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The influence of gear selectivity and spawning behavior on a data-poor assessment of a spawning aggregation fishery

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ABSTRACT

We applied several data-poor techniques to perform an assessment of the Gulf corvina (*Cynoscion othonopterus*) fishery in the Gulf of California from 1997 to 2012 and to investigate the effects of gear selectivity and age-dependent variation in spawning frequency on estimates of sustainability in spawning aggregation fisheries. The length composition of the catch varied significantly among years but showed no clear directional pattern. However, the average length was above the long term average after the implementation of a regulation that standardized mesh size of nets, and the average length of fish captured after the implementation was significantly higher than during previous periods. Results using three simple metrics based on catch length compositions indicated that fishing activities were sustainable due to the exclusion of juveniles from the fishery and the targeted harvest of adults at the optimal length. However, the low proportion of older, fecund fish in the fishery is a serious cause for concern. Modeled estimates of spawning potential ratios (SPR) were consistently higher when spawning frequency was assumed to be age invariant and were significantly higher after the implementation of gear regulations. However, SPR values only reached levels above 35%, a common reference point for sciaenid fishes, during the current fishing period (2010–2012) under conditions of age invariant spawning frequency. Results of this study support previous claims that suggest estimates of reproductive potential are highly sensitive to age-dependent variation in spawning frequency and imply that such details related to spawning behavior require more attention, particularly for fisheries that target spawning aggregations. Our results also suggest that spawning aggregations can be harvested sustainably through conventional regulations if juveniles are excluded, fish are harvested at optimal length, and older, fecund individuals are protected from harvest. Given the uncertainty of the status of the corvina fishery based on the discordant results of this study and the inherent vulnerability of the species to overfishing, We recommend the precautionary approach be applied to management decisions until more robust information is acquired on stock abundance, the relationship between spawning frequency and age or length, and reproductive output.

1. Introduction

Many fishes migrate to form massive spawning aggregations at specific locations and during specific periods, and these events support or have supported some of the most productive, small-scale fisheries in coastal regions throughout the world. Noteworthy examples include historical fisheries for the Nassau grouper (*Epinephelus striatus*) in the Caribbean (Sadovy and Eklund, 1999) and the totoaba (*Totoaba macdonaldi*) in the Gulf of California (Cisneros-Mata et al., 1995), and the live reef food fish trade in Southeast Asia (Sadovy and Vincent, 2002). The high abundance of fish present at aggregations during predictable periods and at known locations, which can range from tens to even millions of individuals confined to small areas, generates the ideal scenario for small-scale fishers with limited resources; large catches and sizeable earnings with minimal effort (Sadovy de Mitcheson and Erisman, 2012). However, these same characteristics render aggregation fisheries particularly vulnerable to overfishing, as targeted

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harvesting of fish from aggregations may result in the rapid removal of large proportions of an entire population. When left unmanaged, overfishing of aggregations is associated with severe declines in fish stocks, fishery collapses, ecosystem imbalances, and in the most extreme cases, the complete extirpation of aggregations from specific areas or regions (Johannes, 1997; Sala et al., 2001; Dulvy et al., 2004; Erisman et al., 2011).

Awareness of both the productivity of aggregation fisheries and their vulnerability to overfishing has steadily increased over time (reviewed in Sadovy de Mitcheson and Colin, 2012), and fish spawning aggregations are beginning to emerge as a focal point of fisheries management and marine conservation (Russell et al., 2012; SCRFA Fish Aggregation Database, 2013 and references therein). The most commonly applied management measures for fisheries on species that aggregate to spawn are seasonal bans during the reproductive period when the species cannot be fished or traded, or the protection of aggregation sites during the spawning season or within no-take marine protected areas. Such strategies have proven effective in stimulating the recovery of depleted aggregation sites while also supporting sustainable fisheries in adjacent areas (Nemeth, 2005; Heppell et al., 2012).

Less information is available on the ability of conventional management tools such as gear restrictions, catch limits, or size limits to protect aggregations while also permitting sustainable harvest levels from the aggregations themselves. It is often assumed that such methods alone are incapable of sufficiently protecting aggregations since many collapsed aggregation fisheries are managed using conventional fisheries regulations, and the most well documented cases of recovery occurred under scenarios of targeted spatial or temporal management (Sadovy and Domeier, 2005; Russell et al., 2012). Yet the dynamics of spawning aggregations vary greatly among species in terms of their timing, duration, and distribution (Sadovy de Mitcheson and Erisman, 2012). Likewise, the relative importance of spawning aggregations to fisheries also varies considerably from those that exclusively target aggregations, to those that only partially exploit them, to those that do not target aggregations at all (Erisman et al., 2010; Erisman et al., 2012; Tobin et al., 2013). Moreover, fisheries use a variety of gear types with different selectivities, resulting in large differences in escapement. Thus, it is reasonable to expect that no single type of management is useful for all aggregating species, and there may be circumstances under which conventional tools may be sufficient, without time or area closures. Thoughtful exploration of such circumstances is warranted, because unnecessary spatial or seasonal restrictions may impose undue hardship on coastal communities that receive significant social, economic, and cultural benefits from the harvesting of spawning aggregations (Sadovy de Mitcheson and Erisman, 2012). Also, seasonal or spatial closures may not be effective if uncontrolled fishing mortality outside of the closures dissipates all of the biological benefits of the closures, resulting in additional fishing costs with no gain in yield or sustainability.

Small-scale fisheries that target the spawning aggregations of coastal fishes tend to be underfunded for research, undermanaged, and unmonitored (Sadovy, 2005). Consequently, they resemble most other small-scale fisheries that lack the necessary catch or population data to perform quantitative stock assessments using complex models to generate robust estimates of stock status, various management targets or reference points, and sustainable yield (Dick and MacCall, 2011). However, a growing body of information on methods to assess data-poor, small-scale fisheries has emerged in recent years (e.g., Dulvy et al., 2004; Froese, 2004; Honey et al., 2010), providing resource managers with useful insights into the status and trends of inter alia spawning aggregation fisheries and facilitating the development of science-based management policies even when data are scarce. Noteworthy examples include methods that use life history parameters and length data to estimate biological reference points such as total and fishing mortality (Gedamke and Hoenig, 2006), optimal length at capture (Froese, 2004; Cope and Punt, 2009), and spawning potential ratio (SPR – the ratio of the total fecundity of the fished population under a given exploitation rate to the total fecundity of the unfished population; Goodyear, 1993). Resulting outputs include estimates of exploitation rates and reproductive potential, which can be used in an adaptive management framework. For example, estimated exploitation rate and SPR can be compared to commonly used reference values or rules of thumb (e.g., F should be close to M, SPR should be above 35%) to inform adjustments to catch or other measures aimed at controlling fishing mortality.

Aggregating behavior in fishes can pose significant challenges to stock assessment and the interpretation of stock status indicators. Specifically, aggregation fisheries often exhibit hyperstability, in which catch rate declines at a slower rate than stock abundance (MacCall, 1976; Erisman et al., 2011). This can lead to overestimates of stock size and delay management responses to stock declines if assessment models assume catch rates are proportional to abundance (Rose and Kulka, 1999; Claro et al., 2009). Therefore, stock assessments for fisheries that target spawning aggregations should avoid the use of CPUE and other catch rate metrics as proxies for population abundance if the relationships between these metrics and abundance are not well understood. Certain data-poor assessment methods may provide more easily interpretable and therefore more useful outputs. For instance, changes in length frequency distributions of catch are often directly related to fishing mortality and provide a basis for recognizing declines in stock condition that may be less visible with metrics such as CPUE.

Most fishes that form spawning aggregations are seasonal batch spawners with indeterminate fecundity (Sadovy de Mitcheson and Colin, 2012), which poses serious challenges for assessments that use some measure of reproductive potential of the population (e.g., SPR). Quantifying reproductive potential for these types of fishes requires estimates of batch fecundity, spawning frequency, and spawning season duration (Murua et al., 2003). These data must be obtained with estimates of how each may vary with size or age, as it is becoming increasingly known that the frequency and duration of spawning increases with age for most marine fishes (Lowerre-Barbieri et al., 2011; Fitzhugh et al., 2012). In fact, if spawning patterns are assumed to be age invariant, modeling studies indicate substantial sensitivity of estimates of spawning potential ratio and reproductive value, and a tendency for overestimating these biological reference points for setting harvest rates (Fitzhugh et al., 2012). Failure to consider such sensitivity can lead to management decisions that either place unnecessary restrictions on fishers (over-management) or that fail to prevent depletion to unsustainable levels or stimulate recovery in depleted populations (under-management). Therefore, more insight into how variation in spawning frequency influences data-poor assessment should result in better assessments and management of fisheries on spawning aggregations, particularly with respect to tools such as catch limits, size limits, and gear restrictions.

Here, we provide a data-poor assessment of a spawning aggregation fishery for the Gulf corvina (*Cynoscion othonopterus*) from the Gulf of California, Mexico. This fishery is particularly suitable to explore the use of data-poor assessments for understanding the effects of conventional fisheries regulations (i.e., gear restrictions and selectivity) and spawning behavior (i.e., age-dependent variations in spawning frequency) on assessments of spawning aggregation fisheries. This species forms a massive spawning aggregation comprised of millions of fish at a single location during brief yet highly predictable periods (Erisman et al., 2012). Nearly all of the annual fishing effort and landings occur during this period. As a result, the species is thought to be quite vulnerable to overfishing and stock collapse (Musick et al., 2000; Chao et al., 2010), and the fishery is currently the focus of intense monitoring and management efforts. Related to this, the fishery is highly regulated by gear restrictions; fishers have been required to use gill nets of a specific mesh size since 2005 (Solana-Sansores et al., 2012). Finally, sufficient biological and fisheries information is available (Erisman et al., 2012; Gherard et al., 2013) to test the effects of gear restrictions and spawning behavior on stock sustainability using contemporary data-poor methods and compare the results with those that have used equilibrium models to estimate stock condition directly from catch and effort data (Ruelas-Peña et al., 2013).

2. Materials and methods

2.1. Study species and its fishery

The Gulf corvina is a large sciaenid fish (Teleostei: Sciaenidae) endemic to the northern Gulf of California, Mexico, with a highly restricted geographic range that extends from the Colorado River Delta south to the Midriff Islands region (Robertson and Allen, 2008). Individuals can reach 1013 cm in total length, 12 kg in body mass, and 9 years in age (Gherard et al., 2013). Gulf corvina are synchronous, multiple batch spawners with indeterminate annual fecundity that reproduce through broadcast spawning (Gherard et al., 2013). The entire spawning stock of adult corvina migrates into the Colorado River Delta to spawn within aggregations from late February through early June, with peak spawning occurring in March and April, coincident with the timing of the spring tides, during the weeks prior to the new and full moons (Erisman et al., 2012).

