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

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Abstract

Fish spawning aggregations (FSAs) are vulnerable to overexploitation, yet quantitative assessments of FSA spawning 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 growth, recruitment, and spawning biomass of Nassau Grouper on Little Cayman following protection. Bimodal length distributions in 2017–2019 indicated a large recruitment pulse (4–8x 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 in 2011 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 if population recovery is dependent upon sporadic recruitment, then success takes time; and (iii) FSA fishery management targets may need to be higher than commonly recommended (i.e. $SPR > 0.6$ instead of 0.4).

Keywords: fish spawning aggregation (FSA), stock assessment, data-limited, length-based, spawning potential ratio (SPR), population recovery, coral reef fishery

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 100s of meters; 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, 2014). 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 is 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 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 versus 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 x 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 Deleveau 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 (Fig. 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 1987-2001 (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 7,000 fish at the time of discovery (Bush et al. 2006; Whaylen et al. 2007). Intense fishing by local fishermen using handlines removed around 4,000 fish in two consecutive one-week spawning seasons (ca. 2,000 in 2001 and 1,934 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 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 2004-2010 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 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 (Fig. 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 (Fig. 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 x 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 (Fig. 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 (Fig. 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 1978–2002 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 one 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 two years it was heavily fished (approximately 2,000 fish in 2001 and 1,934 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 HeroTM video camera attached in front (Fig. 2). We aimed to collect 500–1,000 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 Supplemental Information for details of laser caliper and stereo camera calibration, measurement error estimation, video collection, and data processing (Figs. S1-S3).

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 2005-2018 (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 (MCMC) 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, $S_{50\%}$:

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

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 (Fig. S4).

Estimating island-specific growth

To estimate growth, we used the length-age data from 1988-1992 collected at the three main historic FSAs ($n = 99, 132$, and 246 from Little Cayman, Cayman Brac, and Grand Cayman; Fig. 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,

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

$$\varepsilon_i \sim N(0, \sigma_{\varepsilon_i}^2),$$

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

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_{ε}^2 . 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 2; Ogle 2016). As in Helser and Lai (2004), we modelled the growth parameter vectors for each island j , $\theta_j = (L_{\infty j}, \ln K_j, a_{0j})$, as random effects assumed to follow a multivariate normal distribution with mean $\mu = (L_{\infty}, \ln K, a_0)$ and covariance matrix Σ , i.e.,

248

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

249

$$\Sigma = \begin{bmatrix} \sigma_{L_{\infty}}^2 & \sigma_{L_{\infty} \ln K} & \sigma_{L_{\infty} a_0} \\ \sigma_{L_{\infty} \ln K} & \sigma_{\ln K}^2 & \sigma_{\ln K t_0} \\ \sigma_{L_{\infty} a_0} & \sigma_{\ln K t_0} & \sigma_{t_0}^2 \end{bmatrix}$$

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This model was attractive because it accounts for parameter correlations and borrows strength across islands in order 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 (TMB), 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 less than 0.0001. To select the most parsimonious of the eight nested models, we used marginal Akaike's Information Criterion, $\text{AIC} = -2\log\mathcal{L} + 2p$, where \mathcal{L} is the marginal likelihood evaluated at the MLE and p is the number of estimated parameters (Table 2; 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'.

262 *Estimating natural mortality*

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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 3, Fig. 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 (Fig. 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 (Fig. 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, 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 4; Hordyk 2017).

LBSPR assumes an equilibrium population state and only considers one length distribution at a time (either one 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 one 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 selectivity and that the selectivity was the same for both gears. These assumptions seemed reasonable because large fish, greater than 70 cm, were well-represented in the Little Cayman catch length data from 2002 (Fig. 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 (Fig. 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 Information).

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 two years of catch data (ca. 2,000 fish in 2001 and 1,934 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 two 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 $M \pm 0.05 \text{ yr}^{-1}$. 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-multinomial 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 5 and the ‘LIME’ R package (Rudd 2018), starting the model in 1999 to include four years of roughly known, extreme variation in F before protection: two years in which F was near zero (1999-2000), followed by two 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, $F_{t+1} \sim N(F_t, \sigma_F^2)$ to facilitate convergence. As this was not appropriate for the extreme F

fluctuations from 1999-2003, 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 1 for a summary of the data used to fit each model.

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 (Fig. 3). Of the hierarchical growth models, only those that allowed one or fewer parameters to vary by island converged (Table 2). 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 yr^{-1} , 95% CI: 0.125–0.156) than Cayman Brac (0.160 yr^{-1} , 95% CI: 0.143–0.178) or Grand Cayman (0.164 yr^{-1} , 95% CI: 0.146–0.182; Table 3, Fig. 3).

We estimated natural mortality as $M = 0.276 \text{ yr}^{-1}$ (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 yr^{-1} ; Thompson and Munro 1978) and is very close to estimates from methods recommended in a

recent meta-analysis ($M_{Hoenig_{nls}} = 0.224 \text{ yr}^{-1}$ using $t_{\max} = 29 \text{ yr}$; $M_{Pauly_{nls-T}} = 0.245 \text{ yr}^{-1}$; Then et al. 2015).

