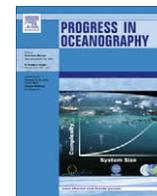




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Local management of a “highly migratory species”: The effects of long-line closures and recreational catch-and-release for Baja California striped marlin fisheries

Olaf P. Jensen^{a,*}, Sofia Ortega-García^b, Steven J.D. Martell^c, Robert N.M. Ahrens^c, Michael L. Domeier^d, Carl J. Walters^c, James F. Kitchell^a

^a Center for Limnology, University of Wisconsin – Madison, 680 N Park St., Madison, WI 53703, USA

^b Centro Interdisciplinario de Ciencias Marinas, Av. Instituto Politecnico Nacional s/n, Col. Playa Palo de Santa Rita Apdo. Postal 592, La Paz, Baja California Sur, Mexico

^c Fisheries Centre, Aquatic Ecosystems Research Laboratory, 2202 Main Mall, The University of British Columbia, Vancouver, Canada BC V6T 1Z4

^d Marine Conservation Science Institute, 2809 South Mission Rd. Suite G, Fallbrook, CA 92028, USA

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ABSTRACT

Management of highly migratory fish species is generally assumed to require complicated international agreements. The effects of spatial closures for such species are thought to be diluted by their extensive movements. We tested these assumptions using a case study of striped marlin (*Kajikia audax*) fisheries off of Baja California, Mexico. Beginning in 1977, Mexico instituted a series of long-line fishery closures and closed areas to reduce commercial fishing mortality rates on billfishes. Using data from the Japanese long-line fishery and the recreational billfish fishery in a stock reduction analysis (SRA) model, we show that temporary closures of Mexico's EEZ to long-lining from 1977–1980 and 1984–1985 had a rapid effect on local abundance of striped marlin. Regional striped marlin abundance likely increased by 12–22% following the 4-year closure and 6–12% following the 2-year closure. Increases near Baja California may have been larger. Recreational catch-and-release appears to have a more modest effect because catches in the recreational fishery are substantially smaller than historic long-line catches. A 100% release rate over the 10-year period for which recreational catch data were available would likely have increased regional abundance by 2.8–7.5% relative to no recreational release. There is also evidence for a small effect of the El Niño Southern Oscillation (ENSO) on recruitment or net immigration, with stronger recruitment or net immigration during the cooler La Niña phase.

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1. Introduction

Billfish populations around the world have experienced serious declines (Myers and Worm, 2003, 2005), and one species, white marlin (*Kajikia albidus*, formerly *Tetrapturus albidus*; Collette et al., 2006) has been considered (but ultimately rejected) for listing under the US Endangered Species Act (NMFS, 2001). Istiophorid billfish (a family that does not include swordfish, hereafter referred to simply as billfish) are taken primarily as bycatch in pelagic long-line fisheries (Peel et al., 2003). Directed fisheries for striped marlin (*Kajikia audax* formerly *Tetrapturus audax*; Collette et al., 2006) have occurred, however, in Mexican (Sosa-Nishizaki, 1998) and Australian (Findlay et al., 2003) waters, and striped marlin have, at times, commanded higher prices in Japan than all tuna species,

other than bluefin (King, 1989). Recreational fisheries can also be an important source of mortality for marine fish populations (Coleman et al., 2004), and in some limited cases, may constitute a larger mortality source for billfish than commercial fishing. For example, Cramer (2004) suggests that the US recreational white marlin fishery may be a greater source of mortality for white marlin than the US Atlantic long-line fishery.

Catch-and-release practices (including catch-tag-and-release) have become more common in many marine recreational fisheries (Bartholomew and Bohnsack, 2005) and are commonly practiced in recreational fisheries for billfish around the world (Peel et al., 1998). Catch-and-release rates for white marlin in US recreational fisheries are near 99% (Goodyear and Prince, 2003). Catch-and-release is less universal, but still common, elsewhere (e.g., 72–87% of fish caught by billfish tournament anglers in Puerto Rico were released, Ditton et al., 1999). Because of post-release mortality, even strict catch-and-release fisheries can have an impact on fish populations when effort is high (Coggins et al., 2007; Nelson, 2002). One factor that influences post-release survival rates for billfishes is the

* Corresponding author. Present address: University of Washington, School of Aquatic & Fishery Sciences, Box 355020, Seattle, WA 98195-5020, USA. Tel.: +1 410 812 4842.

E-mail address: ojensen@u.washington.edu (O.P. Jensen).

type of fishing gear used (e.g., circle hooks vs. “J” hooks), with estimates for recreational fisheries ranging from 65% to 100% (Pepperell and Davis, 1999; Domeier et al., 2003; Horodysky and Graves, 2005; Graves and Horodysky, 2009). While the effects of hook type on post-release survival are increasingly well known (Cooke and Suski, 2004), the broader impact of recreational catch-and-release on fish populations is less well studied (but see Pine et al., 2008).

Concern about billfish population declines and conflict between recreational and commercial fisheries have led to the creation of areas closed to fishing by commercial long-liners in Mexico (Sosa-Nishizaki, 1998), Australia (Findlay et al., 2003; Bromhead et al., 2004), and US waters of the Atlantic and Gulf of Mexico (NMFS, 2000). The impact of closed areas for highly migratory species such as billfishes is difficult to predict or even separate from other factors in retrospect. Most theoretical models of marine protected areas have concluded that high movement rates of adults result in decreased effectiveness of reserves (Gerber et al., 2003; Walters et al., 2007). Martell et al. (2005) found that the effect of marine protected areas on marlins depended on assumptions regarding the rates and drivers (random or fitness-based) of fish movements.

With the advent of pop-up satellite archival tag (PSAT) technology (Block et al., 1998), we now know much more about the movement patterns of pelagic fish, including billfishes (Gunn et al., 2003; Hoolihan, 2003; Prince et al., 2005; Domeier, 2006). While many billfish species move freely across ocean basins, PSAT tracks from 46 striped marlins tagged off Baja California and tracked for an average of 98 days show relatively restricted movements (Domeier, 2006). Such apparently limited movements provide the potential for effective conservation outside the framework of international management institutions, which are often slow to reach consensus on fishing restrictions (Hilborn et al., 2005). Several analyses of striped marlin population dynamics in the southwest Pacific (Campbell et al., 2002; Holdsworth et al., 2003; Langley et al., 2006) show evidence that changes in regional long-line fishing intensity can affect catch rates in nearby recreational fisheries. Despite the current interest in marine protected areas in general (Lubchenco et al., 2002), and the use of closed areas specifically for conservation of billfishes, we know of no empirical studies which have attempted to quantify the abundance of billfishes before and after spatial closures.