The commercial fishery for the Gulf corvina is characterized as a small-scale fishery based primarily in two locations of the Delta, the coastal community of El Golfo de Santa Clara and seasonal fishing camps at El Zanjón, which combine to represent more than 92% of the annual landings for the entire species (Erisman et al., 2012). The fishery lies mainly within the Upper Gulf of California and Colorado River Delta Biosphere Reserve, which includes a no-take zone to protect the spawning and nursery habitat of *C. othonopterus* and its endangered relative, the totoaba (*T. macdonaldi*). All fishing activities occur from pangas, small (8–9 m) fiberglass vessels with outboard engines, in which fishers use the technique known as “encierre” to harvest fish. Briefly, fishers deploy gill nets around an aggregation and then drive the panga in a circle around the aggregation at high speed while continuing to deploy the net. Immediately after deployment, the net and all entangled fish are retrieved while the panga drifts with the current.The fishery harvests up to 5900 tons of fish per year (mean = 3500 tons from 1997 to 2012), with an average of 98.5% of fish harvested during the spawning season (Erisman et al., 2012). Fishing activities are intense during this period, with more than 500 pangas harvesting up to 1.8 million fish in less than 25 days of fishing within a short fishing season of mid-March through April, in an area less than 1149 km^2. The corvina fishery addresses the large demand in Mexico for fish during Lent, which covers a period of approximately six weeks before Easter Day. Fishing is synchronized with the spawning cycle such that 90% of landed fish are harvested during the days when fish are spawning, which occurs from five to two days before the full and new moon (Erisman et al., 2012). Small numbers of juvenile and adult corvinas are landed as bycatch in other gill net fisheries, although these landings are negligible compared to the magnitude of fish harvested during the main fishing season (Walsh et al., 2004; Pérez-Valencia, 2012).

Since 2005, the Gulf corvina fishery has been regulated by an official standard (NOM-063-PESC-2005). Fishers have been required to use gill nets of minimum mesh size of 14.6 cm and a maximum length of 293 m since 2005, and there is evidence that compliance of this regulation is relatively high (Solana-Sansores et al., 2012). There is a minimum size limit of 65 cm TL, but 35% of the catch can be under this length without triggering sanctions. Therefore, discarding of undersized fish is virtually non-existent (Pérez-Valencia, 2012). Only one net is allowed per panga or fisherman, and fishing is restricted to daylight hours. The National Fisheries Commission (CONAPESCA) recognizes the no-take zone of the biosphere reserve as a restricted area, but the exclusion of fishers from the area during the corvina fishery has proven to be a challenge. For example, it is estimated that 86 and 90% of fish were harvested from the no-take zone in 2009 and 2010, respectively (Erisman et al., 2012). The fishery is closed from May 1st to August 31st each year to protect a portion of spawning adults (some spawning occurs in May and early June; BE, unpublished data) and juveniles that inhabit the biosphere reserve during that period. The National Fisheries Institute (INAPESCA) is required by law to recommend a quota for each fishing season, which is published by the Fisheries Secretary in the Official Diary of the Federation.

2.2. Annual and periodic trends in length composition of catch

Several types of analyses, each of which required a series of methods and calculations, were used to assess the status of the corvina fishery. A description of each analysis is summarized in Table 1. As a first means of assessing the corvina fishery, we investigated annual trends in the length composition data from the official surveys conducted from 1997 to 2012. Length and mass data from surveys of the corvina fishery conducted annually during the peak fishing and spawning season (March and April) were used to generate length-frequency distributions of the catch. Briefly, fish were sampled randomly and opportunistically from commercial fishers at El Golfo de Santa Clara (Sonora) and El Zanjón (Baja California) during days the commercial fishery landed corvina (total = 15,312 fish; mean = 1030 fish per year), and data on total length (1 mm) and body mass (1 g) were recorded for each fish. Life history parameters related to growth, sexual maturity, and fecundity were taken from a recent study by Gherard et al. (2013) (Table 2).

A Kruskal–Wallis (non-parametric) test was used to distinguish significant changes in annual median length of harvested fish, as length data did not conform to the assumptions of parametric testing. Pairwise multiple comparisons tests were then used to identify any directional changes in length (i.e., increases or decreases in median length at capture) over that time period. As another method to identify directional changes in length, we calculated the standardized anomaly (*z*-score) for each year by subtracting the grand mean length at capture across the entire period (1997–2012) from the annual mean length at capture for the given year and dividing it by the standard deviation of the mean. A subset of length data were also pooled into three time periods (Early = 1998, 1999, 2002; Implementation = 2005–2007; Current = 2010–2012) to test for changes in median length by time period in relation to changes in gear regulations after 2005 and to compare the results directly to those obtained by analyses of SPR (see below).

2.3. Froese’s indicators of sustainability

As a second method to assess the corvina fishery, we calculated the three indicators of sustainability proposed by Froese (2004) from catch length compositions for each year from 1997 to 2012: (1) the proportion of mature fish (P_{mat}) in the catch, with 100% as target; (2) the proportion of fish within 10% of optimum length (P_{opt}) in the catch, with 100% as target; and (3) the proportion of “mega-spawners” (P_{mega}) in the catch with 30–40% as representative of a sustainable stock structure. The proportion of mature fish (P_{mat}) was calculated for each year by dividing the number of fish of lengths greater than the average length at maturity (295 mm TL;

Table 1
Summary of analyses used to assess the status of the Gulf corvina (*Cynoscion othonopterus*) fishery, include the methods applied and the resulting outputs.

Analysis	Methods and outputs
Annual trends in length composition	• Length and mass data from surveys: generated length-frequency distributions of the catch. • Kruskal–Wallis (non-parametric) test: distinguished significant changes in annual median length. • Pairwise multiple comparisons tests: Identified directional changes in length. • Standardized anomaly (*z*-score) for each year: identified directional changes in length. • Length data pooled into three time periods: tested for changes in median length by time period in relation to changes in gear regulations and results of SPR analysis.
Froese's sustainability indicators	• Percentage of mature fish in the catch with 100% as target. • Percentage of fish with optimum length (±10%) in catch with 100% as target. • Percentage of "mega-spawners" in catch with 30–40% as representative of a sustainable stock structure. • Data pooled into three time periods: For direct comparison with length-based and SPR analyses.
Synthetic cohort model	Generated a simulated size structure of an unfished adult population of corvina. Used in SPR analysis.
Spawning behavior	• Created three discrete models of spawning behavior to test the effects of age-related variations in spawning frequency on SPR outputs.
Mortality and exploitation rate	• Generated a range of estimates for total mortality and exploitation rate to estimate total fecundity of the fished population for each time period and behavior model. Used in SPR analysis.
Spawning potential ratio (SPR)	• SPR values compared by time period: identified whether implementation of gear regulations resulted in a change in total fecundity of the stock. • Calculated SPR values across a range of exploitation rates from 0 to 1: used to understand the relationship between time period and spawning behavior model. • Estimated the exploitation rate of the fishery for each spawning behavior model in all three time periods: Used to make inferences as to whether overfishing is occurring. • Calculated SPR using combinations of two estimates for *M* and three estimates of *E* for each spawning behavior model in all three time periods: Used to calculate and plot median SPR values to provide a semi-quantitative assessment of the fishery.

Table 2
Life history parameters in *C. othonopterus* used in the assessment from Gherard et al. (2013).

Parameter	Value
Asymptotic length (L_∞)	1006 mm TL
Growth parameter (K)	0.255
Theoretical age at zero length (t_0)	0.616 years
Length (L_t) to weight relationship	Weight = 2E−05 × $L_t^{2.8834}$
Batch fecundity (BF) to length relationship	BF = 2867.5 × L_t − 1422110
Total length (TL) at 50% maturity (females)	295 mm TL
Age at 50% maturity (females)	2.3 years

Table 2) by the total number of fish sampled. Optimum length (L_{opt}) was calculated using growth and mortality parameters (Froese and Binohlan, 2000) as follows:

$$\log(L_{opt}) = 1.0421 \times \log(L_\infty) - 0.2742 \quad (1)$$

Mega-spawners are defined as old, highly fecund fish that are more than 10% longer than the optimum length (Froese, 2004). The resulting proportions were summed ($P_{mat} + P_{opt} + P_{mega}$) to calculate annual values to distinguish the selectivity pattern of the corvina fishery (P_{obj}). We then followed the decision-tree created by Cope and Punt (2009) to determine whether the spawning stock biomass likely met or exceeded target reference points and thus would be considered sustainable. Proportional data were also pooled into three time periods (Early, Implementation, Current) to make direct comparisons with length-based analyses (above) and SPR analyses (below).

We assumed the behavior of the fishery, in which gillnets are actively used to surround and envelop fish in a manner similar to purse seines (called "encierre"; Erisman et al., 2012), means there is no upper size limit to the fishery (i.e., large fish do not escape capture). We support this assumption with several lines of evidence. First, fish sampled from the commercial fishery reach lengths greater than the longest previously recorded for the species, despite nearly a century of exploitation of this species in the region (Robertson and Allen, 2008; Erisman et al., 2012). Second, fishers are known to infrequently capture aggregations of totoaba (*T. macdonaldi*) as incidental bycatch of lengths greater than 1 m using this same gear and methodology (BE, pers. obs.). Third, surveys of commercial fisheries from an adjacent community (San Felipe) that harvest Gulf corvina throughout the year using multiple gear types (e.g., hook and line; gill nets of variable mesh sizes) and fisheries-independent surveys of adult Gulf corvina both show length compositions that are similar to those in this study (Román-Rodríguez, 2000; BE, unpublished data). Finally, there is no evidence of size-selectivity in the fishery due to seasonal or area closures, since compliance for such regulations is extremely low (Erisman et al., 2012).

2.4. Spawning potential ratio

Spawning potential ratio (SPR) is defined as the ratio of the total fecundity of the fished population under a given exploitation rate (E) to the total fecundity of the unfished population (adapted from Goodyear, 1993). This measure assumes constant selectivity, fishing mortality and stationarity in terms of growth rate, natural mortality, and maturity schedules. While sometimes referred to as "equilibrium SPR", its application need not be limited to equilibrium conditions as constant recruitment is not a requirement (Mace et al., 1996).

