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Balancing conservation and utilization in spawning aggregation fisheries: a trade-off analysis of an overexploited marine fish

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Although the management of fish spawning aggregations (FSAs) often requires a precautionary approach that initially emphasizes conservation, understanding the dynamics of spawning and interactions with fishing activities can help identify long-term management solutions that balance conservation with utilization. We designed a parsimonious, per-recruit model to evaluate the potential effects of seven time-closure scenarios implemented during the spawning season on egg-production-per-recruit (EPR; a conservation metric) and yield-per-recruit (YPR; a fisheries metric) of Gulf corvina (*Cynoscion othonopterus*), a vulnerable marine fish that experiences persistent overfishing at its only known spawning grounds in the Gulf of California, Mexico. Five of seven scenarios provided measurable increases in EPR (11–48%) and were accompanied by proportional increases in YPR (29–36%) that resulted in a sustainable fishery. Increased mortality of juveniles and small adults through targeted fishing or as bycatch in other fisheries, however, would erode both the fisheries and conservation benefits of these time closures. Our results demonstrate that information on spawning and fishing activities can be combined with stakeholder input to identify regulations that permit the sustainable harvesting of FSAs. Furthermore, the implementation of brief, temporal fishing effort restrictions can represent a viable, less restrictive alternative to marine protected areas for the management of FSAs.

Keywords: fisher ecological knowledge, fisheries management, fish spawning aggregations, marine conservation, precautionary principle, small-scale fisheries

Introduction

The difficult challenge of managing fisheries is to achieve a sustainable balance between conservation and utilization through the consideration and maintenance of ecological, economic, and social components (Stephenson *et al.*, 2018). The precautionary principle, as applied to fisheries management, advocates for conservative fishing activities to sustain or replenish marine stocks (FAO, 1996). It may require that measures be taken first to avoid irreversible harm to species and ecosystems that are deemed vulnerable on the basis of plausible and immediate concern, placing the burden of proof on the fishing industry and giving priority to preventive management in the absence of convincing evidence or scientific consensus as a means to ensure long-term, resource sustainability (González-Laxe, 2005). However, the precautionary principle also considers the risks of irreversible social and economic harm to fisheries and livelihoods when unnecessary restrictions are allowed to persist and requires that restrictive measures be relaxed if research convincingly demonstrates how and to what degree resources can be extracted to achieve the long-term goal of balanced sustainability (Garcia, 1994). Conflicts between conservation and utilization, and subsequent fisheries management failures due to non-compliance, are a well-reported symptom of overly restrictive fisheries management that exclude stakeholder input in decision-making processes (Healey and Hennessey, 1998; De Santo and Jones, 2007). Such conflict scenarios are particularly common for small-scale fisheries in developing countries in which coastal communities are often highly and directly dependent on the utilization of fishes for livelihoods and food security, whilst conservation groups aiming to protect threatened species and habitats are plentiful (Aburto-Oropeza *et al.*, 2018).

Fisheries that target fish spawning aggregations (FSAs) are emblematic of the historical and contemporary challenges and imbalances associated with precautionary fisheries management. It has been unequivocally demonstrated that many FSAs are highly susceptible to overfishing due to increased catchability during spawning coupled with a suite of behavioural and life history traits that reduce their resilience to fishing pressure (Erisman *et al.*, 2011; van Overzee and Rijnsdorp, 2015). Unfortunately, these demonstrations have emerged from a consistent trend of rapid and severe declines in fisheries and stocks that target FSAs but are not managed specifically for spawning (Sadovy de Mitcheson *et al.*, 2008). Declining stock trends have triggered the justifiable and oftentimes urgent need to implement precautionary management measures that emphasize fish conservation as the first steps towards population recovery, rebuilding stocks, staving off imminent fisheries collapses, and achieving the long-term goal of sustainable and resilient fisheries (Grüss *et al.*, 2014b). In many cases, measures taken can be very restrictive to fishers [e.g. no-take marine protected areas (MPAs) and seasonal closures], yet they can substantially increase annual reproductive output and may be necessary to guard against irreversible harm to the fished populations (Arendse *et al.*, 2007; Russell *et al.*, 2012; Grüss and Robinson, 2015). Moreover, evidence continues to grow that targeted protection of FSA sites can provide both conservation and fisheries benefits and build consensus support when stakeholders are involved in the design and implementation of management measures (Hamilton *et al.*, 2011; Granados-Dieseldorff *et al.*, 2013). However, the implementation of MPAs and seasonal closures can result in strong conflicts with and non-compliance by fishers when their design fails to adequately consider fisher ecological knowledge (FEK) and socio-economic factors (Bennett *et al.*, 2015; Carr and Heyman, 2016), which points to the need to explore other viable alternatives for the management of FSAs.

In line with the precautionary principle, research on FSAs has incrementally built a sound knowledge base on the factors that determine the vulnerability and resilience of spawning fish to fishing (Robinson *et al.*, 2015; Lowerre-Barbieri *et al.*, 2017). We now understand that FSAs vary greatly in their intrinsic and extrinsic vulnerability and thus should be monitored and managed on a case-by-case basis (Grüss and Robinson, 2015; Erisman *et al.*, 2017). In addition, there has been a steady increase in research focused on combining information on the spatio-temporal and behavioural dynamics of FSAs, fishing activities, FEK, and socio-economic factors to identify, assess, and monitor the effectiveness of a range of management options that support ecologically and economically viable fisheries (Armstrong *et al.*, 2013; Zemeckis *et al.*, 2014). Such efforts are feasible due to the emergence of efficient, low-cost, and relatively simple analytical methods for estimating potential reference points in fisheries with limited data and resources available for monitoring and management (Carruthers and Hordyk, 2018). Considering the global importance of FSAs to capture (consumptive) fisheries production, recreational fisheries, and subsistence fisheries (Sadovy de Mitcheson and Erisman, 2012; Erisman *et al.*, 2017), this progressive shift away from diagnostic research and towards solutions-based science needs to continue if FSAs are to be integrated into fisheries management that account for conservatism of the precautionary principle whilst not being unnecessarily restrictive, constraining what may represent productive and sustainable fishing practices.

For this study, we explored opportunities for balancing conservation and utilization in the gill net fishery for the Gulf corvina (*Cynoscion othonopterus*; hereafter "corvina"), a commercially important marine fish endemic to the northern Gulf of California, Mexico, that typifies the challenges facing the management of FSAs. The species is currently overfished and has experienced persistent overfishing for close to two decades due to the intense, targeted exploitation of its FSAs during its peak spawning period in March and April in which nearly the entire annual fisheries catch of corvina occurs at their only known spawning grounds (Ruelas-Peña *et al.*, 2013; Erisman *et al.*, 2014). Long-standing, widespread concerns over unsustainable fishing practices associated with the corvina fishery have resulted in a series of precautionary management measures focused on conservation, beginning with the design and implementation of a no-take MPA that encompasses the principle spawning grounds and later evolving in complexity to include a seasonal harvest quota and a regulated mesh size for gill nets to exclude the capture of juveniles and small, young adults (Ortiz *et al.*, 2016). While these policies were implemented under the assumption that they are necessary to ensure a sustainable fishery (DOF, 2007), alternative management options that are less restrictive and seek sustainable solutions that balance the vulnerability of the species with the socio-economic needs of coastal communities have not been explored (Erisman *et al.*, 2012). Meanwhile, low market values for corvina meat coupled with an exponential rise in the international market value of corvina swim bladders, as well as increased restrictions placed on other fisheries in the region to protect the critically endangered harbour porpoise (*Phocoena sinus*) and totoaba (*Totoaba macdonaldi*), have accelerated the "race to fish" for corvina (EDF, 2015, 2016). As a result, sector conflicts and illegal fishing of corvina inside the MPA are an ongoing challenge for management and validate the need for pursuing alternative management strategies that incentivize compliance among fishers and improve the efficiency of enforcement (Erisman *et al.*, 2012; Ortiz *et al.*, 2016).

Fishers have long suggested that brief time closures during peak spawning periods could serve as a more practical, effective management strategy to the existing no-take MPA that would streamline enforcement, increase compliance, and ensure economically viable fisheries yields while also protecting spawning fish (MacCall *et al.*, 2011; Erisman *et al.*, 2012; see *Species and fishery background* below). In response, we synthesized existing biological and fisheries data to complete a trade-off analysis to evaluate the relative benefits to conservation and utilization if the no-take MPA was replaced by fishing bans during specific periods within the spawning and fishing season for corvina. We enacted seven different time-closure scenarios and then estimated egg-production-per-recruit (EPR) (reproductive capacity; a conservation metric) and yield-per-recruit (YPR) (exploitable biomass; a fisheries metric) for each scenario. We also examined the potential effects of exploiting small, young adults on EPR and YPR of corvina.