We used a retrospective analysis of striped marlin population dynamics to examine the impact of historical long-line fishery closures and recreational catch-and-release in the Eastern Tropical Pacific (ETP) near Mexico. A unique aggregation of striped marlin exists in this region with commercial and recreational catch rates higher than anywhere else in the world. A previous analysis of catch per unit of effort (CPUE) before and after a temporary closure of Mexican waters showed evidence of rapid recovery of marlin populations (Squire and Au, 1990). Genetic studies (McDowell and Graves, 2008) and tagging data (Domeier, 2006) suggest limited exchange between Baja California Sur (BCS) and other regions. Striped marlin are the target of a valuable recreational fishery in BCS (Ditton and Stoll, 2003), and a catch-and-release ethic is developing among many anglers. Targeted commercial fishing for striped marlin is currently prohibited in Mexican waters, but they are caught as bycatch by long-line vessels targeting tuna and sharks. There has been pressure by long-line fishermen to reopen closed areas including a 50 nautical mile zone surrounding the coast established in 1984 and a Billfish Conservation Zone (BCZ) created in 1987 (Sosa-Nishizaki, 1998). The goal of this analysis is to assess the effects on regional striped marlin abundance of commercial long-line closures and recreational catch-release within Mexican waters. If unilateral action to reduce billfish mortality can have an appreciable effect on abundance – and, by extension, catch rates in the valuable recreational fishery – there is greater

incentive for Mexico to pursue billfish conservation independent of international institutions.

2. Materials and methods

2.1. Catch and effort time series and fishery history

In 1976, Mexico asserted a claim to a 200 nautical mile Exclusive Economic Zone (Sosa-Nishizaki, 1998). Japanese long-line vessels, which had been targeting striped marlin near the southern tip of Baja California since 1964 (ISC, 2006), were forced offshore by early 1977 when Mexico began enforcing the EEZ (Squire and Au, 1990). The catch of striped marlin in this region, which at its height in the late 1960s, had accounted for 30–50% of the total global Japanese long-line catch of striped marlin, dropped dramatically (Fig. 1). By 1980, the first Mexican and joint venture long-line vessels began operating in Mexico's EEZ. Raw CPUE trends before and after this temporary *de facto* closure of the long-line fishery in Mexican waters show evidence of a recovery (Squire and Au, 1990). The long-line CPUE trends examined by Squire and Au (1990) support their “core area” hypothesis; however, as with all analyses of raw CPUE (Sibert et al., 2006), it is not clear how much of this increase can be explained by changes in abundance rather than variability due to observation error or changes in oceanographic conditions. In particular, striped marlin recreational catch rates off of Baja California are known to vary with sea surface temperature (SST; Ortega-Garcia et al., 2003), and observations of striped marlin as far north as the coast of Washington and Oregon have been reported during El-Niño events (Percy, 2002).

During the 1980s, striped marlin catch by Japanese long-line vessels fluctuated and began to be replaced by catches from other nations (Fig. 1) including a Mexican commercial long-line fishery targeting billfishes (Sosa-Nishizaki, 1998). From the spring of 1984 to the fall of 1985, the permits allowing long-line vessels to operate within Mexico's EEZ were withheld (Squire and Au, 1990) providing another *de facto* fishery closure. Mexican long-line vessels have been officially prohibited from targeting billfish since 1990, however incidental catches of billfish taken while legally targeting sharks and tunas can still be sold (Sosa-Nishizaki, 1998). Catch (Fig. 1) and catch rates (Fig. 2) in the long-line and recreational fisheries show evidence of a rebound in the mid to late 1990s after lows in the early 1990s. A number of changes to the recreational and commercial fishing regulations in the early 1990s (Sosa-Nishizaki, 1998) make it difficult to attribute this spike to a specific management action.

A recreational fishery for striped marlin off Baja California has existed at least since the 1930s (Sosa-Nishizaki, 1998). Anecdotal reports suggest that catch-and-release is becoming more common in this fishery, and current release rates are roughly estimated at 75% (ISC, 2006). Survival rates of striped marlin released in the recreational fishery depend on the type of fishing gear used, but are on average approximately 75% (Domeier et al., 2003). We assumed that 50% of the recorded annual recreational catch was killed (i.e., 75% release rate multiplied by 75% post-release survival rate). Since the recreational catch is low relative to peak commercial harvests, parameter estimates were insensitive to assumptions regarding historical release rates.

We used a commercial and a recreational CPUE time series as indices of striped marlin relative abundance. For the commercial time series, we used Japanese long-line CPUE (Fig. 2) from 1963 to 1998 within the five 5° latitude by 5° longitude grid cells (5 × 5 cells) near the southern tip of Baja California (Fig. 3). Striped marlin catch rates in this region are typically around 20 times higher than elsewhere in the North Pacific (ISC, 2006), and CPUE trends for such a small region are less sensitive to changes in the

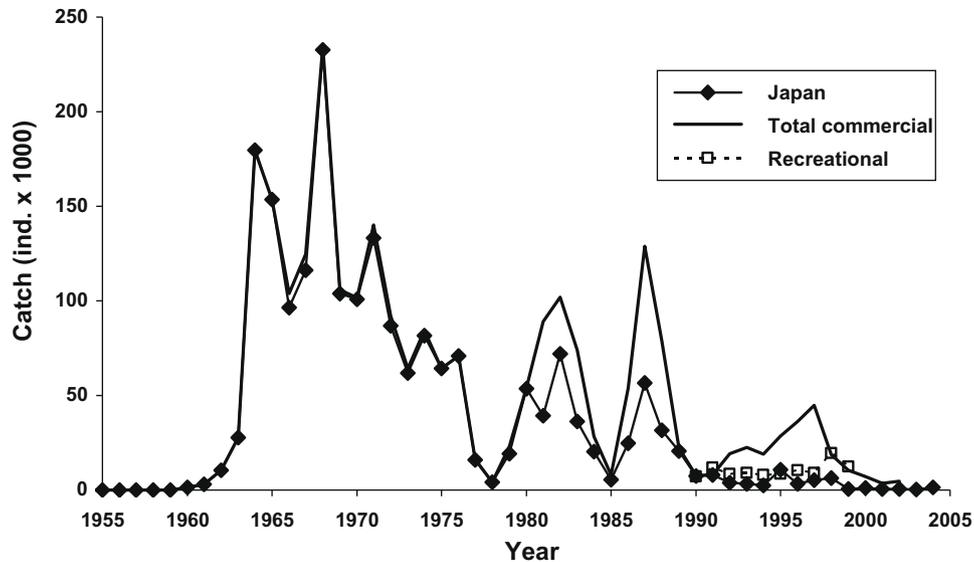


Fig. 1. Catch of striped marlin (1000s of individuals) for the Japanese long-line fleet (solid line and filled diamonds), all long-line fleets combined (thick line), and the recreational fleet based in Cabo San Lucas (open squares and dotted line; Ortega-García et al., 2003).