We examined SPR as a third means of assessing the status of the corvina stock. To determine how SPR changed by fishing period, SPR values were compared by fishing period to identify whether the implementation of gear regulations resulted in a change in the total fecundity of the stock. To test the sensitivity of SPR to the conventional assumption of age-invariant spawning frequency, we calculated SPR for three discrete models of spawning behavior: age invariant, incremental increases in spawning frequency with increasing age, and a model in which age 2–5 fish spawned half as frequently as age 6–9 fish.

For each fishing period and behavior model, we calculated SPR values across a range of exploitation rates from 0 to 1 (in 0.1 increments) to understand the relationship between the two parameters. However, we also estimated the exploitation rate of the fishery for each model of spawning behavior and within each fishing period to make inferences as to whether overfishing is occurring. We used an SPR value of 0.35 as our limit reference point for overfishing based on its common use in other *Cynoscion* fisheries (Murphy et al., 2006; Jensen, 2009), such that values meeting or exceeding the reference point would indicate overfishing.

For each spawning behavior model within each fishing period, six individual estimates of SPR were calculated using combinations of two estimates for M (Pauly and Jensen methods; see below) and three estimates of E (from estimates of Z using catch curves, Beverton–Holt, and SEINE methods described below). The results were then used to calculate and plot median SPR values (±95% confidence intervals) to provide a semi-quantitative assessment of the fishery.

The SPR analyses required a series of calculations. First, we used a synthetic cohort model (Section 2.5) to generate a simulated size structure of the unfished adult population of corvina. Next, we used a series of methods to generate a range of estimates for mortality and exploitation rate (Section 2.6), which in turn allowed us to estimate total fecundity of the fished population for each period and spawning behavior model (Section 2.7).

2.5. Synthetic cohort model

Since fisheries-independent data on the abundance or size distribution of the spawning population of Gulf corvina do not exist, we treated the size-frequency distribution of the commercial catch (Fig. 1) from each of three separate time periods (Early, Implementation, Current) as cohorts and constructed a growth projection model for each one that simulated the size structure and relative abundance of this cohort at past and future times. In this case, we defined a cohort (a group of individuals to which no new members can be added, but from which members can only be lost by mortality) based on the collection of fish caught in a single year's fishery, as if we had imaginarily tagged them. This is justified by the unusual circumstances of this fishery—its apparently high intensity and short duration at the only spawning site for the entire stock produces a "snapshot" of the age and size composition of available fish (Section 2.1). The somatic growth rate is high, so we can then estimate the sizes and relative abundances this cohort would have attained in preceding and following years. Importantly, the lack of overlap of projected size frequencies in adjacent years is an indicator of high fishing intensity, and substantial overlap would greatly weaken the utility of this approach.

The cohort growth model takes the catch length composition as input and estimates the expected growth of each individual to project the length composition of the fish in following years if they were not fished. Assuming Von Bertalanffy growth, the relationship between fish lengths in successive years is given by Ford (1933) equation:

$$L_{t+1} = L_t + (L_\infty \times (1 - e^{-K}) + L_t \times e^{-K}) \tag{2}$$

L_t represents the length of an individual fish at age t. Assuming deterministic growth, length groups can be treated as cohorts, and in the absence of fishing are subject only to natural mortality, so that for each cohort:

$$N_{t+1} = N_t \times e^{-M} \tag{3}$$

where N is numerical abundance, t is time, M is natural mortality, and k is the Von Bertalanffy growth coefficient. Length compositions sampled at time t were projected into future years by combining Eqs. (2) and (3). To avoid erroneous conclusions related to the calculation of reproduction of an unfished population (see methods on SPR below), length compositions were projected forward and backward to create eight synthetic age classes (Mace et al., 1996). These age classes ranged from age 2 to age 9, commensurate with the range of age classes in the unfished population that are capable of reproduction (Gherard et al., 2013). The number of fish within each size class of each synthetic cohort of the unfished population was calculated by

$$N_{t+1} = N_t \times e^{-M} \tag{4}$$

$$N_{t-1} = N_t \times e^{M} \tag{5}$$

Survivorship of each size class within each synthetic cohort of the fished population was calculated by:

$$N_{t+1} = (N_t - C_t) \times e^{-M} \tag{6}$$

$$N_{t-1} = (N_t - C_t) \times e^{M} \tag{7}$$

where N is numerical abundance, t is time, C is catch, and M is natural mortality. Note that we used exploitation rate (E) rather than the more conventional fishing mortality rate (F) in this study, because the fishing season is very short. To calculate yield of both the fished and unfished populations, mean weight per length class was calculated according to the following equation from Gherard et al. (2013)

$$W_t = 2e^{-5} \times L_t^{2.8834} \tag{8}$$

where W is body weight (g) and L is total length (mm). Weights were then multiplied by the number of individuals to obtain a total weight per length class for each cohort. We then calculated yield per recruit (biomass at E) for each cohort of the fished population by

$$\text{Yield}_t = \sum_{t-3}^{t+4} ((N_t \times E_t) \times W_t) \tag{9}$$

Total yield per recruit (biomass at E) was calculated as:

$$\text{Total Yield per Recruit (YPR)} = \sum_{t-3}^{t+4} (\text{Yield}_t) \tag{10}$$

Egg production for each cohort of both the fished and unfished populations were calculated as:

$$\text{Egg production}_t = \sum_{t-3}^{t+4} \left((2867 \times L_t - 1422110) \times \frac{N}{2} \right) \tag{11}$$

based on the relationship between body length and batch fecundity by Gherard et al. (2013). Total fecundity was then calculated by

$$\text{Total fecundity} = \sum_{t-3}^{t+4} (\text{Egg production}_t) \times (\text{spawn frequency}_t) \tag{12}$$

2.6. Mortality and exploitation rate

Based on recommendations by Kenchington (2013), we calculated two estimates of natural mortality for corvina from the length data, both of which assume that estimates of K and L_∞ from Gherard et al. (2013) are reliable, to generate upper and lower bounds with respect to various biological reference points. The first estimate was based on Pauly (1980):

$$M = 0.9849 \times L_\infty^{-0.279} \times K^{0.6543} \times \tau^{0.4634} \tag{13}$$

where M is natural mortality, L_∞ equals asymptotic length, K is the growth coefficient, and τ equals mean sea surface temperature. For this study, τ was set at 23.9 °C, the mean sea surface temperature in the waters off the coast of El Golfo de Santa Clara during the period of 1997–2012. The second estimate was based on Jensen (1996):

$$M = 1.5 \times K \tag{14}$$

Estimates of total mortality (Z) were calculated using three methods to generate upper and lower bounded estimates of biological reference points of sustainability (i.e., SPR). First, life history parameters on growth were used to create a predicted age-frequency

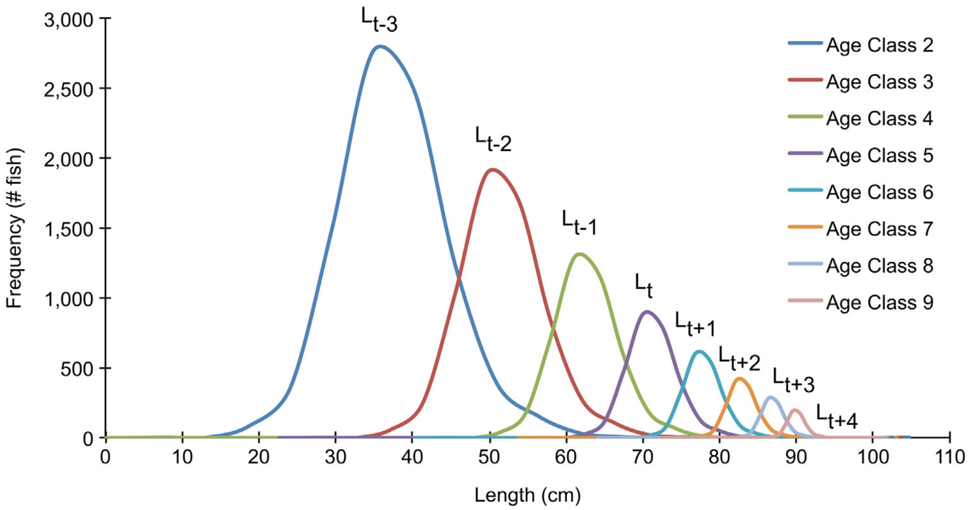

Fig. 1. Synthetic cohort model of a population of Gulf corvina (*Cynoscion othonopterus*) in the absence of fishing pressure.

distribution from the length-frequency distribution. The linearized catch curve method was used to estimate the total mortality coefficient (Z) by plotting age groups versus the natural logarithm of the relative abundance of each group, applying linear regression analysis on points at the peak age of recruitment to the fishery and older (Ricker, 1975; Smith et al., 2012). Estimates of Z based on length to age conversions are problematic, because they assume that selectivity is independent of age above the age at first capture and tend to overestimate the proportion of older fish in the population (Pauly and Morgan, 1987). Therefore, we also calculated Z using the Beverton–Holt mortality estimator (Beverton and Holt, 1956, 1957):

$$Z = \frac{K(L_\infty - L)}{L - L_c} \tag{15}$$

where L is length at age and L_c is the length at first capture by the fishery. The Beverton–Holt mortality estimator has been widely used due to its applicability in data-limited situations. However, the model assumes equilibrium conditions in which catch rate is proportional to abundance, which is difficult to meet in real-world situations and often violated by fisheries that target spawning aggregations (Erisman et al., 2011). Therefore, we also calculated Z using the Survival Estimation in Non-Equilibrium (SEINE) situations model (Gedamke and Hoenig, 2006), a variant of the Beverton–Holt estimator that allows a series of mortality rates to be estimated from mean length data representing non-equilibrium conditions in multiple years. For each method, resulting values of Z were used to calculate fishing mortality (F) from $Z = F + M$. Exploitation rate (E) was then calculated from $E = F/Z$. Again, please note that we focused on exploitation rate (E) rather than fishing mortality rate (F), because the fishing season is very short.

2.7. Models of spawning behavior

Estimates of spawning frequency at age or length are not available for *C. othonopterus* but may have a marked effect on estimates of sustainability as indicated by calculations of SPR (Fitzhugh et al., 2012). Therefore, we created three scenarios to test the potential relationship between length (or age)-based patterns in spawning frequency and SPR (Fig. 2). Spawning frequency was assumed to be invariant with age under the Equal model. Spawning frequency was assumed to increase proportionally with increasing age under the Incremental model. Lastly, fish of ages 2–5 were assumed to spawn half as frequently as fish of ages 6–9 in the Dual model.

