ICES Journal of
Marine Science

ICES Journal of Marine Science (2021), 78(1), 277–292. doi:10.1093/icesjms/fsaa221

Original Article

Pulse recruitment and recovery of Cayman Islands Nassau Grouper (*Epinephelus striatus*) spawning aggregations revealed by *in situ* length-frequency data

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Stock, B. C., Heppell, S. A., Waterhouse, L., Dove, I. C., Pattengill-Semmens, C. V., McCoy, C. M., Bush, P. G., Ebanks-Petrie, G., and Semmens, B. X. Pulse recruitment and recovery of Cayman Islands Nassau Grouper (*Epinephelus striatus*) spawning aggregations revealed by *in situ* length-frequency data. – ICES Journal of Marine Science, 78: 277–292.

Received 16 April 2020; revised 14 October 2020; accepted 29 October 2020; advance access publication 8 January 2021.

Fish spawning aggregations (FSAs) are vulnerable to overexploitation, yet quantitative assessments of FSA populations are rare. We document an approach for how to conduct such an assessment, evaluating the response of Critically Endangered Nassau Grouper (*Epinephelus striatus*) to protections in the Cayman Islands. We assessed pre-protection status on all islands using length data from fishery catch. We then used 17 years of noninvasive length-frequency data, collected via diver-operated laser calipers, to estimate recruitment and spawning biomass of Nassau Grouper on Little Cayman following protection. Bimodal length distributions in 2017–2019 indicated a large recruitment pulse (4–8× average) derived from spawning in 2011. Biomass recovered to 90–106% of the pre-exploitation level after 16 years, largely driven by the strong 2011 year class. Length distributions were also bimodal in 2017–2019 on nearby Cayman Brac, implying a synchronous recruitment pulse occurred on both islands. Our results demonstrate that: (i) *in situ* length data can be used to monitor protected FSAs; (ii) spatiotemporal FSA closures can be effective, but success takes time if population recovery depends upon sporadic recruitment; and (iii) FSA fishery management targets may need to be higher than commonly recommended (i.e. spawning potential ratio >0.6 instead of 0.4).

Keywords: coral reef fishery, data limited, fish spawning aggregation, length based, population recovery, spawning potential ratio, stock assessment

Introduction

Fisheries management based on traditional stock assessments and effort controls has been effective at reducing overfishing for many fish populations (Beddington *et al.*, 2007; Worm *et al.*, 2009; Hilborn *et al.*, 2020). However, one longstanding challenge occurs when fish exhibit aggregating behaviour that sustains high total catch and catch rates [i.e. catch-per-unit-effort (CPUE)] while abundance steeply declines. The formation of transient fish spawning aggregations (FSAs) is one such behaviour that leads to extremely high biomass density, readily predictable in space and time, and therefore often targeted by fisheries (Johannes, 1998; Claro and Lindeman, 2003; Sadovy and Domeier, 2005; Sadovy de Mitcheson and Erisman, 2012). Failing to recognize the "hyperstability" of FSA fisheries has contributed to notable collapses, such as for northern cod (Rose and Kulka, 1999) and orange roughy (Clark, 2001). Although less well publicized and smaller scale, many fisheries that target FSAs of large-bodied tropical reef species such as grouper (Epinephelidae) and snapper (Lutjanidae) have also collapsed (Johannes, 1998; Sadovy de Mitcheson *et al.*, 2008; Claro *et al.*, 2009; Robinson *et al.*, 2015). In response to these declines, spatiotemporal closures are increasingly advocated as a practical and enforceable way to reduce fishing mortality (*F*) at FSAs, which can be very intense over small temporal and spatial scales (e.g. days and 100 s of metres; Russell *et al.*, 2012; Sadovy de Mitcheson, 2016).

Many spatiotemporal closures have been implemented to conserve FSAs, and cost-effective data collection and assessment methodologies are urgently needed to evaluate these protections (Claro and Lindeman, 2003; Grüss *et al.*, 2014; Sherman *et al.*, 2016). In most cases, populations continue to decline after protection or their status is unknown (Table 11.1 in Russell *et al.*, 2012). Well-documented cases of FSA population increase following spatiotemporal protection do exist (Russ and Alcala, 2004; Nemeth, 2005; Luckhurst and Trott, 2009; Hamilton *et al.*, 2011; Sadovy de Mitcheson and Colin, 2012; Waterhouse *et al.*, 2020), but these are uncommon and rarely based on population dynamics models that can help explain the mechanisms underlying recovery through estimation of *F* and recruitment. Fisheries-dependent indices of abundance (e.g. CPUE) data can be cost effective to collect for non-protected FSAs but must be interpreted with caution due to concerns about hyperstability (Rose and Kulka, 1999; Robinson *et al.*, 2015). Fisheries-independent surveys based on underwater visual census, mark-recapture, or acoustics techniques are informative but require more resources. Length-frequency data are relatively cost-effective to collect, and length-based analyses of FSAs soon after protections have shown increases in the mean size of fish, as expected due to reduced *F* (Beets and Friedlander, 1999; Nemeth, 2005; Luckhurst and Trott, 2009). Longer-term population recovery, however, is indicated by the recruitment of smaller fish and a trend toward an unfished length structure with a broad range of sizes (Heppell *et al.*, 2012). Ideally, length-frequency data could be collected over multiple years and used in an assessment model that can distinguish between changes in size due to changes in *F* vs. changes in recruitment (e.g. Rudd and Thorson, 2018). For protected FSAs, scientists can use noninvasive methods such as underwater visual census, stereo cameras, or laser calipers to obtain length measurements (Colin, 2012a; Heppell *et al.*, 2012). At FSAs where harvest is allowed, scientists can also collect length and weight data from the catch.

Study species: Nassau Grouper

Overfishing of FSAs has driven striking declines of Nassau Grouper (*Epinephelus striatus*) throughout the Caribbean Sea, providing a classic example of the challenge that aggregation behaviour poses for fisheries management (Sala *et al.*, 2001; Sadovy de Mitcheson *et al.*, 2020). Like many large-bodied (mature adults range from 45 to 90 cm total length), long-lived (at least 29 years), high trophic level reef fish, Nassau Grouper, are both highly sought after and vulnerable to fisheries (Sadovy and Eklund, 1999; Patrick *et al.*, 2010; Hobday *et al.*, 2011). Nassau Grouper are territorial and solitary outside spawning season but form extremely dense FSAs at highly predictable sites and times to spawn (e.g. 30 000 individuals in a 100 m × 500 m area; Smith, 1972). Nassau Grouper FSAs historically supported one of the most important finfish fisheries in the Caribbean, but intense and uncontrolled FSA fishing has led to the disappearance of two-thirds of known Nassau Grouper FSAs and a *Critically Endangered* listing by the IUCN (Sadovy de Mitcheson *et al.*, 2008; Sadovy *et al.*, 2018). The United States has prohibited take and possession of Nassau Grouper since 1990 and recently listed the species as *Threatened* under the U.S. Endangered Species Act (NMFS, 2016). Several governments, including Mexico, Belize, the Cayman Islands, and The Bahamas, have instituted spatial protections at known Nassau Grouper FSA sites and/or temporal protections covering the spawning season. These efforts have generally been successful at reducing *F*, but recovery has been variable and quantitative estimates of population responses—either abundance or size frequency—are rare (Ehrhardt and Deleveaux, 2007; Heppell *et al.*, 2012; Sadovy de Mitcheson and Colin, 2012; Cheung *et al.*, 2013; Waterhouse *et al.*, 2020).

In the Cayman Islands, a UK Overseas Territory in the Caribbean Sea, Nassau Grouper FSAs historically formed at five known locations (Figure 1). An additional FSA exists at Pickle Bank, an offshore seamount whose political jurisdiction is unclear due to the overlapping Exclusive Economic Zones of the Cayman Islands and Cuba. Fishermen have targeted Cayman FSAs with small boats and handlines around the full moons in January and February since the early 1900s (Bush *et al.*, 2006). Responding to fishermen's concerns over declining numbers and size of Nassau Grouper, in 1985 the Cayman Islands government restricted fishing FSAs to only residents using hook-and-line gear. In 1987, the Cayman Islands Department of the Environment (CI-DoE) began monitoring CPUE and collecting biological data (length, weight, sex, and age; Bush and Ebanks-Petrie, 1994). This study produced the most complete growth curve and oldest recorded individual for the species (29 years) and showed that total catch, CPUE, and mean size declined at all the main Cayman FSAs from 1987 to 2001 (Bush *et al.*, 2006).

In 2001, local fishermen discovered a new FSA off the west end of Little Cayman and divers estimated that the aggregation had roughly 7000 fish at the time of discovery (Bush *et al.*, 2006; Whaylen *et al.*, 2007). Intense fishing by local fishermen using handlines removed around 4000 fish in two consecutive 1-week spawning seasons (ca. 2000 in 2001 and 1934 in 2002; Whaylen *et al.*, 2004). In 2003, the Cayman Islands Marine Conservation Board banned fishing on the aggregation site. Since 2003, the Grouper Moon Project, a collaboration between the CI-DoE, Reef Environmental Education Foundation (REEF), and academic scientists, has published several findings relevant to FSA assessment: (i) acoustically tagged adult fish on Little Cayman and Cayman Brac do not cross deep water to other islands and the vast

