Demographic Recovery of a Reef Fish Population Over 30 Years of Spawning Aggregation Site Protection

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Over 200 species of reef fish around the world form spawning aggregations to reproduce at specific times and locations. The locations of many reef fish spawning aggregations in the Caribbean have been known and fished for decades. Red Hind (*Epinephelus guttatus*), a species of grouper important in Caribbean fisheries, migrate to form spawning aggregations which have historically experienced intense fishing pressure. The Red Hind Bank Marine Conservation District (MCD) was established in the United States Virgin Islands to protect a known Red Hind spawning aggregation site. The MCD was closed seasonally to fishing in 1990 and then permanently in 1999. Our goal was to evaluate the success of this marine conservation effort by assessing how the Red Hind population at the spawning aggregation responded to changing levels of protection. We documented Red Hind population demographics at the spawning aggregation site in the MCD during peak spawning events from 2018 to 2020. After 30 years of protection, the mean size of Red Hind at the spawning aggregation increased by >35% and the population sex ratio of females to males was less skewed compared to population characteristics at the spawning aggregation prior to protection. To evaluate stock status relative to management benchmarks, we used length-based stock assessment models that included *in situ* size distribution data spanning 1988 to 2020 to estimate population spawning potential ratio (SPR) over time. We found that the SPR of the Red Hind population at the spawning aggregation prior to protection was 0.32 (95% CI: 0.25, 0.39) and under seasonal protection, The SPR increased slightly to 0.35 (95% CI: 0.28, 0.42). Under permanent protection, The SPR increased to its highest value yet at 0.49 (95% CI: 0.42, 0.56), which is above the benchmark value considered sustainable for many fish species. Our work demonstrates demographic recovery of the protected Red Hind spawning population and highlights the value of using size distribution data to evaluate the response of data-limited reef fish populations to seasonal and permanent protection at spawning aggregation sites.

Keywords: fisheries management, length-based assessment, spawning potential ratio, size distribution, sex ratio, Serranidae, Caribbean

INTRODUCTION

Seasonal migrations for reproduction are important life history events across phyla which function to connect individuals distributed across broad geographic areas (Dingle and Drake, 2007). Globally, over 200 species of marine fishes, representing 44 families, reproduce by forming resident or transient spawning aggregations at specific times and locations (Sadovy De Mitcheson et al., 2008; Nemeth, 2009; Russell et al., 2014), with some species migrating tens to hundreds of kilometers to spawn (Colin, 1992; Bolden, 2000). This strategy works well from an evolutionary perspective but presents a bottleneck when that life history strategy is disrupted by exploitation (Sadovy De Mitcheson et al., 2008), habitat loss (Reed et al., 2007), or climate change (Asch and Erisman, 2018). The timing of spawning events is often driven by changing photoperiod and lunar cycle, making the formation of spawning aggregations a predictable event (Nemeth, 2009). Fish spawning aggregations are susceptible to intense fishing pressure due to their predictability and the hyperstability of catch rates (Sadovy De Mitcheson and Domeier, 2005; Sadovy De Mitcheson et al., 2008; Erisman et al., 2011).

The locations of many reef fish spawning aggregations in the Caribbean have been known and fished for decades (Beets and Friedlander, 1992; Sadovy De Mitcheson et al., 2008). Intense fishing pressure has led to the extirpation of some reef fish spawning aggregations, most notably of Nassau grouper (*Epinephelus striatus*), which led to its listing as *Threatened* under the United States Endangered Species Act (Erisman et al., 2013). In the United States Virgin Islands (USVI), when Nassau grouper spawning populations collapsed, Red Hind (*Epinephelus guttatus*), which shared some spawning aggregation sites with Nassau grouper, were intensively targeted instead (Beets and Friedlander, 1992). Red Hind, like many other serranids (groupers and sea basses) undergo seasonal migrations to form spawning aggregations to reproduce (Colin et al., 1987; Sadovy De Mitcheson et al., 1992; Zeller, 1998; Heyman et al., 2005; Nemeth, 2005; Lopez-Rivera and Sabat, 2009; Rowell et al., 2015). Red Hind are protogynous hermaphrodites (changing sex from female to male as they age), so they may be more vulnerable to size-selective fishing pressure that disproportionately removes the larger males (Heppell et al., 2006; Brooks et al., 2008). By the late 1980s, the Red Hind population near St. Thomas, USVI showed signs of decline with a decrease in mean fish size and an extremely skewed sex ratio (Beets and Friedlander, 1992). This decline has led to increasingly restrictive harvest guidelines.

Red Hind is an important species in commercial, recreational, and subsistence fisheries in the Caribbean, particularly in Puerto Rico and the USVI, where Red Hind have historically comprised the majority of finfish landings (Cummings et al., 1997). Over the last 30 years, fishery managers have implemented regulations to improve the declining Red Hind populations and to protect spawning aggregation sites. In 1990, the Red Hind Bank Marine Conservation District (MCD) was established to protect a fish spawning aggregation site south of St. Thomas, USVI by seasonally closing the area to fishing during the months of peak spawning activity (December through February). In 1999, the MCD was permanently closed to fishing. Several studies (Beets and Friedlander, 1992; Sadovy De Mitcheson et al., 1992; Beets and Friedlander, 1999; Nemeth, 2005; Nemeth et al., 2007) have surveyed the Red Hind population at the spawning aggregation in the MCD in the intervening years, but to date, no holistic analysis of the change in population status, compiled using all extant data, has been conducted.