Material and methods

Species and fishery background

The corvina is a large-bodied (to 1 m in total length, TL), relatively short-lived (to 9 years) sciaenid fish species endemic to the northern Gulf of California, Mexico (Gherard *et al.*, 2013; Bolser *et al.*, 2018). Unlike most sciaenids but common among fishes in this region (Hastings *et al.*, 2010), the corvina has a very restricted geographic range that extends from the Colorado River Delta south to the Midriff Islands region (Robertson and Allen, 2008), but the environmental factors that shape its distribution are poorly understood. Dispersed among coastal and deeper benthic habitats throughout the northern Gulf for much of the year, the entire adult population of the species migrates on a semi-lunar rhythm during the spring months (late February to early June) into the Colorado River Delta to spawn within massive FSAs that can involve several million individuals and extend over 20 km along the main channels of the river mouth (Erisman and Rowell, 2017). Aggregations form the week before the new and full moons, with mass synchronous spawning occurring during the strong outgoing tides from 5 to 1 day before the new and full moon, and peak spawning occurring 3 and 2 days before the new and full moon (Erisman *et al.*, 2012; Rowell *et al.*, 2017). After the final day of spawning, corvina quickly disperse out of the region before returning the week prior to the next new or full moon. However, the Delta constitutes the principal nursery grounds for the species, as juvenile corvina settle and reside in the region for the first 2 years of their life (Rowell *et al.*, 2005).

The corvina supports a small-scale, commercial gill net fishery in the Upper Gulf of California that is based in coastal communities that surround the Delta. Nearly all the annual fishing effort and landings of the fishery occur during the peak spawning months of corvina in March and April (Erisman *et al.*, 2014; EDF, 2015), when there is a large domestic demand in Mexico for fish over a 6-week period associated with Lent and the Easter holiday season (EDF, 2016). Fishing and spawning activities are synchronized such that peaks in fisheries catch, fishing effort, and catch-per-unit effort completely overlap with the exact timing and locations of peak spawning activity which occur during the weeks preceding the new and full moons (Erisman *et al.*, 2012). Fishing activities involve the use of a single, monofilament gill net that is deployed by two or three fishers from a small "panga" (a 24' length fibreglass boat with a single outboard engine) to entrap schools of corvina during their pre-spawning and spawning activities; the fishing technique is referred to as "encierre." A single panga with one gill net deployed by two fishers can harvest over a ton of corvina in <20 min during the outgoing tide when fish are actively spawning (Erisman *et al.*, 2012). As much as 94% of corvina landings take place during the spawning period, and despite the existence of a no-take MPA intended to protect the corvina during spawning, up to 90% are caught within the MPA (Erisman *et al.*, 2012). Moreover, indigenous communities that reside along the river are permitted to fish within the no-take MPA, which creates ongoing conflicts with the commercial fishing sector (Navarro *et al.*, 2013).

The commercial fishing fleet of over 500 pangas has captured an average of 3600 tons per year during the corvina spawning season since 1998 (EDF, 2016; Ortiz *et al.*, 2016; Supplementary Figure S1a), and the annual exploitation rate of large adults >65 cm TL is estimated at 0.825 (Erisman *et al.*, 2014; see below). During the peak periods of fishing, the fleet's fishing capacity is thought to be saturated (MacCall *et al.*, 2011). That is, even if corvina abundance were much higher, the fleet could not catch more fish due to limitations of time on the water and transportation bottlenecks on both water and land, including ability to deliver the fish to the processor before they spoil. Ex-vessel market prices for corvina are consistently low (<$2 USD kg; EDF, 2016), and daily landings of over 1000 tons during the peak spawning days often create market gluts that result in rapid declines in market prices, complete market closures, and large volumes of wasted, unsold fish (Erisman *et al.*, 2014; EDF, 2016).

While nearly all of the old adults of corvina may be harvested during the spawning season, evidence suggests that due to restrictions on mesh size, the young adults and juveniles of the species escape fishing during the spawning season and that their annual fishing mortality rate due to bycatch is negligible (Pérez-Valencia, 2012; Rowell and Erisman, 2016). As a result, the persistence of the population and the fishery is dependent on survivorship of juvenile corvina and the reproductive success of small (<65 cm TL) adult corvina of 2–4 years of age (Erisman *et al.*, 2014; Rowell and Erisman, 2016). However, harvest rates of juveniles and small adults could increase in the near future in response to recent trends in the corvina fisheries and regional fisheries regulations. Mean length at capture has decreased steadily and significantly over the past decade (Ortiz *et al.*, 2016; Supplementary Figure S1b), indicating that larger adults are becoming increasingly rarer in the population due to fishing, which could force fishers to target smaller fish to maintain economically viable harvest levels.

Time closures have long been advocated by commercial fishers in the Colorado River Delta region as a management option for the sustainable exploitation of corvina, and although the management plans based on time closures have been recommended for consideration (DOF, 2012), these options have not been explored prior to this study. The low market value of corvina results in a situation in which commercial fishers need to catch large volumes to make a profit, which is only possible inside the no-take MPA where corvina aggregate and spawn (Erisman *et al.*, 2012; EDF, 2015, 2016). Likewise, fishers from indigenous communities limit their corvina fishing to the MPA (Navarro *et al.*, 2013). While fish are present outside the no-take MPA prior to the days of spawning, the corvina schools are much more dispersed, which requires substantially more effort (distance, time, deployments) and resources (fuel) to fish and results in significantly lower catches (Erisman *et al.*, 2012, 2015). Once spawning activity ceases by the day of the full or new moon, the corvina population disperses quickly out of the region, allowing very little opportunity for fishers to legally harvest fish (i.e. outside the MPA) in numbers sufficient to warrant their efforts.

Fishers are aware and concerned about the effects of fishing during spawning and have suggested allowing fishing inside the no-take MPA but restricting all fishing activities during designated periods (MacCall *et al.*, 2011; Erisman *et al.*, 2012). This approach could ameliorate some of the existing negative impacts of fishing the spawning aggregation by allowing the fish to spawn undisturbed during peak spawning days or periods. A switch from area to time closures would also streamline and improve enforcement by reducing the area and time allocated to enforcement efforts. The current strategy to restrict fishing inside the MPA involves the patrol of one or more government surveillance vessels along its southern entrance during the peak fishing days. The large size of the MPA coupled with the extremely high ratio of fishing vessels to enforcement vessels severely limits its effectiveness, as evidenced by pervasive fishing activity inside the restricted area throughout the corvina fishing season and during periods when enforcement vessels are present (Erisman *et al.*, 2012, 2015). Moreover, strong tidal fluctuations of 10–12 m, dangerous currents, shallow waters, and shifting sand bars in the area pose significant challenges for enforcement and threaten the safety of both enforcement officers and fishers. Conversely, implementing temporary fishing bans could markedly improve the efficiency and quality of enforcement efforts, because fishing and spawning activities related to corvina are predictable in time and space, there are only a few possible locations to land corvina within the three communities, and all fish are sold and processed at a handful of existing commercial plants. Therefore, enforcement agencies could streamline their efforts around these specific times and locations where fish and fishers must converge. Compliance for fishing regulations would also likely improve, because the social, legal, and economic conflicts associated with fishing inside the MPA would be removed. Voluntary compliance also tends to be higher when fishery regulations include fishers in the process, because the perceived legitimacy of regulations and regulatory authority increases (Hatcher *et al.*, 2000). Of course, effective enforcement strategies also reduce incentives to fish illegally (Nielsen, 2003).

Study design

We designed a parsimonious, non-spatial, per-recruit model that estimates the EPR and YPR of corvina in relation to the annual exploitation rates of the young adults (E_{YA}) and old adults (E_{OA}) of the species. Our model assumes that corvina is harvested only during the spawning season and that all the juveniles and young adults of the species escape fishing currently (i.e. $E_{\mathrm{YA}} = 0$). It also assumes that the encierre technique used by the corvina fishery means that there is no upper size limit to the fishery (i.e. the largest corvinas do not escape capture). These assumptions are supported by several lines of evidence, as described in Erisman *et al.* (2014). Our model, which is based on Erisman *et al.* (2014) and a preliminary study by MacCall *et al.* (2011), relates the annual exploitation rate of old adults of corvina to their daily catch patterns during the spawning season.