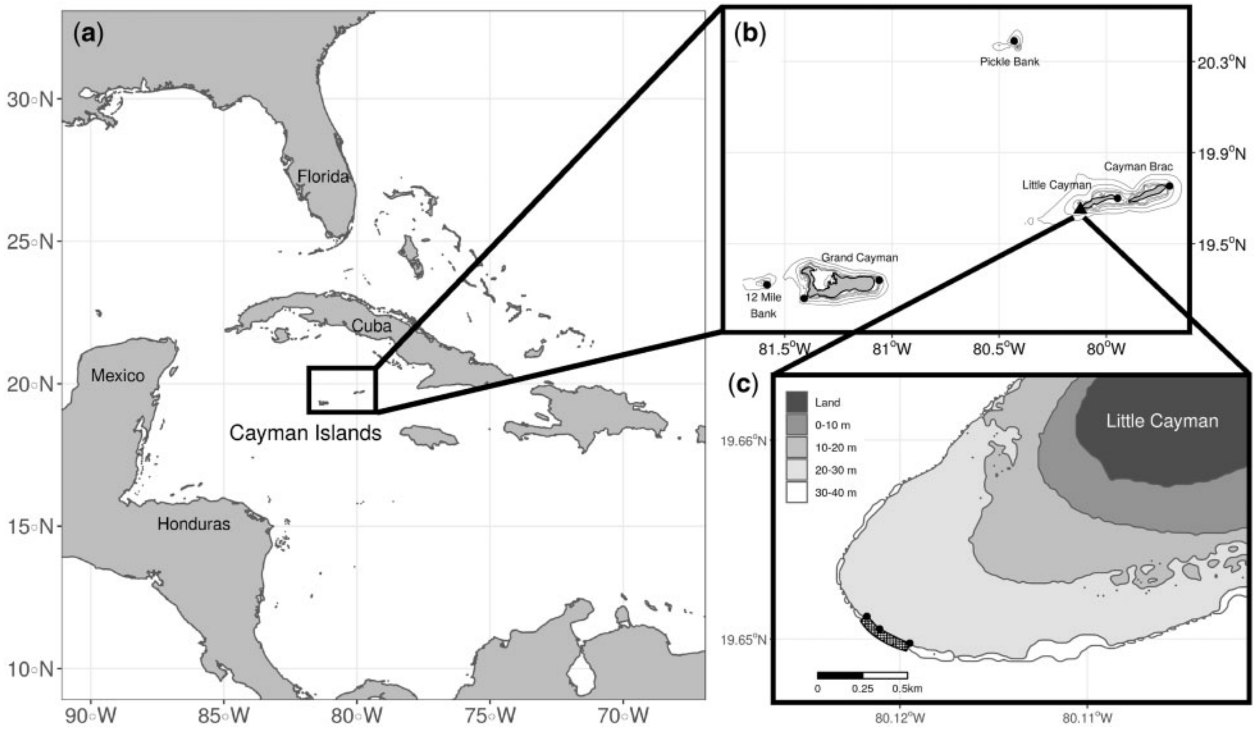

Figure 1. Map showing the location of historic and current Nassau Grouper spawning aggregations in the Cayman Islands. (a) Location of the Cayman Islands within the western Caribbean Sea. Aggregations (FSAs, black points in b) are found either at shelf edges near reef promontories (Grand Cayman, Little Cayman, Cayman Brac) or offshore seamounts that rise to within 30 m of the surface (Twelve-Mile Bank, Pickle Bank). The FSA off the west end of Little Cayman (black triangle in b, hatched area in c) is currently the largest and the focus of this study. In (b), bathymetry is shown with grey contour lines at 50, 100, 200, 500, and 1000 m. Acoustically tagged adult Nassau Grouper have not crossed deep water between islands (>200 m). In (c), the FSA site (hatched area) is defined by three moorings (points) and the shelf edge at 30–40 m.

majority of reproductive fish attend the one FSA on their island to spawn (Semmens *et al.*, 2007, 2009); (ii) a decrease in mean length coupled with an increase in size range from 2004 to 2010 suggests that recruitment occurred on Little Cayman (Heppell *et al.*, 2012); and (iii) since protection, fish numbers have increased substantially on Little Cayman, tentatively on Cayman Brac, and not at all on Grand Cayman (Waterhouse *et al.*, 2020). Based on this evidence, the Cayman Islands government renewed the initial FSA fishing bans and subsequently enacted comprehensive Nassau Grouper management via legislation (no take during spawning months, bag and slot limits away from FSAs in the rest of the year; Cayman Islands Cabinet, 2016; Waterhouse *et al.*, 2020). Management is currently settled by this legislation, and the primary objective is to ensure viability of the FSAs (i.e. FSAs form and spawning is observed) while allowing small amounts of recreational and artisanal catch outside of spawning season.

We present a case study highlighting the value of using length-frequency data to evaluate the response of Cayman Islands Nassau Grouper populations to 16 years of spatiotemporal FSA protection. We first analyse pre-protection fishery catch data to estimate growth, mortality, and sspawning potential ratio (SPR) at FSAs throughout the Cayman Islands. We then combine 17 years of *in situ* length-frequency data with an estimate of abundance into a length-based stock assessment model for the Little Cayman FSA. We specifically address the following:

(I) What was the population status at FSAs throughout the Cayman Islands before and after protections?

(II) How have population size structure and biomass changed on Little Cayman and Cayman Brac since protection?

(III) How variable was recruitment during the recovery monitoring period?

(IV) Did growth rates differ by island before or after protections?

Methods

Historical Cayman FSA sites

Of the five FSAs which supported fisheries before the closures in 2003, the CI-DoE collected fishery-dependent data (described below) primarily at the three with the vast majority of the catch, located on the east ends of Grand Cayman, Cayman Brac, and Little Cayman (Figure 1b; Bush *et al.*, 2006). Few data were collected from the other two FSAs near Grand Cayman: the southwest FSA was no longer fished after it disappeared in 1990 and Twelve-Mile Bank was sporadically exploited and yielded lower numbers of fish. We excluded these data from our analyses. Pickle Bank is not regularly exploited, but 159 fish were opportunistically caught and measured in 2000.

West end Little Cayman FSA site

Since 2003, the Grouper Moon Project has logged thousands of diver-hours observing spawning behaviour and collecting fishery-independent data (described below) at the new FSA off the west end of Little Cayman (Figure 1c; Whaylen *et al.*, 2004, 2007). For 7–10 days following the full moons in January and February, Nassau Grouper aggregate in a roughly 300 m × 50 m area well defined by three project-placed moorings, the insular shelf edge, and dive navigation lines connecting the three moorings to the shelf edge (Figure 1c).

Stock structure assumption: FSAs represent populations

Acoustic tagging of mature fish on- and off-FSA sites on Little Cayman and Cayman Brac has directly shown that only one FSA forms on each island, the vast majority (98%) of fish attend the FSA on their island, and fish do not cross deep water to other islands (Semmens *et al.*, 2007, 2009). Thus, we assumed that distinct populations exist on each island (possibly linked via larval dispersal), and that data collected from the FSAs represent the entirety of the adult population on each island. Given that Pickle Bank is smaller than either Little Cayman or Cayman Brac, surrounded by deep water, and far from either the Cayman Islands or Cuba (Figure 1), the same is likely true for Pickle Bank. Although Grand Cayman is larger and formerly supported two FSAs, the southwestern FSA disappeared by 1990 and we assumed that the 1988–1997 data from the northeastern FSA represented the entire reproductive population.

Fisheries-dependent biological data

We used biological data collected from fisheries catch at the three main FSAs between 1978 and 2002 before protections were implemented (Colin *et al.*, 1987; Bush and Ebanks-Petrie, 1994; Bush *et al.*, 2006). These data included total length, weight, and sex of commercial catch and sagittal otoliths for ageing. Colin *et al.* (1987) measured standard lengths at the Little Cayman FSA in 1978, and we converted these to total lengths using the published relationship with largest sample size and nearest proximity to the Cayman Islands (Claro 1990 in Sadovy and Eklund, 1999). The ageing method was validated by Bush *et al.* (1996) using oxytetracycline injections in captive fish. Following the methods of Bush and Ebanks-Petrie (1994) and Bush *et al.* (2006), we added 1 year to otolith ring counts because all fish were caught on FSAs and had "plus" growth. Finally, total catch estimates were available from the newly discovered west end Little Cayman FSA for the 2 years it was heavily fished (~2000 fish in 2001 and 1934 in 2002; Whaylen *et al.*, 2004).

In situ length-frequency data

For each year from 2003 to 2019, we collected noninvasive length data from the west end Little Cayman FSA using diver-operated laser calipers. In addition to the aluminium bracket system described in Heppell *et al.* (2012), we created a new system with two red laser diodes placed 20 cm apart inside a waterproof acrylic housing, with a GoPro Hero^{TM} video camera attached in front (Figure 2). We aimed to collect 500–1000 length measurements per year because simulation studies of length-based assessment methods show a performance plateau above this sample size (Hordyk *et al.*, 2015b; Rudd and Thorson, 2018). The number of dives and days necessary to achieve this sample size varied by year, primarily depending on dive conditions and currents. We also collected *in situ* length data from the Cayman Brac FSA in 2017–2019, although we were not able to collect large sample sizes ($n = 107$, 125, and 115) because there were fewer and more dispersed fish, and the site typically has challenging boat operation and dive conditions (high seas, strong currents, deeper site). See Supplementary material for details of laser caliper and stereo camera calibration, measurement error estimation, video collection, and data processing (Supplementary Figures S1–S3).

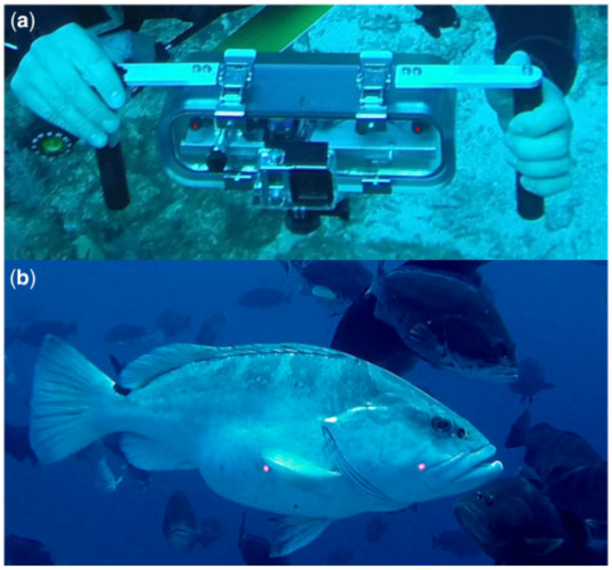

Figure 2. Laser caliper system used to measure fish lengths *in situ*. Two parallel laser diodes are placed 20 cm apart inside a custom-machined acrylic housing, with a GoPro Hero^{TM} camera in separate housing mounted in front. (a) A diver using the system. (b) Example still-frame image with the two laser dots on a fish perpendicular to the camera. The known distance between the laser dots is used as a scale to measure total length.