In the most recent Red Hind stock assessment (SEDAR, 2014), the types of management benchmarks that could be set were constrained as there were limited data to perform a traditional stock assessment reliant on an estimate of the stock-recruitment relationship. Data-limited fisheries assessments often lack age, growth, and maturation data or abundance indices from which stock-recruitment relationships are derived, but size distribution data are easily collected and can be the only source of information for some stocks (Quinn and Deriso, 1999; Rudd et al., 2019). The population spawning potential ratio (SPR) can be used as a proxy for maximum sustainable yield when traditional population metrics are unavailable (Rudd and Thorson, 2018). The SPR describes the proportion of the reproductive population remaining in a fished population relative to its unfished state (Goodyear, 1993; Walters and Martell, 2004). The SPR can be used to evaluate population status and to set target benchmarks for fisheries management (Myers et al., 1994; Slipke et al., 2002; Ault et al., 2008; Brooks et al., 2010; Hordyk et al., 2015a; Prince et al., 2015; Stock et al., 2021), with harvest strategies that are expected to result in 40% unfished spawning stock biomass (SPR ≥ 0.4) considered risk adverse for many species (Clark, 1993; Clark 2002; Mace, 1994; Rudd and Thorson, 2018). Length-based assessment methods provide a way to evaluate stock status of data-limited fisheries because SPR can be calculated using knowledge of basic life history ratios and size distribution data (Pauly and Morgan, 1987; Basson et al., 1988; Gulland and Rosenberg, 1992; Beverton and Holt, 2012; Hordyk et al., 2015a; Hordyk et al., 2015b). Other less data-intensive metrics used to evaluate population status or recovery at fish spawning aggregations are the change in population mean size, size distribution, and sex ratio (Coleman et al., 1996; Beets and Friedlander, 1999; Nemeth, 2005; Heppell et al., 2012; Nemeth et al., 2020; Waterhouse et al., 2020).

Our study (1) uses contemporary *in situ* size distribution and sex ratio data to document population demographics at the Red Hind spawning aggregation in the MCD during peak spawning events from 2018 to 2020, and (2) includes these data with historical size distribution data collected over the previous 30 years in length-based stock assessment models to track changes in the SPR of the Red Hind population under seasonal and then permanent spawning aggregation site protection. The results of our work highlight the value of using length-based methods to assess the response of Red Hind in the USVI to increasing levels of protection and the potential of this method to be applied for other data-limited reef fish populations.

METHODS
Study Site
There are two known Red Hind spawning aggregation sites in the USVI, one located near St. Thomas, and one located near St. Croix. These two spawning aggregation sites are located 80 km apart and are separated by the Virgin Islands Trough (4,000 m deep) and likely serve two separate populations (Nemeth et al., 2007); this study focuses on the Red Hind population at the spawning aggregation in the Red Hind Bank Marine Conservation District (MCD; **Figure 1**). The MCD is located approximately 16 km south of St. Thomas and approximately 25 km southeast of Culebra, Puerto Rico. Red Hind that spawn at this location are known to have home reefs as far west as Culebra (Nemeth et al., 2007).
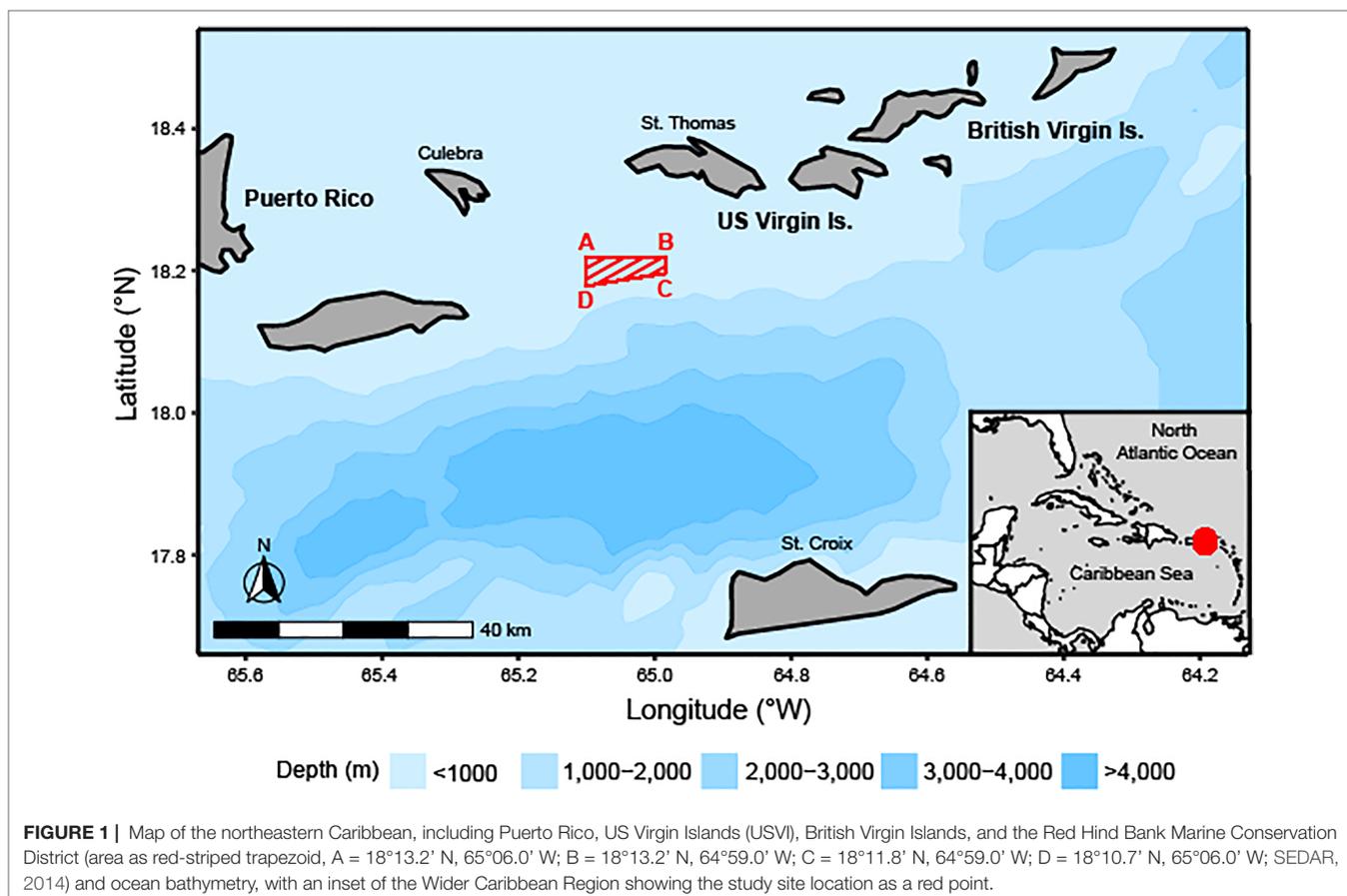
Population Demography
We sampled Red Hind at the spawning aggregation in the MCD to target peak spawning events in December 2018, January 2019, December 2019, and January 2020. With assistance from the USVI Division of Fish and Wildlife and local fishers, we captured Red Hind using baited hook and line, which is a sampling technique used in several studies to describe the size distribution and sex ratio within a spawning aggregation (Beets and Friedlander, 1992; Shapiro et al., 1993b; Beets and Friedlander, 1999; Nemeth,