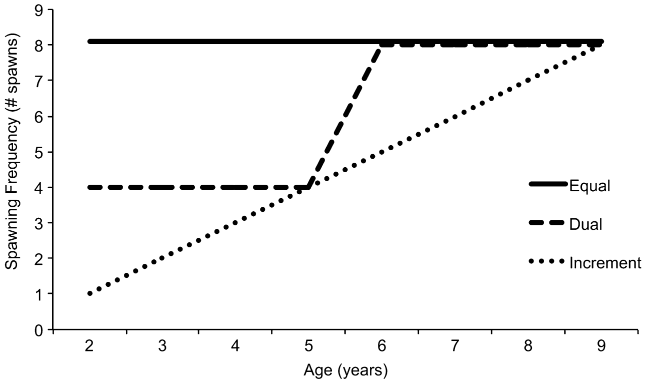

Fig. 2. Three proposed scenarios of spawning behavior in relation to age for Gulf corvina (*Cynoscion othonopterus*).

Differences in median egg production of the unfished population by time period and spawning behavior were tested using Kruskal–Wallis nonparametric ANOVA, since data did not conform to the assumptions of parametric testing. We compared estimates of median exploitation rate among calculations using values of natural mortality obtained from the Pauly (1980) method compared to the Jensen (1996) method using a Kruskal–Wallis ANOVA. The same method was used to compare differences in exploitation rate by method used to calculate Z. However, differences in mean exploitation rate by time period were analyzed with a 1-way ANOVA, as data were normally distributed and homoscedastic. A 2-way ANOVA was used to compare differences in mean SPR by fishing period and spawning model, and a Tukey HSD posthoc test for pairwise comparisons.

3. Results

3.1. Assessment from catch length compositions

Annual median length at capture ranged from 614 mm TL (2003) to 730 mm TL (2008) between 1997 and 2012 (Fig. 3A), with an overall median length of 685 mm TL for the entire study period. Therefore, harvested fish ranged from 319 mm to 435 mm larger than the mean size at sexual maturity (L_{50} = 295 mm TL; Table 2). When length data were converted determinisically to predicted age, the median age at capture ranged from 4.8 (2003) to 5.7 years (2008), with an overall median age of 5.1 years (1997–2012). Given

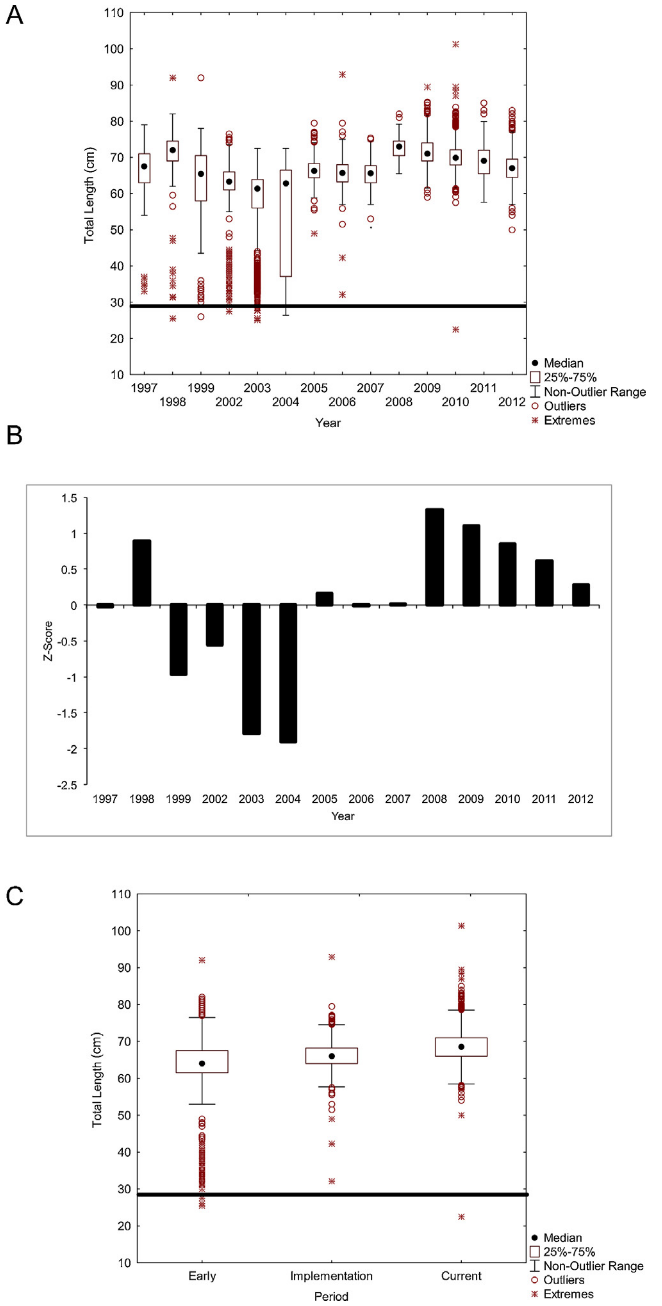

Fig. 3. Trends in catch length composition of the Gulf corvina (*Cynoscion othonopterus*) fishery from 1997 to 2012. (a) Box and whisker plots showing within group variance in length by year; (b) mean length anomaly (*z*-score) by year; (c) Box and whisker plots showing within group variance in length by fishing period (bottom graph). Black horizontal line shows the mean length at sexual maturity (L_{50}) for Gulf corvina.

an age at first maturity (A_{50}) of 2.3 years (Table 2), fish were capable of spawning for 2.5–3.4 years before reaching the median age at capture.

Median length at capture was significantly different among years (Kruskal–Wallis ANOVA by Ranks, df = 13, n = 15,312, H = 5918.673, $p < 0.001$); however, pair-wise comparisons of individual years showed no clear directional trend (i.e., decreasing or increasing) with respect to median length at capture over time (Fig. 3A). Variability in the size range of harvested fish was much greater prior to 2005 (when gear regulations were implemented), and length composition in the catch was much more truncated afterwards. *Z*-score values corresponding to annual average length at capture were consistently below the long-term mean just prior to the regulation change and consistently above it after the change, indicating the gear regulation had a positive impact on the fishery (Fig. 3B). Finally, there was a significant difference in average length by time period (Kruskal–Wallis ANOVA by Ranks, df = 2, n = 10,449, H = 978.891, $p < 0.001$), and pairwise comparisons revealed differences in average length between each time period ($p < 0.001$; Fig. 3C) such that the average length of the catch increased progressively from the Early period to the Current period.

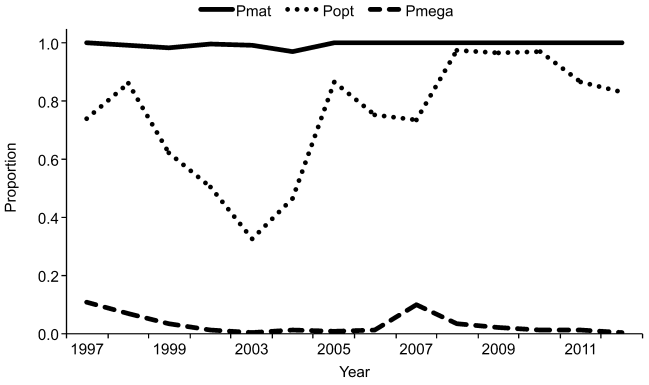

Fig. 4. Froese's indicators of sustainability. Graph showing changes in the annual proportion of mature fish (P_{mat}), proportion of fish harvested at optimal size (P_{opt}), and the proportion of mega-spawners (P_{mega}) in the Gulf corvina (*Cynoscion othonopterus*) fishery.

3.2. Assessment from Froese's indicators of sustainability

The proportion of mature fish (P_{mat}) was calculated for each year by dividing the number of fish of lengths greater than 295 mm TL by the total number of fish sampled. Juveniles were largely excluded from harvest throughout the study period, as the proportion of adults in the catch (P_{mat}) ranged from 0.970 to 1.00, with a mean of 0.996 ± 0.002 sem (Fig. 4). Optimum length at capture (L_{opt}) was calculated to be 715 mm TL, and the proportion of fish near optimum length (P_{opt}) was calculated for each year by dividing the number of fish sampled with lengths ranging from 644 to 787 mm TL, by the total number of fish sampled. The fishery targeted the harvest of fish at or near L_{opt}; the proportion of fish within 10% of L_{opt} (P_{opt}) ranged from 0.327 to 0.975, with a mean of 0.750 ± 0.026 sem. The proportion of mega-spawners harvested by the fishery (P_{mega}) was calculated for each year by dividing the number of fish of lengths greater than 787 mm TL by the total number of fish sampled. Annual values for P_{mega} ranged from 0.003 to 0.109, with a mean of 0.033 ± 0.006 sem. Therefore, P_{mega} was well below the desired range of 0.30–0.40 set by Froese throughout the study period. P_{obj} ranged from 1.322 to 2.00, with a mean of 1.778 ± 0.057 sem. A mean P_{obj} value of <2 placed the selectivity of the fishery in the category of "fish maturity ogive". Under this scenario, the fishery would be determined to exceed the limit reference points, because $L_{mat} < 0.75L_{opt}$ and $P_{mat} > 0.90$ during all years. During each of the three time periods, the proportion of mature fish was at or near 1.0 and the proportion of mega-spawners was at or below 0.02 (Table 3). The proportion of fish harvested at optimal length was consistently higher after the implementation of gear and harvest regulations.