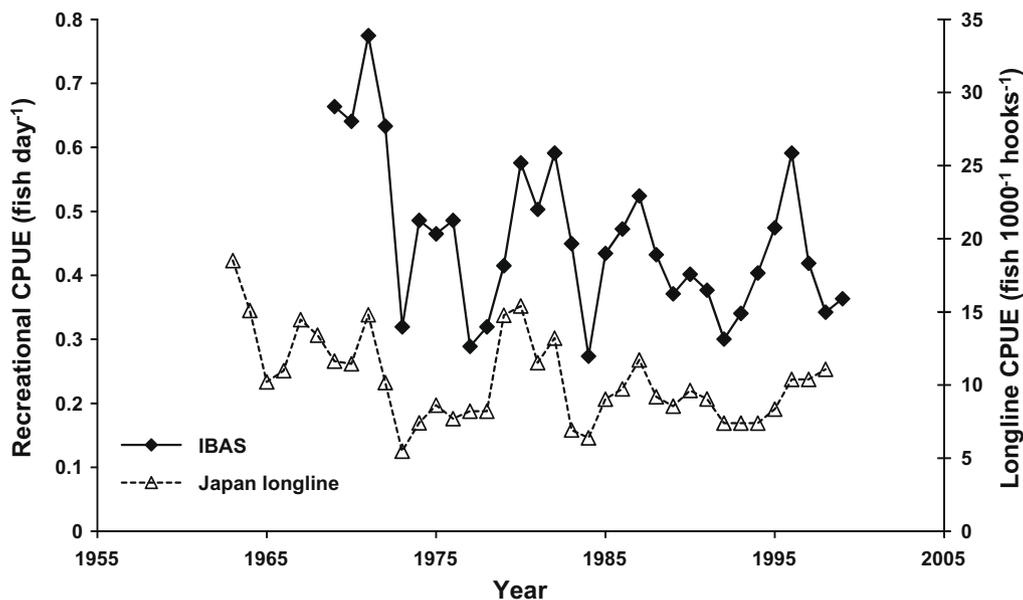


Fig. 2. Catch per unit of effort (CPUE) from the International Billfish Angler Survey (IBAS, filled diamonds, solid line) of anglers fishing near Baja California and catch per unit of standardized effort from the Japanese long-line fishery (open triangles, dotted line) averaged over the five grid cells near Baja California shown in Fig. 3 using the spatial backfilling method of Walters (2003).

spatial distribution of fishing effort. Assuming effort is distributed at random within a 5×5 cell or strata, Walters (2003) suggests a more appropriate abundance index can be derived by treating the catch rate data as a random stratified sample. A relative abundance index for the study area in each year was calculated as the spatially weighted average of strata catch rates. Walters (2003) notes that catch rate information is required for all spatial areas for all times, requiring estimates of catch rate to be made for those areas not fished. Prior to fishing within a cell, catch rate was assumed to be the average of the first three catch rates observed in that cell. Once an area received no further effort, catch rate was assumed to be the last observed catch rate. To prevent bias due to seasonal variation in effort distribution, the “spatial filling” and averaging method was performed for each quarter and the final relative abundance trend was estimated as the average of quarterly

trends. The only information that was available to correct for potential changes in fishing power due to hook depth was the mean hooks per basket. Using gear configuration information available in Bigelow et al. (2006) to estimate mainline, leader and float-line lengths, hook depth was estimated using catenary algorithms (Suzuki et al., 1977) and reduced by 20% to account for gear shoaling (Bigelow et al., 2006). Using coefficients available in Ward and Myers (2005) relating hook depth to striped marlin catchability, we standardized (relative to 1950) catch rate in each 5×5 cell for changes in hook depth resulting from changes in the number of hooks per basket. Despite this correction for changes in hook depth, other changes in fishing methods may have resulted in changes in catchability over the time series. CPUE time series cannot be adjusted for such potential changes without detailed, set-level data, which were not available for this analysis.

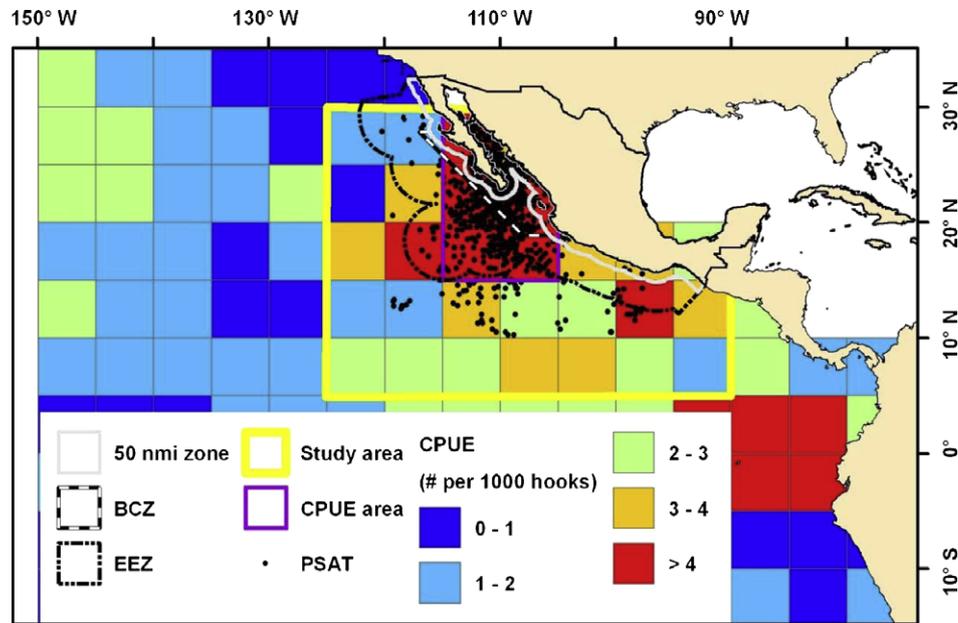


Fig. 3. Striped marlin catch per unit of effort (CPUE, number of individuals 1000 hooks⁻¹) from the Japanese long-line fishery averaged over the period 1964–1975. Also shown are Mexico's 50 nautical mile zone (gray), billfish conservation zone (BCZ, black and white dashed), and 200 nautical mile exclusive economic zone (EEZ, black dashed); the study area for the population model (yellow); and the five grid cells near the tip of Baja California from which the commercial CPUE time series was developed (CPUE area, purple). Geolocations (>38 days post-release) of striped marlin tagged with pop-up satellite archival tags (PSAT) are also shown (data from Domeier, 2006).

We used CPUE from a survey of recreational billfish anglers (Fig. 2) as an additional index of abundance. The International Billfish Angler Survey is a mail survey of billfish anglers administered by the National Marine Fisheries Service – Southwest Fisheries Science Center (NMFS–SWFSC) that provides annual catch and effort data by species and region since 1969 (Squire, 1987). Participating anglers are asked to return a mail-in card each year with totals by quarter and location for the number of days they fished for billfish and their catch by species. We used this catch and effort data for the “Baja California” and “Mazatlan” regions combined. There was a significant correlation (Pearson $r = 0.65$, $p < 0.001$) between the recreational and commercial CPUE time series. Port sampling of recreational catch and effort has only been conducted in Cabo San Lucas since 1990, making a port sample CPUE time series too short to be used in this analysis.

While the two indices of abundance are derived from catch and effort within a small area near the tip of Baja California, the population model is based on a larger study area that surrounds this region (Fig. 3). The study area was roughly delineated based on Japanese long-line CPUE patterns to include the entire area of contiguous high striped marlin catch rates. The constraints on the size of the study area were: (1) that it be small enough that the CPUE trends from the area of directed striped marlin fishing are likely to be representative of population dynamics of the entire study area and (2) that it be large enough so that fishery removals within the study area can have an observable impact on population dynamics within the study area. For smaller areas, the population dynamics are likely to be dominated by immigration and emigration rather than local removals and recruitment. In our population models, we explored three scenarios that represent varying degrees of potential immigration and emigration between the study area and surrounding waters.