2005; Luckhurst et al., 2006; Nemeth et al., 2006). All species caught were documented; non-target species were immediately recompressed at depth (ranging from 38.5 m to 48.5 m) using a commercially available descending device (SeaQualizer™), while Red Hind were retained briefly for data and sample collection and then released in a similar manner. Our work was completed with approval from the National Oceanic and Atmospheric Administration National Marine Fisheries Service Sustainable Fisheries Division and followed an approved protocol from the Institutional Animal Care and Use Committee at Oregon State University.

Size Distribution
We measured the total length (TL) of each Red Hind to the nearest millimeter and recorded the date, time, location, and depth at capture. To minimize the effects of barotrauma, this process was conducted as quickly as possible. Typically, fish were on deck less than two minutes.

Analyses of size distribution data were conducted using R version 4.0.3 (R Core Team, 2020). Alpha levels for all statistical tests were 0.05. Size distribution data for each sampling event were evaluated as to whether data met assumptions of parametric testing. Size distribution data were tested for normality with a Shapiro-Wilk test and were square transformed if $p \leq 0.05$. To investigate how fish size varied between spawning events,

FIGURE 1 | Map of the northeastern Caribbean, including Puerto Rico, US Virgin Islands (USVI), British Virgin Islands, and the Red Hind Bank Marine Conservation District (area as red-striped trapezoid, A = 18°13.2' N, 65°06.0' W; B = 18°13.2' N, 64°59.0' W; C = 18°11.8' N, 64°59.0' W; D = 18°10.7' N, 65°06.0' W; SEDAR, 2014) and ocean bathymetry, with an inset of the Wider Caribbean Region showing the study site location as a red point.

we ran a one-way analysis of variance (ANOVA) test with fish size as the response variable and sampling event (December 2018, January 2019, December 2019, and January 2020) as the predictor variable and conducted a Tukey's HSD *post-hoc* test for multiple comparisons. We calculated mean fish size (TL) of individuals for each spawning event. Data were pooled, and we calculated mean fish size (TL) of individuals over the 2018–2020 study period. Size distribution data of females and males over the 2018–2020 study period were evaluated as to whether data met assumptions of parametric testing. Data were tested for normality with a Shapiro-Wilk test and were square transformed if $p \le$ 0.05. The size distribution of females was normal (Shapiro-Wilk test, $p > 0.05$), whereas the size distribution of males was left-skewed (Shapiro-Wilk test, $p < 0.001$); both distributions were transformed for statistical comparison. To investigate whether females were smaller than males (as expected for protogynous hermaphrodites), we ran a two-sample, one-sided t-test with fish size as the response variable and fish sex as the predictor variable.

Sex Ratio

For each Red Hind captured, we attempted to collect a blood sample to determine fish sex. If the seas were too rough or the fish had been on deck for too long, we refrained from taking a blood sample. We collected blood samples from the caudal vein using a heparinized syringe and samples were stored on ice until centrifuged to separate out the plasma. Plasma samples were then frozen until analysis. We determined sex based on relative hormone concentrations of estradiol and 11-ketotestosterone using commercially available enzyme-linked immunosorbent assays (ELISAs; Cayman Chemical Company, 2022). We randomly selected a subsample from all plasma samples available for analysis. Plasma samples were first tested for interference to evaluate the need for purification. Interference levels were determined to be sufficiently high (>20%) to warrant purification, so samples were extracted prior to measuring hormone levels. Estradiol and 11-ketotestosterone levels in blood plasma were measured following protocols from the manufacturer (Cayman Chemical Company, 2022). The ratio of estradiol to 11-ketotestosterone was used to determine fish sex (Heppell and Sullivan, 2000). The derived sex ratios (F:M) represent the ratio of female fish relative to one male.

Population Demographics Over Time

To evaluate how Red Hind population demographics have changed over time at the spawning aggregation, we compared population sex ratio, mean fish size (TL), mean size (TL) of females, and mean size (TL) of males from this study period (2018–2020) and historical studies conducted at the spawning aggregation site under increasing levels of protection (**Table 1**). Historical size distribution data were extracted from published manuscripts using a free online tool, WebPlotDigitizer (Rohatgi, 2021). For studies that included multiple years of size distribution data, all years were pooled to represent a study period. Size distribution data from each study period were evaluated as to whether data met assumptions of parametric testing. Size distribution data were tested for normality with a Shapiro-Wilk test and were square transformed if $p \le 0.05$. To investigate how fish size varied between study periods, we ran a one-way analysis of variance (ANOVA) test with fish size as the response variable and study period as the predictor variable and conducted a Tukey's HSD *post-hoc* test for multiple comparisons.

