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SPECIAL FEATURE

Social hysteresis and ecological hysteresis

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Modeling responses of coupled social–ecological systems of the Gulf of California to anthropogenic and natural perturbations

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Abstract Key elements of the rapidly expanding field of ecosystem-based management include: (a) understanding connections among social and ecological systems and (b) developing analytical approaches to inform the necessary trade-offs among ecosystem services and human activities in coastal and marine areas. To address these needs, we investigate the impacts of multiple economic sectors on the marine ecosystem and dependent human community in the Gulf of California with an ecological-economic model. We focus on the spotted rose snapper (*Lutjanus guttatus*), an economically important species targeted concurrently by the nearshore artisanal fleet, the sportfishing fleet, and by the industrial shrimp fleet as bycatch. Economic returns to the local community are driven by the artisanal fishery catch and the number of tourists who engage in the sportsfishery, and these variables are in turn impacted by fish abundance. We find that the coexistence of the two sectors (and production of both seafood and tourism services) creates stability in key elements of the coupled systems. When the coupled systems are perturbed by changes in exploitation and climate variability, the artisanal fishery responds more rapidly and to a greater degree than the sportsfishery to shifts in the fish population. Our results suggest that vital components of coupled systems may well respond differently to climate variability or other perturbations, and that management strategies should be developed with this in mind. Models like ours can facilitate the development and testing of hypotheses about the form and strength of interactions between ecosystems, services, and the human communities that rely on them.

Keywords Trade-offs · Marine ecosystem services · Social–ecological system · Ecosystem-based management · Modeling · Ecological-economics · Fisheries

Introduction

Human effects upon coastal and ocean ecosystems are greater in magnitude and extent than ever before (MA 2005; UNEP 2006). More than 40% of the world's oceans are heavily impacted by human activities, including coastal development, overexploitation, pollution, and climate change (Halpern et al. 2008). Given the degree of humans' influence on ocean ecosystems, there is increasing interest in more integrated, ecosystem-based approaches to managing human interactions with coastal and marine ecosystems (UNCED 1992; USCOP 2004). Key elements of ecosystem-based management include: (a) understanding connections among social

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and ecological systems and (b) developing analytical approaches to inform the necessary trade-offs among human activities in coastal and marine areas (Leslie and McLeod 2007). Linkages between coastal and marine ecosystems and the human communities that rely upon them are often mediated by ecosystem services, i.e., the goods and services that are generated by functioning ecosystems (Daily 1997; McLeod and Leslie 2009).

A key principle of marine EBM is managing human interactions with ecosystems so as to ensure delivery of the full range of ecosystem services these systems provide. This approach recognizes the diversity of ways that humans value coastal and marine systems (McLeod and Leslie 2009). In contrast, management activities focused on the provision of a single service or human activity can create negative effects on other services and/or economic sectors (e.g., Barbier et al. 2008; Chan et al. 2006; Rosenberg and Sandifer 2009). Consequently, in order to move forward with ecosystem-based approaches, there is a pressing need for the development of analytical tools to aid in the assessment of trade-offs among services and sectors. Explicit consideration of these trade-offs—as opposed to the present implicit calculus—will increase opportunities to identify win–win outcomes as well as to forecast the likely consequences (positive and negative) of particular strategies (Tallis et al. 2008).

Many models of the linkages between ecosystems and people (and their social and economic institutions) exist, and have developed from diverse disciplinary roots and with varying scientific and pragmatic purposes. In the interest of space, we focus here on fisheries models. Classical bioeconomic models of fish populations and fishermen date to the work of Gordon (1954) and Clark (1990) and are reviewed comprehensively by Hilborn and Walters (1992). Analytical approaches may be used to develop management strategies (i.e., broad advice) but when it comes to specific tactics (e.g., setting of quotas, selection of closed areas), the flexibility of simulation models have made the latter the dominant approach (Hilborn and Walters 1992). More recently, simulation models that incorporate more than fish and fishermen, and go so far as to model whole marine ecosystems have been developed (e.g., Christensen and Walters 2004; Kaplan and Levin 2009; Smith et al. 2007). Our approach falls in the middle; we do not attempt to model the entire system, but rather focus on key linkages between the social and ecological domains. While we employ simulations, we also simplify and solve our model analytically initially to get a basic understanding of the fish population dynamics.

Here we investigate the impacts of multiple economic sectors on the resilience of key components of the marine ecosystem and dependent human community in the Gulf of California by using an ecological-economic modeling approach. Our goal is to explore the qualitative behavior of coupled social–ecological marine systems so as to better understand the trade-offs among different ecosystem services and the implications for management, rather than to prescribe or evaluate particular management strategies. We expect that this work will inform more detailed (and potentially, predictive) modeling and empirical work in the future. We define resilience (sometimes called robustness, e.g., Levin and Lubchenco 2008) as the extent to which a system can maintain its structure, functioning, and identity in the face of disturbance, after Folke et al. 2004 and Holling 1973. We explore how two key services generated by coupled social and ecological systems (tourism and seafood) respond to climate variability and changes in management. In the context of our model, the magnitude of the fluctuations in the adult fish population size and the catch per unit effort and returns of the fishing fleets associated with each of the services are used as indicators of the coupled systems' resilience.

The ecological and economic value of the Gulf of California (also known as the Sea of Cortés), along with the strong interest in sustainability by stakeholders in the region (see Carvajal et al. 2004), make it a logical focus for our approach. Bordering five Mexican states, it is 260,000 km^2 in area, and one of the most biologically productive areas of the world's oceans. The Gulf's biodiversity includes 770 endemic marine species and 39 IUCN red-listed species. Terrestrial and marine ecosystems in the region respond dramatically to El Niño-Southern Oscillation events, which occur every several years (Polis et al. 2002; Velarde et al. 2004). During El Niño years, ocean waters warm, wind and tidally driven upwelling slows, rainfall increases tremendously, and ocean productivity declines. Terrestrial productivity varies inversely with marine productivity; during El Niño years, plants and higher terrestrially dependent trophic levels flourish while marine-dependent species falter (Polis et al. 2002).

While the region's remarkable biodiversity has considerable conservation value, it also is of substantial social and economic importance. The region is home to almost 9 million people, and in 2000, produced 10% of Mexico's gross domestic product (Carvajal et al. 2004). In addition to fisheries and agricultural production, other key ecosystem services include fresh water for human consumption, industry, and other uses, and recreation and tourism in coastal and nearshore areas.

While ultimately it makes sense to examine the trade-offs among all the priority ecosystem services in a region like the Gulf of California, for tractability, we start by examining the human–environment linkages involved in two of the most important services: seafood production and tourism (specifically sportfishing). Shrimp, sardines, and squid are among the largest fisheries by volume in the Gulf (SAGARPA 2001), and 50% of Mexico's commercial fish catch comes from the Sea of Cortés, including one of the country's most valuable exports, shrimp (Carvajal et al. 2004). Sportfishing also generates substantial revenues and jobs and brings hundreds of thousands of visitors to the region each year (Southwick Associates et al. 2008).

We begin with only one fish species to facilitate our focus on the dynamics of the coupled systems, rather than on the details of the ecological or social domain per se. Inclusion of multispecies dynamics (e.g., Arreguin-Sanchez et al. 2004) would add depth to the biological domain of this model, but with this detail will come more complexity, which will complicate interpretation of our results and understanding of the coupling between the social and ecological domains.

We chose the spotted rose snapper (*Lutjanus guttatus*), an economically important species, to represent the ecological domain as it is impacted by multiple sectors. This relatively large, demersal fish is highly valued as a game fish, and also is exploited by artisanal fishermen, who use a variety of gears, including hook and line, spearfishing, gillnets, and longlines, to catch it throughout the year. Snappers exhibit relatively slow growth rates and thus are considered vulnerable to overfishing (Ralston 1987). In fact, estimates of the fishing and natural mortality of this species in Sinaloa, in the southern part of the Gulf, suggest that it is overfished, and Sinaloan fishermen have remarked that catches of the snapper are half of what they were 10 years ago (Amezcua et al. 2006). Comparative data are not available from the northern region, although the species is thought to be under significant fishing pressure there as well (R. Cudney-Bueno, pers. obs.). Finally, sub-adult spotted rose snappers are caught as bycatch by the industrial shrimp fishery (Perez-Mellado and Findley 1985; Young and Romero 1979). This last impact is thought to exert a major pressure on the stock (Amezcua et al. 2006), but estimates of the biomass taken or the added mortality created by this industry are not available.