2.2. Estimation of population trajectory using stock reduction analysis

We used a stock reduction analysis (SRA) model to estimate abundance trends and population dynamics parameters for striped marlin within the study area from 1953 to 2002. SRAs can be used

with a time series of fishery removals (catch) and a time series of relative abundance to estimate how large and productive a stock must have been for the observed removals to result in the observed changes in relative abundance. The term SRA refers to the general approach of treating catch as a known removal from the population rather than a quantity to be predicted by the model. This approach is also known as conditioning on catch and does not imply a specific population model. Although SRAs have traditionally been used in a deterministic framework (Kimura and Tagart, 1982; Kimura et al., 1984), they can also be applied in a stochastic context (Walters et al., 2006), where distributions, rather than single values, are estimated for each of the model parameters and some process error is admitted in the stock-recruitment relationship. The process error is typically incorporated in the form of annual “recruitment” deviations. These deviations can account for variability around the mean stock-recruitment relationship, for example, variation due to oceanographic conditions. They can also account for other changes in population size that cannot be explained by mean recruitment, harvest or natural mortality, including net immigration or emigration.

Following Walters et al. (2006), we used an age-structured SRA model to keep track of numbers of age a (1–15) individuals in year t ($N_{a,t}$, 1953–2002):

$$N_{a+1,t+1} = N_{a,t}S(1 - v_a U_t), \quad (1)$$

where $S = e^{-M}$ is the natural survival rate, v_a is the vulnerability of an age a fish to fishing (assumed constant over time), and U_t is an estimate of the exploitation rate on fully vulnerable fish ($v_a = 1$):

$$U_t = \frac{C_t}{\sum_a N_{a,t} v_a}, \quad (2)$$

where C_t is the annual catch in numbers. Although size and age composition data were unavailable, an age-structured model allows information contained in the maturity and vulnerability schedules to be incorporated in the model.

A lognormal prior on the natural mortality rate (y^{-1}), $\ln(M) \sim N[\mu = \ln(0.368), \sigma = 0.033]$, was set based on the M/K Beverton–Holt invariant: $M = 1.59 K$ (Beverton and Holt, 1959; Jensen, 1996) and

an estimate of the von Bertalanffy growth rate parameter (K) of 0.23 y^{-1} based on striped marlin from the BCS recreational fishery (Melo-Barrera et al., 2003). Similar life history based approaches to estimating M have been used for striped marlin stock assessment (Hinton and Bayliff, 2002).

An asymptotic vulnerability schedule was used to describe vulnerability-at-age:

$$v_a = \frac{1}{1 + \exp(-(a - ah)/0.5)}, \quad (3)$$

where ah is the age at 50% vulnerability. A histogram of catch-at-length (see Fig. 2.3.1 in Hinton and Bayliff, 2002) for the northern part of the eastern Pacific Ocean shows a mode near 160 cm (4 years old) in the 1980s, with a somewhat larger size distribution in the 1970s and a smaller size distribution in the 1990s. To estimate an appropriate mode for the prior distribution of ah , we examined a graph of v_a multiplied by the stable age distribution for a given value of ah and total mortality rate. The product of v_a and numbers-at-age is proportional to catch-at-age. Across a range of plausible total instantaneous mortality rates (0.4–0.6), an age at 50% vulnerability (ah) of 3 years (144 cm) results in a mode near 160 cm for the product of vulnerability and numbers-at-age. We allowed for uncertainty in ah by placing a normal prior on this parameter centered at 3 years, with an arbitrary standard deviation of 0.5. The vulnerable population size in year t (N_t) is the sum of the element-wise product of the vulnerability schedule and the numbers-at-age.

Although changes are apparent in the catch-at-length data (Hinton and Bayliff, 2002), indicating changes in either age structure or the vulnerability schedule, there were not enough size composition data available to fit more complicated length-based models. We did not attempt to account for potential differences in the vulnerability schedule between the recreational and commercial fisheries or changes through time in the vulnerability schedule. Changes in vulnerability can result from changes in fishing methods; however, such changes cannot be estimated without age composition time series. Even where age or length composition data are available, changes in vulnerability-at-age are frequently confounded with changes in age structure.

Annual recruitment to the first age class was assumed to follow a Beverton–Holt stock-recruitment function with lognormal recruitment deviations (w_t):

$$N_{1,t} = \left(\frac{\alpha E_{t-1}}{1 + \beta E_{t-1}} \right) \exp(w_t). \quad (4)$$

The E_{t-1} are the number of spawners in the previous year, the product of the numbers-at-age vector $N_{1-15,t}$ and an asymptotic maturity schedule (analogous to Eq. (3)), m_a , with an age at 50% maturity of 3 years (144 cm, Kume and Joseph, 1969). The stock-recruitment parameters α and β were parameterized in terms of the Goodyear (1980) recruitment compensation ratio (K) as:

$$\alpha = \frac{K}{\varphi_E} \quad \text{and} \quad \beta = \frac{(K-1)}{(N_{1,0} \varphi_E)}, \quad (5, 6)$$

where φ_E is the spawners per recruit at unfished equilibrium (the sum of the element-wise product of the natural survival to age and maturity schedule vectors) and $N_{1,0}$ is the mean recruitment in year zero, a parameter to be estimated. The Beverton–Holt function was chosen because it appears to be the most common form of stock-recruitment relationship seen in empirical analyses (Myers et al., 1999), and there is no evidence that the mechanisms believed to generate Ricker stock-recruitment relationships (i.e., strong cannibalism, spawning site destruction by adults, or disease transmission; Hilborn and Walters, 1992) are relevant to striped marlin populations. The w_t represent a combination of apparent variability in recruitment that is not explained by the Beverton–Holt model

and net immigration of recruits from outside the study area. These two factors are not distinguishable.

We used Markov Chain Monte-Carlo (MCMC) simulation in AD Model Builder (Otter Research Ltd., Sydney, British Columbia) to integrate over uncertainty in the model parameters. Fitting was conducted using two leading parameters: MSY , the maximum sustainable yield, and F_{MSY} , the instantaneous fishing mortality rate that results in MSY . Martell et al. (2008) suggest using these leading parameters rather than K and $N_{1,0}$ because this approach reduces correlation between the leading parameters and therefore improves model fitting. The relationship between model parameters, $N_{1,0}$ and K , and the leading parameters used for fitting, F_{MSY} and MSY is given in Eqs. (4) and (5) in Martell et al. (2008). We drew 200,000 MCMC samples, discarded the first 100,000, and retained every 50th sample from the remaining 100,000. Convergence was assessed using Gelman and Rubin's potential scale reduction factor for two independent MCMC chains (Gelman et al., 2000).

We placed priors on both leading parameters. The prior on MSY was lognormal, corresponding to a normal distribution with mean equal to the long-term average annual harvest (70,000) and a CV of 25%. A lognormal prior corresponding to a normal distribution with mean = M and a CV of 50% was used for F_{MSY} . Assuming that the CPUE time series are proportional to vulnerable stock size (N_t) with lognormal observation error, the objective function for the data was the concentrated log likelihood of the parameters given the catch and the two CPUE time series:

$$\ln L = - \sum_{t=1}^n \left(\ln(\sigma^2) + \frac{(z_t - \bar{z})^2}{2\sigma^2} \right), \quad (7)$$

where σ^2 is the observation error variance, $z_t = \ln(\text{CPUE}_t N_t^{-1})$ and \bar{z} is the mean of the z_t , i.e., the natural log of the maximum-likelihood estimate of the catchability coefficient, q (Walters and Martell, 2004).