Fishery-independent abundance estimate, Little Cayman post-protection

In the context of assessing small-scale FSA fisheries, it is rare to have fishery-independent data on abundance. We were fortunate to have access to yearly estimates of the number of mature fish at the west end Little Cayman FSA from 2005 to 2018 (Waterhouse *et al.*, 2020), which we used as an index of abundance in a length-based stock assessment model for the Little Cayman population (described below). Waterhouse *et al.* (2020) fit a state-space model of the number of spawners, modelling the population as a random walk with drift in log-space, i.e. $\log(S_{t+1}) = \log(S_t) + \mu + \varepsilon_t$, where S_t is the number of spawners in year t, μ is the mean population growth rate, and ε_t is the annual deviation in growth rate in year t. The model was then fit to diver-collected mark-resight and video census data using Markov Chain Monte Carlo sampling. Since the assessment model (described below) assumed that the yearly abundance estimates were independent, we re-analysed the mark-resight data without the assumption that population growth is a function of population size, i.e. we removed Eq. 1 from Waterhouse *et al.* (2020) and simply estimated S_t using the number of fish tagged, K_t, and the proportion of tagged sides of fish in mark-resight surveys, p_t: $S_t = K_t/2p_t$. We also allowed for the possibility that the credible interval widths were too small to use as the index observation error, σ_I, in the assessment. We approximated σ_I as the mean of the approximate Z-scores from the Waterhouse *et al.* (2020) median posterior estimates of the number of spawners, $S_{50\%}$:

$$\frac{S_{97.5\%} - S_{2.5\%}}{2 \times 1.96 \times S_{50\%}},$$

where $S_{97.5\%} - S_{2.5\%}$ is the 95% *CI* width. We then considered this value, $\sigma_I = 0.103$, as a lower bound in our assessment model and conducted a sensitivity analysis on σ_I (Supplementary Figure S4).

Estimating island-specific growth

To estimate growth, we used the length-age data from 1988 to 1992 collected at the three main historic FSAs ($n = 99$, 132, and 246 from Little Cayman, Cayman Brac, and Grand Cayman, respectively; Figure 3; Bush *et al.*, 2006). We also included 25 lengths of un-aged fish presumed to be 1-year old in February 2012 on Little Cayman from a large recruitment event from February 2011 spawning (Camp *et al.*, 2013; Semmens *et al.*, 2013). We modelled the length-at-age of fish i, $L[a_i]$, using the von Bertalanffy function:

$$L[a_i] = L_\infty \left[1 - e^{-K(a_i - a_0)}\right] + \varepsilon_i,$$

$$\varepsilon_i \sim \mathrm{N}\left(0, \sigma^2_{\varepsilon_i}\right),$$

$$\sigma_{\varepsilon_i} = CV_L \times L_\infty \left[1 - e^{-K(a_i - a_0)}\right],$$

where L_∞ is the asymptotic length, K is the growth coefficient, a_0 is the theoretical age when length is zero, and the variation of length-at-age increases with mean length and is normally distributed with variance, σ^2_ε. Since exploratory analysis showed potential differences in length-at-age between the three islands, we fit a series of hierarchical growth models that allowed for island-specific deviations from the overall mean parameters (Kimura, 1980; Helser and Lai, 2004). These ranged in complexity from the simplest model, m1, with no island-specific deviations, to the full model, m8, with all parameters varying by island (Table 1; Ogle, 2016). As in Helser and Lai (2004), we modelled the growth parameter vectors for each island j, $\boldsymbol{\theta_j} = (L_{\infty j}, \ \mathrm{ln}K_j, \ a_{0j})$, as random effects assumed to follow a multivariate normal distribution with mean $\boldsymbol{\mu} = (\mathrm{L}_\infty, \ \mathrm{lnK}, \ \mathrm{a}_0)$ and covariance matrix Σ, i.e.:

$$\boldsymbol{\theta_j} = \begin{pmatrix} L_{\infty j} \\ \mathrm{ln}K_j \\ t_{0j} \end{pmatrix} \sim \mathrm{MVN}(\boldsymbol{\mu}, \ \Sigma),$$

$$\Sigma = \begin{bmatrix} \sigma^2_{L_\infty} & \sigma_{L_\infty \mathrm{ln}K} & \sigma_{L_\infty a_0} \\ \sigma_{L_\infty \mathrm{ln}K} & \sigma^2_{\mathrm{ln}K} & \sigma_{\mathrm{ln}Kt_0} \\ \sigma_{L_\infty a_0} & \sigma_{\mathrm{ln}Kt_0} & \sigma^2_{t_0} \end{bmatrix}.$$

This model was attractive because it accounts for parameter correlations and borrows strength across islands to estimate island-specific growth parameters, despite some islands having few samples of older or younger fish. We implemented the hierarchical growth model in Template Model Builder, which uses Laplace approximation to provide maximum likelihood estimates (MLEs) of the fixed effects and empirical Bayes estimates of the random effects (Kristensen *et al.*, 2016). We assessed model convergence by confirming that the Hessian was positive definite and that the absolute values of all final gradients were <0.0001. To select the most parsimonious of the eight nested models, we used marginal Akaike's Information Criterion, $\mathrm{AIC} = -2\log\ell + 2p$, where ℓ is the marginal likelihood evaluated at the MLE and p is the number of estimated parameters (Table 1; Burnham and Anderson, 2002). Finally, we fit the length-weight relationship as a log-linear model, $\log(W) = \alpha + \beta \log(L)$, with the R function "lm".

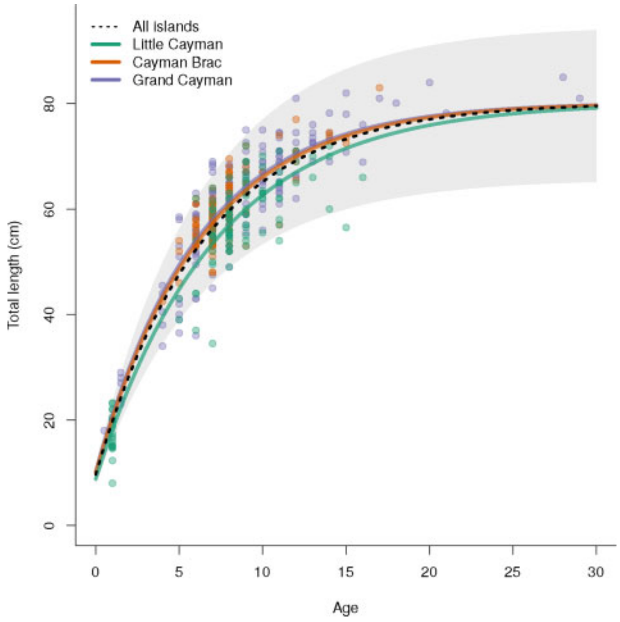

Figure 3. Island-specific Nassau Grouper growth curves from the Cayman Islands. Fish age-4 and older were sampled from 1988 to 1992 FSA catch on Little Cayman, Cayman Brac, and Grand Cayman ($n = 99$, 132, and 246). Little Cayman age-1 fish ($n = 25$) were sampled away from the FSA in February 2012. The black dashed line and shading depict the predicted length at age and 95% *CI* from the overall growth curve. Growth curve parameter estimates are given in Table 2.

Estimating natural mortality

We estimated natural mortality, M, using catch-curve analysis of the length data from Pickle Bank ($n = 159$). First, we converted length data to ages using the mean parameters from the best-fit hierarchical growth model (Table 2 and Figure 3), and then followed the guidance of Smith *et al.* (2012) to use the Chapman-Robson estimator (Chapman and Robson, 1960), implemented in the "FSA" R package (Ogle *et al.*, 2018). This estimate of M depends on the assumption that Pickle Bank is unexploited, and M will be biased upwards if this is not true. We consider the assumption that fishing pressure on Pickle bank is low to be reasonable given how small and isolated Pickle Bank is from the Cayman Islands and Cuba (Figure 1). In addition, adult Nassau Grouper are extremely unlikely to leave Pickle Bank and experience fishing pressure elsewhere, given that they do not appear to move between Little Cayman and Cayman Brac (acoustic and floy tagging data not shown) despite the islands being separated only by 8 km and 250 m deep water. Furthermore, the substantial proportion of large fish caught on Pickle Bank indicates a high probability of a natural age structure (Figure 4).

Length-based assessment models

To assess the status of all Cayman Islands Nassau Grouper FSAs before protections, when only fishery length data were available,

Table 1. Hierarchical von Bertalanffy growth models for Cayman Islands Nassau Grouper, where $\hat{L}[a] = L_{\infty j}[1 - e^{-K_j(a-a_{0j})}]$ for island *j*.

Model	Island-specific parameters	No. fixed effect parameters	Converged and pos. def. Hessian	AIC	ΔAIC
m1	–	4	Yes	3 112.8	34.4
m2	K	5	Yes	3 078.4	0
m3	L_∞	5	Yes	3 082.2	3.8
m4	a_0	5	Yes	3 087.9	9.5
m5	K, L_∞	7	No	3 090.7	12.3
m6	L_∞, a_0	7	No	3 086.4	8.0
m7	K, a_0	7	No	3 088.7	10.3
m8	K, L_∞, a_0	10	No	–	–

Table 2. Estimated von Bertalanffy growth function parameters from model m2, which allowed K_j to vary by island, i.e. $\hat{L}[a] = L_\infty[1 - e^{-K_j(a-a_0)}]$ for island *j*.

Parameter	Overall/mean	Little Cayman	Cayman Brac	Grand Cayman
L_∞ (cm)	80.2 (76.8, 83.7)	–	–	–
K_j (1/year)	0.155 (0.134, 0.175)	0.140 (0.125, 0.156)	0.160 (0.143, 0.178)	0.164 (0.146, 0.182)
a_0	−0.832 (−0.984, −0.680)	–	–	–
CV_L	0.092 (0.087, 0.098)	–	–	–
No. fish	502	124	132	246

95% confidence interval limits are given in parentheses.