Like other snappers, the spotted rose snapper exhibits ontogenic habitat shifts, such that larvae occupy the pelagic environment, juveniles (particularly first year fish) live in mangroves and coastal lagoons, and adult fish are associated with rocky reefs and other high relief environments (Thomson et al. 2000). They are generalized, opportunistic carnivores, feeding primarily within a few meters of the bottom on smaller fish, crabs, and shrimp (Allen 1985; Parrish 1987). Parrish (1987) observed that there is little direct evidence that snappers are prey-limited, but that competition for shelter may be more of an issue. In reviewing the causes and magnitude of natural mortality in groupers and snappers, Ralston (1987) notes that predation is likely size-dependent and most severe on young fish.

In terms of the socioeconomic context, within which the sportfishing and artisanal fishing in the Gulf occur, ongoing research by PANGAS (http://pangas.arizona.edu/) indicates that for some species, both artisanal fishermen and sportfishing operators (i.e., those who take tourists out sportfishing) are active in the same geographic areas (R. Cudney-Bueno, pers. obs.). Our model is based upon the situation in various communities of the Gulf, where individuals specialize in one of these two sectors, and do not regularly switch between them. This situation differs from many other artisanal fishing contexts, where membership in a given fishery may be more fluid through time (Allison and Ellis 2001).

In the following pages, we first explore the dynamics of the coupled systems under different exploitation scenarios. We then investigate how changes in the biophysical environment and management regime impact the coupled systems, and discuss the implications of our model for ecosystem-based management efforts in the Gulf of California and elsewhere.

Model description

The ecological domain: fish population dynamics

We model the population dynamics of the spotted rose snapper with two distinct subpopulations, a juvenile and an adult, to represent the ontogenic shift in habitat use observed in this and many other snapper species (Fig. 1). We consider all individuals that are not mature and recruited to the artisanal and sportsfisheries to be juveniles, although we recognize that the actual life history is more complex (see "Discussion"). We use a discrete time model with overlapping generations because of the seasonality of reproduction and recruitment and the relatively long lifespan of the species. Our approach is roughly based on ecological-economic models that consider simultaneous exploitation by multiple sectors of adult fish populations (e.g., Laukkanen 2001; Olaussen and Skonhoft 2005) and is consistent with the biomass dynamic-type models advocated when data on species life history and exploitation rates and effects are sparse (Hilborn and Walters 1992). However, our model goes beyond those by considering the juveniles and adults as two distinct stocks that are affected by different environmental and harvesting pressures, and are linked through recruitment and immigration. We explicitly include the adult harvest mortality generated by two sectors—the artisanal fleet and the sportfishing fleet—and also include juvenile mortality due to bycatch pressure from the industrial shrimp fleet. For the purposes of this model, we assume that adult mortality due to the industrial shrimp fishery is minimal.

Let $X_{J,t}$ and $X_{A,t}$ be the abundance of juvenile and adult snappers, respectively, in two distinct locations, at time t. Larval fish recruit to the juvenile population based on production of new juveniles by the adult population with a probability ψ according to a Ricker-type spawner-recruit relationship. In this context, b represents the competitive effects among the young-of-the-year (i.e., the first-year juveniles). Juvenile survival within the juvenile population (S_J) is influenced by the total natural mortality, M_J (which is a combination of density-dependent and density-independent mortality), H_J, the probability of bycatch mortality due to the industrial shrimp fishery, and I, the probability of immigration of juveniles from coastal estuaries to the adult snapper population on rocky reefs (Eq. 1). Approximately one-quarter of the surviving juvenile fish immigrate to the adult population every year; we arrived at this proportion based on knowledge of the life history of this snapper and related species (see Amezcua et al. 2006; Polovina and Ralston 1987).

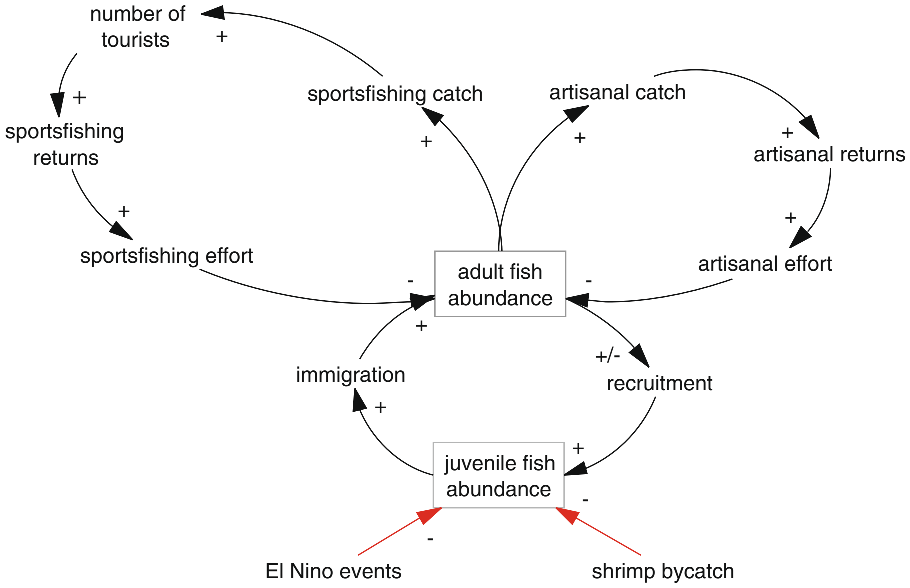

Fig. 1 Major feedback driving the model of the coupled social–ecological systems. Juvenile and adult fish populations are affected by different environmental and exploitation pressures and are linked through immigration and recruitment. Adults are harvested by the sportsfishing and artisanal fleets, while the largely immature individuals are impacted by the industrial shrimp fleet via bycatch. The effort employed by the sportsfishing and artisanal fleets are driven by the returns to each respective sector. See text for details

The size of the adult population (in numbers of fish) at time *t* is $X_{A,t}$. Adult snapper are exploited by both the artisanal fishery and the sportsfishery. H_A is the cumulative probability of mortality of adult snappers caused by the two sectors, while M_A is the natural mortality probability of adults. The population increases through migration of $I \times X_{J,t}$ juveniles to the adult population. The surviving adults and the immigrated juveniles form the adult population at time $t + 1$ (Eq. 2). This yields the following dynamics:

$$X_{J,t} = S_J * X_{j,t-1} + \psi * X_{A,t-1} * e^{-b*X_{A,t-1}} \tag{1}$$

$$X_{A,t} = S_{A,t-1} * X_{A,t-1} + IX_{J,t-1} \tag{2}$$

where $S_J = 1 - M_J - H_J - I$ and $S_A = 1 - M_A - H_{A,t\text{-}1}$.

$H_{A,t}$—the cumulative catch probability by the sportsfishery and the artisanal fishery in time t—is a function of effort ($E_{Y,t}$) and catchability (q_Y) in each sector *Y* (where $Y = S$ for the sportsfishery and *F* for the artisanal fishery; Eq. 3). The effort in the artisanal fishery ($E_{F,t}$) and sportsfishery ($E_{S,t}$) are determined by the returns in each sector (see below; Eqs. 7–8).

$$H_{A,t} = E_{S,t} * q_S + E_{F,t} * q_F \tag{3}$$

The social domain

We assume that the returns from the sports and artisanal fisheries contribute to community well-being, and are utilized and controlled within the geographic region. While there is a market for the fish caught by the artisanal fleet, it is quite local in extent (R. Cudney-Bueno, pers. obs.). The returns from both activities determine the actual fishing effort $E_{F,t}$ and $E_{S,t}$ in the artisanal fishery and sportsfishery (see Eqs. 7–8).