We allowed for the possibility that $N_{1,0}$ may have been lower than unfished equilibrium recruitment by introducing an additional parameter (F_0), the equilibrium fishing mortality rate experienced by the population before the start of the modeled period (i.e., before 1953). The first recorded catch of striped marlin in the study area by the Japanese long-line fleet occurred in 1954. It is possible, however, that earlier catches of striped marlin outside the study area by the Japanese fleet or inside the study area by recreational and artisanal fishermen could have affected abundance and recruitment within the study area. We placed a beta prior on F_0 : [$F_0 \sim \text{Beta}(1, 3)$].

We considered three scenarios: purely deterministic recruitment ($\rho = 1$, i.e., observation error only), moderate process error ($\rho = 0.75$), and high process error ($\rho = 0.5$), where ρ is the proportion of the total error variance (κ) due to observation error ($\rho\kappa = \sigma^2$). For the $\rho = 1$ scenario, we tested the hypothesis that the Southern Oscillation Index (SOI) can explain some of the apparent variability around the mean stock-recruitment relationship:

$$w_t = r \cdot \text{SOI}_t, \quad (8)$$

where SOI_t is the z-standardized SOI, and r is a coefficient (equivalent to the Pearson correlation coefficient between the deviations and the SOI) to be estimated in the model. For the models with process error, the w_t were assumed to be normally distributed random deviations with mean zero and standard deviation = $\sqrt{(1-\rho)\kappa}$. The concentrated log likelihood for the models with process error is then:

$$\ln L = - \sum_{t=1}^n \left(\ln(\sqrt{\rho\kappa}) + \frac{(z_t - \bar{z})^2}{2\rho\kappa} \right) - \sum_{t=1}^n \left(\ln(\sqrt{(1-\rho)\kappa}) + \frac{w_t^2}{2((1-\rho)\kappa)} \right). \quad (9)$$

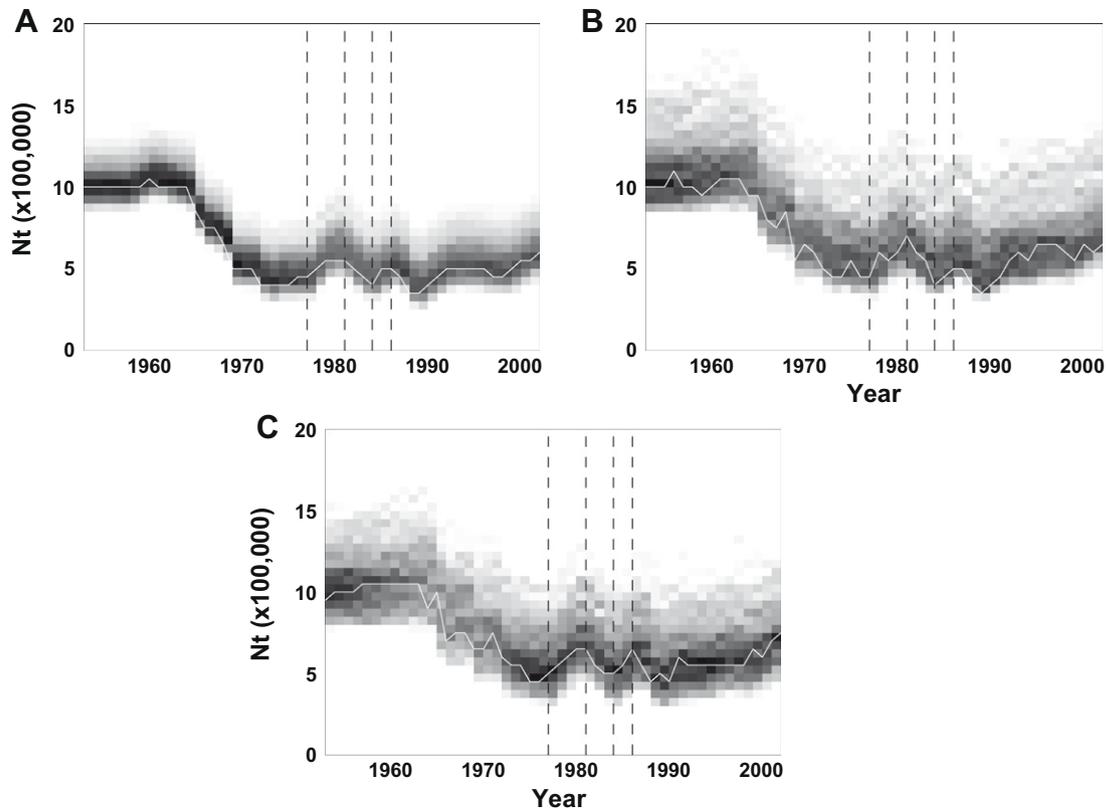


Fig. 4. Time series of modeled vulnerable population size ($N_t \times 100,000$) for the (A) deterministic, (B) 25% process error, and (C) 50% process error scenarios. High probability values are shown in darker regions, low values in light regions. The white line represents the modal value. Vertical dashed lines denote the two commercial long-line closures.

For each scenario, we assessed the effects of closing Mexico's EEZ to long-lining during each of the two closures (1977–1980 and 1984–1985) by estimating the marginal posterior distribution of the ratio of abundance in the first year of the closure to the abundance in the year following the closure. We assessed the potential impact of catch-and-release by calculating the ratio of population size in the year 2000 under two extremes: 100% release of the recreational catch and 100% retention during the years 1990–1999 (the decade for which reliable recreational catch data were available). We assumed a 90% survival rate of released fish. This rate is optimistic (Domeier et al., 2003) and assumes that the least harmful recreational fishing gear (lures) and best release practices would be used.

3. Results

The three model scenarios resulted in similar time series of vulnerable abundance (N_t), with an initial period of declining abundance from the early 1960s until the mid 1970s followed by two distinct increases coincident with the two closures, and a constant or slightly increasing trend from the late 1980s to 2002 (Fig. 4). Estimates of the percent increase in vulnerable abundance during each of the closures indicate substantial local rebuilding during the earlier (1977–1980; Fig. 5, column 1) 4-year closure and modest increases during the later (1984–1985; Fig. 5, column 2) 2-year closure. The posterior mode of the percent increase during the 4-year closure was 21% (90% Bayesian Credible Interval, BCI = 12–36) under the observation error only scenario, 12% (BCI = 0–36) under the 25% process error scenario, and 22% (BCI = 3–51) under the 50% process error scenario. For the 2-year closure, the posterior mode of the percent change in vulnerable numbers was 12%

(BCI = 3–23) under the observation error only scenario, 6% (BCI = –1 to 28) under the 25% process error scenario, and 9% (BCI = –2 to 34) under the 50% process error scenario.

The effect of recreational catch-and-release was smaller (Fig. 5, column 3). Relative to 100% retention of the recreational catch, a policy of 100% recreational catch-and-release during the 1990s would have led to increases in abundance by the year 2000 of 7.5% (BCI = 3.4–9.5) under the observation error only scenario, 2.8% (BCI = 1.3–7.9) under the 25% process error scenario, and 3.4% (BCI = 1.4–8.2) under the 50% process error scenario.

There was a weak, but statistically significant effect of the SOI on recruitment deviations (Fig. 6). The posterior mode of r , the Pearson correlation coefficient, between the SOI and the recruitment deviations, was 0.14 (BCI = 0.04–0.22). A positive correlation coefficient indicates that the recruitment deviations were generally positive (i.e., recruitment was higher than predicted by the stock-recruitment model) in above average SOI years, which are associated with cooler, La Niña conditions. Values of r are not meaningful (and were not calculated) under the scenarios with process error because a fixed fraction of the total variability is assigned *a priori* to random recruitment deviations.