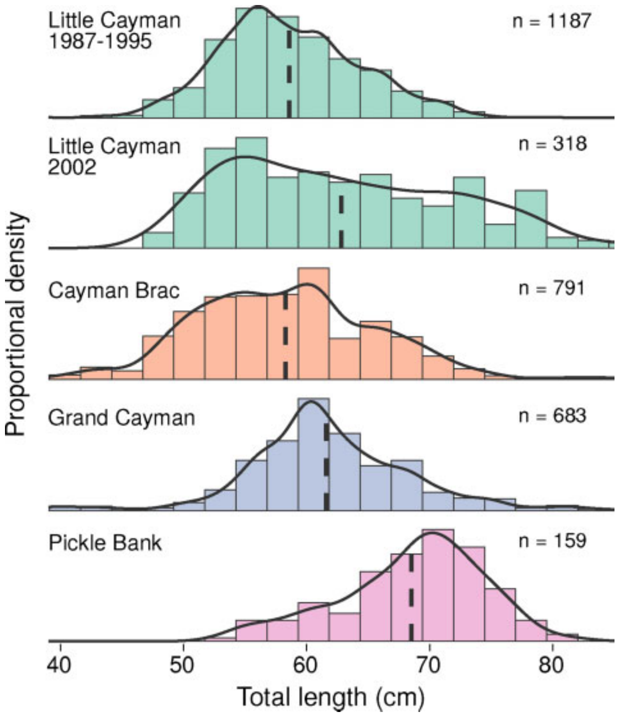

Figure 4. Nassau Grouper catch length distributions from FSA fisheries in the Cayman Islands before protections. Data are pooled across years for Cayman Brac (1990–1995, 1998, 2000), Grand Cayman (1988–1989, 1993, 1995, 1997), and Pickle Bank (2000). Data from Little Cayman were divided into two separate periods, 1987–1995 and 2002, because (i) no FSA fishing occurred for 6 years between 1995 and 2001 and (ii) data from 1987 to 1995 are from the historic east end site while data from 2002 are from the rediscovered west end site. Dashed lines indicate the mean total length for each FSA.

we used the Length-Based Spawning Potential Ratio (LBSPR) model developed by Hordyk *et al.* (2015a,b, 2016). LBSPR is a promising method for populations with limited monitoring data, since SPR can be calculated from life history parameters and length-frequency data under the assumptions of logistic selectivity and maturity. In a comparison of several length-based assessment methods, Chong *et al.* (2020) showed that LBSPR outperformed others using only one length distribution. We fit LBSPR to pre-protection catch length-frequency data from four FSAs: Little Cayman, Cayman Brac, Grand Cayman, and Pickle Bank (Hordyk *et al.*, 2016). On the two islands for which we had length data following protections, Little Cayman and Cayman Brac, we also fit the LBSPR model to *in situ* length-frequency data to compare pre- and post-protection status. We used the island-specific parameters from the best-fit hierarchical growth model and the "LBSPR" R package (Table 3; Hordyk, 2017).

LBSPR assumes an equilibrium population state and only considers one length distribution at a time (either 1 year of data or multiple years pooled). Rudd and Thorson (2018) relaxed this equilibrium assumption in their Length-based Integrated Mixed Effects (LIME) model. LIME estimates time-varying recruitment and fishing mortality in a state-space framework and can be run using only length data (as with the LBSPR) or include fishery catch and an index of abundance if they exist. Otherwise, LIME makes the same assumptions as LBSPR. We chose to use LBSPR to assess pre-protection status because only length data were available, and LBSPR has been shown to outperform LIME when fit to only 1 year of length data (Chong *et al.*, 2020). However, LIME was appropriate to assess the Little Cayman FSA after protections because it capitalizes on the available time series of length, abundance estimates, and catch to relax the assumption that the population is at equilibrium. For both LBSPR and LIME, we assumed that the gears used before (hook and line, catch) and after (laser calipers, non-extractive) protections had logistic

Table 3. Parameters used to fit the LBSPR model.

Parameter		LC	CB	GC	PB	Source
L_∞	Asymptotic length (cm)	80.2	80.2	80.2	80.2	This study (Table 2 and Figure 3)
K	Growth coefficient (1/year)	0.140	0.160	0.164	0.155	This study (Table 2 and Figure 3)
M	Natural mortality (1/year)	0.276				This study
α	Length-weight intercept	3.725×10^{-6}				This study
β	Length-weight slope	3.384				This study
L_{50}	Length at 50% maturity (cm)	47.4				Sadovy and Eklund (1999)
L_{95}	Length at 95% maturity (cm)	55.7				Sadovy and Eklund (1999)
CV_L	Coefficient of variation of L	0.096				This study (Supplementary Figure S8)
	Bin width (cm)	1				
	Maximum length (cm)	100				
	Minimum length (cm)	1				

Island abbreviations: CB, Cayman Brac; GC, Grand Cayman; LC, Little Cayman; PB, Pickle Bank. Length-weight parameters were fit to the log-linear model, $\log(W_i) = \alpha + \beta \log(L_i)$, with weight in kg and length in cm.

selectivity and that the selectivity was the same for both gears. These assumptions seemed reasonable because large fish, >70 cm, were well-represented in the Little Cayman catch length data from 2002 (Figure 4), as well as in the sample caught by hook and line for acoustic tagging (12/144 greater than L_∞, data not shown). In addition, we observed similar proportions of smaller fish, 40–50 cm, in the laser caliper and fishery catch data aggregated across years (Figure 5). Based on the behaviour of fish at the FSA and our data collection protocol, we believe that the probability of measuring a fish with the laser calipers was independent of size, given the fish was mature and at the FSA (Supplementary material).

We fit LIME to 17 years of *in situ* length-frequency data (this study), a 14-year estimate of absolute abundance (numbers of mature fish; Waterhouse *et al.*, 2020), and 2 years of catch data (ca. 2000 fish in 2001 and 1934 fish in 2002; Whaylen *et al.*, 2004). The main purpose for using LIME was to estimate recruitment and depletion (SSB/SSB_0) of the Little Cayman population through time following protections, which do not depend on the biomass scale. Still, we included the 2 years of catch data to inform the model about the very high F in 2001–2002. We used the value of M estimated from the catch-curve analysis and conducted sensitivity runs using $M \pm 0.05$/year. We chose to estimate annual recruitment deviations directly without incorporating a stock–recruit relationship, i.e. we set steepness (h) at 1, because the LIME model was not intended to calculate MSY-based reference points or generate catch advice. Nevertheless, we also conducted a sensitivity run using $h = 0.7$. Finally, we explored the sensitivity of LIME to data weighting parameters—the observation errors for the index, σ_I, and catch, σ_C, as well as the length composition likelihood. LIME uses the Dirichlet-multinominal distribution by default, which estimates an effective sample size for the length-frequency data that can be lower than the input sample size. We also fit LIME using the multinomial distribution with effective sample sizes calculated using Francis weighting (TA1.8 in Francis, 2011). We used the parameters in Table 4 and the "LIME" R package (Rudd, 2018), starting the model in 1999 to include 4 years of roughly known, extreme variation in F before protection: 2 years in which F was near zero (1999–2000), followed by 2 years of high F (2001–2002).

We modified LIME in three ways. First, we integrated the best-fit hierarchical growth model, m2, with LIME to estimate L_∞, a_0, island-specific K_j, and σ_K^2 internally. This "LIME-integrated" model thus explicitly accounts for uncertainty in growth parameters, addressing the commonly cited concern that data-limited assessments assume life history parameters are known without error (Pons *et al.*, 2019, 2020). We compared these results with LIME run with growth parameters fixed at the values estimated externally, as usual, which we refer to as the "LIME-fixed-K" model. Second, LIME includes a penalty on annual F deviations as a random walk, $F_{t+1} \sim N\left(F_t, \sigma_F^2\right)$ to facilitate convergence. As this was not appropriate for the extreme F fluctuations from 1999 to 2003, we modified LIME to penalize F deviations only beginning in 2004. Last, we specified that the index was in units of number of spawners, as opposed to total (or spawning) biomass, by replacing the predicted spawning biomass in year t, $\hat{B}_t$, with the predicted number of spawners in year t, $\hat{S}_t$, in the equation for the predicted index in year t, i.e. $\hat{I}_t = q\hat{S}_t$ instead of $\hat{I}_t = q\hat{B}_t$, where $\hat{S}_t = \sum_a \hat{N}_{t,a} Mat_a$, $\hat{N}_{t,a}$ is the number of age a fish at time t, and Mat_a is the maturity-at-age a. We then fixed catchability, q, at 1 because the Waterhouse *et al.* (2020) model directly estimates S_t in absolute, not relative, numbers. We admitted the possibility that the abundance index could be biased 10% low or high by conducting sensitivity runs using $q = 0.9$ and $q = 1.1$. See Table 5 for a summary of the data used to fit each model. The data and code underlying our analysis are available at https://github.com/brianstock/cayman-grouper-assess.

Results

Growth and natural mortality

In the pre-protection period with fishery data, 1988–1992, Nassau Grouper were smaller at given age on Little Cayman than the other islands (Figure 3). Of the hierarchical growth models, only those that allowed one or fewer parameters to vary by island converged (Table 1). Model m2, with island-specific random effects on the growth coefficient, K_j, and shared L_∞ and a_0, had the lowest AIC and estimated a lower growth coefficient on Little Cayman (0.140/year, 95% *CI*: 0.125–0.156) than Cayman Brac (0.160/year, 95% *CI*: 0.143–0.178) or Grand Cayman (0.164/year, 95% *CI*: 0.146 − 0.182; Tables 1–2 and Figure 3).

We estimated natural mortality as $M = 0.276$/year (95% *CI*: 0.17–0.38). This estimate falls within the range reported by previous catch-curve analysis for Nassau Grouper ($M = 0.17$–0.30/year; Thompson and Munro, 1978) and is very close to estimates from methods recommended in a recent meta-analysis ($M_{Hoenig_{nls}} = 0.224$/year using $t_{\max} = 29$ years; $M_{Pauly_{nls-T}} = 0.245$/year; Then *et al.*, 2015).