In the following, we first present the assumptions made regarding the growth and reproductive patterns of corvina and then detail the process for calculating of EPR and YPR for the species. Next, we summarize the current exploitation rates and catch patterns of corvina in the absence of time closures based on recent monitoring data, before describing the estimation of reference points for the species and the sensitivity analysis we conducted. Finally, we explain how we evaluated time-closure scenarios for corvina and the potential consequences of harvesting young adult corvinas.

Life history and reproductive parameters

Following the growth parameters generated by Bolser *et al.* (2018), corvina is assumed to grow in length according to a von Bertalanffy growth function (Figure 1a):

$$L(a) = L_{\infty}\left(1 - \mathrm{e}^{-K(a-a_0)}\right), \tag{1}$$

where $L(a)$ is the body length at age a (in mm TL); L_{∞} is the maximum body length (951.30 mm TL); K is the Brody growth coefficient (0.25 year^{-1}); and a_0 is the theoretical age at zero length (−0.33 years). Then, based on the work by Gherard *et al.* (2013), the body weight of corvina at age $a, w(a)$, in g, is estimated as (Figure 1b):

$$w(a) = 2 \cdot 10^{-5} \cdot L(a)^{2.8834}. \tag{2}$$

Corvina are synchronous, multiple batch spawners with indeterminate annual fecundity (Gherard *et al.*, 2013). To account for this, our per-recruit model considers the batch fecundity of corvina at age and its spawning frequency at age. The batch fecundity of corvina at age a, $\mathrm{BF}(a)$, in numbers of eggs, is given by Gherard *et al.* (2013; Figure 2):

$$\mathrm{BF}(a) = 115\ 689 \cdot a^{1.036558}. \tag{3}$$

Estimates of spawning frequency at age are not available for corvina, but may have a large impact on the reproductive capacity of the species (Erisman *et al.*, 2014). Therefore, in this study, we considered the three alternative scenarios for spawning frequency at age as defined and examined by Erisman *et al.* (2014): the "Equal spawning frequency," the "Incremental spawning frequency," and the "Dual spawning frequency" scenarios (Figure 3). Under the Equal spawning frequency scenario, spawning frequency is invariant with age. Under the Incremental spawning frequency scenario, spawning frequency increases proportionally with increasing age. Finally, under the Dual spawning frequency scenario, fish of ages 2–5 spawn half as frequently as fish of ages 6–9.

Estimation of EPR and YPR

We estimated EPR as follows:

$$\begin{aligned}\mathrm{EPR} = {} & \frac{\mathrm{SR}}{1+\mathrm{SR}}\int_{aR}^{a\mathrm{OA}} \mathrm{e}^{-M(aR-0)}\left[\mathrm{e}^{-M(a-aR)}\left(1-E_{\mathrm{YA}}\right)^{(a-aR)}\right] \\ & \times \mathrm{BF}(a)\phi(a)da + \frac{\mathrm{SR}}{1+\mathrm{SR}}\int_{a\mathrm{OA}}^{a\mathrm{MAX}} \mathrm{e}^{-M(aR-0)} \\ & \times \left[\mathrm{e}^{-M(a\mathrm{OA}-aR)}\left(1-E_{\mathrm{YA}}\right)^{(a\mathrm{OA}-aR)}\right] \\ & \times \left[\mathrm{e}^{-M(a-a\mathrm{OA})}\left(1-E_{\mathrm{OA}}\right)^{(a-a\mathrm{OA})}\right]\mathrm{BF}(a)\phi(a)da\end{aligned} \tag{4}$$

where SR is the female to male sex ratio of corvina [assumed to be 1:1 based on Erisman *et al.* (2015)]; M is the annual natural mortality rate [0.26 year^{-1}; estimated in Erisman *et al.* (2014) using Pauly's (1980) relationship, assuming a temperature of 23.9°C for the Gulf of California]; E_{YA} is the annual exploitation rate of young adults [and, therefore, $(1 - E_{\mathrm{YA}})$ is the escapement rate of young adults]; E_{OA} is the exploitation rate of old adults [and, therefore, $(1 - E_{\mathrm{OA}})$ is the escapement rate of old adults]; aR is the age of sexual maturity (2 years; Gherard *et al.*, 2013); $a\mathrm{OA}$ is the age of transition from the young adult stage to the old adult stage (i.e. 5 years); and $a\mathrm{MAX}$ is the maximum age (9 years; Gherard *et al.*, 2013). It is necessary to use exploitation rates rather than the more conventional fishing mortality rates for young and old adult corvina, because the corvina fishing season is very short and thus behaves as a pulse fishery (see MacCall *et al.*, 2011 and Erisman *et al.*, 2014 for more details).

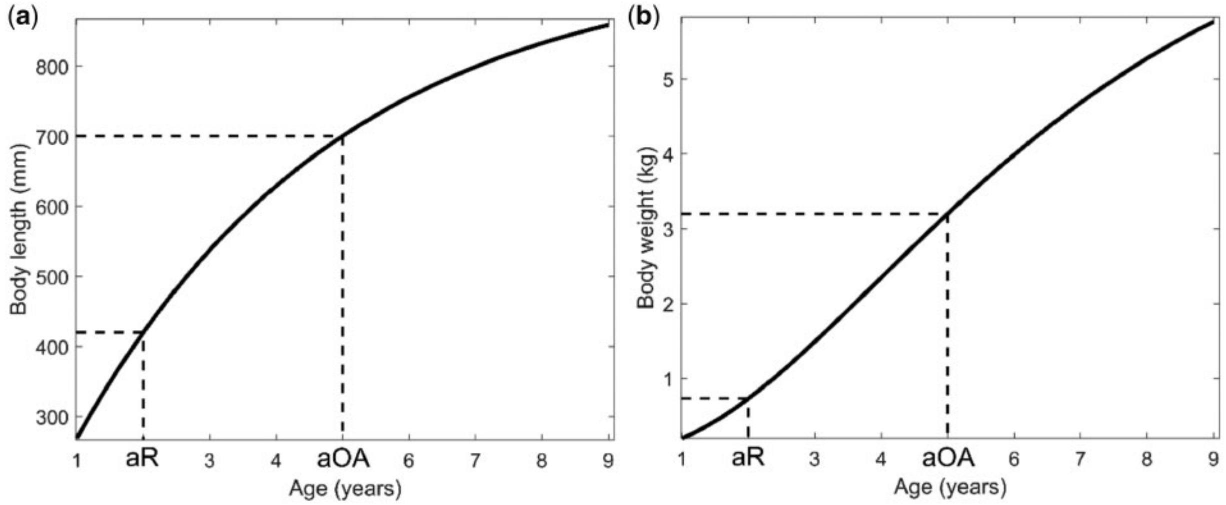

Figure 1. (a) Length-at-age and (b) weigh-at-age relationships considered for Gulf corvina (*C. othonopterus*) in this study. a_R is the age of sexual maturity (2 years; Gherard *et al.*, 2013); a_{OA} is the age of transition from the young adult stage to the old adult stage (5 years).

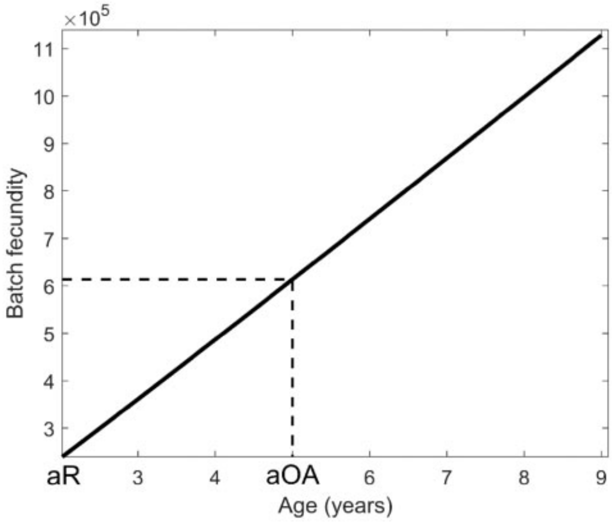

Figure 2. Batch fecundity-at-age relationship considered for Gulf corvina (*C. othonopterus*) in this study. a_R is the age of sexual maturity (2 years; Gherard *et al.*, 2013); a_{OA} is the age of transition from the young adult stage to the old adult stage (5 years).