Let $R_{F,t}$ and $R_{S,t}$ be the returns from artisanal fishing and sports fishing, respectively (Eqs. 4–5). Let P_F represent the price per unit of fish, P_S the price per tourist that fishes on a fishing boat, C_F the costs of fishing for artisanal and C_S the price for taking a tourist on a boat for sportfishing. N_t is the number of tourists involved in sportfishing. The returns from artisanal fishing are a function of the actual fish catch while the returns from sportfishing are determined by the number of tourists that engage in sportfishing. We recognize that returns are impacted by variable costs and prices, caused for example by fluctuations in the domestic and international markets or subsidies; as a starting point we keep these parameters constant.

$$R_{F,t} = (P_F q_F * X_{A,t} - C_F) * E_{F,t} \tag{4}$$

$$R_{S,t} = (P_S - C_S) * N_t \tag{5}$$

The number of tourists that participate in sportfishing (N_t) is a function of the number of adult snappers caught by the sportsfishery in the previous time step ($E_{S,t\text{-}1} * q_S * X_{A,t\text{-}1}$). We based this on the assumption that a higher sportfishing catch will attract more tourists, as sportsfishermen are motivated by catch as well as non-catch considerations (Fedler and Ditton 1994). The function *N* approaches K_T, the maximum number of tourists that can be supported by this area, with a slope determined by the parameter λ (Eq. 6).

$$N_t = \frac{\lambda E_{S,t-1} * q_S * X_{A,t-1} * K_T}{K_T + \lambda E_{S,t-1} * q_S * X_{A,t-1}} \tag{6}$$

Linking the ecological and social domains

While there is a federal fisheries-management structure in Mexico and effort is intended to be managed via limited entry through the provision of fishing permits and concessions due to limited enforcement, both the artisanal fishery and the sportsfishery in this region are largely de facto open-access fisheries (Cudney-Bueno et al. 2009a). Effort in each sector is driven by the size of the revenues from selling the catch of the artisanal fisheries, or taking tourists sportfishing. Some sportsfishermen operate independently, and do not rely on tourist charters; for the purposes of this initial model, we group these sportsfishermen with the 'tourists'.

We assume that with high returns there will be more financial capital, which will allow an increase in the physical (and labor) capital. We developed our own formalizations for each sector's effort dynamics (Eqs. 7, 8), in keeping with well-accepted bioeconomic approaches (Clark 2006; Hilborn and Walters 1992). Effort in the artisanal fishery ($E_{F,t}$) increases if the level of returns per unit effort is above the threshold R_C, and otherwise is at a minimum level, $E_{F(\min)}$ (Eq. 7). This minimum level of effort, even when profits are low, could be caused by several factors, e.g., incidental capture (while fishers may shift their activities to another species, they still are likely to capture snappers while searching for those other fish), time lags in fisher responses to changes in the ecology or economics of the system, and the heterogeneous behavior of individual fishers (some being more conservative than others). The threshold reflects the assumption that artisanal fishers need a certain minimum return before they will start increasing their effort.

$$E_{F,t} = \begin{cases} \frac{a(R_{F,t-1}/E_{F,t-1} - R_C)}{1+c(R_{F,t-1}/E_{F,t-1} - R_C)} + E_{F(\min)} & \text{if } R_{F,t-1}/E_{F,t-1} > R_C \\ E_{F(\min)} & \text{if } R_{F,t-1}/E_{F,t-1} \le R_C \end{cases} \tag{7}$$

Effort in the sportsfishery ($E_{S,t}$) increases linearly with returns from sportfishing (Eq. 8). Unlike in the artisanal fishery, effort in the sportsfishery can drop to zero (i.e., there is no minimum effort present regardless of the returns/size of the fish population). The scaling parameter β is the investment factor for the sportfishing sector. That is, we interpret an increase in β as a reflection of more investment and consequently, higher sportfishing effort in the following year.

$$E_{S,t} = \beta R_{S,t-1} \tag{8}$$

Steady-state analysis of the fish population model without harvesting

Analysis of the steady state of the model gives the following equilibrium states for the juvenile and adult fish population abundance, X_J and X_A, respectively (Eqs. 9–10):

$$X_J^* = -\frac{1-S_A}{b*I} * \ln\left(\frac{(1-S_J)(1-S_A)}{\psi * I}\right) \tag{9}$$

$$X_A^* = -\frac{1}{b}\ln\left(\frac{(1-S_J)(1-S_A)}{\psi * I}\right) \tag{10}$$

Thus, to assure that such an equilibrium can exist, necessary conditions are

$$0 < (1-S_J)(1-S_A) < \psi * I$$

In other words, there must be some mortality in both age-classes (or else the population will explode and then crash due to density-dependent recruitment), and recruitment and immigration rates must be sufficiently large to compensate for mortality. The equilibrium is stable under the conditions that $\psi * I < \left(\frac{e^T}{T}\right)$ with $S_J = S_A = S$ and $T = \frac{1}{(1-S)}$. Thus, for very low survival probabilities we can approximate $\psi * I < e^2$. For high survival probabilities, the upper bound on $\psi * I$ disappears. For a full stability analysis of the fish population model and a graph of the stable parameter region, please see Electronic Supplementary Material, Appendix A1 and Fig. A1.

Model parameterization

Model parameters were chosen to reflect biological and economic knowledge of the system where possible. Otherwise, following extensive sensitivity analyses, we selected parameters in order to stay in a parameter region where behavior in the single sector models is not chaotic (see Table 1). Specifically, we parameterize the immigration probability, I, to reflect knowledge that the juvenile fish remain in the juvenile habitat for approximately 4 years before immigrating to the adult population (as described above). We consider a range of biologically reasonable values for ψ and H_J to explore these parameters' effects on the system as part of the scenarios (see "Influence of perturbations on the coupled systems"). As a starting point, we assume that the catchability parameters in each sector are equivalent ($q_S = q_F$). The cost parameters are scaled so that they are proportionally equivalent between the two sectors ($C_S = 0.025 * C_F$).

Results

We first investigate the dynamics of the coupled systems under three conditions: no exploitation, single-sector fishing, and two-sector exploitation. We then explore how two types of disturbance, climate variability and a change in management of the shrimp fishery that alters the magnitude of juvenile bycatch, influence the dynamics of the fish population and the generation of ecosystem services and monetary benefits to each sector.

No exploitation condition

When there is no exploitation, juvenile abundance is highest when immigration (I) is low (but non-zero) and

Table 1 Model parameters and initial conditions

		Value	Range explored
Fish population parameters			
Reproductive probability	ψ	2.5	1.25
YOY competition parameter	b	0.001	
Probability of natural adult mortality	M_a	0.2	
Probability of natural juvenile mortality	M_J	0.2	
Probability of bycatch mortality	H_J	0.1	0, 0.1, 0.2, 0.3, 0.4, 0.5
Immigration probability	I	0.25	
Effort function parameters			
Minimum artisanal effort	E_F (min)	0.05	
Artisanal effort threshold	R_C	50	
Artisanal effort parameter 1	a	0.015	
Artisanal effort parameter 2	c	0.02	
Sportfishing investment factor	β	0.0108	0.005, 0.15
Return function parameters			
Fish price	P_F	0.4	
Tourist price	P_S	1	
Artisanal catchability parameter	q_F	1	
Sportfishery catchability parameter	q_S	1	
Artisanal cost parameter	C_F	20	
Sportfishery cost parameter	C_S	0.5	
Tourism function parameters			
Tourism slope parameter	λ	2	
Tourism carrying capacity	K_T	100	
Initial conditions			
Juvenile population size, $t = 0$	$X_{J,0}$	200	
Adult population size, $t = 0$	$X_{A,0}$	50	
Number of tourists, $t = 0$	N_0	10	
Artisanal returns, $t = 0$	$R_{F,0}$	10	
Sportfishery returns, $t = 0$	$R_{S,0}$	10	
Artisanal effort, $t = 0$	$E_{F,0}$	0.2	
Sportfishery effort, $t = 0$	$E_{S,0}$	0.2	

'Range explored' refers to the values used in the scenarios. Please see text for relevant references and sensitivity analyses

the reproductive probability (ψ) is high (Electronic Supplementary Material, Fig. A2). Adult fish abundance increases with increases in the values of the reproductive and immigration probabilities. At high immigration probabilities, the adult population is more sensitive to changes in the reproductive probability, whereas the juvenile population is generally more sensitive to changes in immigration probability.