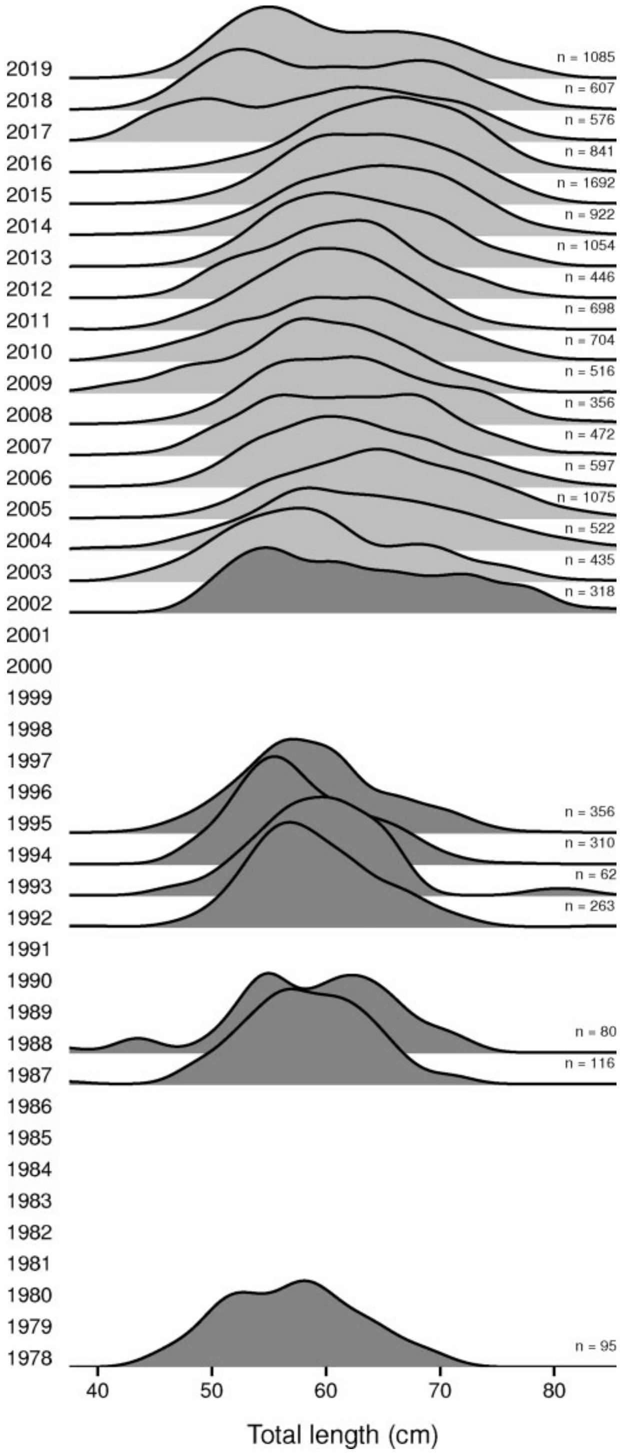

Figure 5. Length distributions from Little Cayman Nassau Grouper spawning aggregations (FSAs). Pre-protection data are from fisheries catch (dark shading, 1978–2002), and post-protection data are from *in situ* laser calipers (light shading, 2003–2019). The size structure recovery following 5 years of no FSA fishing (1996–2000) and subsequent protection is shown by wider distributions from 2002 to 2019. The 2017–2019 distributions are bimodal with wide range, showing a pulse of recruits. The sample sizes (n) for each year are displayed at right.

Length-frequency analysis

The pre-protection catch length distributions from the three historic FSAs on Little Cayman, Cayman Brac, and Grand Cayman were similar, except that lengths from Grand Cayman had a smaller range and were about 3 cm larger on average (Figure 4). Pickle Bank had much larger fish—the average was 10 cm larger than the three main historic Cayman Islands FSAs. Individuals >70 cm were rare at the three historic FSAs, whereas they comprised roughly half of the catch on Pickle Bank (Figure 4). All recent years (2002–2019) of length distributions from the west end Little Cayman FSA had wider range and larger individuals than catches at the historic east end Little Cayman FSA (1978–1995, Figure 5). This was true both for fisheries catch immediately before protection (2002) and for *in situ* laser caliper data after protection (2003–2019) and reflects the fact that there was no FSA fishing from 1995 to 2001.

The 2017–2019 length distributions were bimodal on both Little Cayman and Cayman Brac, with a pulse of small fish 45–55 cm not seen in the other 22 years (Figure 6). On Little Cayman, the modes (local maxima, dashed lines in Figure 6) clearly stepped right from 2017 to 2019 on both islands, as expected if the modes represent growth of a single strong cohort. The Little Cayman modes aligned well with the predicted lengths from the Little Cayman growth curve assuming the cohort was spawned in 2011 (i.e. age 6 in 2017, age 7 in 2018, age 8 in 2019; Figure 6). The 2018 and 2019 modes were slightly lower than the growth curve predictions for age-7 and age-8 fish, by 0.91 and 2.05 cm, respectively. In all years, the modes were larger on Cayman Brac than Little Cayman, which is consistent with the higher estimated growth coefficient on Cayman Brac (Figure 6 and Table 2). The 2017–2018 Cayman Brac modes aligned well with the growth curve predictions under the assumption the cohort was spawned in 2011, although this was not the case for 2019.

Length-based assessment models

Before protections, LBSPR-calculated SPR at the three historic FSAs ranged from 0.45 to 0.53 (Figure 7). The lightly exploited Pickle Bank FSA had higher SPR at 0.73 (95% *CI*: 0.59–0.87). SPR for the Little Cayman population in 2002, following 6 years of no FSA fishing, was estimated to increase from 0.48 to 1.00. Following 2 years of intense aggregation fishing in 2001 and 2002, the Little Cayman SPR decreased to 0.60 (95% *CI*: 0.56–0.63) before increasing to 0.94 (95% *CI*: 0.86–1.00) in recent years. SPR for Cayman Brac also dramatically increased following protection, from 0.50 to 1.00.

In the LIME models for the Little Cayman population from 1999 to 2019, including different amounts of uncertainty in the growth parameters and length composition data led to slightly different but consistent trends in spawning biomass, numbers, mean size, and recruitment (Table 6). Francis weighting gave less weight to the length composition data than the default Dirichlet-multinomial ($w = 0.08$ compared to $w = 0.54$, where w is the multiplier for effective sample size). This substantially improved the model fit to both the mean length and the index (Supplementary Figure S5). We found that $\sigma_I = 0.175$ and $\sigma_C = 0.20$ resulted in the lowest negative log-likelihood and therefore considered the LIME-integrated model with these values and

Table 4. Parameters used to fit the LIME models to assess the Little Cayman FSA.

Parameter		Model		Source
		LIME-fixed-K	LIME integrated	
L_∞	von Bertalanffy asymptotic length (cm)	80.2	^{a}81.2 (77.9, 84.3)	This study (Table 2 and Figure 3)
K	von Bertalanffy growth coefficient (1/year)	0.140	^{a}0.141 (0.126, 0.156)	This study (Table 2 and Figure 3)
a_0	Age at zero length	−0.832	^{a}−0.802 (−0.951, −0.654)	This study (Table 2 and Figure 3)
M	Natural mortality (1/year)	0.276		This study
L_{50}	Length at 50% maturity (cm)	47.4		Sadovy and Eklund (1999)
L_{95}	Length at 95% maturity (cm)	55.7		Sadovy and Eklund (1999)
S_{50}	Length at 50% selectivity (cm)	^{a}61.9 (59.4, 64.4)	^{a}61.8 (59.2, 64.4)	
S_{95}	Length at 95% selectivity (cm)	^{a}66.1 (59.9, 72.4)	^{a}66.0 (59.4, 72.6)	
α	Length-weight intercept	3.725×10^{-6}		This study
β	Length-weight slope	3.384		This study
σ_F	Fishing mortality process error	0.3		Default
σ_C	Catch observation error	0.2		Sensitivity analysis (Supplementary Figure S4)
σ_I	Abundance index observation error	0.175		Sensitivity analysis (Supplementary Figure S4)
σ_R	Recruitment process error	^{a}0.87 (0.60, 1.25)	^{a}0.83 (0.57, 1.21)	
CV_L	Growth curve coefficient of variation	0.096		Likelihood profile (Supplementary Figure S8)
q	Abundance index catchability	1		
h	Steepness of Beverton–Holt	1		Default
	Bin width (cm)	1		
	Maximum length (cm)	100		
	Minimum length (cm)	1		

^{a}Estimated in model (MLE with 95% *CI* in parentheses). Otherwise fixed at specified value.

Francis weighting the final model (Supplementary Figure S4). LIME generally fit the abundance index and length-frequency data well, including the bimodal distributions in 2017–2019 (Supplementary Figures S6–S7). LIME models that attempted to estimate the growth curve coefficient of variation, CV_L, did not converge. However, a grid search with CV_L ranging from 0.08 to 0.11 found that the negative log-likelihood was minimized at $CV_L = 0.096$ and this value was used in the final LIME-integrated model (Supplementary Figure S8).

On Little Cayman, the LIME-integrated model estimated a two-step decline in spawning biomass, driven by both decreasing size and numbers of fish during two periods of high fishing mortality (2001–2002 and 2006–2009, Figure 8). The 2 years of heavy FSA fishing immediately prior to protection, 2001–2002, reduced SSB by 54% (95% *CI*: 46–61%). Depletion (SSB/SSB_0) reached a low of 0.23 (95% *CI*: 0.17–0.32) in 2009 and then dramatically increased to 0.90 (95% *CI*: 0.65–1.25) in 2019 (Figure 8d and Table 6). The number of spawners similarly reached a minimum in 2008, increased slightly from 2008 to 2012 due in part to slightly higher recruitment in the 2003–2006 period, and then increased dramatically from 2014 to 2018 (Figure 8b and c). Mean size went through five alternative periods of decrease (2000–2002, 2005–2010, 2016–2018) and increase (2003–2005, 2010–2016) corresponding to pulses in F and recruitment (Figure 8a).