3.3. Assessment from SPR analyses

Egg production peaks at the nominal age 5 cohort for the Equal and Incremental spawning scenarios and at nominal age 6 cohort under the Dual spawning scenario (Fig. 5). Total egg production of an unexploited population ($E = 0$) showed

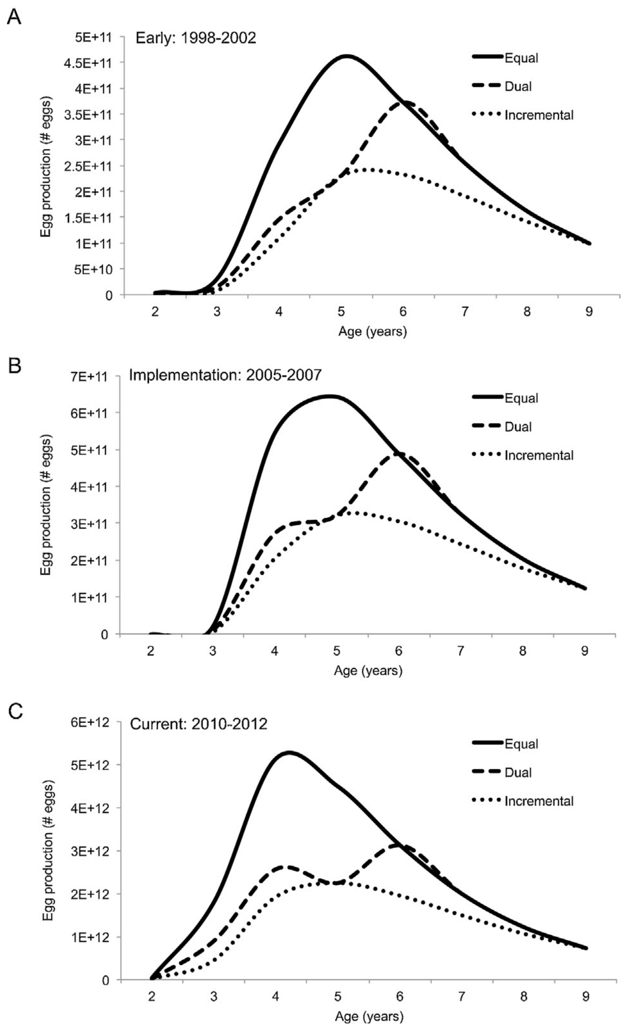

Fig. 5. Egg production of an unexploited population of Gulf corvina (*Cynoscion othonopterus*) in relation to spawning behavior scenario: (top) Early period; (middle) Implementation period; (bottom) Current period.

significant differences with respect to fishing period (Kruskal–Wallis ANOVA by ranks: df = 2; $n = 18$; $H = 13.345$; $p = 0.0013$) such that egg production of an unexploited population during the Current fishing period was higher than it was in both the Implementation ($p < 0.0001$) and the Early ($p < 0.0001$) periods. However, total egg production did not vary significantly with respect to spawning behavior (Kruskal–Wallis ANOVA by ranks; df = 2, $n = 18$; $H = 2.6666$; $p = 0.2636$).

The estimated natural mortality (M) from the Pauly, 1980 method was 0.26 year^{-1}, whereas the value obtained from the Jensen, 1996 method was 0.38 year^{-1}. Median annual exploitation rate was higher for calculations using values of natural mortality obtained from the Pauly (1980) method compared to the Jensen, 1996 method (Kruskal–Wallis ANOVA by ranks; df = 1; $n = 18$; $H = 7.2684$; $p = 0.007$) (Fig. 6A). However, median annual exploitation rate did not vary significantly among the three methods for estimating total mortality (Kruskal–Wallis ANOVA by ranks; df = 2; $n = 18$; $H = 2.144778$; $p = 0.3422$) (Fig. 6B), nor did mean annual exploitation rate vary by period (1-way ANOVA; $F_{2,\ 15} = 2.6407$; $p = 0.1041$) (Fig. 6C).

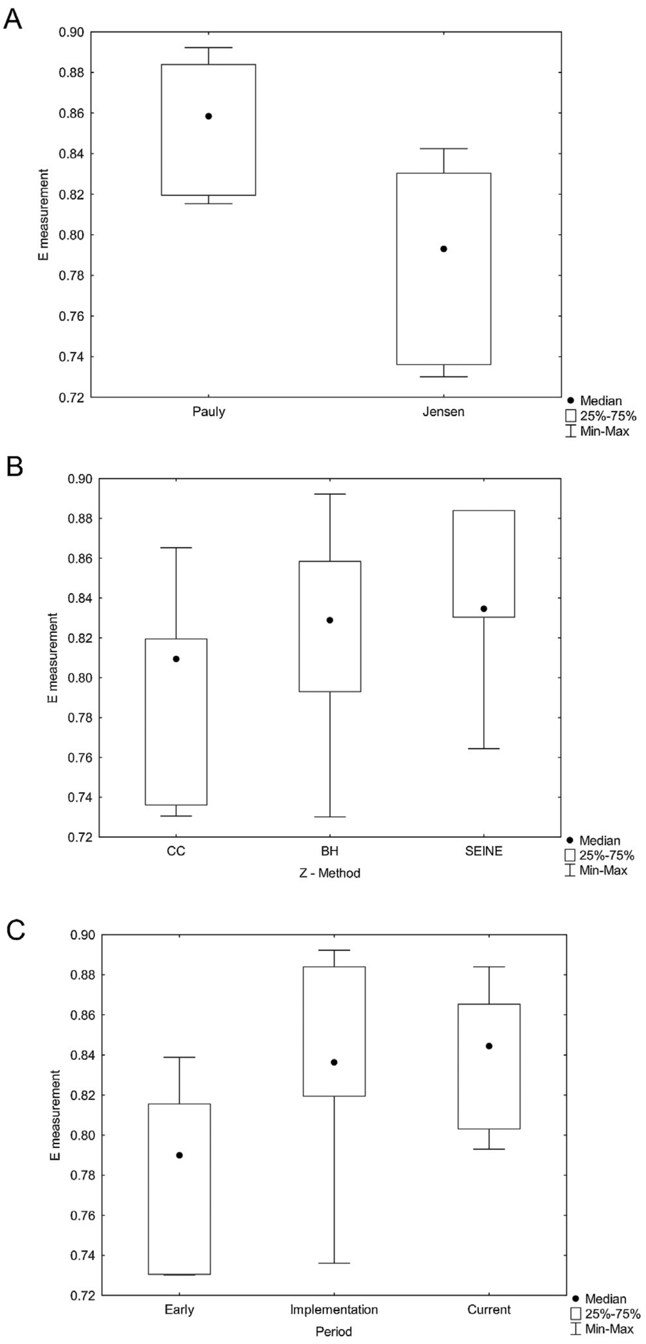

Fig. 6. Box and whisker plots showing within group variance in estimates of exploitation rate of the Gulf corvina (*Cynoscion othonopterus*) fishery in relation to method used to calculate natural mortality (top), method used to calculate total mortality (middle), and fishing period (bottom).

Table 3
Summary of estimates of Froese's indicators of sustainability by fishing period. P_{mat} = the proportion of mature fish in the catch. P_{opt} = the proportion of fish within 10% of the optimal length at harvest. P_{mega} = the proportion of the catch represented by old, highly fecund fish that are more than 10% longer than the optimal length. $P_{obj} = P_{mat} + P_{opt} + P_{mega}$, represents the selectivity of the fishery (see Cope and Punt, 2009).

Period	Years	P_{mat}	P_{opt}	P_{mega}	P_{obj}
Early	1998–2002	0.998	0.570	0.021	1.589
Implementation	2005–2007	1.000	0.822	0.012	1.834
Current	2010–2012	1.000	0.888	0.010	1.898

When we calculated SPR and YPR values across the entire range of exploitation rates from 0 to 1, estimates of SPR were consistently higher under the Equal spawning scenario compared to the Incremental and Dual scenarios in all three periods, whereas the latter two scenarios produced consistently similar results in each

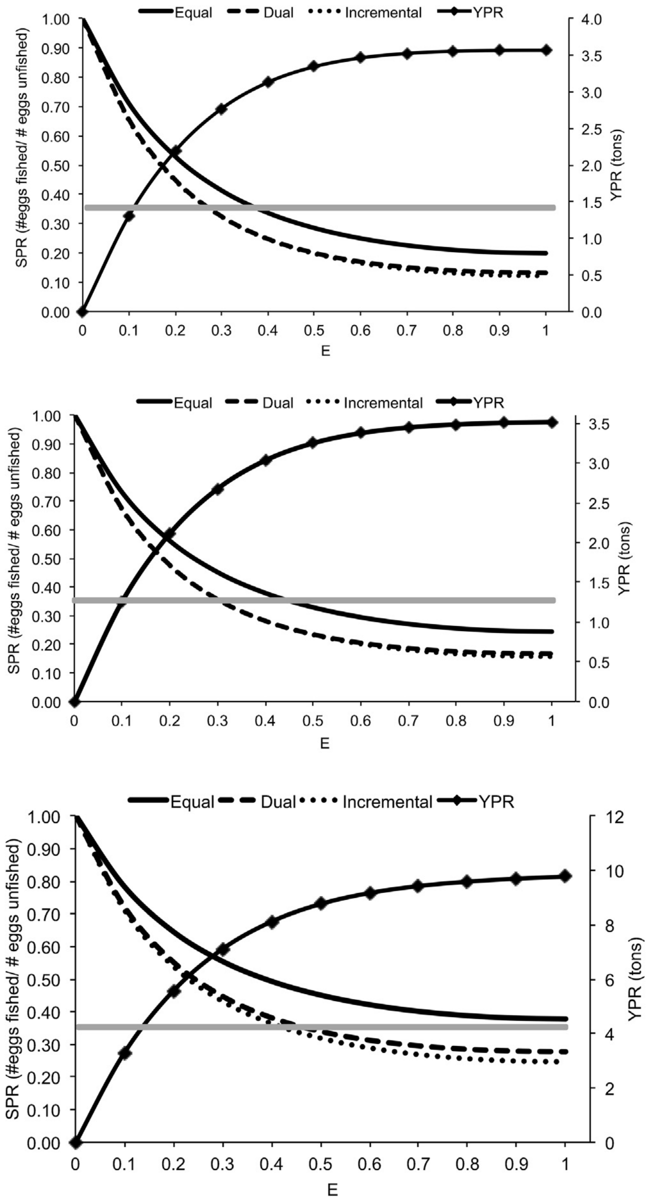

Fig. 7. Estimates of Spawning Potential Ratio (SPR) and Yield per Recruit (YPR) in relation to exploitation rate (*E*) for the Gulf corvina (*Cynoscion othonopterus*) fishery. (top) Early period; (middle) Implementation period; (bottom) Current period. Gray horizontal horizontal line represents $SPR_{0.35}$, the reference point for overfishing.

period (Fig. 7). For the Early and Implementation periods, SPR values dropped below the reference point of 0.35 at exploitation rates less than 0.50 under all spawning scenarios (Fig. 7A and B). During the Current period, SPR values in the Equal spawning scenario exceeded the limit reference point at exploitation rates that approach 1. Conversely, SPR values fell below the reference point at exploitation rates above 0.5 under the Incremental and Dual scenarios (Fig. 7C). During the Early period, YPR began to asymptote at exploitation rates above 0.6. During the Implementation period, YPR began to asymptote at $E = 0.7$, whereas it began to asymptote at $E = 0.9$ for the Current period.

When estimates of SPR were generated from estimates of exploitation rate (see above), Median estimates of SPR were significantly different among fishing periods (ANOVA, $F_{2,\ 49} = 31.3035$, $p < 0.001$) and among spawning behavior scenarios (ANOVA, $F_{2,\ 49} = 16.1520$, $p < 0.001$), but the interaction between these two parameters was not significant (Fig. 8). Moreover, the Equal spawning scenario produced significantly higher SPR values than both the Incremental and Dual scenarios (Tukey HSD posthoc, $p < 0.001$). No differences in SPR were detected between the Incremental and Dual scenarios (Tukey, $p = 0.685244$). Similarly, the Current fishing period produced significantly higher SPR values than the Early and Implementation periods (Tukey, $p < 0.001$), but there was no difference in SPR between the Early and Implementation periods (Tukey, $p = 0.194325$). SPR values exceeded the limit reference point (SPR = 0.35) only for the Current fishery period under the Equal spawning scenario.