Spawning Potential Ratio (SPR)

We used the length-based spawning potential ratio (LBSPR) method developed by Hordyk and colleagues (Hordyk et al., 2015a; Hordyk et al., 2015b) to estimate the SPR of the Red Hind population at the spawning aggregation site over time. The LBSPR method provides a way to evaluate stock status of data-limited fisheries because SPR can be calculated using knowledge of basic life history ratios and size distribution data (Hordyk et al., 2015a; Hordyk et al., 2015b). We fit LBSPR models to Red Hind size distribution data collected between 1988 and 2020 at the spawning aggregation in the MCD using the 'LBSPR' R package (Hordyk, 2019) and R version 4.0.3 (R Core Team, 2020). We included female-only size distribution data from historical datasets as well as our contemporary data to estimate the SPR before and after changes in spawning aggregation site protection (**Table 1**).

The LBSPR method assumes a population at equilibrium, that fish growth conforms to the von Bertalanffy equation, that there is a normal distribution of size-at-age, natural mortality rates are constant across age classes, growth rates are constant

TABLE 1 | Timeline of spawning aggregation site protections and size distribution data used to estimate population demographics and length-based spawning potential ratio over time.

Time period	Source	*n* (total sampled, females, males)	Capture method
Pre–1988	*No protections of fish spawning aggregation site*		
1988–1989	Beets and Friedlander (1992)	495, 177, 8	Baited traps, hook and line
1990	*Seasonal protection of fish spawning aggregation site*		
1997	Beets and Friedlander (1999)	395, 300*, 91	Baited traps, hook and line
1999	*Permanent protection of fish spawning aggregation site*		
2001–2003	Nemeth (2005); Nemeth et al. (2006); Nemeth et al. (2007)	2499, 545, 193	Diver surveys, baited traps, hook and line
2006–2009	R. S. Nemeth, unpublished data	1398, 491, 850	Diver surveys, baited traps
2018–2020	This study	1203, 104, 115	Hook and line

*Sample size (n) is reported for the total number of fish sampled, and the number of positively identified females and males in each study. *Authors included 36 individuals of unidentified sex that were not distinguished from females in their report.*

across cohorts, and that selectivity is asymptotic. While there is some potential for dome-shaped selectivity in fishery-dependent sampling of Red Hind landings in the USVI due to market demands for plate-sized individuals (SEDAR, 2014), the size distribution data we used to estimate SPR resulted from fishery-independent sampling at the spawning aggregation in the MCD with methods satisfying the assumption of asymptotic selectivity.

We used female-only size distribution data in our LBSPR models to avoid bias in size distribution associated with varying population sex ratio. The sex ratio (F:M) at the spawning aggregation varies widely based on the day of sampling relative to peak spawning (Shapiro et al., 1993a; Sadovy De Mitcheson et al., 1994; Beets and Friedlander, 1999; Nemeth, 2005; Whiteman et al., 2005; Nemeth et al., 2007). Since Red Hind transition from female to male with age, the larger individuals in the population are generally male. If the sex ratio is heavily skewed towards males in a given time period, but both females and males are included in LBSPR models, then during periods of extremely skewed sex ratio, SPR estimates may be biased because of the size distribution of a population with a relatively disproportionate number of larger individuals.

The life history parameter inputs to the LBSPR models included mean asymptotic size (L_∞), variability of size-at-age (CV_L), the ratio of natural mortality divided by von Bertalanffy growth coefficient (M/k), and the size at maturity schedule (**Table 2**). We included female-only size distribution data and a female-only maturity schedule (size at which 50%, L_{50}, and 95%, L_{95}, of females are mature) in the LBSPR models. The growth curve estimated for Red Hind is assumed to describe female growth (Sadovy De Mitcheson et al., 1992). Fishing mortality may differ for males and females (Sadovy De Mitcheson et al., 1994; Nemeth, 2005), but natural mortality was assumed to be the same. Life history parameters should be estimated from studies conducted in close spatial proximity to the population of interest (Prince et al., 2015), so we chose parameters calculated specifically for Red Hind at the spawning aggregation in the MCD.

The LBSPR method is particularity sensitive to the underestimation of L_∞ because as the larger-sized individuals in a sample begin to approach L_∞, estimates of SPR increase rapidly (Hordyk et al., 2015b). To better understand the influence of our selected parameters on model output, we conducted a sensitivity analysis of model-derived SPR to the values of L_∞, M, and k in each study period: 1988–1989, 1997, 2001–2003, 2006–2009, and 2018–2020. We varied each parameter (L_∞, M, and then k) by ± 10% while holding the other parameters constant.