We estimated a large recruitment pulse from 2011 spawning on Little Cayman that was 5.3 times average (95% *CI*: 0.6–9.9, Figure 8b). This was robust to assuming different amounts of uncertainty in the growth parameters and length composition data (Figure 9), as well as values of M (Supplementary Figure S9 and Supplementary Table S1) and steepness (Supplementary Table S2). Under these various parameterizations, the magnitude of the 2011 recruitment pulse varied from 4.4–7.8 times average recruitment (Table 6 and Supplementary Tables S1 and S2). Including uncertainty in the growth parameters and downweighting the length composition data increased the uncertainty in the timing of the recruitment pulse as well as the magnitude (wider confidence intervals for 2010 and 2012 recruitment in Figure 9).

Discussion

On Little Cayman and Cayman Brac, Nassau Grouper population size structure and SPR clearly recovered following 16 years of FSA protections. Using a time series of *in situ* length data is an effective method for monitoring protected FSAs, where all mature fish aggregate at high density and can be efficiently measured. Both the laser caliper and stereo camera systems were accurate enough to detect bimodal length distributions on Little Cayman and Cayman Brac in 2017–2019, which implied recruitment of a very strong year class spawned in 2011. On Little Cayman, spawning biomass was reduced by 54% in 2 years of intense FSA fishing and then took 16 years to recover to near pre-exploitation levels (Figure 8d). This recovery was largely driven by the one strong year of recruitment in 2011. These results attest to the value of monitoring FSA size structure in addition to numbers of fish—combining length and abundance data in an assessment allow for a more complete picture of population status and can attribute increases or decreases to changes in fishing mortality vs. recruitment.

The differences in growth coefficients (Table 2 and Figure 3) and 2017–2019 length distributions (Figure 6) between Little Cayman and Cayman Brac strongly suggest synchrony in the 2011 large recruitment event on both islands. There is, nevertheless, an alternate hypothesis for the difference in length modes between the two islands: fish grew at the same rate on both islands but are 1 year older on Cayman Brac, i.e. a large recruitment event took place on Cayman Brac in 2011 followed by the same on Little Cayman in 2012. This possibility is not supported by the above model outputs, and the presence of numerous 1–1.5-year-old (12–23 cm) juveniles on Little Cayman in February–July 2012

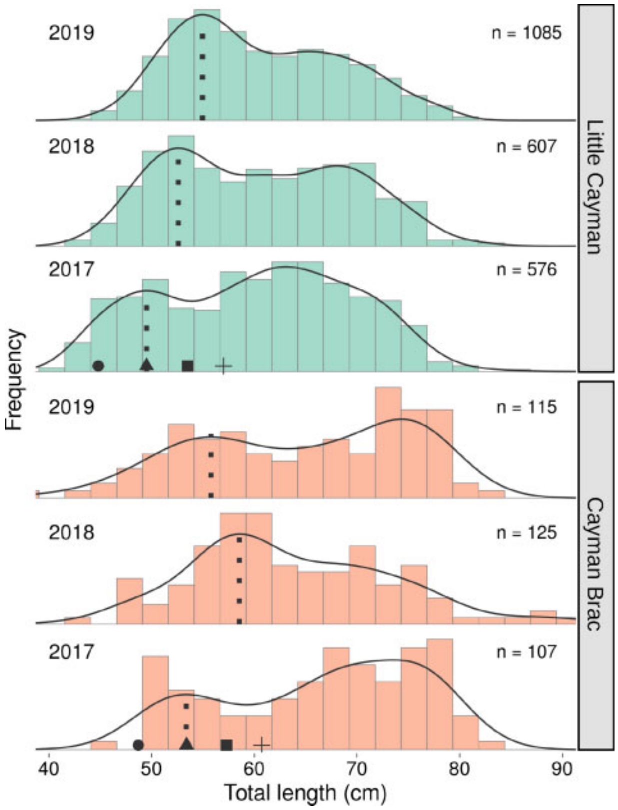

Figure 6. Bimodal length distributions from Little Cayman and Cayman Brac for the years 2017–2019. The modes (local maxima, dashed lines) shift right from 2017 to 2019 on both islands, and the modes are larger on Cayman Brac (CB) than Little Cayman (LC) in all years. Predicted lengths from the Cayman Brac growth curve are: 48.7 cm at age 5 (CB circle), 53.4 cm at age 6 (CB triangle), 57.3 cm at age 7 (CB square), and 60.7 cm at age 8 (CB cross). Predicted lengths from the Little Cayman growth curve are: 44.8 cm at age 5 (LC circle), 49.5 cm at age 6 (LC triangle), 53.5 cm at age 7 (LC square), and 57.0 cm at age 8 (LC cross).

(Camp *et al.*, 2013; Semmens *et al.*, 2013) provides further evidence against two major recruitment events. Nearly zero juveniles were sighted in all years 2004–2017 except for 2012 (Semmens *et al.*, 2013). Furthermore, it is not unreasonable that Little Cayman and Cayman Brac would show strong recruitment in the same year, because they are only separated by 8 km and late-stage larvae are easily capable of swimming this distance against currents (Leis *et al.*, 2009). The most likely explanation is that recruitment on both islands was paired. If true, direct and indirect evidence indicates that growth coefficients were consistently lower on Little Cayman during two separate time periods, 1987–1992 and 2011–2019.

It is not clear why Nassau Grouper growth would be slower on Little Cayman than Cayman Brac or Grand Cayman. The biomass of Nassau Grouper on Little Cayman increased nearly fourfold from 2008 to 2019 and was much higher than on Cayman Brac despite similar habitat area (Supplementary Figure S10, McCoy, 2019). Thus, growth may plausibly be slower on Little Cayman in recent years if there are density-dependent growth effects. This could also help explain why the Little Cayman 2018–2019 length modes were 0.9–2.0 cm smaller than the growth curve predictions for age-7 and age-8 fish (Figure 6) since the age-length data used to fit the model are from a period with lower population density. However, while slower growth at higher density is consistent with density-dependent growth, it is not direct evidence, and future work would be necessary to evaluate the hypothesis. Furthermore, density dependence is only one possible mechanism underlying the slower growth on Little Cayman vs. Cayman Brac in recent years, and it does not explain why growth was also slower on Little Cayman compared to the other islands in 1987–1992. Cayman Brac has relatively more “spur and groove” and patch reef habitat, and differences in benthos may be related to prey density and growth rate (McCoy, 2019). Instead of intraspecific competition, Nassau Grouper on Little Cayman may have less access to food because there are more large snappers and groupers in general, and thus, interspecific competition may be greater. Prey may be harder to capture on Little Cayman, requiring Nassau Grouper to allocate more energy to active metabolism and less to growth. Behaviour may differ—when DOE scientists attempted in-water capture to acoustically tag Nassau Grouper *in situ*, they noted that Cayman Brac fish were markedly warier and more skittish than their counterparts on Little Cayman (B. Johnson, pers. comm.). Nassau Grouper on Little Cayman may have matured earlier than their counterparts on Cayman Brac, which would result in an energy reallocation from somatic growth to reproductive growth. Of these alternative explanations, we can only rule out different ages at maturity because the 2011 cohort was absent from the 2016 length distribution on Little Cayman. Still, there are many conceivable mechanisms behind the difference in estimated growth coefficients, and future work could test for these possibilities.

Another obvious question is: What was special about conditions in 2011 that led to a major recruitment pulse on both islands? Like many reef fish, Nassau Grouper are benthic but are pelagic broadcast spawners, and successful recruitment may largely depend on favourable currents bringing larvae close to suitable reef habitat. The prevailing current around the Cayman Islands flows east-northeast to west-southwest, but the mean current is weak and looping eddies that retain water for months are common (Richardson, 2005). Thus, self-recruitment within the Caymans is a very likely possibility (Colin *et al.*, 1987; Heppell *et al.*, 2009, 2011; Colin, 2012b; Sadovy de Mitcheson and Colin, 2012). Future work could model larval dispersal from Little Cayman using archived remote sensing data and compare 2011 against low recruitment years. Alternatively, strong recruitment in 2011 could have been related to abundant prey or fewer predators at critical space and time scales for larval survival (e.g. Cushing’s match–mismatch hypothesis, with a strong “match” in 2011; Cushing, 1990). It is also possible for physical forcing to positively affect larval dispersal and survival simultaneously (Checkley *et al.*, 1988). While intriguing, these possibilities are difficult to test in hindsight.

Nassau Grouper at different locations throughout the Caribbean appear to spawn during months when the average temperature is around 26°C (Table 2 in Tucker *et al.*, 1993). Sea surface temperatures near Little Cayman were indeed relatively cool in 2011, ~26°C (Supplementary Figure S11). However, temperatures were also lower in 2005, 2006, and 2009, and no large recruitment events were observed in these years. Water temperature around 26°C may be a necessary but insufficient condition for recruitment success. Future work could investigate a possible temperature effect on recruitment, which may be acting as a proxy for effects related to currents, prey, or predators.

Table 5. Summary of the types, years, and locations of data used to fit each model.

	Estimates			Data type				
Model	**Quantity**	**Island**	**Pre/post-protection**	**Length**	**Index**	**Catch**	**Age**	**Result**
Growth	L_∞, a_0, and K	LC, CB, GC	Pre	1988–1992, 2012[b]			1988–1992	Tables 1 and 2 Figures 3 and 6
Catch curve	M	PB	Pre	2000				Tables 3 and 4
LBSPR	SPR	LC	Pre, post	1978–1995, 2002–2019				Figure 7
	SPR	CB	Pre, post	1990–2000				Figure 7
	SPR	GC	Pre	1988–1997				Figure 7
	SPR	PB	Pre	2000				Figure 7
LIME-fixed-K	SSB/SSB$_0$, F, recruitment	LC	Post	2002–2019	2005–2018	2001–2002		Figure 9
LIME integrated	SSB/SSB$_0$, F, recruitment	LC	Post	2002–2019, 1988–1992[a]	2005–2018	2001–2002	1988–1992[a]	Figure 8

Island/FSA abbreviations: CB, Cayman Brac; GC, Grand Cayman; LC, Little Cayman; PB, Pickle Bank. "Pre/post" refers to FSA protection status (FSAs were protected in 2003). Prior to protection, length data were collected from fishery catch, and after protection, length data were collected *in situ* via diver-operated laser calipers.