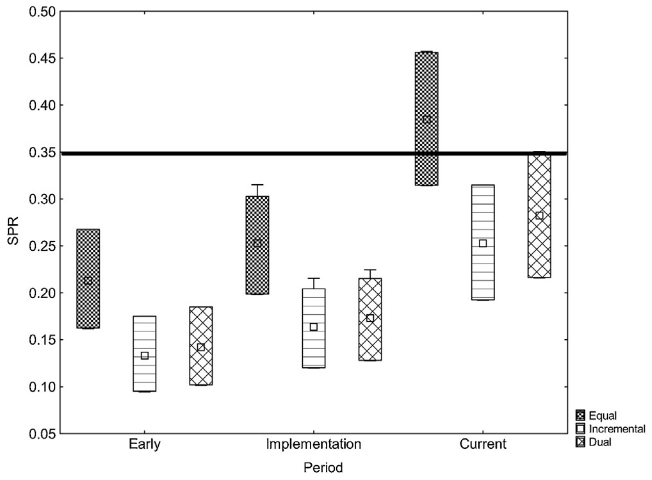

Fig. 8. Box and whisker plots showing within group variance in estimates of Spawning Potential Ratio (SPR) for the Gulf corvina (*Cynoscion othonopterus*) fishery in relation to spawning behavior scenario and fishing period.

4. Discussion

For this study, we employed several data-poor techniques to gain insights into the sustainability of the Gulf corvina fishery in the Upper Gulf of California and improve our understanding of the effects of conventional regulations and spawning behavior on assessments of spawning aggregation fisheries. The results produced from these methods generated somewhat equivocal results regarding whether overfishing is occurring in the fishery. Analyses based on the length composition of the catch indicated that the fishery was likely sustainable as a result of gear selectivity allowing sufficient numbers of fish to escape, although the lack of large, fecund adults in the population was identified as a serious cause for concern. Conversely, analyses based on reproductive potential suggested that overfishing was likely to occur unless spawning frequency was invariant with respect to age. Discordance among the results obtained made it difficult to draw a strong conclusion about the status of the corvina fishery. However, they did produce useful information on the use of conventional tools for managing spawning aggregation fisheries and the importance of understanding age or length related patterns in spawning behavior in stock assessments.

If we assume that the growth model for Gulf corvina (Gherard et al., 2013) is reliable, then simple analyses focusing on the catch length composition of the fishery indicated the implementation of the gear regulation had a positive effect on the fishery. While the length composition of harvested fish varied over time and showed no clear directional change, mean length at capture was consistently above the long-term mean after the implementation of the gear restriction that standardized the legal mesh size for the gill net fishery at 5.75 in. (DOF, 2005). In addition, when length data were binned into three separate time periods, length at capture was significantly higher after the implementation of the gear regulation. Similarly, the proportion of fish harvested at or near the optimal length was consistently higher after regulations were implemented, which suggested that catch length compositions consisted primarily of fish of the size that generate the highest yield from a cohort (Beverton, 1992).

However, the size distribution of the catch was highly truncated throughout the study period, such that the annual proportion of mega-spawners reached 0.10 during only two years. Assuming larger fish do not escape capture of gill nets due to the encircling technique used (see Section 2), this suggests that the large volumes of fish harvested each year by the fishery resulted in the low survivorship of larger, older adults. Nevertheless, these results imply that conventional regulations associated with gear selectivity can produce positive results for aggregation fisheries.

The application of Froese's (2004) indicators of sustainability also suggested that fishing activities for the Gulf corvina were sustainable during most or all years of our study period as a result of gear selectivity. First, the proportion of juveniles in the catch was relatively low throughout the study period and nearly nonexistent after 2005. The mesh size of gill nets selected for fish larger than 61 cm TL, which enhanced the reproductive potential of the stock by allowing adult corvina to spawn up to 3.4 years prior to reaching the size at full selectivity for harvest. The selectivity of the nets also resulted in the targeted harvest of most fish at or near the optimal length of 65 cm TL, or the expected length at which the combination of biomass and reproductive output of the population would peak.

The proportion of large, old adults (mega-spawners) in the catch was extremely low during most years and never met the limit reference point of 30–40%. This indicates high mortality for fish at or above full selectivity, resulting in a low proportion of mega-spawners in the population and the truncation of age structure of the population. Such effects are not unexpected given that the fishery involves a fleet of 500 pangas that harvest an average of 3500 tons of corvina in less than 25 days of fishing each year within a 1149 km^2 area; individual pangas are capable of harvesting more than two tons of fish with a single net of 250 m in length in less than 20 min (Erisman et al., 2012; BE, personal observation). While the role of large fish in this population has not been quantified, their low abundance may represent a significant risk for this fishery, as large fish with disproportionately large reproductive capacity are thought to be important in sustaining other fish populations (Berkeley et al., 2004; Birkeland and Dayton, 2005). Likewise, truncations in the population structure due to selective harvesting can alter the basic dynamics of fish populations, reduces their ability to buffer environmental events, and increases their susceptibility to collapse (Hsieh et al., 2006; Anderson et al., 2008). Despite the negative effects associated with the high mortality rate of mega-spawners, which may be unavoidable for any fishery that utilizes gill nets, the overall conclusion based on Cope and Punt's decision tree is the fishery met or exceeded the reference points associated with sustainability. These results suggest that a conventional regulation that standardizes the minimal length at capture is capable of producing a sustainable aggregation fishery even when fishing pressure on larger adults is extremely high.

Empirical studies on the ability of conventional management regulations such as gear restrictions to successfully enhance stocks of aggregation spawning fishes are less common than those associated with seasonal or area closures that restrict fishing of aggregations altogether. A notable exception relates to the white seabass (*Atractoscion nobilis*), another large sciaenid fish that supports a valuable commercial and recreational fishery in southern California. Landings of white seabass in California waters fluctuated between 200 and 400 tons per year from the 1930s to the 1970s but then collapsed to 10% of its historical catch by the early 1980s (Vojkovich and Crooke, 2001). However, significant increases in commercial catch, CPUE, and the density of wild, juvenile fish have been consistently observed since the early 2000s (Allen et al., 2007). While favorable environmental conditions and the implementation of a hatchery-based stock enhancement program likely contributed to stock productivity (Williams et al., 2007; Hervas et al., 2010), a ban of commercial gill nets in nearshore waters of California in 1994 resulted in the protection of white seabass breeding aggregation sites and is believed to be the main factor in the presumed recovery of the stock (Allen et al., 2007).

Modeled scenarios of reproductive potential as measured by Spawning Potential Ratio (SPR) indicated that overfishing occurred consistently throughout the study period of 1997–2012. In fact, only the Current fishing period under the assumption of age invariant spawning frequency resulted in an SPR that met the target reference point of 0.35. Our model simulations indicate that SPR values are highly sensitive to age dependence in spawning frequency. For example, scenarios under which smaller fish spawn less frequently (i.e. those associated with the Incremental and Dual models) resulted in SPR values well below targeted reference points under moderate to intense fishing pressure. Similar results were found in a recent study by Fitzhugh et al. (2012), who conducted a literature search of spawning patterns in fishes and found that 62% of the species included showed evidence of increased spawning frequency with age or size, and 83% were found to spawn over a longer duration with increasing age or size. Moreover, stock assessment models based on both spawning potential ratios and maximum sustainable yield tended to overestimate the biological reference points used for setting harvest limits when the number of spawning batches increased with age but was incorrectly assumed to be constant (Fitzhugh et al., 2012). Such insufficient incorporation of age or size structure on reproductive potential could lead to erroneous conclusions regarding stock status and the overexploitation of the stock (Witthames and Marshall, 2008). Age or size-related patterns may have particularly important implications for fisheries that target spawning aggregations, since significant proportions of stocks can be removed during the few spawning events that may occur at only a few sites and during only a few days each year. These results highlight the importance of future studies to focus on understanding the influence of spawning behavior on vulnerability of a species to fishing and the need to further investigate variations in spawning frequency with age, location, etc.

The conclusion that assessments built upon estimates of reproductive output are highly sensitive to age-based variations in spawning patterns is not surprising. Such assessment methods are also highly sensitive to variations in estimated values of natural mortality (Williams and Shertzer, 2003). In addition, it is important to note that SPR only reflects the reproductive potential of a stock and not reproductive success. Work by Froese and Luna (2003) reminds us that high fecundity does not necessarily confer greater resilience to fishing pressure; their review of 49 species found no correlation between fecundity and reproductive success and concluded that the number of spawners is more important for reproductive success than reproductive output. Moreover, such misconceptions and the reliance of reproductive potential to set harvest control rules pose a huge threat to populations of highly fecund fishes (Sadovy, 2001).

Ruelas-Peña et al. (2013) assessed the status of the corvina stock using two biomass dynamic models (Schaefer and Pella-Tomlinson), which calculated a historical annual abundance index directly from commercial catch and effort data. They estimated fishing mortality to be 26% higher than the precautionary target reference point of $F_{0.1}$ (i.e. the fishing mortality rate corresponding to 10% of the slope of the yield-per-recruit curve at the origin) which suggested that the stock was overexploited. Similarly, they found the average biomass of the stock was 52% of the optimum level of the fishery (i.e. biomass at maximum surplus production) during the period of 2006–2010 as a result of increased fishing effort after 1999. Results from that study were built upon assumptions of linear relationships between catch, fishing effort, and stock size, which are unlikely to be true given the aggregating behavior of the stock and the fishing behavior of the fleet (Hilborn and Walters, 1992; Erisman et al., 2011; Erisman et al., 2012). In addition, such analyses provide no information on the effects of fishing pressure or gear regulations on the age or length composition and the reproductive potential of the stock. Nevertheless, their conclusions about overfishing do support those found in several of our analyses. This reinforces the argument that data poor assessments can provide important insights on aspects of fish populations that cannot be observed by more conventional assessment methods.