RESULTS
Population Demography

Size Distribution
We caught, measured, and released a total of 1,203 Red Hind at the spawning aggregation site in the MCD over the 2018–2020 study period. Mean size of fish over the entire study period was 40.6 ± 0.42 cm TL (min = 22.6 cm TL, max = 48.2 cm TL; **Figure 2A**). The number of fish sampled and mean fish size (TL) varied by sampling event (one-way ANOVA, $df = 3, 1199$, $F = 12.80$, $p < 0.001$; **Table 3**). There was no evidence that mean fish size (TL) differed between the two months sampled in the 2018–2019 spawning season (Tukey's HSD, $p > 0.05$), but there was strong evidence that mean fish size (TL) differed between the two months sampled in the 2019–2020 spawning season and that mean fish size (TL) differed between both months in the 2019–2020 spawning season compared to both months in the 2018–2019 spawning season (Tukey's HSD, $p < 0.05$). The size distribution was progressively dominated by males towards the upper end of the distribution (**Figure 2B**), as expected for protogynous hermaphrodites. Females (39.6 ± 0.76 cm TL, $n = 104$) were smaller than males (42.6 ± 0.52 cm TL, $n = 115$; two-sample t-test, $t = -8.84$, $df = 217$, one-sided $p < 0.001$).
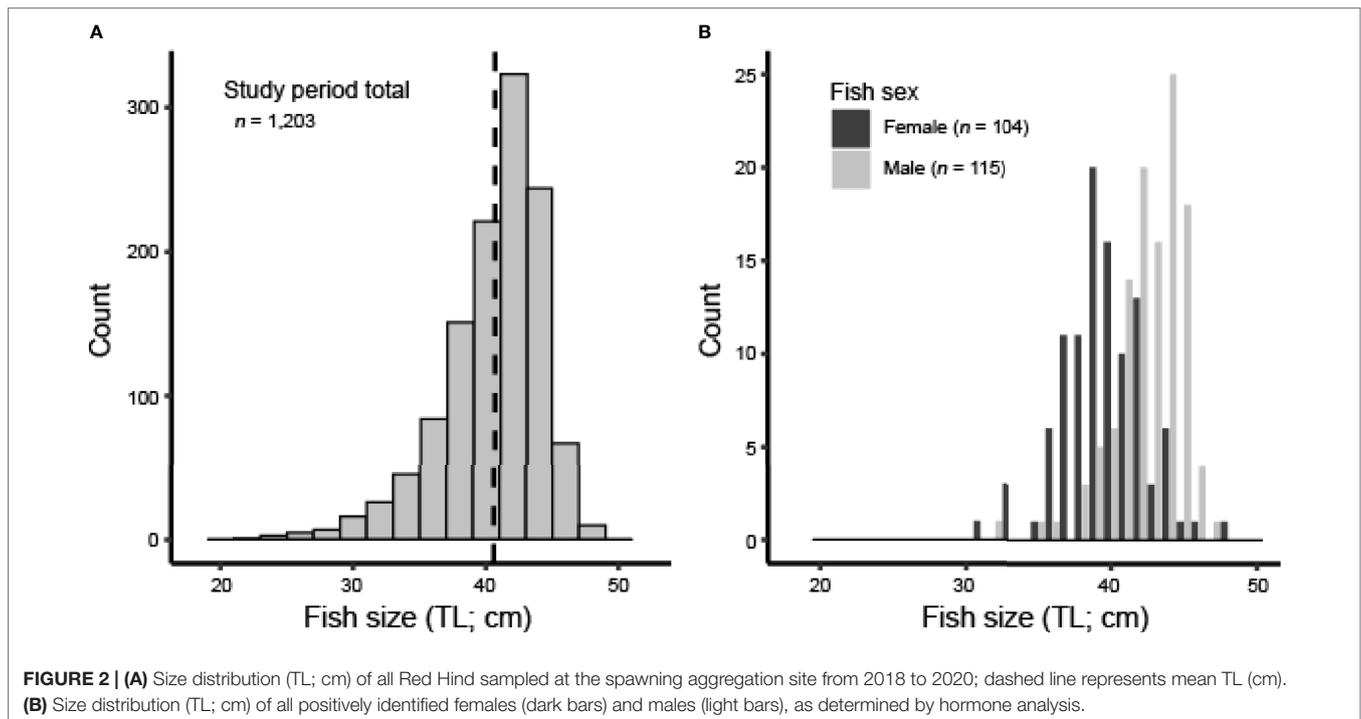
Sex Ratio
Of the 1,203 Red Hind sampled at the spawning aggregation over the 2018–2020 study period, we determined the sex of 219 (18.2%). The ratio of females to males varied between sampling events. Sex ratio was skewed towards males in days leading up to the full moon, whereas the sex ratio was skewed towards females in days following the full moon (**Table 4**). The overall sex ratio for the study period was 0.90:1 (F:M), but comparison of the sex-specific size distributions with the size distribution of all individuals sampled at the spawning aggregation indicated that the sex ratio of the total sample was likely more skewed to females than reported here because the overall mean size (TL) was closer to that of the mean size (TL) of females than of males.

Population Demographics Over Time
The mean size (TL) of fish at the spawning aggregation increased over time and with increased spawning aggregation site protections. The mean fish size (TL) 30 years after protection at the spawning aggregation site was 11.1 cm TL (37.6%) larger than the mean fish size reported from Red Hind landings data in

TABLE 2 | Biological parameters used to fit the length-based spawning potential ratio models.

Parameter		Value	Source
L_∞	Mean asymptotic size (cm)	60.10	Sadovy De Mitcheson et al. (1992)
CV_L	Variability of size-at-age	0.10	Assumed (Hordyk et al., 2015b)
M	Natural mortality (1/year)	0.16	Sadovy De Mitcheson and Figuerola (1992)
k	Growth coefficient (1/year)	0.0705	Sadovy De Mitcheson et al. (1992)
M/k		2.27	
L_{50}	Size at 50% maturity (cm)	21.50	Sadovy De Mitcheson et al. (1994)
L_{95}	Size at 95% maturity (cm)	27.50	Sadovy De Mitcheson et al. (1994)
	Bin width (cm)	1	
	Maximum size (cm)	67	
	Minimum size (cm)	1	

FIGURE 2 | (A) Size distribution (TL; cm) of all Red Hind sampled at the spawning aggregation site from 2018 to 2020; dashed line represents mean TL (cm).
(B) Size distribution (TL; cm) of all positively identified females (dark bars) and males (light bars), as determined by hormone analysis.