Single-sector dynamics

Fishing effort in the two sectors is determined by the returns to each sector (Eqs. 4, 5), and by key parameters of the effort functions that determine the linkage between returns and effort: sportfishing effort ($E_{S,t}$) is a function of the returns from tourism scaled by the sportfishing investment factor β, and artisanal effort is determined by the critical returns-per-effort-threshold (heretofore referred to as the artisanal effort threshold or R_C) and actual returns per effort.

When we examine the response of the fish population to exploitation only by the sportsfishery, we find that with an increase in β, both the juvenile and adult fish populations decline; although the juveniles initially increase in abundance due to the release of density dependence on the adult reproductive output. An increase in β leads to a nearly linear increase in effort as returns increase and then a leveling off when returns start to decline again (Fig. 2). Because $0 \leq E_S < 1$ and effort is proportional to sportfishing returns, the maximum value of β that is possible for the given parameterization and maximum return values is ca. 0.29. The catch, returns, and number of tourists all peak at a fairly low value of β ($=0.009$) where effort is at approximately 0.4 and the catch per unit effort is highest. The actual returns per unit effort decline asymptotically with increasing β. Thus an increase in β and a sportfishing effort exceeding 0.4 leads to a decrease in the returns. The fish population is then fished beyond its optimal level.

When only the artisanal sector is active, increasing the artisanal effort threshold R_C leads to increases in both the juvenile and adult stocks. A higher R_C value means that higher returns per effort are needed before effort is increased beyond the minimum effort. With increasing R_C, effort in the artisanal sector (E_F) declines while catch, total returns, and returns per unit effort increase (Fig. 3). As with sportfishing, catch per unit effort is highest for effort values around 0.4. Once effort is higher, the population and its growth rate are smaller, and catch is less than optimal. This explains why we see an increase in the catch with a decrease in effort. At the same time, at high R_C values ($200 < R_c < 600$), fish abundance, catches, and effort oscillate strongly or become chaotic (results not shown).

Note that the range of values for effort differ between the sectors (artisanal fishing effort varies much less and is higher on average, across the range of R_C values plotted), as does the catch and total returns per sector (here, maximum fish catches are similar but the variance is much higher in the sportfishing; total returns are higher in the artisanal fisheries). For the given parameter values, catch per unit effort for the sportsfishery spans a much larger range as well.

Two-sector dynamics

We then investigate the behavior of the fish population and dependent sectors when both the artisanal and sportfishing fleets are active. Overall, we see that as the sportfishing sector becomes more active with an increase in the sportfishing investment factor β, the effort in artisanal fishing sector decreases (Fig. 4a). The abundance of both juvenile and adult fish changes sharply with changes in β and the artisanal effort threshold (R_C) (Fig. A3). Abundances are highest with high R_C and low β values. Here, as R_C increases, artisanal fishing effort declines

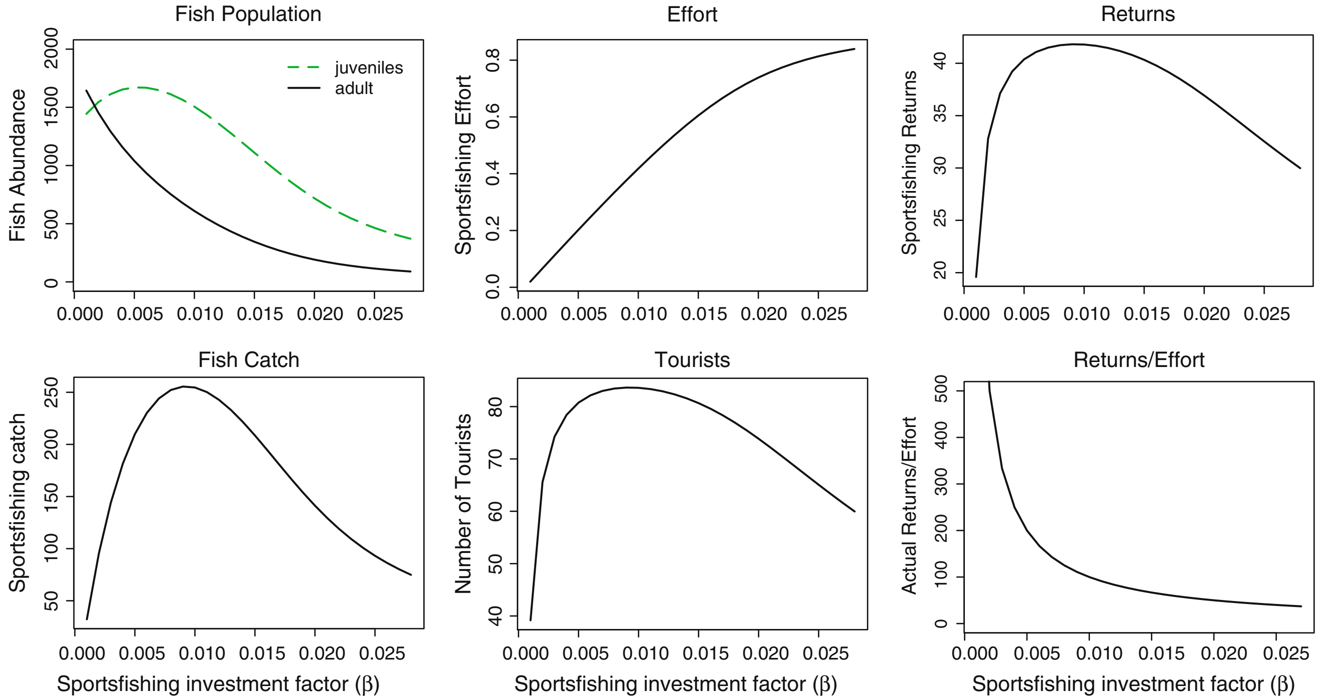

Fig. 2 System dynamics when only the sportsfishery is active. All values are mean values of the last 200 time steps of each run