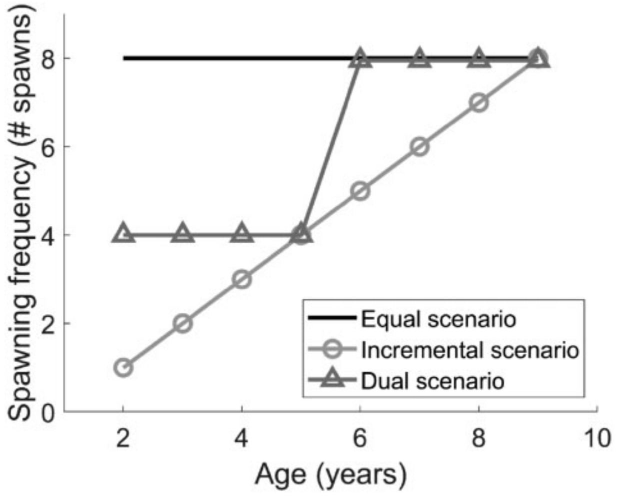

Figure 3. Scenarios of spawning frequency at age considered for Gulf corvina (*C. othonopterus*) in this study.

YPR is given by:

$$
\begin{aligned}
\mathrm{YPR} = {} & E_{\mathrm{YA}} \int_{aR}^{a\mathrm{OA}} \mathrm{e}^{-M(aR-0)} \left[\mathrm{e}^{-M(a-aR)} (1 - E_{\mathrm{YA}})^{(a-aR)} \right] w(a) da \\
& + E_{\mathrm{OA}} \int_{a\mathrm{OA}}^{a\mathrm{MAX}} \mathrm{e}^{-M(aR-0)} \left[\mathrm{e}^{-M(a\mathrm{OA}-aR)} (1 - E_{\mathrm{YA}})^{(a\mathrm{OA}-aR)} \right] \\
& \times \left[\mathrm{e}^{-M(a-a\mathrm{OA})} (1 - E_{\mathrm{OA}})^{(a-a\mathrm{OA})} \right] w(a) da
\end{aligned}
\tag{5}
$$

Estimation of exploitation rates and catch patterns in the absence of time closures

In March and April of 2013–2015, we conducted biological surveys of corvinas landed by commercial fishers at the three principal fishing communities surrounding the Colorado River Delta: El Golfo de Santa Clara, San Felipe, and El Zanjon. For each fish ($n = 4955$), we recorded information on TL to the nearest mm, and length data were combined among years to generate a length frequency distribution for the current fishery.

By applying the methods described by Erisman *et al.* (2014), we determined that E_{OA} is equal to 0.825 based on the length composition data from 2013 to 2015. For determining the value of E_{OA}, we relied on the natural mortality rate M estimated in Erisman *et al.* (2014). We calculated total annual mortality rate Z using the Survival Estimation in Non-equilibrium situations model (Gedamke and Hoenig, 2006), and then employed the M estimate to calculate fishing mortality rate F from $Z = F + M$. Finally, E_{OA} was calculated as $E = {}^{F}/_{Z}$. We assumed that E_{YA} is equal to 0, based on the absence of small adults in our survey data and the results of other monitoring reports (EDF, 2015; Ortiz *et al.*, 2016).

Data on daily catch volumes during the corvina fishing season (late February through April) were collected at El Golfo de Santa

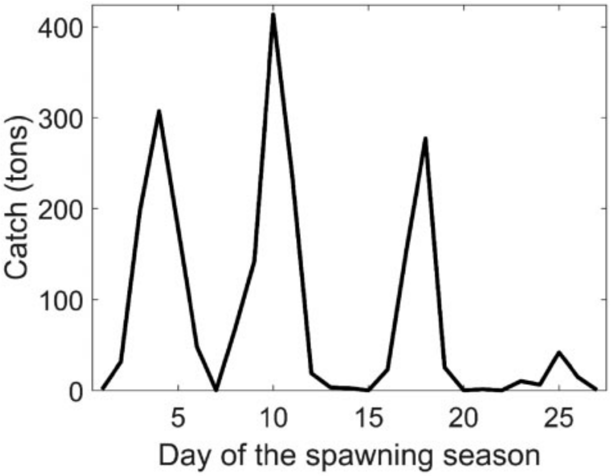

Figure 4. Daily catch patterns of Gulf corvina (*C. othonopterus*) during the spawning season, reconstructed from daily catch data collected between 2013 and 2015.

Clara from 2013 through 2015 by the Environmental Defense Fund as part of an administrative monitoring programme associated with the management of the corvina fishery (EDF, 2015). These data were used to reconstruct the average daily catch patterns of corvina during the spawning season (Figure 4). We assumed that the daily catch patterns shown in Figure 4 resulted in an exploitation rate for old adults of corvina equal to $E_{\mathrm{OA}}=0.825$, so as to be able to estimate a mean annual harvestable biomass for corvina (see "Evaluation of time-closure scenarios" section). Based on the patterns of daily catch patterns from 2013 to 2015 and the results of several previous studies focused on temporal fishing patterns in the corvina fishery (MacCall *et al.*, 2011; Erisman *et al.*, 2012, 2014, 2015; EDF, 2016) that revealed highly predictable, consistent temporal fishing patterns that were synchronized with and dependent on the highly predictable spawning migration of corvina, we assumed that the average daily catch patterns would not change in response to time closures.

Estimation of reference points and sensitivity analyses

To facilitate discussions of our results, before evaluating any scenario, we estimated two reference points for corvina with our per-recruit model: the maximum value of the YPR of corvina, $\mathrm{YPR}_{\max}$; and the natural EPR of corvina (NEPR), i.e. its EPR when E_{OA} is set to 0. Then, we evaluated the sensitivity of the fraction of natural FNEPR of corvina (FNEPR = EPR/NEPR) and of ($\mathrm{YPR}/\mathrm{YPR}_{\max}$) to changes in M. Using Jensen's (1996) relationship, Erisman *et al.* (2014) estimated an M of 0.38 year^{-1} for corvina. Therefore, given that we set the M of corvina to 0.26 year^{-1} in this study [based on Pauly's (1980) method], we chose to explore the consequences of increasing or decreasing the value of the M of corvina by 0.12 year^{-1} for FNEPR and ($\mathrm{YPR}/\mathrm{YPR}_{\max}$).

Evaluation of time-closure scenarios

The individual fishing periods for corvina are commonly referred to as fishing "tides," because they occur during the weeks leading up to the new and full moons when tidal ranges can exceed 8 m. We considered the following time-closure scenarios: (Scenario 1) No fishing during the entire spawning season; (Scenario 2) No fishing during the first tide; (Scenario 3) No fishing during the last tide; (Scenario 4) No fishing during the first two tides; (Scenario 5) No fishing during the last two tides; (Scenario 6) No fishing during the peak day spawning of each tide; and (Scenario 7) No fishing during the peak three days of each tide.

As aforementioned, we assume that the daily catch patterns (Figure 4) result in an exploitation rate for old adults of corvina equal to $E_{\mathrm{OA}}=0.825$. Moreover, over the period 2013–2015, the mean catch of corvina at El Golfo de Santa Clara during the entire spawning season, C, was 2207.3 tons. Therefore, we assume that the harvestable biomass of old adults of corvina over the entire spawning season, B_{harvest}, is equal to: $B_{\mathrm{harvest}}={}^{C}/_{E_{\mathrm{OA}}}=2675.5$ tons. Under these assumptions, it is straightforward to adjust the value of E_{OA} when a specific time-closure scenario is implemented (Figure 5). For example, under Time-Closure Scenario 2, the 763.7 tons of old adult corvina that were supposed to be harvested during the first tide "escape" fishing. Therefore, 2207.3–763.7 = 1443.6 tons of adult corvina are harvested during the spawning season. Consequently, under Time-Closure Scenario 2, the exploitation rate for old adults of corvina is equal to: $E_{\mathrm{OA}}={}^{C}/_{\mathrm{Bharvest}}=0.5396$ (Figure 5).

Evaluation of the consequences of harvesting young, adult corvina

We also conducted an evaluation the consequences of harvesting young, adult corvina during the spawning season. This evaluation consisted of increasing gradually the value of E_{YA} from 0 to 1 (while fixing the value of E_{OA} to 0.825) and examining the impacts of these increases on FNEPR and ($\mathrm{YPR}/\mathrm{YPR}_{\max}$).