[a] Age-length data (1988–1992) were used in the LIME-integrated model to fit the growth parameters, but these data did not contribute to the likelihood of the population length composition (model years: 1999–2019).

[b] Lengths of 25 un-aged fish presumed to be 1-year old were recorded in 2012 on Little Cayman from a large recruitment event from 2011 spawning (Camp *et al.*, 2013; Semmens *et al.*, 2013).

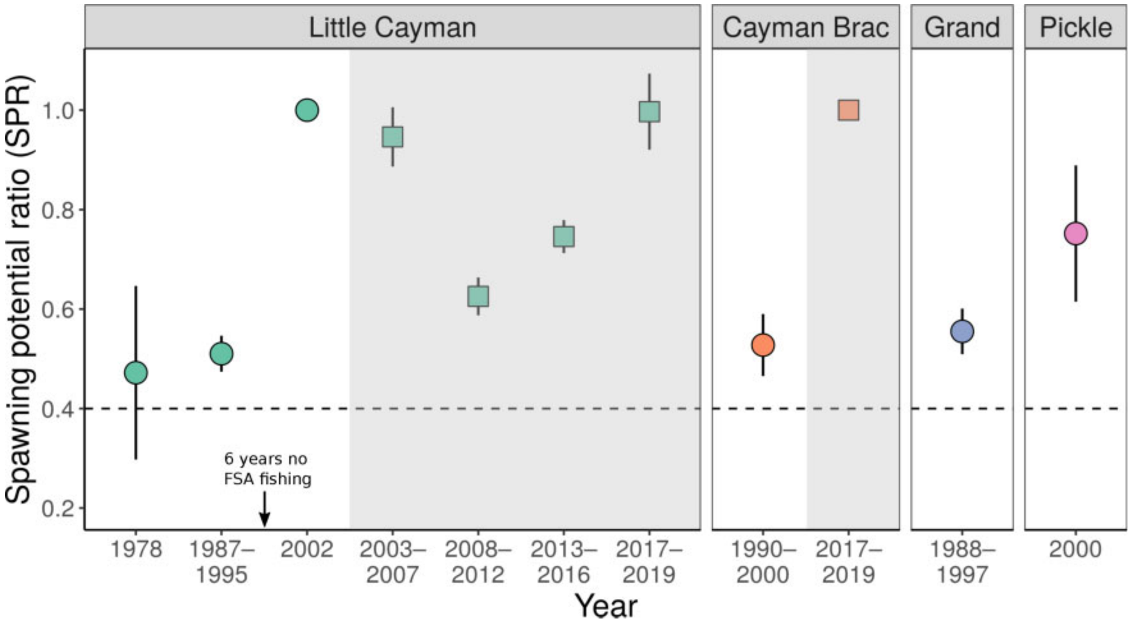

Figure 7. Estimated SPR for Cayman Islands Nassau Grouper spawning aggregations before and after protections implemented in 2003. Pre-protection length data (circles, white background) were collected by sampling FSA catch on Little Cayman, Cayman Brac, Grand Cayman, and Pickle Bank. Although not formally protected until 2003, no FSA fishing occurred on Little Cayman for 6 years between 1995 and 2001. Post-protection length data (squares, grey background) were collected from diver-operated laser calipers on Little Cayman (2003–2019, pooled into 5-year bins) and Cayman Brac (2017–2019).

Aggregation status and management

Out of 17 years of monitoring on Little Cayman, we saw only one year of strong recruitment. This is not surprising since Nassau Grouper are periodic strategists (Winemiller and Rose, 1992): long-lived and highly fecund, capable of withstanding years of recruitment failure sporadically punctuated by large successful spawning events. Given the dramatic decline of Nassau Grouper throughout the Caribbean, it is possible that external recruitment (i.e. from other FSAs) is more sporadic now than in the past. When FSAs were far greater in size and number, the probability of any population receiving larvae from a different FSA was likely higher, and therefore, recruitment less variable. Now, with fewer and smaller FSAs, the remaining FSAs may be more dependent on self-recruitment. Whether or not this is true, we observed high recruitment variability for the Little Cayman FSA that had no correlation with spawning stock biomass. This is important

Table 6. LIME model estimates of min/max depletion (SSB/SSB$_0$), 2011 recruitment pulse, and growth parameters for the Little Cayman FSA, assuming different amounts of uncertainty in the growth parameters and length composition data.

	LIME integrated		**LIME-fixed-K**	
Estimated quantity	**Francis weighting**	**Dirichlet-multinomial**	**Francis weighting**	**Dirichlet-multinomial**
2019 SSB/SSB$_0$	0.90 (0.65, 1.25)	0.96 (0.73, 1.25)	1.06 (0.80, 1.40)	1.04 (0.81, 1.36)
2009 SSB/SSB$_0$	0.23 (0.17, 0.32)	0.29 (0.23, 0.38)	0.27 (0.20, 0.36)	0.33 (0.26, 0.42)
2002 SSB/SSB$_0$	0.46 (0.39, 0.54)	0.55 (0.50, 0.61)	0.53 (0.46, 0.61)	0.59 (0.55, 0.63)
2011 Rec/mean Rec	5.3 (0.6, 9.9)	7.8 (3.1, 12.5)	4.4 (1.6, 7.1)	5.6 (3.6, 7.6)
L_∞	81.2 (78.1, 84.3)	79.3 (77.3, 81.4)	80.2^a	80.2^a
k	0.141 (0.126, 0.156)	0.146 (0.135, 0.158)	0.140^a	0.140^a
a_0	−0.80 (−0.95, −0.65)	−0.78 (−0.90, −0.66)	−0.83^a	−0.83^a

LIME-integrated included uncertainty in growth parameters while LIME-fixed-K did not. Francis data weighting included more uncertainty in the length composition data than using the Dirichlet-multinomial likelihood. Values are MLE with 95% *CI* in parentheses.

[a] Fixed in model, not estimated.

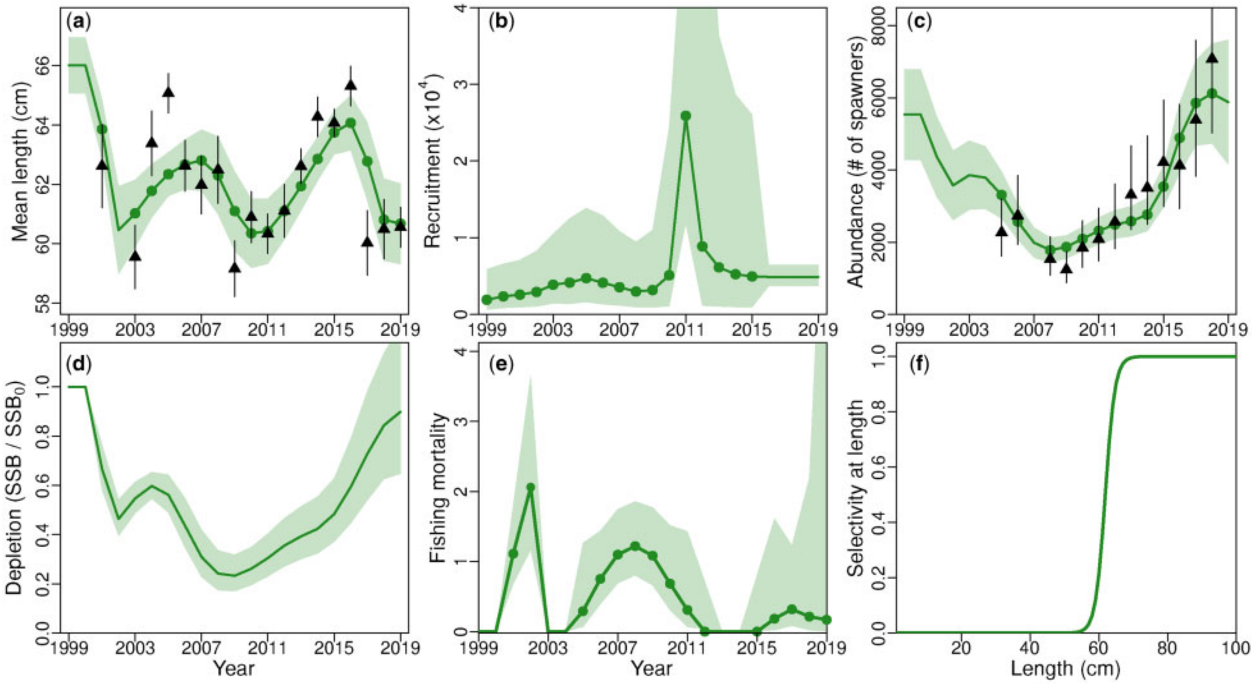

Figure 8. LIME-integrated model output for the Little Cayman Nassau Grouper FSA: (a) mean length (cm), (b) recruitment (age-0), (c) abundance (number of spawners), (d) depletion (SSB/SSB$_0$), (e) fishing mortality, and (f) selectivity. Black triangles show the input data with 95% confidence intervals. Green points, lines, and shading depict the MLEs and 95% confidence intervals. In (a) and (c), model estimates for years without data are distinguished by green lines without points. In (b) and (e), recruitment deviations and fishing mortality were fixed at 0 for years without points.

information for management as it implies that long recovery timelines for this species should be expected. On Little Cayman, where biomass was reduced by 53% in 2 years of intense FSA fishing, the recovery to pre-exploited levels took 16 years and was largely driven by the one strong year of recruitment in 2011.

Waterhouse *et al.* (2020) reported that numbers of Nassau Grouper on Cayman Brac have likely increased since protection but tempered their conclusions due to sparse observations. Two of our results strengthen confidence that the Cayman Brac population has, in fact, increased. First, pre- and post-protection length data used to estimate SPR show a substantial improvement in population status between 1990–2000 and 2017–2019 (Figure 7). Second, the bimodal 2017–2019 length distributions imply that a large recruitment pulse occurred on Cayman Brac as well as Little Cayman (Figure 6). Thus, while we cannot map the Cayman Brac population trajectory in fine detail as we did for Little Cayman, our length data do support the increase in abundance described by Waterhouse *et al.* (2020).