The influence of the priors on F_{MSY} and ah became progressively stronger as more process error was admitted (Fig. 7), while MSY was relatively insensitive to the prior under all three process error scenarios. The prior density for M strongly influenced the marginal posterior density for M , reflecting a lack of information on mortality rate in the non-age-structured CPUE data. The marginal posterior densities of F_0 were relatively independent of the weak prior placed on this parameter.

The stock-recruitment relationship (Fig. 8A) shows unusually weak recruitment compensation (K falls in the range of 1.8 for the deterministic model to 2.2 for the 50% process error model)

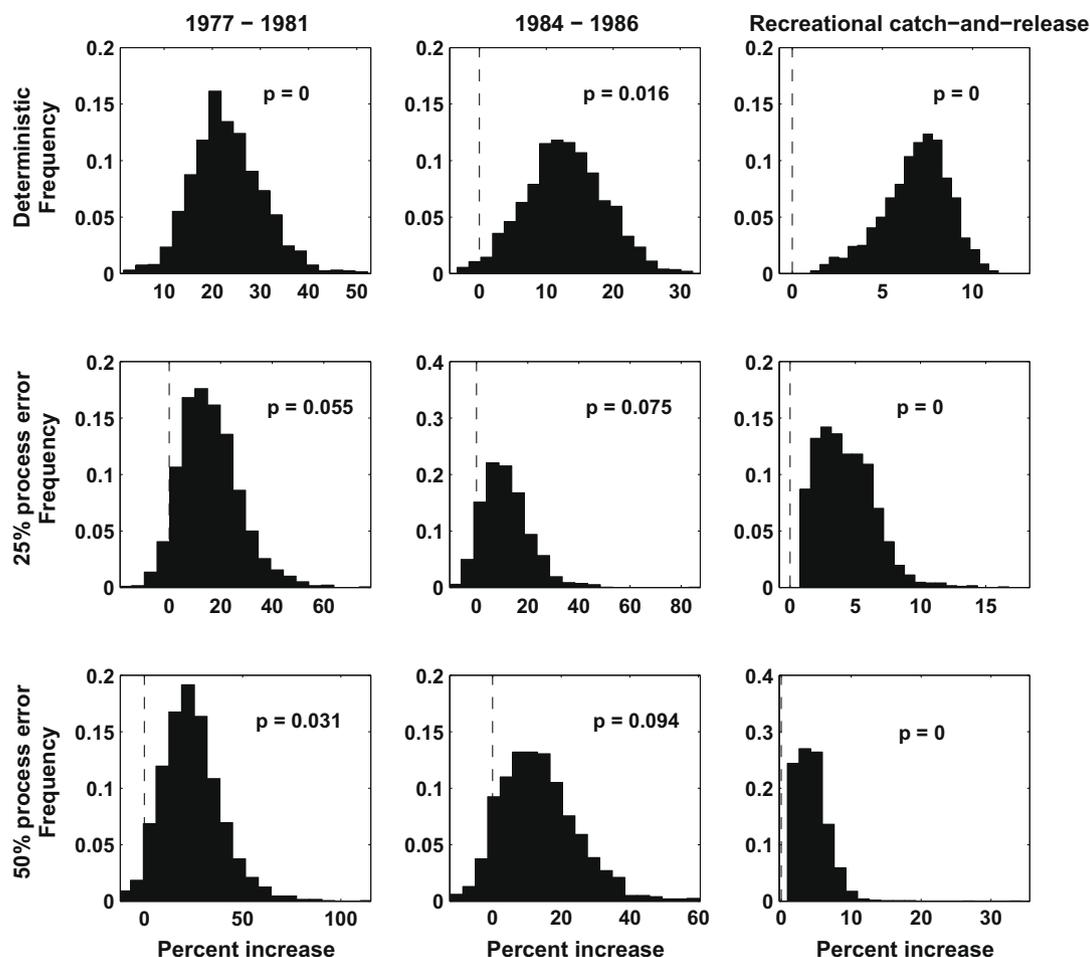


Fig. 5. Marginal posterior distributions for (column 1) the percent increase in vulnerable abundance from 1977–1981 and (column 2) 1984–1986, and (column 3) the percent increase in vulnerable abundance in the year 2000 for strict catch-and-release relative to no catch-and-release during the period 19,901,999. Rows represent (row 1) the deterministic, (row 2) 25% process error, and (row 3) 50% process error scenarios. Posterior distributions are based on 2000 systematic samples from an MCMC chain of length 200,000 where the first 100,000 were discarded to allow for convergence. The proportion of samples for which the percent increase is <0 (p) is given in each panel.

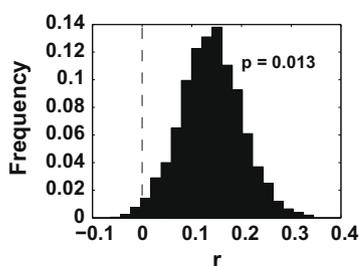


Fig. 6. Marginal posterior distribution of the Pearson correlation coefficient (r) between the Southern Oscillation Index (SOI) and recruitment deviations under the deterministic (i.e. observation error only) scenario. Posterior distribution is based on 2000 systematic samples from an MCMC chain of length 200,000 where the first 100,000 were discarded to allow for convergence.

as the model attempts to explain early declines in CPUE. Although such low values of K are at the lower end of observed values from other populations (Myers et al., 1999), K showed only a modest negative relationship with the percent change in population size during the closures (r^2 ranged from 0.17 for the deterministic model to 0.001 for the 50% process error model). In keeping with the trends in K , recruitment was generally less variable as more process error was permitted (Fig. 8B). Model fits improved as process error increased (Fig. 8C–E); however, even the 50% process error model was unable to fully replicate early declines in CPUE.

4. Discussion

This analysis is unique in that it demonstrates the effect of a closed area for a large pelagic marine species. Most previous analyses of closed areas or marine reserves have focused on relatively sedentary benthic species, particularly coral reef fishes (Halpern, 2003). A network of high-seas marine reserves has been proposed (IUCN, 2004), yet, to date, there is little evidence that marine reserves would be an effective tool for large pelagic fishes. Indeed, model results (e.g. Martell et al., 2005) suggest that such reserves would need to be exceedingly large if they were to offer significant protection to such species. Our results show that this may not always be true.

Under all of the scenarios considered here, our model results confirm Squire and Au's (1990) observation of rapid recovery of striped marlin following the 1977–1980 closure and suggest modest recovery following the shorter 1984–1985 closure as well. However, the magnitude of the recovery appears smaller than raw CPUE data suggest. This discrepancy could have at least two explanations: part of the increase in CPUE during these closures is the result of random unexplained variability, or the population recovered more rapidly in the “core area” near the southern tip of Baja California, following the hypothesis proposed by Squire and Au (1990). Based on our model results, we cannot distinguish between these two explanations.