5. Conclusions

The results of this study support a growing consensus on the importance of applying multiple methods in fisheries assessments, since no one biological reference point is appropriate for all stocks (Clark, 2002; Williams and Shertzer, 2003). This principle is particularly important for assessments of data-poor stocks, which suffer from insufficient data to generate full stock assessments and are often based on the availability of a few life history parameters to which the outputs and may be highly sensitive. Likewise, the application of multiple assessment methods is important for the monitoring and management of fishes that form large spawning aggregations during brief periods at only a few sites. Such species can decline rapidly under intense fishing pressure yet these trends may not be visible depending on the methods used to determine target or limit reference points for their fishery (Sadovy de Mitcheson and Erisman, 2012).

It is important to point out that the results of this study rely on several assumptions due to the limited amount of information on the fishery, which could drastically change if any are violated. The catch length composition indicated an incredibly low incidence of capture of juveniles; however, such data comprise only fish captured by the targeted fishery and do not include the bycatch of juvenile corvina captured by other fisheries in the region. Fishers currently use gill nets of much smaller mesh sizes to capture blue shrimp and other fishes (Pérez-Valencia, 2012), and a new regulation will soon require all fishers involved in the small-scale shrimp fishery to switch from gill nets to small bottom trawls to reduce bycatch of the endangered vaquita porpoise (DOF, 2013). Both gear types are known to capture juvenile corvinas (Aguilar-Ramirez and Rodriguez-Valencia, 2012; Pérez-Valencia, 2012) and could significantly reduce current estimates of the reproductive potential of young adult corvinas that escape the targeted corvina fishery. The impact of such fisheries on the juvenile population of corvina has not yet been quantified. Related to this issue, most of the catch surveys of the corvina fishery have been conducted at El Golfo de Santa Clara, which represents more than 85% of the total landings of the fishery and has been the focus of enforcement activities since regulations were implemented in 2005 (BE, personal observation). Therefore, compliance for the use of the regulation gill nets with 5.75 inch mesh is nearly ubiquitous (BE, personal observation). However, the use of nets with smaller mesh sizes has been observed for fishers from the San Felipe and the Baja Rio and Cucapah communities (I. Mascareñas-Osorio, unpublished data). Estimates of reproductive potential (e.g., SPR) would be expected to decrease even further if non-compliance for the gear regulation is widespread among these communities, which would increase the measured level of fishing pressure.

Despite these important caveats, the lack of mega-spawners suggested by results obtained from length-based approaches in combination with low SPR levels estimated under scenarios in which spawning frequency increases with age point to a clear need to apply the precautionary approach (FAO, 1996) to the management of the corvina fishery. State and federal agencies should adopt cautious measures that take into account existing uncertainties related to the size and productivity of the stock, reference points, the impacts of fishing on the species, the influence of environmental conditions on recruitment and stock dynamics, and the amount of unreported or illegal catch. Such actions are also warranted due to certain life-history factors that indicate an implicit vulnerability of Gulf corvina to overfishing as well as uncertainties and assumptions in the data gathered from the fishery. Notably, this species has a highly restricted geographic range and adults are only known to spawn in the estuary of the Colorado River Delta (Erisman et al., 2012). This, along with its high degree of dependence on precise timing of its spawning aggregation, may indicate its use of an evolutionary strategy that depends on very high fecundity, suggesting high fecundity might not necessarily be associated with high resilience to fishing. The fact that potentially all fish aggregate to spawn at a single location during very brief and predictable periods, and more than 95% of fish are harvested during these periods and at this location, suggests that a collapse of the entire stock could occur very rapidly.

In fact, there is a history of collapses in aggregation fisheries of this region. The commercial fishery for totoaba (*T. macdonaldi*), the world's largest sciaenid fish and a close relative of the Gulf corvina, collapsed in large part from the persistent overfishing of their massive spawning aggregations, which formed in the Colorado River Delta in rhythm with the full moons during the spring months (Cisneros-Mata et al., 1995) just as corvina aggregations form. Similar to the corvina fishery, commercial fishers encircled the aggregations of totoaba during the peak spawning periods with gill nets deployed like purse seines and harvested several thousands of tons during only a few weeks each year (Flanagan and Hendrickson, 1976). The stock of totoaba collapsed in the mid 1950s after several decades of intense fishing pressure on the aggregations, rebounded slightly in the 1960s, and then collapsed again in the early 1970s (Cisneros-Mata et al., 1995). The second collapse was followed by a moratorium on the fishery in Mexico and earned the totoaba the dubious distinction as the first marine fish listed on CITES as an endangered species. Precautionary measures seem prudent for the corvina fishery given these results and the totoaba collapse.

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References

Aguilar-Ramirez, D., Rodriguez-Valencia, A., 2012. Eficiencia y Selectividad de Dos Diseños de Redes de Arrastre para Pescar Camarón Azul (*Litopenaeus stylirostris*) en la Pesquería Artesanal del Alto Golfo de California. INAPESCA, México, 13 pp. Disponible en: http://www.inapesca.gob.mx

Allen, L.G., Pondella, D.J.I.I., Shane, M.A., 2007. Fisheries independent assessment of a returning fishery: abundance of juvenile White seabass (*Atractoscion nobilis*) in the shallow nearshore waters of the Southern California Bight 1995–2005. Fish. Res. 88, 24–32.

Anderson, C.N.K., Hsieh, C., Sandin, S.A., Hewitt, R., Hollowed, A., Beddington, J., May, R.M., Sugihara, G., 2008. Why fishing magnifies fluctuations in fish abundance. Nature 452, 835–839.

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

Beverton, R.J.H., 1992. Patterns of reproductive strategy parameters in some marine teleost fishes. J. Fish Biol. 41 (Suppl. B), 137–160.

Beverton, R.J.H., Holt, S.J., 1956. A review of the methods for estimating mortality rates in fish populations, with special reference to sources of bias in catch sampling. Rapp. P.-V. Réun. Cons. Int. Explor. Mer. 140, 67–83.

Beverton, R.J.H., Holt, S.J., 1957. On the dynamics of exploited fish populations. Fish. Invest., II. Sea Fish 19, 533.

Birkeland, C., Dayton, P.K., 2005. The importance in fishery management of leaving the big ones. Trends Ecol. Evol. 20, 356–358.

Chao, L., Espinosa, H., Findley, L., van der Heiden, A., 2010. *Cynoscion othonopterus*. in: IUCN 2012. IUCN Red List of Threatened Species. Version 2012.2. www.iucnredlist.org (downloaded on 18 June 2013).

Cisneros-Mata, M.A., Montemayor-Lopez, G., Roman-Rodrıguez, M.J., 1995. Life history and conservation of *Totoaba macdonaldi*. Conserv. Biol. 9, 806–814.

Clark, W.G., 2002. $F_{35\%}$ revisited ten years later. N. Am. J. Fish. Manag. 22, 251–257.

Claro, R., Sadovy de Mitcheson, Y., Lindeman, K.C., García-Cagide, A.R., 2009. Historical analysis of Cuban commercial fishing effort and the effects of management interventions on important reef fishes from 1960–2005. Fish. Res. 99, 7–16.

Cope, J.M., Punt, A.E., 2009. Length-based reference points for data-limited situations: applications and restrictions. Mar. Coast. Fish: Dyn. Manag. Ecosyst. Sci. 1, 169–186.

Dick, E.J., MacCall, A.D., 2011. Depletion-based stock reduction analysis: a catch-based method for determining sustainable yields for data-poor fish stocks. Fish. Res. 110, 331–341.

DOF, 2005. Acuerdo por el que se establece veda temporal para la captura de curvina golfina (Cynoscion othonopterus) en las aguas marinas y estuarinas de jurisdicción federal de la reserva de la Biosfera Alto Golfo de California y Delta del Río Colorado, durante el periodo del 1 de mayo al 31 de agosto de cada año. Pub. DOF, 25 de Agosto de 2005.

DOF, 2013. Proyecto de Modificación a la Norma Oficial Mexicana NOM-002-PESC-1993, para ordenar el aprovechamiento de las especies de camarón en aguas de jurisdicción federal de los Estados Unidos Mexicanos, publicada el 31 de diciembre de 1993 y sus modificaciones publicadas los días 30 de julio de 1997 y 28 de noviembre de 2006. Pub DOF, 22 de February de 2013.

Dulvy, N.D., Ellis, J.R., Godwin, N.B., Grant, A., Reynolds, J.D., Jennings, S., 2004. Methods of assessing extinction risk in marine fishes. Fish Fish. 5, 255–276.

Erisman, B.E., Allen, L.G., Pondella, D.J.I.I., Claisse, J., Miller, E., Murray, J., 2011. Illusions of plenty: hyperstability masks collapses in two recreational fisheries that target fish spawning aggregations. Can. J. Fish. Aquat. Sci. 68, 1705–1716.

Erisman, B., Mascareñas, I., Paredes, G., Sadovy de Mitcheson, Y., Aburto-Oropeza, O., Hastings, P., 2010. Seasonal, annual, and long-term trends in commercial fisheries for aggregating reef fishes in the Gulf of California, Mexico. Fish. Res. 106, 279–288.

Erisman, B.E., Aburto-Oropeza, O., Gonzalez-Abraham, C., Mascareñas-Osorio, I., Moreno-Báez, M., Hastings, P.A., 2012. Spatio-temporal dynamics of a fish spawning aggregation and its fishery in the Gulf of California. Sci. Rep. 2, 284.

FAO, 1996. FAO Technical Guidelines for Responsible Fisheries. No. 2. FAO, Rome. 54 pp.

Fitzhugh, G.R., Shertzer, K.W., Kellison, G.T., Wyanski, D.M., 2012. Review of size- and age-dependence in batch spawning: implications for stock assessment of fish species exhibiting indeterminate fecundity. Fish. Bull. 110, 413–425.

Flanagan, C.A., Hendrickson, J.R., 1976. Observations on the commercial fishery and reproductive biology of the totoaba Cynoscion macdonaldi, in the northern Gulf of California. Fish. Bull. 74, 531–544.

Ford, E., 1933. An account of the herring investigations conducted at Plymouth from the years 1924 to 1933. J. Mar. Biol. Assoc. U.K. 19, 305–384.

Froese, R., 2004. Keep it simple: three indicators to deal with overfishing. Fish Fish. 5, 86–91.

Froese, R., Binohlan, C., 2000. Empirical relationships to estimate asymptotic length, length at first maturity and length at maximum yield per recruit in fishes, with a simple method to evaluate length frequency data. J. Fish Biol. 56, 758–773.

Froese, R., Luna, S., 2003. No relationship between fecundity and annual reproductive rate in bony fish. Acta Ichthyol. Piscat. 34, 11–20.

Gedamke, T., Hoenig, J.M., 2006. Estimating mortality from mean length data in nonequilibrium situations, with application to the assessment of goosefish (*Lophius americanus*). Trans. Am. Fish. Soc. 135, 476–487.