Results

Model in the absence of time closures and with no harvest of young adults

The status of the corvina population can be easily determined from the YPR curve (Figure 6) and the EPR curve (Figure 7). The current value of E_{OA} is twice the value of E_{OA} at which YPR reaches a maximum, $E_{\mathrm{OA}}^{\max}$, and the current YPR of corvina is at 73% of its maximum value ($\mathrm{YPR}_{\max}$) (Figure 6). The current EPR of corvina depends on the spawning frequency scenario being considered. Under the Equal spawning frequency scenario, the current EPR of corvina is 56% of its unfished value (Figure 7a). EPR decreases faster with increasing E_{OA} under the Incremental than under the Equal spawning frequency scenario (Figure 7b vs. Figure 7a). Consequently, the FNEPR of corvina (i.e. the EPR of corvina expressed as a fraction of its NEPR) is lower under the Incremental spawning frequency scenario (0.37). EPR also decreases faster with increasing E_{OA} under the Dual than under the Equal spawning frequency scenario (Figure 7c vs. Figure 7a). Consequently, the FNEPR of corvina is lower under the Dual than under the Equal spawning scenario. However, the FNEPR under the Dual spawning scenario is slightly larger than that under the Incremental spawning frequency scenario (0.42 vs. 0.37). If the exploitation rate of corvina old adults was decreased to $E_{\mathrm{OA}}^{\max}$ (i.e. if E_{OA} was set to about half of its current value), corvina FNEPR would range between 0.53 and 0.68, depending on the spawning frequency scenario assumed (while YPR would be at its maximum value).

Decreasing the natural mortality rate M of corvina decreases both the FNEPR and ($\mathrm{YPR}/\mathrm{YPR}_{\max}$) of the species, while increasing M leads to an increase in both FNEPR and ($\mathrm{YPR}/\mathrm{YPR}_{\max}$)

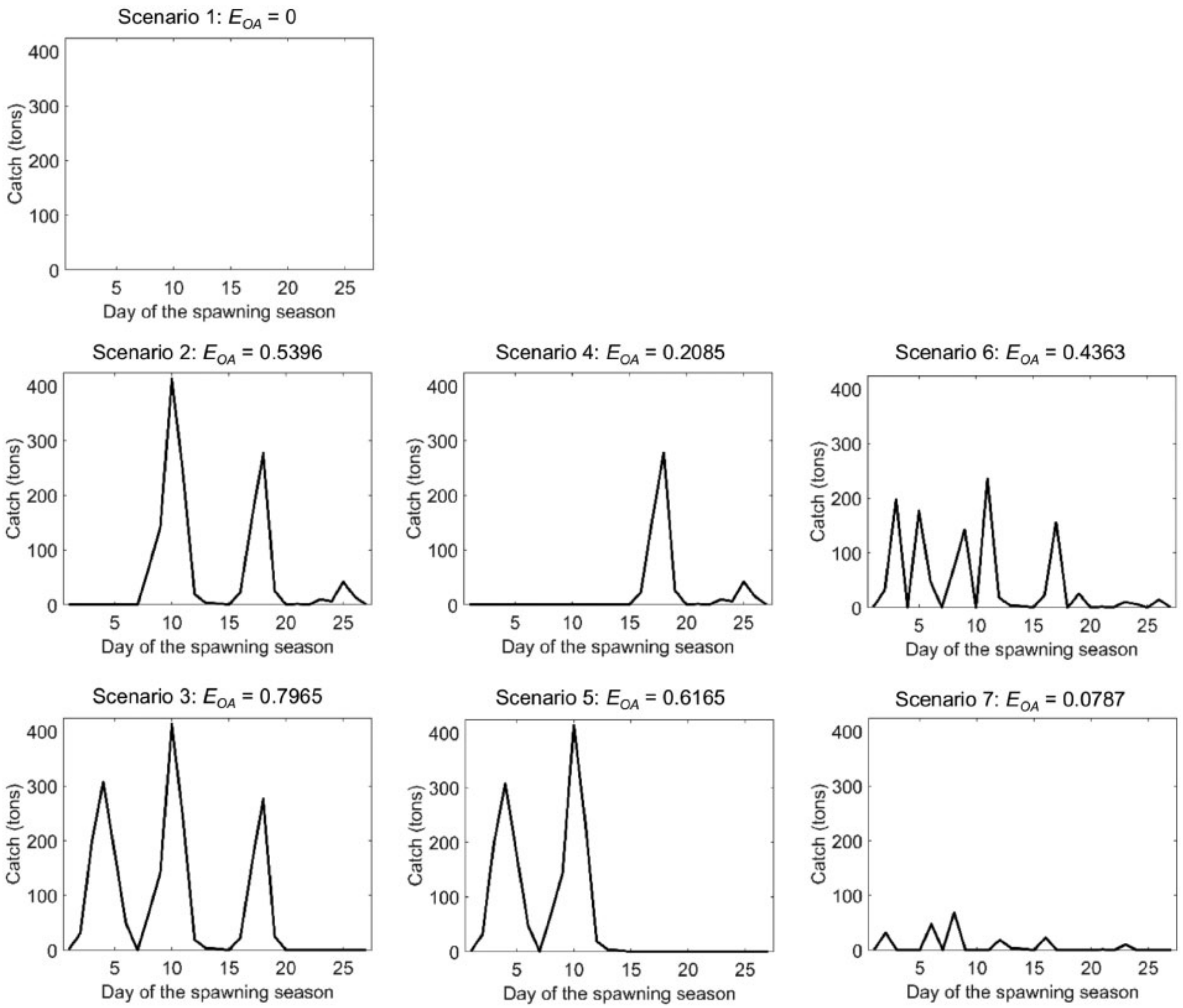

Figure 5. Daily catch patterns during the spawning season and exploitation rate (E_{OA}) of old adults of Gulf corvina (*C. othonopterus*), under seven different time-closure scenarios: (Scenario 1) No fishing during the entire spawning season; (Scenario 2) No fishing during the first tide; (Scenario 3) No fishing during the last tide; (Scenario 4) No fishing during the first two tides; (Scenario 5) No fishing during the last two tides; (Scenario 6) No fishing during the peak day spawning of each tide; and (Scenario 7) No fishing during the peak 3 days of each tide.

(Table 1). Changes in response to a change in *M* are more pronounced for FNEPR than for (YPR/YPR_{max}).

Evaluation of time-closure scenarios

All time-closure scenarios result in an increase in the EPR of corvina (Figure 8 and Supplementary Figures S2 and S3). Yet, the increase in EPR in response to time closures varies greatly depending on the time-closure scenario and spawning frequency scenario considered. As expected, the largest increases in EPR in response to the implementation of time closures occur when there is no fishing during the spawning season (Scenario 1). However, large increases in EPR also occur when there is no fishing during the peak 3 days of each tide (Scenario 7; +67 to 141%) or no fishing during the first two tides (Scenario 4; +48 to 100%). When no fishing occurs during the peak day spawning of each tide (Scenario 6), the EPR of corvina increases by 25–48%, depending on the spawning frequency scenario considered. Increases in EPR in response to time closures are more modest when there is no fishing during the first tide (Scenario 2) or no fishing during the last two tides (Scenario 5) (+11 to 31%). Finally, increases in EPR are negligible (+1 to 3%) when time closures are implemented during the last tide.

Increases in EPR in response to the implementation of time closures are largest under the Incremental spawning frequency scenario and are always more important under the Dual than under the Equal spawning frequency scenario (Figure 8 and Supplementary Figures S2 and S3). Yet, contrasts among the Incremental, Dual, and Equal spawning frequency scenarios are more pronounced when there is no fishing during the spawning season (Scenario 1), no fishing during the peak 3 days of each tide (Scenario 7) or no fishing during the first two tides (Scenario 4) than under the four other time-closure scenarios.