1988, prior to protection (Beets and Friedlander, 1992; **Table 5**). The cumulative size frequency distribution of female fish shifted to larger sizes over time (**Figures 3A, B**). There was strong evidence that the mean size (TL) of females differed between study periods (one-way ANOVA, $df = 4, 1552, F = 68.34, p < 0.001$), except for between 1997 and 2006 to 2009 (Tukey's HSD, $p > 0.05$). The mean size (TL) of females from 2006 to 2009 may have decreased due to a number of females transitioning to males, thereby also causing a decrease in the mean size (TL) of males, with the overall mean size (TL) of fish at the spawning aggregation from 2006 to 2009 continuing to increase (**Table 5**). The decrease in mean size (TL) of females from 2006 to 2009 may have been due in part to the recruitment of smaller females to the population of spawners.

Spawning Potential Ratio (SPR)

Our length-based stock assessment models included size distributions of female fish in the following study periods: 1988–1989, 1997, 2001–2003, 2006–2009, and 2018–2020. In the late 1980s, before seasonal or permanent protection at the spawning aggregation, the SPR of the Red Hind population at the spawning aggregation in the MCD was 0.32 (95% CI: 0.25, 0.39; **Figure 4**). Pre-protection SPR was lower than the traditional target benchmark of

SPR ≥ 0.40. In 1997, following seven years of seasonal protection, the SPR increased slightly to 0.35 (95% CI: 0.28, 0.42). Permanent protection of the spawning aggregation site was put into place in 1999. In the early 2000s, the SPR increased to 0.41 (95% CI: 0.35, 0.46), above the traditional target, but then from 2006 to 2009, decreased to 0.36 (95% CI: 0.31, 0.41), likely due to larger females transitioning to males and the recruitment of smaller females. After 20 years of continued permanent protection of the spawning aggregation site, the SPR increased to its highest level yet at 0.49 (95% CI: 0.42, 0.56).

Sensitivity analysis revealed that estimates of SPR were sensitive to mean asymptotic size (L_∞) and less so to our assumption of natural mortality rate (M) and the growth coefficient (k; **Supplementary Table 1**).

TABLE 3 | Sample size (**n**) and mean fish size (TL; cm) ± SE of Red Hind caught at the spawning aggregation site over the 2018–2020 study period.

Sampling event	n	Mean fish size (TL; cm) ± SE
December 2018	348	40.9 ± 0.86
January 2019	476	40.9 ± 0.55
December 2019	64	38.1 ± 3.26
January 2020	315	40.1 ± 0.73
2018–2020 study period	1,203	40.6 ± 0.42

TABLE 4 | The number of and sex ratio of females to males in daily catches relative to days from the full moon, summarized by month and over the 2018–2020 study period.

Date	Days to full moon	F	M	Ratio (F:M)
12/19/2018	-3	0	7	
12/20/2018	-2	4	8	0.50:1
12/22/2018	0	4	14	0.29:1
December 2018 total:		8	29	0.28:1
01/18/2019	-3	7	17	0.41:1
01/19/2019	-2	7	11	0.64:1
01/21/2019	0	17	14	1.21:1
01/22/2019	+1	12	11	1.09:1
January 2019 total:		43	53	0.81:1
12/15/2019	+3	0	1	
December 2019 total:		0	1	
01/16/2020	+6	27	13	2.08:1
01/17/2020	+7	26	19	1.37:1
January 2020 total:		53	32	1.66:1
2018–2020 study period		104	115	0.90:1

TABLE 5 | Population sex ratio and mean fish size (TL; cm) ± SE of Red Hind at the spawning aggregation site for each study period and mean fish size (TL; cm) ± SE of positively identified females and males.

Study period	Source	Sex ratio (F:M)	Mean fish size (TL; cm) ± SE	Mean size of females (TL; cm) ± SE	Mean size of males (TL; cm) ± SE
1988–1989	Beets and Friedlander (1992)	14.6:1	29.5*	34.0* 33.2** ± 0.38**	39.7*
1997	Beets and Friedlander (1999)	2.9:1	36.6*	35.3** ± 0.19**	41.2* ± 0.48*
2001–2003	Nemeth (2005); Nemeth et al. (2006); Nemeth et al. (2007)	2.8:1	38.0 ± 0.08	36.9 ± 0.14	42.0 ± 0.24
2006–2009	R. S. Nemeth, unpublished data	0.6:1	38.8 ± 0.11	35.5 ± 0.14	40.9 ± 0.09
2018–2020	This study	0.9:1	40.6 ± 0.42	39.6 ± 0.76	42.6 ± 0.52

*As reported in source study. **calculated from published fish size distributions, otherwise calculated from raw data.*

DISCUSSION

This study evaluates the impact of reducing and then eliminating fishing pressure from a spawning aggregation site as a marine conservation effort to aid in the recovery of a reef fish population. Fishing pressure is the predominant factor that affects the size and abundance of groupers in the Caribbean (Sluka et al., 1997; Chiappone et al., 2000), and aggregation fishing is one of the greatest sources of catch for aggregating species (Sadovy De Mitcheson et al., 2008). The MCD south of St. Thomas, USVI was established to protect a known spawning aggregation site from fishing pressure, first seasonally in 1990 and then permanently in 1999. We document the demographic recovery of the Red Hind population at the spawning aggregation in the MCD over 30 years of increasing protections using length-based assessment methods and historical and contemporary *in situ* size distribution data. After 10 years of seasonal protection and 20 years of permanent protection at the spawning aggregation site, the overall mean size (TL) of Red Hind increased by >35%, the population sex ratio is less skewed, and the SPR is above a management benchmark considered conservative for many fisheries (Clark, 1993; Clark 2002; Mace, 1994; Rudd and Thorson, 2018). Population recovery of Red Hind in the USVI has tracked management decisions to increase protections at the spawning aggregation site.