Gherard, K., Erisman, B.E., Rowell, K., Allen, L.G., 2013. Growth, development, and reproduction of Gulf corvina *Cynoscion othonopterus*. Bull. South. Cal. Acad. Sci. 112, 1–18.

Goodyear, C.P., 1993. Spawning stock biomass per recruit in fisheries management: foundation and current use. Can. J. Fish. Aquat. Sci. 120, 67–81.

Heppell, S.A., Semmens, B.X., Archer, S.K., Pattengill-Semmens, C.V., Bush, P.G., McCoy, C.M., Heppell, S.S., Johnson, B.C., 2012. Documenting recovery of a spawning aggregation through size frequency analysis from underwater laser caliper measurements. Biol. Conserv. 155, 119–127.

Hervas, S., Lorenzen, K., Shane, M.A., Drawbridge, M.A., 2010. Quantitative assessment of a white seabass (*Atractoscion nobilis*) stock enhancement program in California: post-release dispersal, growth and survival. Fish. Res. 105, 237–243.

Hilborn, R., Walters, C.J., 1992. Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty. Chapman and Hall, New York.

Honey, K.T., Moxley, J.H., Fujita, R.M., 2010. From rags to fishes: data-poor methods for fishery managers. Managing Data-Poor Fisheries: Case Studies, Models and Solutions, vol. 1, pp. 159–184 (California Sea Grant College Program).

Hsieh, C., Reiss, C.S., Hunter, J.R., Beddington, J.R., May, R.M., Sugihara, G., 2006. Fishing elevates variability in the abundance of exploited species. Nature 443, 859–862.

Jensen, A.L., 1996. Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. Can. J. Fish. Aquat. Sci. 53, 820–822.

Jensen, C.C., 2009. Stock status of spotted seatrout, *Cynoscion nebulosus*, in North Carolina, 1991–2008. North Carolina Division of Marine Fisheries, Morehead City, 90 pp. www.ncfisheries.net/fmps/downloads/SeatroutAssessment2009.pdf

Johannes, R.E., 1997. Grouper spawning aggregations need protection. SPC Live Reef Fish Inform. Bull. 3, 3–14.

Kenchington, T., 2013. Natural mortality estimators for information-limited fisheries. Fish Fish., http://dx.doi.org/10.1111/faf.12027.

Lowerre-Barbieri, S.K., Ganias, K., Saborido-Rey, F., Murua, H., Hunter, J.R., 2011. Reproductive timing in marine fishes: variability, temporal scales, and methods. Mar Coast. Fish. 3, 71–91.

MacCall, A.D., 1976. Density dependence of catchability coefficient in the California Pacific sardine Sardinops sagax caerulea, purse seine fishery. Calif. Coop. Oceanic Fish. Invest Rep. 18, 136–148.

Mace, P., Botsford, L., Collie, J., Gabriel, W., Goodyear, P., Powers, J., Restrepo, V., Rosenberg, A., Sissenwine, M., Thompson, G., Witzig, J., 1996. Scientific review of definitions of overfishing in U.S. fishery management plans. NOAA Tech. Mem. NMFS-F/SPO-21.

Murphy, M.D., Guenther, C.B., Mahmoudi, B., 2006. An assessment of the status of spotted seatrout in Florida waters through 2005. Florida Fish Wild. Conserv. Comm. Fish Wild Res. Inst. IHR 2006-XXX. www.myfwc.com/media/1355905/Spotted_seatrout.pdf

Murua, H., Kraus, G., Saborido-Rey, F., Witthames, P.R., Thorsen, A., Junquera, S., 2003. Procedures to estimate fecundity of marine fish species in relation to their reproductive strategy. J. Northwest Atl. Fish. Sci. 33, 33–54.

Musick, J.A., Harbin, M.M., Berkeley, A., Burgess, G.H., Eklund, A.M., Findley, L.T., Gilmore, R.G., Golden, J.T., Ha, D.S., Huntsman, G.R., McGovern, J.C., Parker, S.J., Poss, S.G., Sala, E., Schmidt, T.W., Sedberry, G.R., Weeks, H., Wright, S.G., 2000. Marine, estuarine and diadromous fish stocks at risk of extinction in North America (exclusive of Pacific salmonids). Fisheries 25, 6–30.

Nemeth, R.S., 2005. Population characteristics of a recovering US Virgin Islands red hind spawning aggregation following protection. Mar. Ecol. Prog. Ser. 286, 81–97.

Pauly, D., 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J. Conseil Int. Explor. Mer. 39, 175–192.

Pauly, D., Morgan, G.R., 1987. Length-based methods in fisheries research. Proceedings of the International Conference on the Theory and Application of Length-Based Methods for Stock Assessment, Sicily, Italy. International Center for Living Aquatic Resources Management, Safat, Kuwait, 468 pp.

Pérez-Valencia, S.A., 2012. Manifestación de Impacto Ambiental para la pesca ribereña responsable en la Reserva de la Biosfera Alto Golfo de California y Delta del Río Colorado: Costa Este. El Golfo de Santa Clara: Centro Intercultural de Estudios de Desiertos y Océanos, A.C. 264 pp.

Ricker, 1975. Computation and interpretation of biological statistics of fish populations. Bull Fish. Res. Board Canada 191, 1–382.

Robertson, D.R., Allen, G.R., 2008. Shorefishes of the Tropical Eastern Pacific online information system. Version 1.0. Smithsonian Tropical Research Institute, Balboa, Panama. www.neotropicalfishes.org/sftep (accessed 05.09.13).

Román-Rodríguez, M.J., 2000. Estudio poblacional del chano norteño, *Micropogonias megalops* y la curvina Golfina *Cynoscion othonopterus* (Gilbert) (Pisces: Sciaenidae), especies endémicas del alto Golfo California, Mexico. Instituto del Medio Ambiente y Desarrollo Sustentable del Estado de Sonora. Informe final SNIB-CONABIO proyecto No. L298. Mexico, D.F. www.conabio.gob.mx/institucion/cgi-bin/datos.cgi?Letras=L&Numero=298

Rose, G.A., Kulka, D.W., 1999. Hyperaggregation of fish and fisheries: how catch-per-unit-effort increased as the northern cod (*Gadus morhua*) declined. Can. J. Fish. Aquat. Sci. 56 (Suppl. 1), 118–127.

Ruelas-Peña, J.H., Valdez-Muñoz, C., Aragón-Noriega, E.A., 2013. Analysis of the corvina gulf fishery as a function of management in the Upper Gulf of California. Lat. Am. J. Aquat Res. 41, 498–505.

Russell, M., Luckhurst, B.E., Lindeman, K.C., 2012. Management of spawning aggregations. In: Sadovy de Mitcheson, Y.J., Colin, P.L. (Eds.), Reef Fish Spawning Aggregations: Biology, Research, and Management. Springer, New York, pp. 371–404.

Sadovy, Y., 2001. The threat of fishing to highly fecund fishes. J. Fish Biol. 59 (Suppl. A), 90–108.

Sadovy, Y., 2005. Trouble on the reef: the imperative for managing vulnerable and valuable fisheries. Fish Fish. 6, 167–185.

Sadovy, Y., Domeier, M., 2005. Are aggregation-fisheries sustainable? Reef fish fisheries as a case study. Coral Reefs 24, 254–262.

Sadovy, Y., Eklund, A.M., 1999. Synopsis of biological data on the Nassau grouper, *Epinephelus striatus* (Bloch, 1792), and the jewfish, *E. itajara* (Lichtenstein, 1822). NOAA Tech. Rep. NMFS 146, 1–65.

Sadovy, Y.J., Vincent, A.C.J., 2002. Ecological issues and the trades in live reef fishes. In: Sale, P.F. (Ed.), Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem. Academic Press, San Diego, pp. 391–420.

Sadovy de Mitcheson, Y., Colin, P.L., 2012. Reef Fish Spawning Aggregations: Biology, Research, and Management. Springer, New York.

Sadovy de Mitcheson, Y., Erisman, B.E., 2012. The social and economic importance of aggregating species and the biological implications of fishing on spawning aggregations. In: Sadovy de Mitcheson, Y.J., Colin, P.L. (Eds.), Reef Fish Spawning Aggregations: Biology, Research, and Management. Springer, New York.

Sala, E., Ballesteros, E., Starr, R.M., 2001. Rapid decline of Nassau grouper spawning aggregations in Belize: fishery management and conservation needs. Fisheries 26, 23–30.

SCRFA Fish Aggregation Database, 2013. Spawning Aggregation Database by Science and Conservation of Fish Aggregations. World Wide Web Electronic Publication. http://www.scrfa.org

Smith, M.W., Then, A.Y., Wor, C., Ralph, G., Pollock, K.H., Hoenig, J.M., 2012. Recommendations for catch-curve analysis. N. Am. J. Fish. Manag. 32, 56–967.

Solana-Sansores, L.R., Dicante, I., Luna, L., Villaseñor Talavera, R., 2012. Selectivity of gill-nets used in curvina (*Cynoscion othonopterus*) fishery in the upper Gulf of California, Mexico. Hidrobiólogica 22, 132–141.

Tobin, A., Currey, L., Simpfendorfer, C., 2013. Informing the vulnerability of species to spawning aggregation fishing using commercial catch data. Fish. Res. 143, 47–56.

Vojkovich, M., Crooke, S., 2001. White seabass. In: Leet, W.S., Dewees, C.M., Klingbeil, R., Larson, E.J., (Eds.), California's Living Marine Resources: A Status Report. Calif. Dept Fish Game, U. C. Agri. Nat. Res. Pub. SG01-11, 592 pp.

Walsh, P., Grant, S., Winger, P., Blackwood, G., Balmori Ramirez, A., Silva Ramirez, T., 2004 An Investigation of alternative harvesting methods to reduce the by-catch of vaquita porpoise in the upper Gulf of California shrimp gillnet fishery. Tech. Rep. Centre for Sust. Aqua. Res. and Inst. Nac. Pesca, México, 32 pp.

Williams, E.H., Shertzer, K.W., 2003. Implications of life-history invariants for biological reference points used in fishery management. Can. J. Fish. Aquat. Sci. 60, 710–720.

Williams, J.P., Allen, L.G., Steele, M.A., Pondella, D.J.I.I., 2007. El Niño periods increase growth of juvenile white seabass (*Atractoscion nobilis*) in the Southern California Bight. Mar. Biol. 152, 193–200.

Witthames, P.R., Marshall, C.T., 2008. The importance of reproductive dynamics in fish stock assessments. In: Payne, A., Cotter, J., Potter, T. (Eds.), Advances in Fisheries Science. Blackwell, Oxford, pp. 306–324.