The YPR of corvina increases or decreases in response to the establishment of time closures (Figure 8 and Supplementary Figures S2 and S3). As expected, YPR decreases by 100% when there is no fishing during the spawning season (Scenario 1). The YPR of corvina also declines (by 50%) when no fishing occurs during the peak 3 days of each tide (Scenario 7). In contrast, the

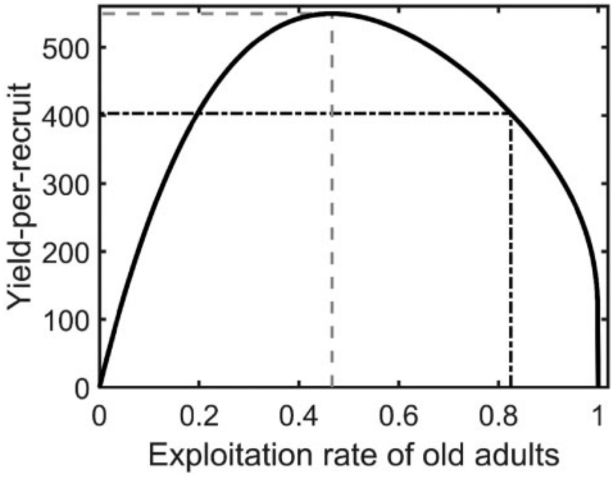

Figure 6. YPR as a function of the exploitation rate of old adults for Gulf corvina (*C. othonopterus*) (thick black curve). The vertical thin black line indicates the current exploitation rate of old adults of Gulf corvina, and the corresponding value of YPR. The vertical thin grey line indicates the exploitation rate of old adults of Gulf corvina at which the YPR of the species reaches a maximum, and the corresponding value of YPR.

YPR of corvina is enhanced under the five other time-closure scenarios. The largest increases in YPR in response to the implementation of time closures occur when no fishing occurs during the peak day spawning of each tide (Scenario 6; +36%), no fishing occurs during the first tide (Scenario 2; +35%), or no fishing occurs during the last two tides (Scenario 5; +29%).

Three of the seven time-closure scenarios offer the best compromises in terms of EPR and YPR, in the following order: Scenario 6 (where no fishing occurs during the peak day spawning of each tide), Scenario 2 (where no fishing occurs during the first tide), and Scenario 5 (where no fishing occurs during the last two tides) (Figure 8). Under these three scenarios, a small to large increase in EPR (+11 to 48%) is accompanied by a large increase in YPR (+29 to 36%) (Figure 8).

Evaluation of the consequences of harvesting young adults of corvina

The YPR of corvina increases very little when E_{YA} increases from 0 to 0.27 and then decreases when E_{YA} exceeds 0.27 (Figure 9a). The FNEPR of corvina decreases nonlinearly with increasing E_{YA} under the three spawning frequency scenarios (Equal, Incremental, and Dual) (Figure 9b). However, FNEPR starts at a higher level and reaches a critically low level more slowly under the Equal scenario than under the two other spawning frequency scenarios. Moreover, FNEPR starts at a lower level and reaches a critically low level more rapidly under the Incremental than under the Dual scenario (Figure 9b).

Discussion

In exploited populations of marine fishes, there exists a fundamental trade-off between maximizing fisheries yield and conserving fish populations via the sufficient protection of spawners to ensure a long-term, healthy reproductive capacity (Schmalz *et al.*, 2016). Evaluations of potential trade-offs between these two conflicting strategies using fisheries status indicators such as YPR and EPR can facilitate the decision-making process by illuminating alternative harvest policies and tactics (e.g. catch limits, MPAs, fishing effort restrictions) to support both thriving fisheries and healthy ecosystems and resolve the proverbial "conserve or catch" conflict among stakeholder groups (Hilborn *et al.*, 2012; Chollett *et al.*, 2017). For fisheries that target FSAs, this approach offers an opportunity to move beyond a reliance on MPAs and seasonal closures as the only solutions to sufficiently protect spawners and to explore potentially less restrictive harvest policies and tactics that consider the socio-economic and cultural needs of fishers and coastal communities in a balanced, meaningful way.

For this study, we evaluated the utility of implementing brief time closures within the spawning season as a viable alternative to no-take MPAs for maximizing fisheries yields, protecting the reproductive capacity of adults during their critical and vulnerable spawning period, and increasing support and compliance by commercial fishers for harvest regulations by including their input within the management policies. The study was designed in response to proposals by both commercial and indigenous fishers from the Colorado River Delta region to consider implementing brief time closures as a potential management strategy to reduce conflicts and non-compliance issues associated with the existing no-take MPA, allow fishers to harvest enough corvina to maintain their livelihoods, protect a sufficient proportion of spawning to maintain the corvina population, and streamline enforcement efforts (Erisman *et al.*, 2012; Navarro *et al.*, 2013). By combining existing biological and fisheries data with FEK on interactions between the spawning dynamics and fishing activities for corvina, we have demonstrated that balanced, sustainable management solutions are possible even for the most extreme examples of aggregation fisheries, in which FSAs are intensively targeted by a fishery whose harvest tactics are synchronized and entirely dependent on the harvest of fish during spawning.

Our approach and our results may serve as a template for the monitoring and management of aggregation fisheries elsewhere, in which the initial steps may involve precautionary management that emphasizes conservation but is later replaced by less restrictive, more practical regulations once a comprehensive understanding of spawning–fishing interactions is achieved through cooperative research and co-management processes with stakeholders. Our per-recruit modelling approach can easily be applied to other case studies, as it relies on a very limited number of parameters, many of which (natural mortality rate, parameters of the length-at-age and weight-at-age relationships, age of sexual maturity, and maximum age) can be very easily obtained (e.g. via FishBase; Froese and Pauly, 2019). Spawning frequency at age and, to a lesser extent, batch fecundity at age, are the two relationships on which our approach relies that will be the hardest to establish in many cases. However, future studies can define alternative spawning frequency scenarios, as we did in this study. Moreover, if information is unavailable for the species of interest or a related species to parameterize batch fecundity at age, future studies can substitute EPR with spawning stock biomass-per-recruit (SSBR) to evaluate management measure effects on reproductive capacity, which relies on a much easier to parameterize weight-at-age relationship (Grüss *et al.*, 2014a). Finally, the unique context of the corvina fishery made it easy to define seven alternative time-closure scenarios for this study, yet the simplicity of our per-recruit modelling approach will allow its future users to straightforwardly determine how management measures may affect fishing mortality rates or exploitation rates from

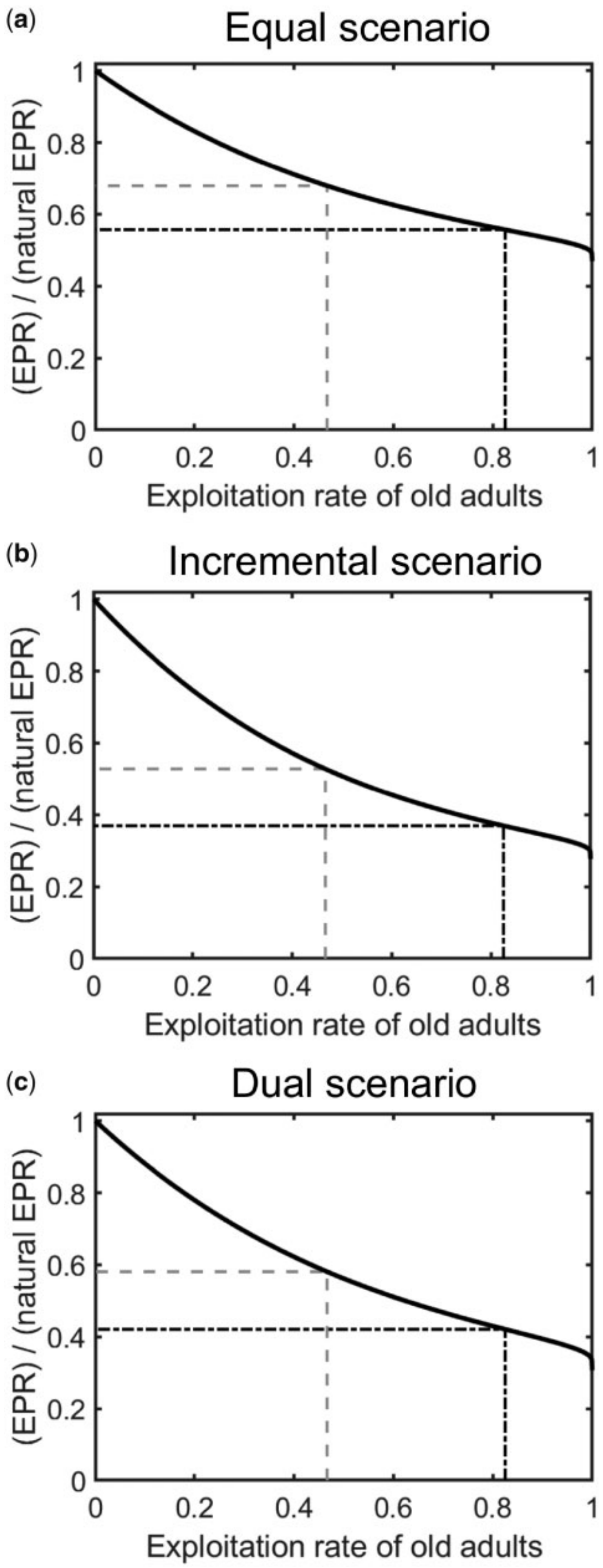

Figure 7. EPR over NEPR as a function of the exploitation rate of old adults for Gulf corvina (*C. othonopterus*) (thick black curve), under (a) the "Equal," (b) the "Incremental," and (c) the "Dual" spawning frequency scenarios. Under the Equal spawning frequency scenario, spawning frequency is invariant with age. Under the

Figure 7. Continued

Incremental spawning frequency scenario, spawning frequency increases proportionally with increasing age. Finally, under the Dual spawning frequency scenario, fish of ages 2–5 spawn half as frequently as fish of ages 6–9. For each panel, the vertical thin dashed black line indicates the current exploitation rate of old adults of Gulf corvina, and the corresponding value of EPR over NEPR. Moreover, for each panel, the vertical thin dashed grey line indicates the exploitation rate of old adults of Gulf corvina at which the YPR of the species reaches a maximum, and the corresponding value of EPR over NEPR.