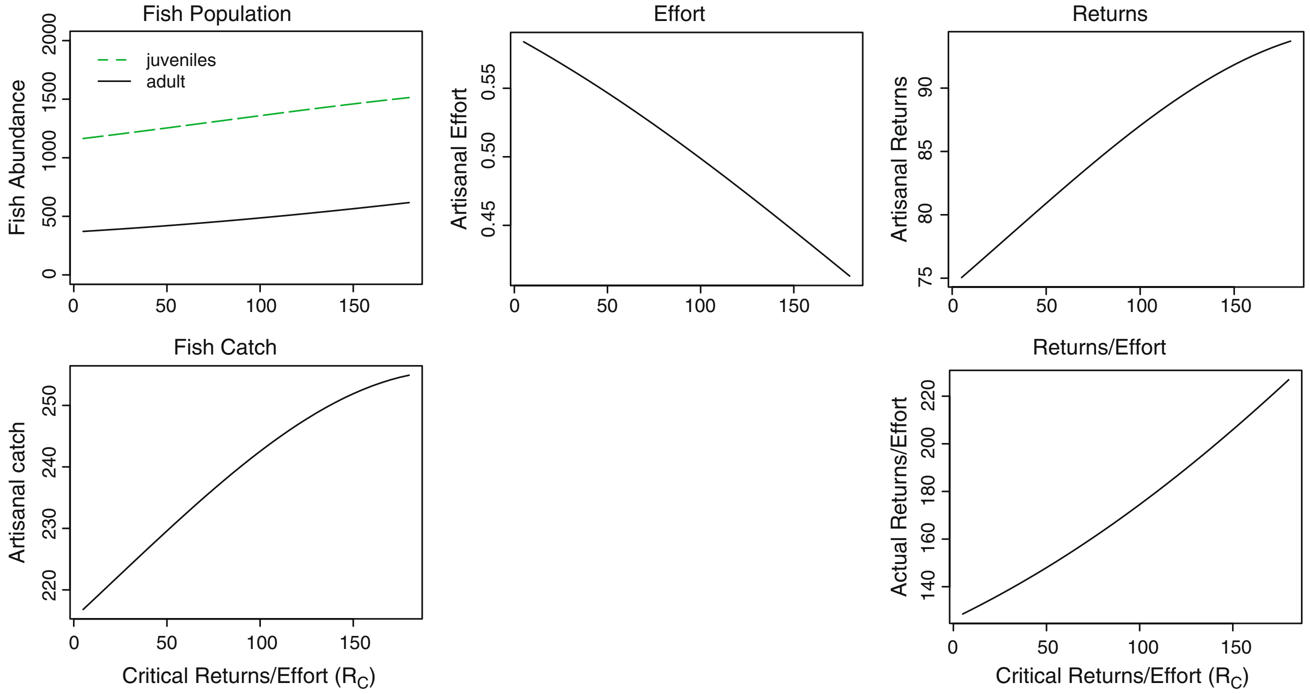

Fig. 3 System dynamics when only the artisanal fishing is active. All values are mean values of the last 200 time steps of each run

(Fig. 4a); sportfishing effort is still low and thus this situation is similar to single sector (only artisanal fishing) scenario. Because of the concurrent decrease in adult fish abundance, the returns received in each sector decrease and total returns decline as well (Fig. 4b, c).

There is clearly a threshold where the system switches from being artisanal fishing dominated to a system where both activities fish with substantial effort to a sportsfishing-dominated one, depending on the values of R_C and β (Fig. 4a). As R_C increases, this area of

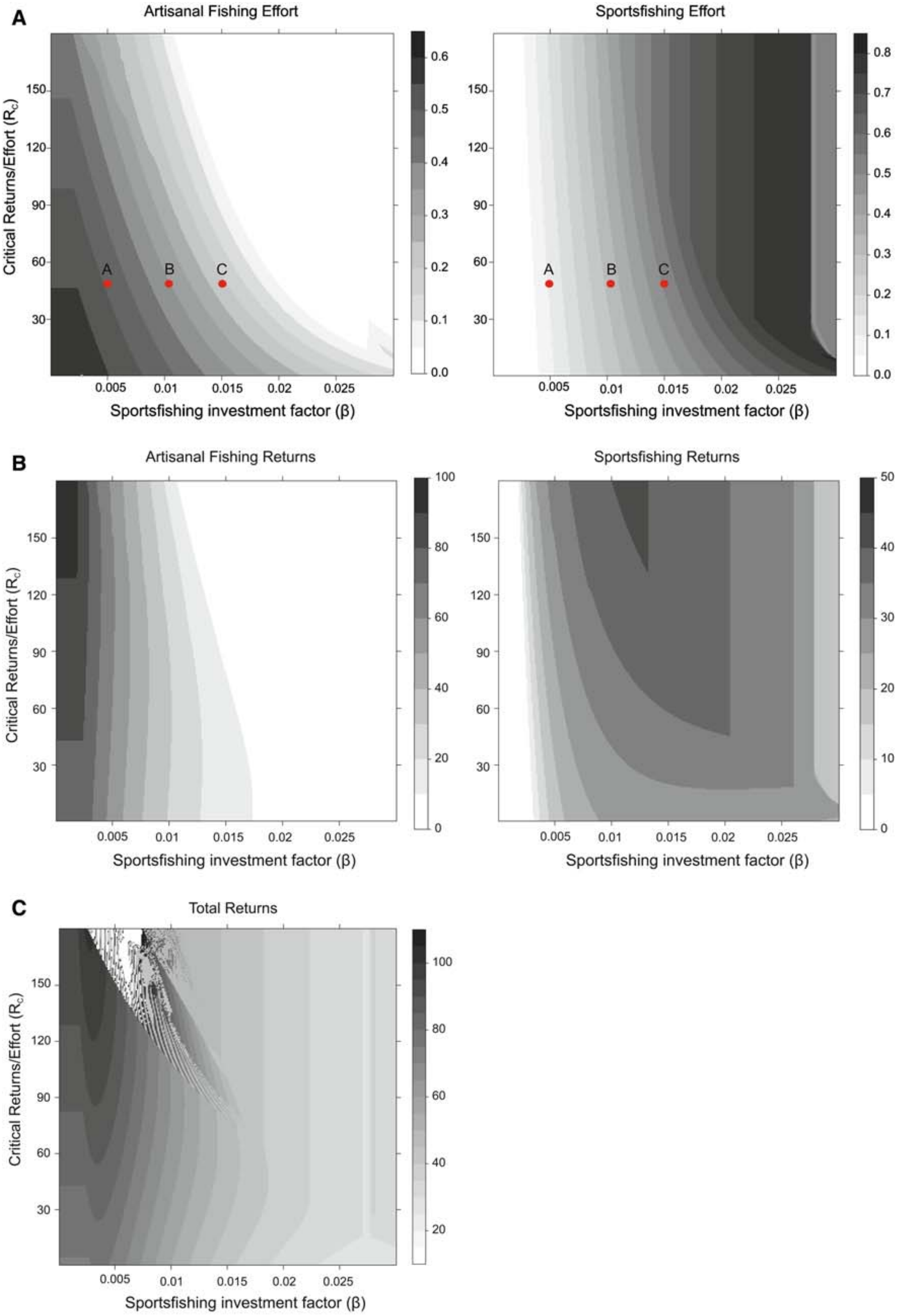

Fig. 4 System dynamics when both sectors are active. **a** Effort, **b** returns for each sector, **c** total returns, **d** standard deviation of the effort for each sector. Three system states are identified in **a**: the artisanal-dominated ($\beta = 0.005$), coexistence ($\beta = 0.01075$) and sportfishing-dominated ($\beta = 0.015$) states ($R_c = 50$ in all three cases)

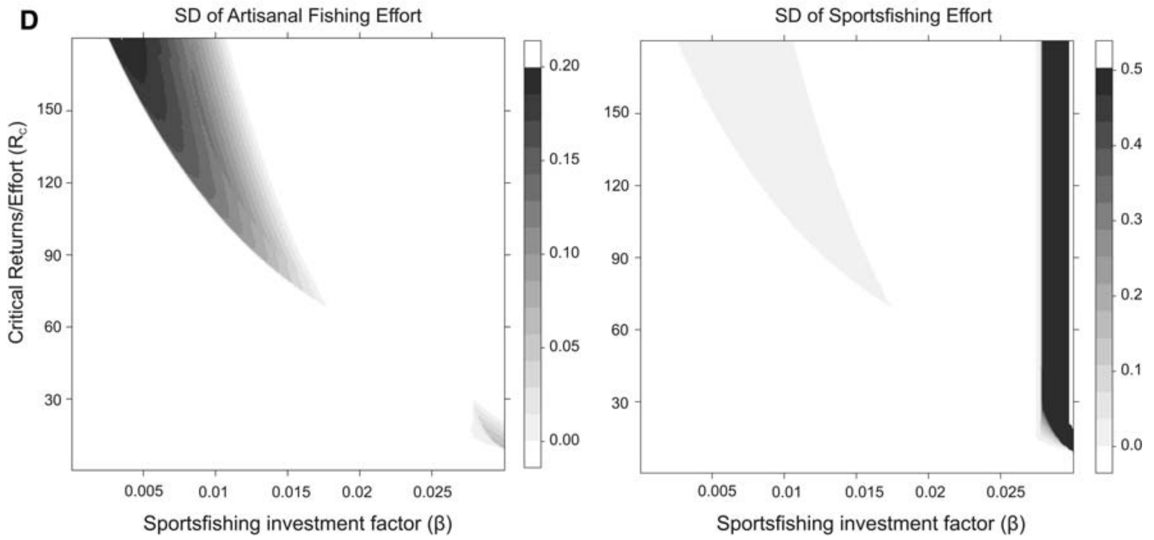

Fig. 4 continued

sportfishing dominance (with minimal artisanal fishing) expands (Fig. 4a). Additional runs of the model with a linear form of the artisanal fisheries effort function (Eq. 9) indicate that the nonlinearity of this function is not responsible for the observed threshold (results not shown).