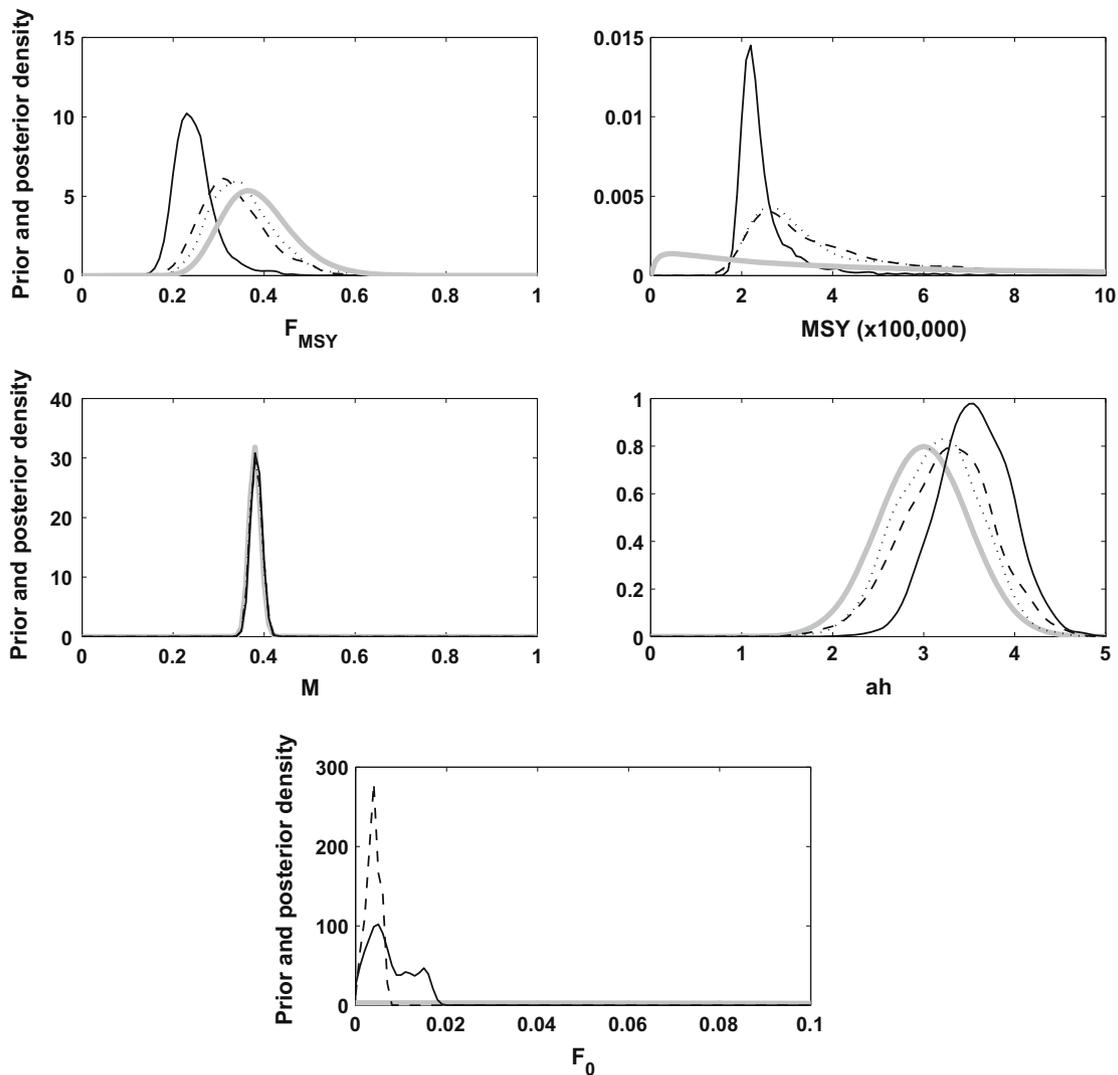


Fig. 7. Normal kernel densities of the marginal posterior distributions (black lines) and the prior distributions (gray line) of model parameters under the deterministic (solid line), 25% process error (dashed line), and 50% process error scenarios (dotted line). Posterior densities are based on 2000 systematic samples from an MCMC chain of length 200,000 where the first 100,000 were discarded to allow for convergence.

Our finding that SOI is related to recruitment or net immigration is consistent with observations that striped marlin respond to extreme El Niño (warm) events by extending their distribution into areas which are otherwise too cold (Pearcy, 2002). Striped marlin are most abundant in California waters during the summer when warm water from the south moves up into the near-shore region off southern California. Expansion of the population to the north (i.e., emigration outside the study area) during warm conditions could explain the finding of negative recruitment deviations during the negative (warm) phase of the SOI.

The relative completeness of the catch data are a source of uncertainty that cannot be represented in the model. There is an artisanal panga (a type of small open boat) fishery in Baja California that catches many pelagic species including striped marlin. The magnitude and trends of catches in this fishery are completely unknown. There has also been increasing conflict between the recreational and commercial fishing sectors in Baja California since the 1980s. Catch records rely heavily on self-reporting. In this environment, commercial fishing vessels may be more hesitant to report high catches of striped marlin. The most recent estimate of the by-catch rate of striped marlin in the Mexican Pacific was 5.8% (Santana-Hernandez, 2001).

An additional significant source of uncertainty not captured by the model is potential changes in catchability not accounted for by our hook-depth standardization. A unit of fishing effort (1000s of long-line hooks or number of angler fishing days) is not equivalent through time as fishing gear and techniques change. Some of the patterns and variability in the CPUE time series are due to changes in catchability rather than changes in abundance, as assumed in the model. In addition to the hook-depth standardization, we addressed this issue by fitting the model to two independent CPUE timeseries. Changes in catchability resulting from changes in targeting or fishing gear are not likely to be correlated between the two time series as these fisheries use different gear and are driven by different motives. This approach reduces, but does not eliminate, the impact of catchability changes on our model outputs. There is a published standardized long-line CPUE time series for striped marlin (see Fig. 4.2.1 in Hinton and Maunder, 2004); however, this CPUE time series is for the entire eastern Pacific Ocean, and is therefore not appropriate for our analysis that is more geographically limited. This standardized CPUE time series is qualitatively similar to the raw CPUE time series, although the extent of early declines in CPUE appears to be somewhat exaggerated by raw CPUE data.

