. Aleuts, sea otters, and alternate stable state communities. Science 200:403–411.

Srinivasan, U. T., R. Watson, and U. Rashid Sumaila. 2012. Global fisheries losses at the exclusive economic zone level, 1950 to present. Marine Policy 36:544–549.

Swartz, W., U. R. Sumaila, R. Watson, and D. Pauly. 2010. Sourcing seafood for the three major markets: the EU, Japan and the USA. Marine Policy 34.

Tallis, H. M., and P. Kareiva. 2006. Shaping global environmental decisions using socio-ecological models. Trends in Ecology and Evolution 21:562–568.

Tissot, B. N., et al. 2010. How U.S. ocean policy and market power can reform the coral reef wildlife trade. Marine Policy 34:1385–1388.

Tlusty, M., R. Hardy, and S. Cross. 2011. Limiting size of fish fillets at the center of the plate improves sustainability of aquaculture production. Sustainability 3:957–964.

Vianna, G. M. S., M. G. Meekan, D. J. Pannell, S. P. Marsh, and J. J. Meeuwig. 2012. Socio-economic value and community benefits from shark-diving tourism in Palau: a sustainable use of reef shark populations. Biological Conservation 145:267–277.

Walker, B., S. Carpenter, J. Anderies, N. Abel, G. S. Cumming, M. Janssen, L. Lebel, J. Norberg, G. D. Peterson, and R. Pritchard. 2002. Resilience management in social-ecological systems: a working hypothesis for a participatory approach. Conservation Ecology 6:14.

Walters, C. J. 1986. Adaptive management of renewable resources. Macmillan, New York, New York, USA.

Wilde, G. R. 1997. Largemouth bass fishery responses to length limits. Fisheries 22:14–23.

Wilson, J., L. Yan, and C. Wilson. 2007. The precursors of governance in the Maine lobster fishery. Proceedings of the National Academy of Sciences USA 104:15212–15217.

Worm, B., et al. 2009. Rebuilding global fisheries. Science 325:578–585.

Zhou, S., A. D. M. Smith, A. E. Punt, A. J. Richardson, M. Gibbs, E. A. Fulton, S. Pascoe, C. Bulman, P. Bayliss, and K. Sainsbury. 2010. Ecosystem-based fisheries management requires a change to the selective fishing philosophy. Proceedings of the National Academy of Sciences USA 107:9485–9489.

SUPPLEMENTAL MATERIAL

Appendix A

Descriptive statistics of logbook data, tables showing estimates of the effect of prices on catch and numbers of fishermen, and figures showing the total catch by size class and cooperative and the effects of the four harvest scenarios under different conditions for initial harvest and new entrants (*Ecological Archives* A023-036-A1).

Appendix B

Detailed description of fish population model (*Ecological Archives* A023-036-A2).

Supplement

Code for age- and stage-based population models of *Lutjanus peru* and four harvest scenarios run under four different conditions (*Ecological Archives* A023-036-S1).