The LBSPR model estimated SPR ranging from 0.45 to 0.53 at the three historic FSAs in the 1980–1990s (Figure 7). These SPR estimates were above 0.40, which is often recommended as a risk-averse reference point in cases where the stock–recruit relationship is not estimable (Clark, 1993, 2002; Mace, 1994; Hordyk *et al.*, 2015b; Rudd and Thorson, 2018). Yet, Nassau Grouper populations in the Cayman Islands subsequently declined; total catch, CPUE, and mean size all decreased to very low levels by 2001 (Bush *et al.*, 2006), and fishermen decided to stop fishing at the Little Cayman east end FSA by 1995. Particularly concerning

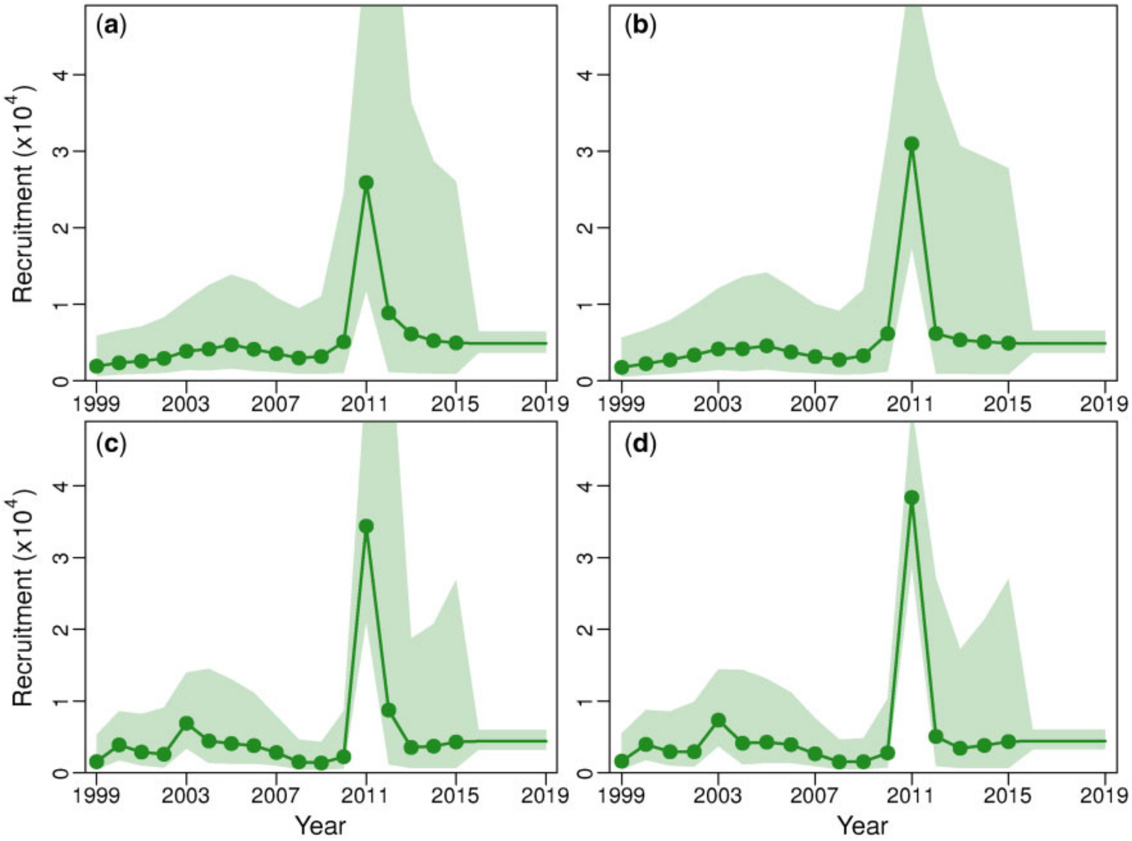

Figure 9. Estimated recruitment for the Little Cayman Nassau Grouper FSA from models with a range of uncertainty and data weighting. The LIME-integrated model (a, c) incorporates uncertainty in growth parameters by estimating them internally, whereas the LIME-fixed-K model (b, d) fixes growth parameters at values estimated externally. Francis weighting (a, b) gives less weight to the length data ($w = 0.08$) than the Dirichlet-multinomial (c, d; $w = 0.54$). Green points, lines, and shading depict the MLEs and 95% confidence intervals. Recruitment deviations are fixed at 0 in years without points (2016–2019) because the data are uninformative (age at first capture >4).

is that the Grand Cayman FSA, with an estimated SPR of 0.53 (95% *CI*: 0.48–0.57) in the 1988–1997 period, has shown no sign of recovery despite 16 years of protection. Recovery on Grand Cayman was a reasonable expectation because (i) SPR on all three islands was similar before protections, (ii) substantial increases in biomass and SPR have occurred on both Little Cayman and Cayman Brac over the same time period with the same management measures (i.e. the FSA closures sufficiently reduced *F* on the other islands), and (iii) Grand Cayman is much larger than either Little Cayman or Cayman Brac (roughly 2.5 times available reef habitat; McCoy, 2019), so should have a higher carrying capacity and potential for rebuilding. However, the few post-protection observations we have from Grand Cayman suggest that the population remains depleted (Waterhouse *et al.*, 2020). All the above strongly suggest that the Grand Cayman population was not being fished at sustainable levels before 2001 (with SPR estimated at 0.53), was very depleted by 2001, and remains depleted. Together with the species' history of exploitation (range-wide dramatic declines in catch, disappearance of FSAs, and failure of lost FSAs to re-form once protected), this indicates that SPR <0.6 may be an unwise reference point for managing Nassau Grouper spawning aggregation fisheries.

It is plausible that a sustainable SPR for Nassau Grouper could be higher than 0.40. Clark (2002) and Brooks *et al.* (2010) demonstrated that the appropriate SPR depends on the slope of the stock–recruit curve at low stock size, and that for less resilient species (i.e. lower stock–recruit steepness) SPR in the range 0.60–0.86 could be warranted. Zhou *et al.* (2020) modelled SPR at MSY (SPR_{MSY}) as a function of life history parameters for 185 stocks and found that nearly two-thirds require $\text{SPR}_{\text{MSY}} > 40\%$. In addition, the species' life history may not follow the assumptions underlying the typical SPR reference point guidelines. First, the guidelines are derived from Beverton–Holt or Ricker stock–recruit relationships that do not admit the possibility of an Allee effect (i.e. depensation, lower recruits per spawner at low stock size; Brooks *et al.*, 2010). The spawning aggregation behaviour of Nassau Grouper may well be a "strong" Allee effect mechanism, whereby FSAs no longer form at population sizes (or densities) below a threshold and few, if any, recruits are produced (Courchamp *et al.*, 2008; Sadovy de Mitcheson, 2016). If such a threshold exists, Nassau Grouper stock sizes need to be kept above it. Second, Nassau Grouper recruitment may be more driven by environmental stochasticity, including variable larval dispersal, and only weakly related to stock size. This is the case for many, if not most, managed fish stocks in the world (Szuwalski *et al.*, 2015). Of course, both these mechanisms may act in concert, such that recruitment is very low or zero at low stock sizes when FSAs cease to form, and then unrelated to stock size above a threshold. This highlights the need for fisheries assessment and management tools to be adapted for aggregating species' life history (Sadovy de Mitcheson, 2016).

Conclusion

The Cayman Islands government should be commended for acting quickly to protect the Nassau Grouper FSAs. While roughly half of the Little Cayman spawning biomass was harvested in the 2 years before protection, the remaining individuals continued to form a spawning aggregation. Had the Caymanians not acted quickly, then recovery, had it occurred at all, would likely have been even more protracted than it was; Nassau Grouper recovery is almost nonexistent at sites throughout the Caribbean where aggregating behaviour has ceased. The recovery of these historic sites may depend on getting a pulse of larvae from a healthy FSA—it is possible this occurred on Cayman Brac in 2011.

The Nassau Grouper FSA on Little Cayman is currently the largest spawning aggregation known for the species, and the status of the Cayman Brac FSA is markedly improved. FSA protections are increasingly common in the Caribbean, and region-wide recovery of Nassau Grouper depends on population responses to these protections. In the Cayman Islands, scientific monitoring following temporary FSA protections bolstered the necessary political will to extend these protections and make them permanent through legislation (no take during spawning months, bag and slot limits away from FSAs in the rest of the year; Cayman Islands Cabinet, 2016; Waterhouse *et al*., 2020). We found that time series of *in situ* length data is an especially effective method for assessing protected FSAs and was even able to detect the recruitment of strong year classes and differences in growth between islands. The methods demonstrated here are useful for assessing FSAs and lend themselves to efforts aimed at managing sustainable reef fisheries.

Supplementary data

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

Data availability

The data and code underlying our analysis are available at https://github.com/brianstock/cayman-grouper-assess.

Acknowledgements

We thank the hard-working CI-DoE staff who have provided years of field support: Bradley Johnson, Ivan Montieth, Keith Neale, Robert Walton, James Gibb, Cody Panton, Michael Guderian, Kevin Jackson, and Chris Dixon. Many REEF staff and volunteer divers helped collect laser caliper video, including Leslie Whaylen, Steve Gittings, Hal Peterson, Todd Bohannon, Cody Panton, Tammi Warrender, and Josh Stewart. Peter Hillenbrand (Southern Cross Club), Jason Belport (Little Cayman Beach Resort), and Cayman Airways generously provided accommodations and logistical support. We thank Patrick L. Colin and Douglas Y. Shapiro for access to the original data of 1978 from Little Cayman. Their work was done under permit from the Cayman Islands government. The manuscript was vastly improved by constructive comments from three anonymous reviewers.

Funding

BCS received support from the Cooperative Institute for Marine Ecosystems and Climate (CIMEC) and the National Science Foundation Graduate Research Fellowship under Grant No. DGE-1144086. ICD was funded by the Scripps Institution of Oceanography Director's Office in support of the 2017 Scripps Undergraduate Research Fellowship (SURF) REU program (NSF-OCE 1659793).

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Handling editor: Katherine Yates