With the reduction in fishing pressure at the spawning aggregation site, a gradual return to a population structure that includes a higher proportion of older and larger fish is expected; however, this recovery can take decades, depending on life history and reproductive strategy (White et al., 2013; Kaplan et al., 2019). Red Hind are long-lived (max. 22 years) and reach their maximum size slowly (Sadovy De Mitcheson et al., 1994). The timing of recovery of the proportion of older and larger individuals in the population (in this case, males) after protection is difficult to predict, particularly for protogynous hermaphrodites (Easter et al., 2020). We note that the size distribution of females sampled in the 2018–2020 study period is normally distributed, but the size distribution of males is left-skewed and is missing the upper tail of larger individuals. The absence of larger males may indicate that the size structure of the population is still filling in after years of protection. Another reason why larger males are less represented in the size distribution may be due to size-selective fishing mortality outside of the MCD, with commercial fishing
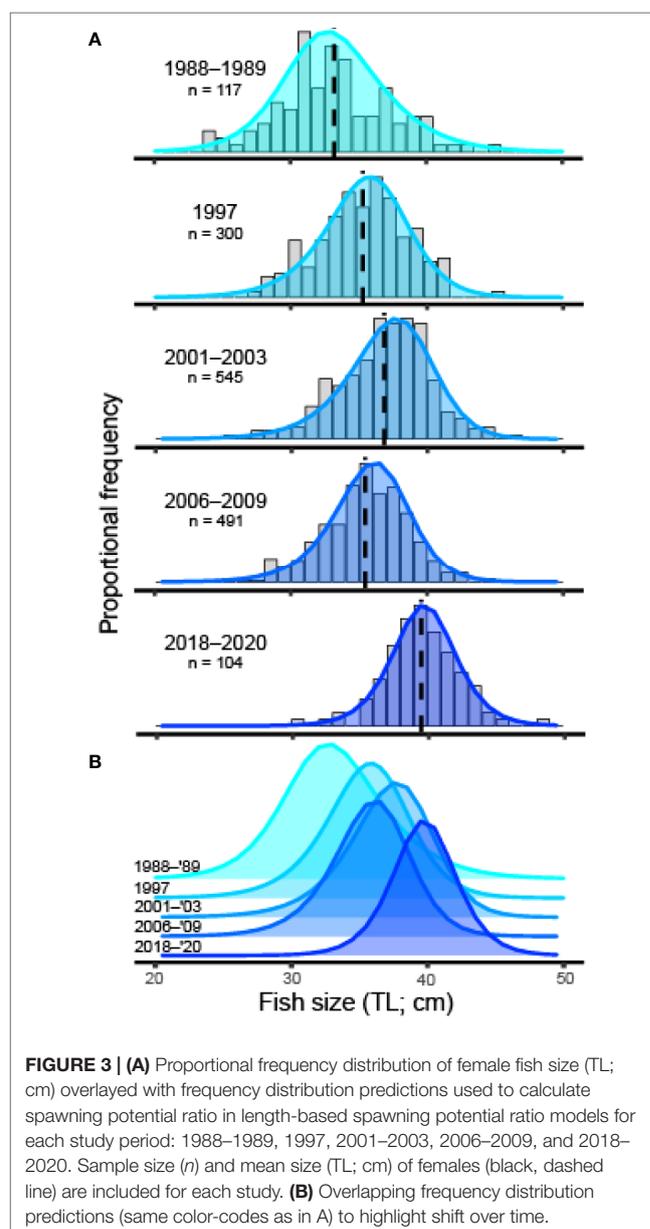
FIGURE 3 | (A) Proportional frequency distribution of female fish size (TL; cm) overlayed with frequency distribution predictions used to calculate spawning potential ratio in length-based spawning potential ratio models for each study period: 1988–1989, 1997, 2001–2003, 2006–2009, and 2018–2020. Sample size (*n*) and mean size (TL; cm) of females (black, dashed line) are included for each study. **(B)** Overlapping frequency distribution predictions (same color-codes as in A) to highlight shift over time.
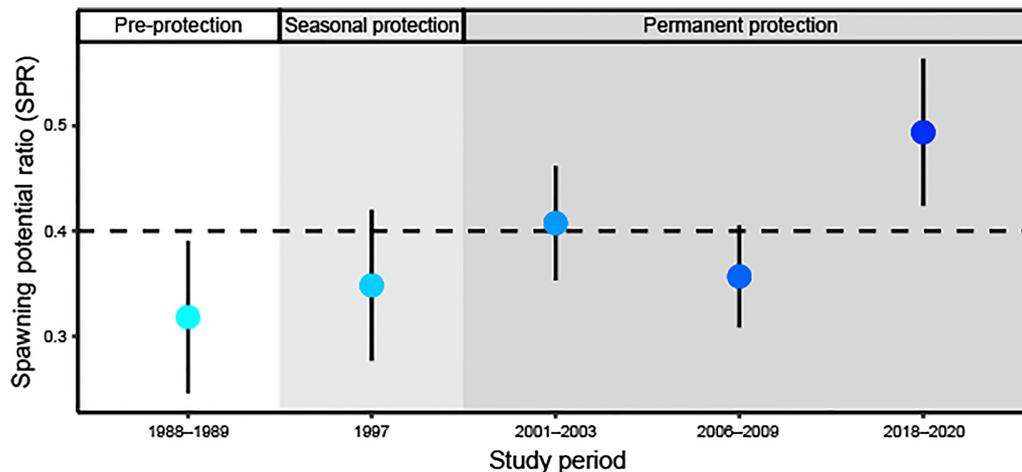
FIGURE 4 | Estimated spawning potential ratio (SPR; ± 95% CI) of Red Hind population over time at the spawning aggregation site under no protection (white background), seasonal protection (light grey background), and permanent protection (dark grey background). The horizontal dashed line at SPR = 0.40 represents the lower limit of what is considered sustainable for most fish species.

activity disproportionately targeting larger males occupying offshore reefs (Nemeth, 2005). It is important then, that this population has been surveyed multiple times over the decades to track changes in population structure to assess recovery.