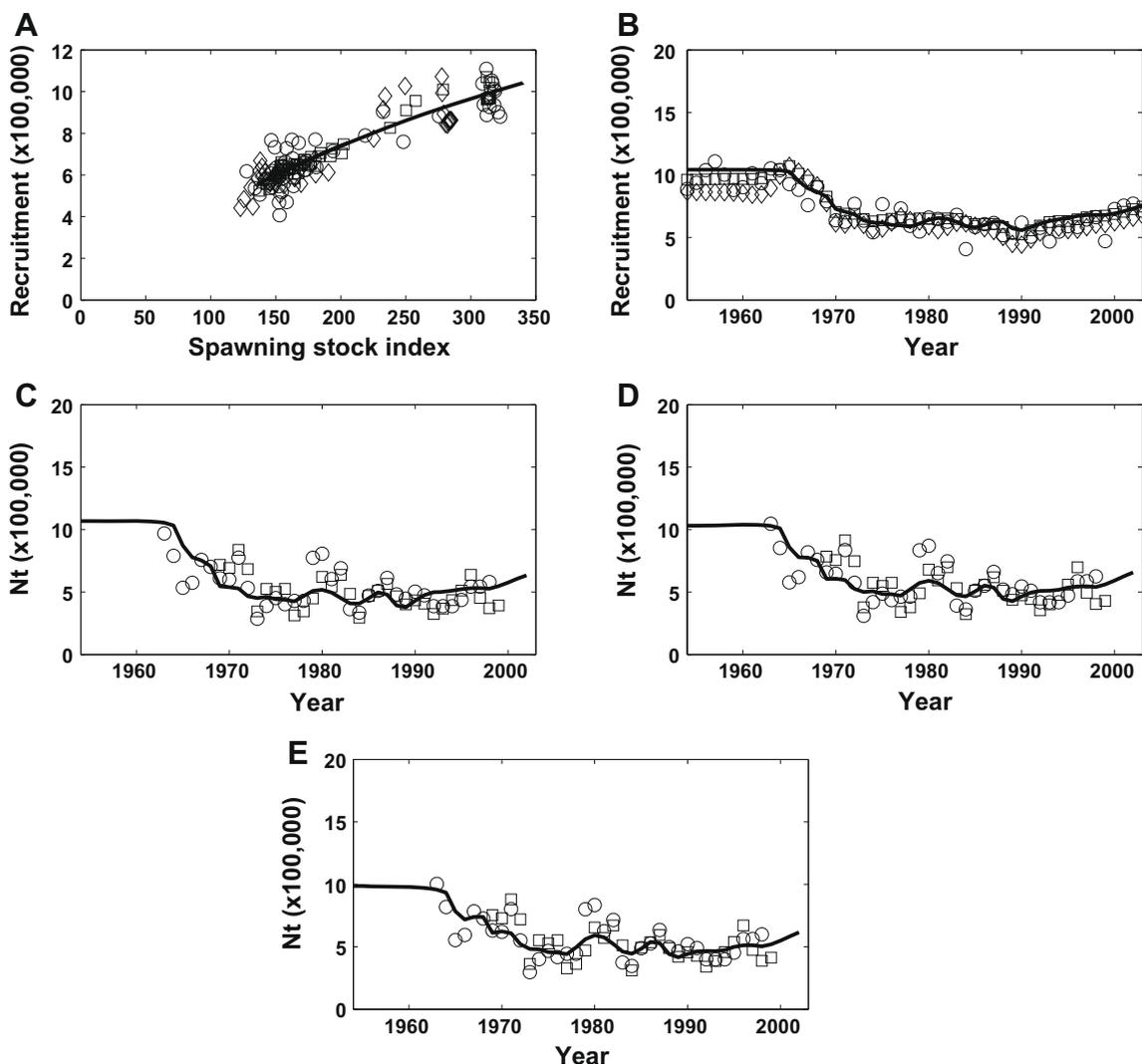


Fig. 8. Stock-recruitment relationship (A) for the deterministic (solid line), Southern Oscillation Index (circles), 25% process error (squares), and 50% process error (diamonds) models; recruitment (age 1) time series (B, same symbols as in A); and modeled vulnerable population size ($N_t \times 100,000$, solid line) for the deterministic (C), 25% process error (D), and 50% process error (E) models. Catch per unit of effort divided by the maximum-likelihood estimate of catchability is shown in C–E for the long-line (circles) and recreational (squares) fisheries.

One of the persistent difficulties in modeling the population dynamics of highly migratory species has been the problem of stock structure. Simply put, it's hard to know where to draw the line marking the extent of a fish stock's distribution when the species in question is capable of transoceanic movements. Mark-recapture studies using individually numbered plastic or stainless steel tags suggest that all billfish are capable of long-distance movements (Ortiz et al., 2003). However, for striped marlin, the vast majority of recaptures typically occur within 1000 km of the release location. For example, 90% of the 360 recaptures of tagged striped marlin occurred within 1000 km of the release location; 83% occurred within 1000 km when only the 157 tags at liberty for over 90 days are considered (Jensen, *unpubl. analysis* of Ortiz et al., 2003 database). It's difficult to know how to interpret these data because most tag returns are from recreational fisheries that have a very limited and discontinuous distribution. Furthermore, fishing effort and reporting rates are generally unknown but likely to vary substantially among regions (Ortiz et al., 2003). For these and other reasons, tag data have not been directly incorporated into other recent stock assessments of striped marlin (Langley et al., 2006).

Genetic studies (Graves and McDowell, 1994; McDowell and Graves, 2008) have also supported the idea that striped marlin can show stock structure at a spatial scale of a few thousand kilometers. More specifically, analysis of multi-locus microsatellite genotypes showed significant genetic heterogeneity between adult striped marlin caught off of Baja California and those from the North Pacific (Taiwan, Japan, Hawaii and California) and Ecuador (McDowell and Graves, 2008). This finding suggests extremely limited interbreeding among these regions but does not rule out mixing among regions for feeding or other non-breeding purposes.

A large PSAT study (Domeier, 2006) showed limited dispersal of adult striped marlin tagged off of Baja California and tracked for up to 9 months (Fig. 3). It is clear that striped marlin aggregate in this region, and both larvae (González-Armas et al., 1999, 2006) and mature females have been found here (Rodríguez-Jaramillo et al., 2007). It is not clear what fractions of adults in the region reproduce and contribute to future generations. Our model results are equivocal on this question. The fact that the closed (observation error only) and open scenarios resulted in broadly similar population trajectories and estimates of recovery during the two long-line closures argues that immigration and emigration may not play as

large a role at this spatial scale as might be expected for a “highly migratory species”.

The question of mixing rates and the spatial distribution of temporary immigrants is critical for the evaluation of marine protected areas. A temporary immigrant that does not spawn in this region has little impact on future population size within the region. Protecting areas made up largely of temporary immigrants would do relatively little to protect local abundance. In contrast, protecting areas made up mostly of spawners would have a disproportionate impact on future local abundance. This question may be solved in the future through genetic sampling of large numbers of striped marlin throughout this region. Our results lend support to McDowell and Graves' (2008) assertion that conservation and management of striped marlin should focus on smaller regions than have been considered in the past.

Uncertainty over stock structure need not delay action to protect striped marlin populations. Under all of the scenarios considered in this analysis, past closures of Mexican waters to long-line fishing lead to rapid increases in abundance. Complete closure of long-line fisheries in Mexican waters would likely involve substantial costs, although long-lining has been declining recently as purse-seining (which involves less billfish bycatch) has become more profitable in the ETP. Billfish caught by long-lines are often alive when the gear is retrieved (Jackson and Farber, 1998; Lee and Brown, 1998). Regulations requiring the release of billfish have been implemented in the US Atlantic long-line fishery (NMFS, 1988), and have been recommended by ICCAT (2007) for all high-seas commercial fisheries in the Atlantic. Similar policies have not yet been enacted in the Pacific, but may prove to be a cost-effective conservation measure. Our analysis shows that any approach that significantly reduces mortality of billfish in Mexican waters will likely result in local increases in striped marlin abundance.

Although our primary results were robust to different levels of process error, there are other sources of uncertainty that could not be fully accounted for. Wider release of catch-at-age data from the Japanese long-line fishery would allow for estimation of the natural mortality rate and provide more information on recruitment variability and vulnerability-at-age. Set-level information on long-line fishing gear (e.g. hooks-per-basket) and technique (e.g. set time and soak time) would permit more sophisticated effort standardization. Future extensions of this work which incorporate these valuable data sources may increase the accuracy and precision of advice regarding the use of area closures for management of striped marlin.

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