Table 1. Per cent change in FNEPR and (YPR/YPR$_{max}$) for Gulf corvina (*C. othonopterus*) in response to two scenarios: (1) a scenario where the natural mortality rate *M* of corvina is set to 0.14 year^{-1} (instead of 0.26 year^{-1} in the baseline situation); and (2) a scenario where *M* is set to 0.38 year^{-1}.

Metric	Spawning frequency scenario	*M* set to 0.14 year^{-1}	*M* set to 0.38 year^{-1}
FNEPR	Equal	−17.5%	+16.8%
	Incremental	−21.6%	+23.8%
	Dual	−20.2%	+21.6%
YPR/YPR$_{max}$	Equal, incremental, and dual	−7.7%	+6.6%

FNEPR is the fraction of natural egg-production-per-recruit (EPR), i.e. the ratio of EPR over NEPR, while YPR/YPR$_{max}$ is the ratio of YPR over its maximum possible value. Results are provided for three different spawning frequency scenarios: the "Equal," the "Incremental," and the "Dual" scenarios. Under the Equal spawning frequency scenario, spawning frequency is invariant with age. Under the Incremental spawning frequency scenario, spawning frequency increases proportionally with increasing age. Finally, under the Dual spawning frequency scenario, fish of ages 2–5 spawn half as frequently as fish of ages 6–9.

interactions with fishers, managers and other stakeholders (Grüss and Robinson, 2015).

The collective results of this study support previous studies that concluded that corvina experience persistent overfishing (Erisman *et al.*, 2014) and are overfished (Ruelas-Peña *et al.*, 2013). Our per-recruit model suggests that the EPR of corvina is at 37–56% of its natural (unfished) value, depending on the spawning frequency assumed for the species. The FNEPR is analogous to the spawning potential ratio, and both are often used interchangeably with SSBR as reference points to gauge the status of a fish population and determine the minimum reproductive potential necessary for a population to replace itself in response to fishing mortality (Goodyear, 1993; MacCall, 1999). The fraction of natural SSBR that causes population collapse typically is in the range of 0.1–0.6 and lower for short-lived fish species such as corvina (Myers *et al.*, 1999). However, it is equally plausible that the SSBR reference point should be higher for fishes like corvina that spawn in large groups within massive aggregations, because reductions in spawner biomass below some critical threshold could lead to mating system Allee effects (i.e. depensation) that disproportionately reduce reproductive output at low population sizes (Sadovy de Mitcheson and Erisman, 2012; van Overzee and Rijnsdorp, 2015). Therefore, the current EPR of corvina may be at a critically low level (0.37; Incremental scenario) or not (0.56; Equal scenario), depending on the relationships among spawning frequency, age structure, and spawner biomass, which are currently unknown. Moreover, the current value of the

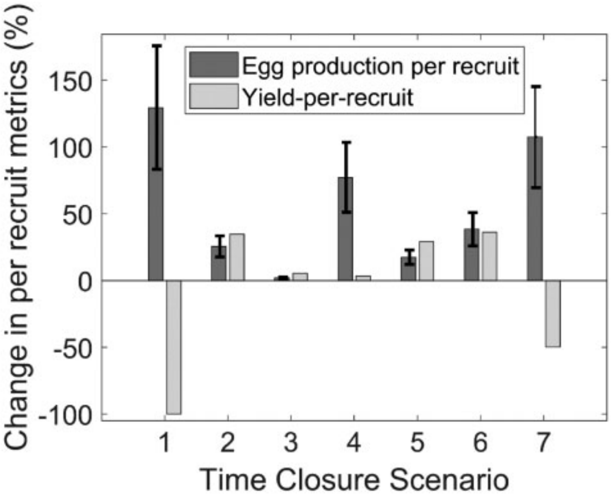

Figure 8. Changes in EPR and YPR for Gulf corvina (*C. othonopterus*) relative to the baseline situation (where no time closures are implemented), under seven different Time-closure Scenarios: (Scenario 1) No fishing during the entire spawning season; (Scenario 2) No fishing during the first tide; (Scenario 3) No fishing during the last tide; (Scenario 4) No fishing during the first two tides; (Scenario 5) No fishing during the last two tides; (Scenario 6) No fishing during the peak day spawning of each tide; and (Scenario 7) No fishing during the peak 3 days of each tide. In the case of EPR, Time-closure Scenarios were simulated under three different spawning frequency scenarios: the "Equal," the "Incremental," and the "Dual" scenarios (Figure 3). Thus, in that case, plain bars indicate mean relative changes in EPR over the three spawning frequency scenarios, while error bars indicate standard deviations in relative changes in EPR over the three spawning frequency scenarios.

exploitation rate of larger (>65 cm TL), older (4+ years) adult corvinas is nearly double the value at which the YPR is predicted to reach a maximum.

The results of the time-closure scenarios explored in our study indicate that the proposal presented by fishers has the potential to improve the resilience of the corvina population while also maintaining a productive fishery. One may expect that increases in the biomass and reproductive capacity of corvina resulting from the implementation of time closures would be at the expense of the corvina fishery by decreasing the total exploitable biomass. However, our results suggest that the implementation of time closures implemented during specific periods within the spawning season can benefit both corvina—by enhancing the reproductive capacity of the species—and its fishery—by increasing the exploitable biomass of corvina. Among the seven time-closure scenarios that we explored, the scenario that offered the best compromise in terms of reproductive capacity and exploitable biomass was the one that prohibited fishing during the peak day spawning of each fishing tide. Under that scenario, the EPR of corvina was enhanced by 38% on average over all the spawning frequency scenarios considered, while its YPR increased by 36%.

While the implementation of brief time closures during the spawning season as a replacement for the existing MPA has the potential to enhance reproductive output, maintain high fishery yields, improve enforcement, and increase fisher compliance in the corvina fishery, they do not address the market issues that maintain the race-to-fish mentality and drive overfishing. Eliminating fishing during the peak spawning day could help address the issue of episodic landing gluts and waste in the corvina fishery; landings volumes during the peak spawning day can greatly exceed the demand and capacity of local buyers and processors, which causes market prices to plummet, markets to close, and tons of fish to be discarded into local landfills (Erisman *et al.*, 2015; EDF, 2016). However, the long-term sustainability and productivity of the corvina fishery will require increased efforts by all sectors to reduce fishing pressure by raising and stabilizing the value of corvina fillets in commercial markets in Mexico and managing the seemingly insatiable demand (and skyrocketing market prices) for corvina swimbladders in China (EDF, 2015, 2016).