For example, when we hold R_C constant and increase β, sportfishing effort increases rapidly (Figs. 4a, A4). Adult fish abundance decreases, as does the artisanal fishing effort. When β is ≥0.02, artisanal fishing effort is at the minimum level (Fig. 4a). Total returns decline strongly, which is in contrast to the high increase in sportfishing effort. We see a change in the dynamics of the fish population and the sportfishing effort once artisanal fishing effort is at a minimum. This response is caused by the fact that we are constraining artisanal effort at a minimum value and not letting it decline to zero. Thus, even with the decline in the adult fish population, both sectors continue to fish.

Artisanal and sportfishing catch changes with increasing β as well (Fig. A4). Artisanal catch declines in a fashion similar to the artisanal effort, but more steeply because the fish population also declines. While sportfishing catch increases initially, returns do not increase in the same manner. After an initial increase, they remain nearly constant due to the effect of the tourism function, which buffers the effect of an increase in sportfishing effort.

In general, we observe that the higher the value of β (the investment factor that controls sportfishing effort and thus returns) the more variable the response from the sportfishing sector. As β approaches 0.03, the system becomes unstable because this change forces combined effort from the sectors to approach 1.

The range of fish population size and fishery effort in R_C/β—parameter space reveals that there are three system states: one where the artisanal fishery dominates, a second where the two sectors coexist, and a third where the sportsfishery dominates. In the first case, both the effort and the returns of the artisanal sector greatly exceed those of the sportsfishery (Fig. 4a, point ‘A’); while in the final case, the sportsfishery returns and effort exceed the values for the artisanal fishery (Fig. 4a, point ‘C’). Coexistence is characterized by near-equal effort and returns in each sector (Fig. 4a, point ‘B’). These differences are more clearly visible when we plot the returns and effort for each sector for each of the three states (Fig. A5).

The returns per effort in the two scenarios where one of the sectors dominates are higher than in the coexistence scenario. In other words, the presence of the other sector reduces the returns of the first. With two sectors present, the abundance of adult fish declines and subsequently the returns to each sector. At the same time, when both sectors are active at approximately the same level of effort (the coexistence scenario), the returns to each and the fish population abundance oscillate less. Thus coexistence creates stability in some key elements of the coupled systems.

Influence of perturbations on the coupled systems

We focus on the coexistence scenario (Fig. 4a, point ‘B’) to examine how the connections between the marine ecosystem and human community impact the generation of key ecosystem services (seafood provision, tourism opportunities) in the face of disturbance.

First we explore the impact of climate variability. Investigations from the Gulf and other marine systems have demonstrated the bottom-up effects of El Niño events (e.g., increased ocean temperatures, decreased primary productivity, and alterations in habitat) on higher trophic levels (Aburto-Oropeza et al. 2007; Glynn

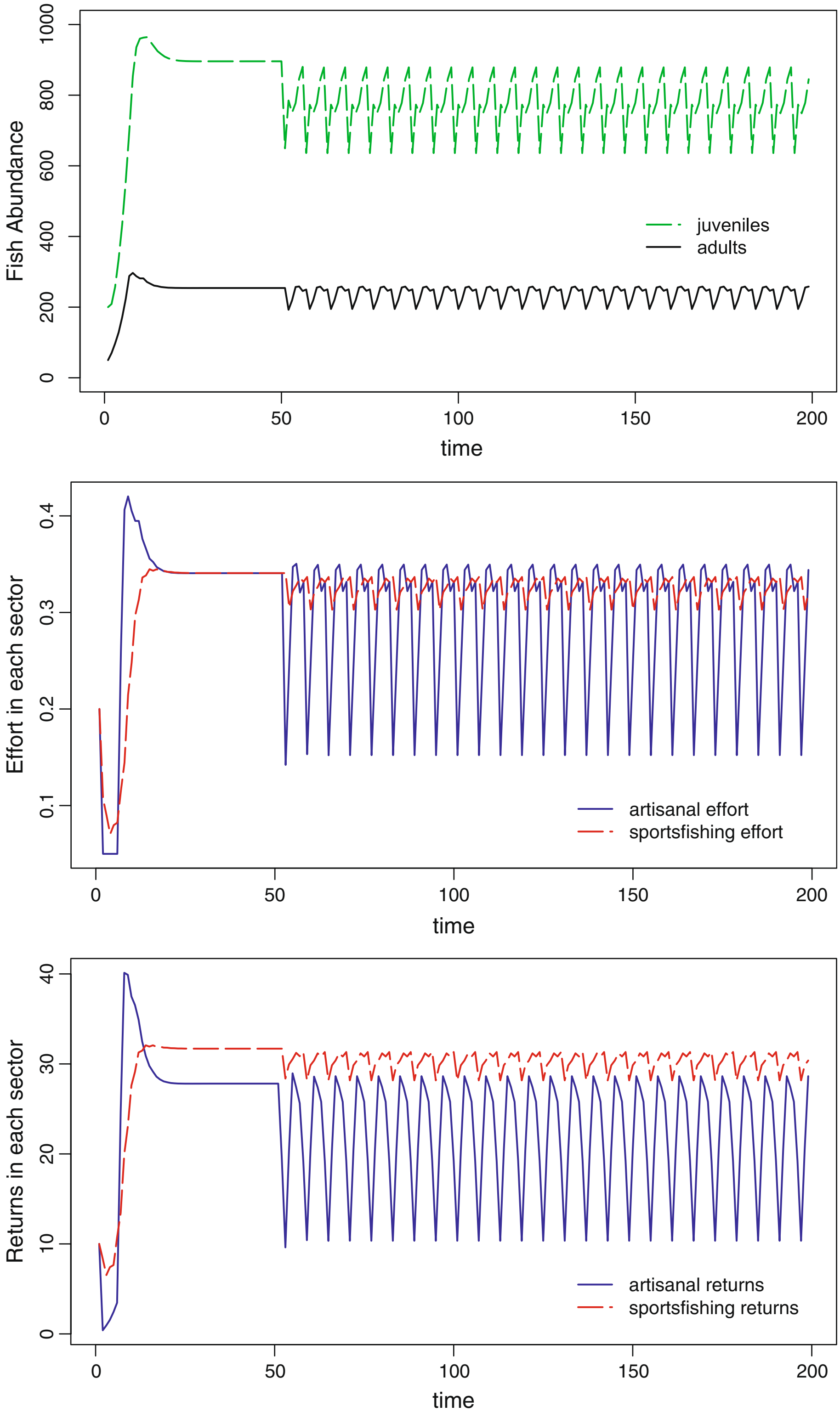

Fig. 5 System responses to El-Niño like shocks under the coexistence conditions ($\beta = 0.01075$, $R_c = 50$). See text for details. **a** Fish abundance, **b** effort, and **c** returns

1988; Hare and Mantua 2000; Thomson et al. 2000; Velarde et al. 2004). This may happen directly (e.g., through changes in prey availability, as suggested by McGowan et al. 1998) or indirectly (e.g., due to changes in habitat availability, as described by Aburto-Oropeza et al. 2007). On average, moderate El Niño events occur every 6 years, and strong events occur every 12 years (Glynn 1988). Here we explore the effect of El Niño events specifically on the fish population, and assume that during an El Niño year, the fishes' reproductive probability declines 50% because of a reduction in survivorship of pre-settlement larval fish due to lack of food