The recovery of the population size structure may lead to an increase in reproductive potential. The mean size of female fish at the spawning aggregation increased from 34.0 cm TL pre-protection (Beets and Friedlander, 1992) to 39.6 cm TL in the 2018–2020 study period, with the overall size distribution of females gradually shifting to larger fish. A survey of the Red Hind population at the spawning aggregation site found that female Red Hind larger than 37.0 cm have higher potential fecundities than those smaller than 37.0 cm and there is a rapid increase in potential fecundity with total length (Whiteman et al., 2005). The mean size of females in the 2018–2020 study period, after 30 years of protection, is above the 37.0 cm threshold, indicating that a greater proportion of the population may be contributing significantly more to larval production. Our study did not estimate reproductive output, nor did we investigate whether recruitment rates have changed over time, but both may be worth future experimental or theoretical studies to understand if the increase in mean size of females over time has impacted stock recruitment.

Heavy exploitation of spawning aggregations can alter sex ratios of hermaphroditic species (Beets and Friedlander, 1992; Carter and Perrine, 1994; Coleman et al., 1996; Koenig et al., 1996; Domeier and Colin, 1997). Before the MCD was established, the sex ratio of the population at the spawning aggregation site was heavily skewed towards females (15 females per male; Beets and Friedlander, 1992). A population with a highly skewed sex ratio may experience a decrease in reproductive success. Red Hind mate in small clusters of multiple females per male (Colin et al., 1987; Shapiro et al., 1993a), and gonad size of males and females is similar (Sadovy De Mitcheson et al., 1994), indicating that sperm limitation is unlikely unless the sex ratio is so skewed towards females to the point that there is lower fertilized egg output (Alonzo and Mangel, 2004; Heppell et al., 2006).

The sex ratio after 30 years of protection at the spawning aggregation site is within the range considered biologically balanced for this population (Whiteman et al., 2005). The sex ratio is skewed towards males in days leading up to the full moon and is skewed towards females in days following the full moon. This pattern of occupancy of the spawning aggregation site is consistent with that observed at this site previously and at other Red Hind spawning aggregation sites in the Caribbean, with the sex ratio skewed more towards males prior to spawning and then towards females during peak spawning (Sadovy De Mitcheson et al., 1994; Beets and Friedlander, 1999; Whiteman et al., 2005; Nemeth et al., 2007).

A challenge for sustainable fisheries management is developing cost-effective ways to determine stock status of data-limited fisheries. Length-based assessment methods have been employed around the world because they offer a way to assess the stock status of fisheries without requiring expensive data inputs (Prince et al., 2015; Stock et al., 2021). The LBSPR method that we use in this study has also been applied to other data-limited populations of grouper (Serranidae) in the Caribbean to assess population status at fish spawning aggregations before and after protection. In the Cayman Islands, Nassau grouper spawning aggregation site protection led to the recovery of the population size structure and SPR after 16 years of protection, but the rate and extent of recovery may have been driven by successful periodic recruitment (Stock et al., 2021). Although SPR ≥ 0.40 is considered sustainable for many fish species, adjusting the target upwards may be necessary to achieve maximum sustainable yield for vulnerable fish life histories (Clark 2002; Brooks et al., 2010; Zhou et al., 2020).

After 10 years of seasonal protection and 20 years of permanent protection from fishing pressure in the MCD, the SPR of the Red Hind population at the spawning aggregation has increased from 0.32 (95% CI: 0.25, 0.39) to 0.49 (95% CI: 0.42, 0.56), above the benchmark considered sustainable for many fisheries (Clark, 1993; Clark 2002; Mace, 1994; Rudd and Thorson, 2018). Red Hind that are resident within the MCD gained additional protection when

protection became year-round. This particular Red Hind population has experienced demographic recovery after spawning aggregation site protection at a different rate than other Red Hind populations in the Caribbean, possibly due to historic fishing pressure or other population dynamics (Sadovy De Mitcheson and Figuerola, 1992; Nemeth et al., 2006). The increase in the SPR of the population of Red Hind represents a conservation success, but it is possible that the target SPR of the population needs to be higher still to maintain a sustainable fishery.

Spawning aggregations are necessary for the successful reproduction of many reef fishes, but fishing at spawning aggregations has led to the decline of many important fishery species around the world (Sadovy De Mitcheson et al., 2008). Fish spawning aggregation site protection is used as a management tool to aid in population recovery (Grüss et al., 2014). To evaluate the effectiveness of spawning aggregation site protection, it is necessary to assess stock status over time as it may take decades for the population structure to fully recover (White et al., 2013; Kaplan et al., 2019). Our study uses historical and contemporary data to monitor recovery of a Red Hind population over 30+ years, from 1988 to 2020. The population of Red Hind at the spawning aggregation site south of St. Thomas, USVI has recovered according to multiple population metrics: an increase in overall mean fish size (TL), a less skewed sex ratio, and an increase in the population SPR. The USVI Red Hind fishery has tracked recovery of the population at the spawning aggregation site, with an increase in mean size of landed Red Hind and a perceived increase in catch rates (Beets and Friedlander 1999; Nemeth, 2005). Most fishers are supportive of the spawning aggregation site closure because of the perceived enhancement of the local fishery (Beets and Friedlander, 1999; Nemeth, 2005). Management decisions, participation of fishers in acknowledging closures, and long-term monitoring have contributed to the conservation success that is the recovery of the Red Hind population at the spawning aggregation site south of St. Thomas, USVI.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: https://github.com/rclairer/population_recovery_with_marine_conservation.

ETHICS STATEMENT

The animal study was reviewed and approved by Institutional Animal Care and Use Committee at Oregon State University.

AUTHOR CONTRIBUTIONS

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.931409/full#supplementary-material

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