Despite evidence of persistent overfishing, landings of several thousands of tons of corvina have been maintained for two decades (EDF, 2016; Supplementary Figure S1a), because young adult corvina are able to spawn while escaping capture by gill nets with mesh sizes that select for larger fish (Erisman *et al.*, 2014;

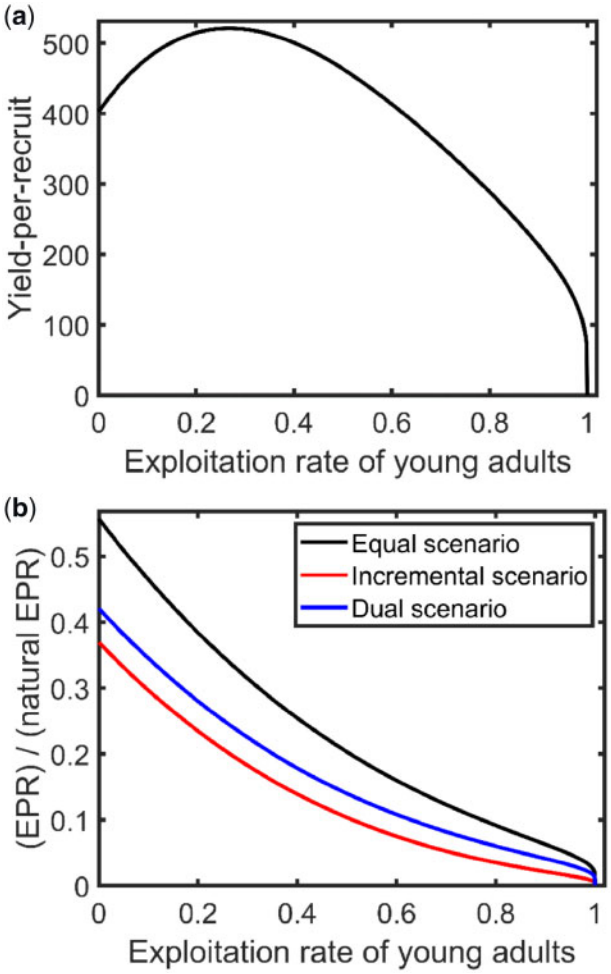

Figure 9. (a) YPR and (b) EPR over NEPR as a function of the exploitation rate of young adults for Gulf corvina (C. othonopterus). Results for EPR over NEPR are provided for three different spawning frequency scenarios: the "Equal," the "Incremental," and the "Dual" scenarios. Under the Equal spawning frequency scenario (top line), spawning frequency is invariant with age. Under the Incremental spawning frequency scenario (bottom line), spawning frequency increases proportionally with increasing age. Finally, under the Dual spawning frequency scenario (middle line), fish of ages 2–5 spawn half as frequently as fish of ages 6–9.

Rowell and Erisman, 2016). Our results suggest that exploiting the young adults of corvina would decrease the reproductive capacity of the species while not increasing or decreasing the exploitable biomass of corvina. Therefore, any changes to regulations or fishing practices that increase the direct or indirect (e.g. bycatch) mortality rates of juvenile and young adult corvina could be detrimental to the sustainability of the fishery and undermine any conservation and fishery benefits provided by time closures. Evidence of increased fishing pressure on younger adults is mounting; recent studies have demonstrated that the mean length of landed corvina has decreased steadily over the past 10 years, the number of fish landed below the legal minimum size of 65 cm TL has increased, and very large adults (>80 cm TL) have not been recorded in the fishery since 2015 (Erisman *et al.*, 2014; Ortiz *et al.*, 2016; Supplementary Figure S1b).

Several avenues of research would improve model performance, estimates of reproductive potential in response to exploitation rates, and the quality of population and fishery assessments for corvina. First, assumptions on age-related patterns in spawning frequency had a large effect on the estimated status of the corvina population, EPR values under various time-closure scenarios, and the consequences of harvesting the young adults on EPR. These results support previous studies that emphasized that estimates of reproductive capacity are highly sensitive to assumptions about spawning frequency and imply that such details related to spawning behaviour require more research attention (e.g. empirical data on spawning frequency at age; Fitzhugh *et al.*, 2012), particularly for fisheries that target FSAs (Erisman *et al.*, 2014). Rowell *et al.* (2017) provided the first estimates of the abundance, distribution, and biomass of corvinas within a single aggregation period. However, further research is needed to determine how spawning seasonality, migration and spawning periodicity, and spawning frequency vary with length and age as a means to reduce uncertainty in model outputs. Second, our per-recruit model assumes the population is at equilibrium such that recruitment is constant (Beverton and Holt, 1957). However, the settlement, growth, survivorship, and fishery recruitment of corvina during their early life history appears to be influenced by the environmental conditions of the Delta (Rowell *et al.*, 2005), and climatic conditions during the birth year of corvina are positively correlated with fisheries landings 5 years later when adults are fully recruited to the fishery (Reed, 2017). Therefore, future studies that incorporate environmental considerations into our per-recruit model would offer more accurate insights into the potential impacts of time closures for corvina. Lastly, fishing activities can exert strong negative effects on the reproductive success of aggregation spawners that go beyond removals from the spawning stock (Dean *et al.*, 2012). For instance, any measurable impacts of the intense boat and engine noise, net deployments, and other observed disturbances that define the chaotic activities of the current corvina fishery on the mating behaviour of corvina would reduce estimates of EPR in relation to brief time closures, and they would reinforce the value of maintaining and enforcing the no-take MPA in parallel to the implementation of time closures to ensure sufficient reproductive activity to sustain the corvina population.

The per-recruit models used in this study represent one of many simple, effective, and widely available analytical tools to identify sustainable limits of fishing on FSAs in data-limited situations (e.g. http://www.datalimitedtoolkit.org). However, future studies employing our approach for other FSA-forming populations will likely need to switch from a per-recruit model relying on exploitation rates to a per-recruit model relying on fishing mortality rates similar to that of Grüss and Robinson (2015). Using exploitation rates in our study was necessary, because the corvina gill net fishery is an extreme pulse fishery. However, most exploited FSA-forming populations are targeted over a long period of the year and the use of fishing mortality rates in per-recruit models will be more appropriate to decompose total annual fishing mortalities into relevant spatio-temporal components (e.g. to decompose the total annual fishing mortality of adults into the fishing mortality rate exerted on them at spawning sites during the spawning season and the fishing mortality rate exerted on them in normal residence areas outside the spawning season; Grüss and Robinson, 2015). Moreover, because per-recruit models do not integrate a stock–recruitment relationship, they can inform only about the potential effects of management measures on exploitable biomass and not about their potential effects on fisheries yields. Therefore, for FSA-forming populations that are data-rich, we encourage the development of a more sophisticated approach combining per-recruit quantities with stock–recruitment relationships (Hart, 2006) to provide more comprehensive insights into management decision impacts for FSA fisheries.

Conclusions

FSAs represent ideal model systems for improving our understanding of the reproductive resilience of fish populations in response to variability in fishing and other anthropogenic disturbances, because the spatial and temporal structure and dynamics of exploited fish populations are tightly linked to productivity and the complexity of spawner–recruit systems (Lowerre-Barbieri *et al.*, 2017). Related to this, there is a growing number of empirical and modelling studies on the impacts of fishing on mating behaviour and reproductive success, the effects of spatial behavioural types and spawning migrations on catchability and fisheries selectivity, the impacts of temporal and area closures on spawning-stock biomass, and related topics (Alós *et al.*, 2019; MacCall *et al.*, 2019). When sufficient data on the spatio-temporal dynamics of spawning behaviour are coupled with life history, catch, and effort data, it is possible to synthesize such information to produce various metrics (e.g. YPR, EPR) and to estimate reference points (e.g. $\mathrm{YPR}_{\max}$) that can be used by stock assessment scientists and fishery managers, thereby creating a roadmap for the further integration of reproductive dynamics into fisheries management frameworks.

We recommend that after first establishing vulnerability and determining precaution, fishing–spawning interactions are measured, monitored, and used in a practical way to explore the degree to which FSAs can be sustainably exploited. Moreover, we can employ the many tools that have been developed in fisheries science to accomplish this task (e.g. for temperate salmonid and gadid fisheries; Thorstad *et al.*, 2008; Zemeckis *et al.*, 2014), and by doing so, we can forge a path for integrating FSAs into fisheries management frameworks rather than setting them apart as exceptional cases that require some unique set of management tools and complete exclusion from fishing. This approach can help improve the protection, productivity, and sustainability of FSAs and facilitate development of more fine-tuned tools by scientists tasked with assessing stocks to focus on FSA fisheries as interesting case studies. Including stakeholder ideas and the socio-economic importance of FSAs in this process is vital, and through quantitative evaluations of their proposed management strategies, it is possible to generate mutually agreeable solutions that ensure the resilience and productivity of fish stocks are maintained.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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Author contributions

B.E.E. conceived the ideas, designed the study, completed the preliminary data analysis, and drafted the manuscript; A.G. designed the analysis, constructed the models, analysed the data, and assisted B.E.E. with drafting of the manuscript; B.E.E., I.M.-O., C.L.-S., and H.L.-G. collected the biological and fisheries data; All authors contributed to the editing and revising of the manuscript.

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