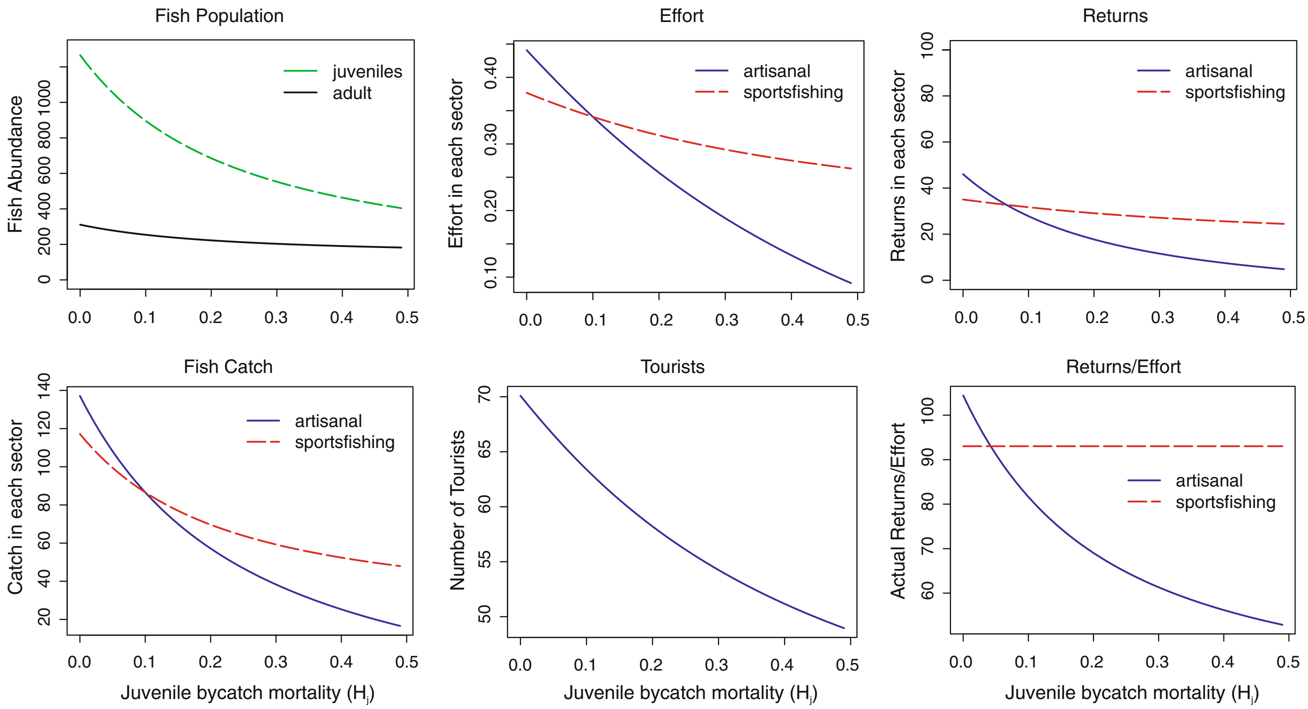

Fig. 6 System responses to an increase in the probability of juvenile bycatch mortality under the coexistence conditions ($\beta = 0.01075$, $R_c = 50$)

resources. This perturbation lasts for 1 year, and then the reproductive probability returns to the normal value until the next event (6 years later). There are clearly other types of biological responses that we could explore, but we start simply in order to understand the responses of both the ecological and social domains of the coupled systems to climate variability.

Because we model El Niño perturbations as an impact on reproduction, both juvenile and adult populations oscillate over time, although the juveniles respond to a greater degree (Fig. 5). The mean effort and returns to both sectors are reduced in response to the El Niño-like event. Sportfishing effort and returns vary less than the artisanal fishery's. We also see a lag in the sportfishing sector's response, such that it takes longer for this sector to recover to the equilibrium level that preceded the perturbations. We attribute the magnitude and timing in the sportfishing response to the way that we have linked the fish population and the sportfishing effort via changes in the number of tourists, and ultimately, via returns to this sector. The artisanal sector's effort and returns slightly overshoot following the perturbations; this does not occur in the sportsfishery.

Second, we explore how changes in the proportion of juvenile bycatch (H_J) impact the dynamics of the fish population and the economic returns to the human community. The proportion of bycatch of the snapper *L. guttatus* by the shrimp fishery is unknown (Amezcua et al. 2006), and thus we explore a range of values rather than a particular increase or decrease. A change in bycatch could occur due to a variety of management strategies, including alteration in fishing effort (via the size of the fleet or number of days at sea); implementation of fully protected marine reserves or other marine protected areas, or changes in gear.

We find that as the proportion of juvenile bycatch (H_J) increases, the juvenile population declines sharply and the adult fish population declines as well, although not nearly as markedly (Fig. 6). Effort, returns, and returns per effort in the artisanal sector decline with increasing H_J. Effort and returns (as well as the numbers of tourists) also decline in the sportsfishing sector, although to a smaller degree. Because of the linear relationship between returns and effort in the sportsfishing sector, returns per effort are constant and thus only change with a change in the parameter β. Catch declines with increasing H_J in both sectors. In sum, the sportsfishery is more resilient to increasing H_J than the artisanal fishery.

Sensitivity analyses

We performed sensitivity analyses for those parameters not well supported by literature such as the immigration and reproductive probabilities, as mentioned above (Fig. A2). Changes in those parameters cause quantitative changes in equilibrium abundances but do not affect the qualitative behavior, except at very low immigration probabilities where juvenile abundances peak because of very little losses to the adult population. Similarly, changes in the b parameter of the Ricker function of the fish population sub-model influence the quantitative results by shifting equilibrium abundances up or down, but do not influence the qualitative behavior of the model. Thus, overall, the model is robust against parameter uncertainties of the fish population sub-model and these uncertainties do not change the qualitative interpretation of our results. As discussed above, the model is sensitive to any changes that affect the relationship between the returns of the two sectors, such as the relation between artisanal and sportsfishing prices and costs, or the scaling parameters in the artisanal effort or tourism functions as well as the structure and parameterization of the linkage between the ecological and social domains. However, the qualitative behavior of the interaction of both remains the same, e.g., with a doubling of the price per fish caught in the artisanal fisheries, artisanal fishing effort and thus artisanal returns remain higher for a larger range of the sportsfishing investment factor (β). Thus the switch between an artisanal fishing-dominated system to a sportsfishing-dominated one happens at higher β values. The qualitative behavior of the model characterized by the dominance of single sectors at respective extreme values and the gradual transition region of coexistence of both sectors is robust.

Discussion

We developed an ecological-economic model based on the situation in the Gulf of California in order to explore how coupled social and ecological marine systems and the ecosystem services they provide are impacted by natural and anthropogenic disturbances. Three aspects of our findings are of particular interest: the clear trade-offs among the sectors and services we modeled; the influence of the typology of the social–ecological linkages (i.e., how ecosystems, services, and human communities are connected); and the influence of varying magnitude of the social–ecological linkages. We discuss each of these in turn, and then conclude with the scientific and management implications of our findings.

Trade-offs between ecosystem services

Our results highlight the inherent trade-offs between different ecosystem services that depend on a common component of the ecosystem (in this case, the snapper population). In the model, economic returns to the human community are driven by the catch in artisanal fisheries and the number of tourists who engage in sportsfishery, and these variables are in turn impacted by adult fish abundance. We observe that when both seafood and tourism services are generated in this system, the abundance of fish and the total economic returns tend to be lower and less variable through time than when the artisanal sector dominates (Figs. 4c, d, A5). Thus coexistence of the two sectors (and production of both the seafood and tourism services) creates stability in some key elements of the coupled social and ecological systems. Because of the decrease in adult fish abundance with increasing β, the returns received per effort in each sector decrease and total returns decline as well. This is also due to the fact that the per-fish return from sportsfishing is lower than that in artisanal fishing. Depending on the effort dynamics of each sector, which we do not impose but rather emerge from the interactions of the two sectors with the fish population, variable dynamics in the ecological and socioeconomic domains result.

In many cases, marine managers and society at large structure economic incentives and institutions so as to encourage diversity of economic activities. Indeed, diversity in economic activities at the household and community level is considered a hallmark of socially resilient human communities (e.g., Adger et al. 2005; Nelson et al. 2007). In our modeled systems, such diversity comes at a real economic cost, due to an increase in total effort which reduces the adult fish population to lower-than-optimal levels, resulting in lower catches and overall returns when both the artisanal fishery and sportsfishery are active. In the actual management of human interactions with the Gulf's marine environment, it may be more difficult to monitor and control effort when multiple sectors or impacts are influencing the same component of the ecosystem, as has been observed in other marine systems (Rosenberg and Sandifer 2009).

Typology of social–ecological linkages

Second, the typology of the social–ecological linkages varies significantly between the sectors, and this variation has considerable influence on the response of each sector to perturbations and the subsequent provision of seafood and tourism services. The sportsfishery is more resilient to both El Niño-like shocks and changes in management of the shrimp fishery that lead to an increase in the probability of juvenile bycatch mortality. The artisanal fishery responds more rapidly and to a greater degree than the sportsfishery to both types of perturbations. This is an intriguing result and one that again highlights the value of maintaining diverse activities in a given coastal area, so as to increase the likelihood that the human community is buffered from and able to adapt to changing environmental and economic conditions. Fletcher and Hilbert (2007) illustrate an analogous tension and trade-off between profit maximization and resilience in the context of a grazing social–ecological system.

Our results also suggest that some services and sectors are more vulnerable than others to particular perturbations, and thus mitigation and adaptation strategies (if implemented) would need to be tailored accordingly. We attribute these differences in response to the way that the fish population and sportsfishing or artisanal effort are connected. The interaction between the fish population and sportsfishing is mediated by tourists; sportsfishing operators are essentially fishing for tourists. Tourists then catch fish, which results in returns to the sector and controls the effort in the following year. This results in a lag in the sportfishery's response to perturbations; the tourists thus act like a buffer. In contrast, in artisanal fishery, returns (and thus effort) react much stronger and directly to a change in fish abundance; there is not the same mediation by the tourists. Moreover, returns per effort in artisanal fishery must exceed a critical level before effort can increase the next year. The threshold causes the oscillations at high R_c values: the fish population can increase substantially before the threshold is crossed, then once the system crosses it, effort is increased rapidly beyond minimum effort, which decreases the fish resources and returns per effort quickly below the threshold, causing effort to drop to a minimum again; this then repeats. The fast response of the artisanal fisheries causes the high variability and overshooting observed in response to the El Niño-like shocks.

Magnitude of social–ecological linkages

Finally, we also observe the varying magnitude of social–ecological linkages in this model system. Two key parameters have particularly strong effects: the sportsfishing investment parameter (β) that controls the increase in sportsfishing effort with increase in returns and the artisanal effort threshold (R_C). The higher the value of β, the stronger the response from the sportsfishery. In the extreme case, where β approaches 0.03, the system becomes unstable. We interpret this parameter as related to the sportsfishery operators' expectations of future conditions; i.e., with a higher β, sportsfishery agents are more willing to engage in risky behavior and push the system to its limits. We see a similar but opposite influence of the artisanal effort threshold (R_C), which controls the level of returns at which the artisanal sector expends more effort in the next time step. Consequently, understanding how returns are re-invested or otherwise allocated is likely to be particularly important in order to understand the interactions within and among coupled social–ecological systems of the Gulf and similar systems.

Future work

Like all models, ours involves a number of critical assumptions and simplifications. While some of these, such as the natural mortality probabilities, are well supported by the literature, we relied on sensitivity analyses to investigate the impacts of the remaining parameter choices. Those analyses indicated that the qualitative behavior of the model was robust to changes in parameter values. Nonetheless, the model would be strengthened by the collection of further empirical information specific to the social and ecological systems of the Gulf of California. Information on the economic costs and benefits of exploiting nearshore marine fish populations (as well as other elements of this ecosystem) and effort dynamics would be particularly informative, as would data on the social networks, mobility, and preferences of the fishermen, tourists and other key actors. Investigation of how changes in functional forms, e.g., the relationships between catch and artisanal and sportsfishing effort, influence the ecological and social dynamics of our model systems, would be beneficial as well.

Here we explore only one set of the many potential connections between ecosystems, services, and people. We see this work as a first step toward a more general set of models that would elucidate these linkages in coastal and marine systems. For example, another model could examine how services produced by two different species (or spatially distinct habitats) vary in response to key perturbations, or how the number of nodes or connection points between the ecosystem, service, and human beneficiaries influence the systems' dynamics. Such a set of general models could well benefit from the burgeoning field of food web theory, where ecologists have explored how the structure and magnitude of linkages among diverse nodes influence system dynamics (Belgrano et al. 2005).

Extensions of this model would also benefit from more ecological realism. In terms of the fish population model, the addition of age structure is a logical next step, as it is known to strongly impact the modeled dynamics of fish populations and the outcomes of fisheries management (Gaylord et al. 2005; Levin and Goodyear 1980). The fish's actual life cycle is more complex than we have modeled it: snappers tend to spend their first year in mangrove and other nearshore habitats, and then are recruited to the three fisheries (shrimp, artisanal, and sportsfishery) differentially. For example, the shrimp trawl fishery tends to catch both immature individuals (2 to 3-year-old fish) and adults (R. Cudney-Bueno, pers. obs.), while the sportsfishery exploits primarily adult fish. Also, integration of information on larval dispersal and connectivity among populations (Cudney-Bueno et al. 2009b), as well as knowledge of the degree of overlap in fishing areas targeted by artisanal and sportsfishermen, is vital if this approach is to be used in the management arena (e.g., Smith and Wilen 2003).

A number of extensions in the social domain are of interest, as well. Our model explores the reaction of the two sectors to changes in their economic performance without any active management of the effort invested in each activity or consideration of the immediate and long-term outcomes of the choices made. We assume that a single manager allocates effort within each sector without knowledge of the effort in the other sector: extensions of the model could explore other ways of allocating effort either by a social manager or individual decision-making agents based on internal or external constraints, market-dynamics or information about ecological or social conditions. Moreover, we model the industrial shrimp fishery as an external perturbation on the snapper population, which then indirectly influences the returns to the other two sectors. This static, exogenous approach to the shrimp fishery limits our analysis of interactions between this sector and the other two.

Marine resource governance in the northern Gulf is changing as this article goes to press: with the passage of a new national fisheries law in 2007, fisheries are intended to be managed via science-based regional fisheries management plans, giving more management weight to a broader set of actors from the local to federal levels (Hernández and Kempton 2003; Poder Ejecutivo Federal 2007). We are interested in incorporating the likely effects of this law (e.g., the development of diverse ways of allocating effort, of different decision-making mechanisms, and of alternative markets for artisanal products) into the model. We could then contrast scenarios based on these elements with an optimization approach, and investigate the impact of different economic measures (e.g., fishing regulations or economic incentives) to achieve optimal effort levels. Regardless of the levels of complexity we incorporate into future models, fish abundance and effort will always be uncertain in the real system. Therefore, it might be more realistic to further investigate robust rather than optimal strategies that perform well in face of those uncertainties and perturbations.

The model also could be expanded to help guide development of tactical management strategies, such as the definition of sector-specific quotas. There is growing interest from Mexico's National Commission of Fisheries to implement catch-share programs for certain fisheries (R. Cudney-Bueno, pers. obs.). If an ecosystem-based approach is deemed desirable, then allocating catch shares for a specific fishing sector should include consideration of interactions with other components of the ecosystem—including interacting fishing sectors and environmental factors such as El Niño effects.

In conclusion, our results illustrate the value of understanding the diverse ways in which humans influence and are influenced by marine ecosystems and the services they produce. Using the Gulf of California as an example, we focused on two key services (seafood and tourism) that make use of the same component of the marine ecosystem, a valued fish species. Our model suggests that one of the two sectors (and the service it generates) may be more robust to both anthropogenic and natural perturbations. While there is ample room for further empirical and theoretical exploration of this result, our findings suggest that understanding the typology and magnitude of the connections between marine ecosystems, the services they produce, and the human communities that rely on them could contribute vital information to the design, implementation and evaluation of marine ecosystem-based management strategies in Mexico and elsewhere.

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