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 (Fig. 4). Pickle Bank had much larger fish—the average was 10 cm larger than the three main historic Cayman Islands FSAs. Individuals greater than 70 cm were rare at the three historic FSAs, whereas they comprised roughly half of the catch on Pickle Bank (Fig. 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, Fig. 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 (Fig. 6). On Little Cayman, the modes (local maxima, dashed lines in Fig. 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; Fig. 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 (Fig. 6, Table 3). 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 (Fig. 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 six years of no FSA fishing, was estimated to increase from 0.48 to 1.00. Following two 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 1999-2019, 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 (Fig. 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 Francis weighting the final model (Fig. S4). LIME generally fit the abundance index and length-frequency data well, including the bimodal distributions in 2017–2019 (Figs. S6-7). 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 0.08-0.11 found that the negative log-

likelihood was minimized at $CV_L = 0.096$, and this value was used in the final LIME-integrated model (Fig. 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, Fig. 8). The two 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 (Fig. 8d, Table 6). The number of spawners similarly reached a minimum in 2008, increased slightly from 2008–2012 due in part to slightly higher recruitment in the 2003-2006 period, and then increased dramatically from 2014–2018 (Fig. 8b-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 (Fig. 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, Fig 8b). This was robust to assuming different amounts of uncertainty in the growth parameters and length composition data (Fig. 9), as well as values of M (Fig. S9, Table S1) and steepness (Table S2). Under these various parameterizations, the magnitude of the 2011 recruitment pulse varied from 4.4–7.8 times average recruitment (Tables 6, 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 Fig. 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 two years of intense FSA fishing, and then took 16 years to recover to near pre-exploitation levels (Fig. 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 versus recruitment.

The differences in growth coefficients (Table 3, Fig. 3) and 2017–2019 length distributions (Fig. 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 one 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 (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 four-fold from 2008 to 2019 and was much higher than on Cayman Brac despite similar habitat area (Fig. 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 (Fig. 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 versus 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,

472 requiring Nassau Grouper to allocate more energy to active metabolism and less to growth.
473 Behaviour may differ—when DOE scientists attempted in-water capture to acoustically tag
474 Nassau Grouper *in situ*, they noted that Cayman Brac fish were markedly warier and more
475 skittish than their counterparts on Little Cayman (B. Johnson, pers. comm.). Nassau Grouper on
476 Little Cayman may have matured earlier than their counterparts on Cayman Brac, which would
477 result in an energy reallocation from somatic growth to reproductive growth. Of these alternative
478 explanations, we can only rule out different ages at maturity because the 2011 cohort was absent
479 from the 2016 length distribution on Little Cayman. Still, there are many conceivable
480 mechanisms behind the difference in estimated growth coefficients, and future work could test
481 for these possibilities.

482 Another obvious question is: What was special about conditions in 2011 that led to a
483 major recruitment pulse on both islands? Like many reef fish, Nassau Grouper are benthic but
484 are pelagic broadcast spawners, and successful recruitment may largely depend on favourable
485 currents bringing larvae close to suitable reef habitat. The prevailing current around the Cayman
486 Islands flows east-northeast to west-southwest, but the mean current is weak and looping eddies
487 that retain water for months are common (Richardson 2005). Thus, self-recruitment within the
488 Caymans is a very likely possibility (Colin et al. 1987; Heppell et al. 2009, 2011; Colin 2012b;
489 Sadovy de Mitcheson and Colin 2012). Future work could model larval dispersal from Little
490 Cayman using archived remote sensing data and compare 2011 against low recruitment years.
491 Alternatively, strong recruitment in 2011 could have been related to abundant prey or fewer
492 predators at critical space and time scales for larval survival (e.g. Cushing’s match-mismatch
493 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 Jr 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, around 26°C (Fig. 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.

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 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 two 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 (Fig. 7). Second, the bimodal 2017–2019 length distributions imply that a large recruitment pulse occurred on Cayman Brac as well as Little Cayman (Fig. 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 1980-90s (Fig. 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 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 (1) SPR on all three islands was similar before protections, (2) 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 (3) 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 $SPR_{MSY} > 40\%$. Additionally, 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 two 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 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 material

The following supplementary material is available at *ICESJMS* online:

Table S1. Sensitivity analysis of LIME-integrated model parameters and derived quantities to the assumed value of M .

Table S2. Sensitivity analysis of LIME-integrated model parameters and derived quantities to the assumed value of steepness, h , and survey catchability, q .

Description of methods: laser caliper calibration, measurement error, and data collection.

Figure S1. Measurement error of the laser caliper system as a function of distance-to-camera and angle offset from perpendicular.

Figure S2. Length distributions for major versus minor spawning months.

Figure S3. Length distribution comparison from the stereo camera and laser calipers.

Figure S4. Sensitivity analysis of the LIME-integrated model to data weighting parameters σ_C (catch observation error) and σ_I (abundance index observation error).

Figure S5. Distributions of standardized residuals for the index and mean length from the LIME-integrated model with Dirichlet-multinomial versus Francis weighting.

Figure S6. Fits to the length-frequency data from the LIME-integrated model with Francis weighting.

Figure S7. Standardized residuals for the index and mean length from the LIME-integrated model with Francis weighting.

Figure S8. Likelihood profiles for the coefficient of variation of length-at-age, CV_L , and von Bertalanffy asymptotic length, L_∞ .

Figure S9. Sensitivity analysis of the LIME-integrated model to assumed value of M .

Figure S10. Habitat area available to Nassau Grouper on Little Cayman and Cayman Brac.

Figure S11. Sea surface temperature surrounding Little Cayman after spawning events from 2004–2018, 7-day average.

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Figure 1. Map showing the location of historic and current Nassau Grouper spawning aggregations in the Cayman Islands. 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.

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™ 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.

Figure 3. Island-specific Nassau Grouper growth curves from the Cayman Islands. Fish age-4 and older were sampled from 1988-1992 FSA catch on Little Cayman, Cayman Brac, and Grand Cayman ($n = 99, 132, \text{ and } 246$). 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 3.

Figure 4. Nassau Grouper catch length distributions from fish spawning aggregation (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 1987–1995 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.

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 2002-2019. 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.

Figure 6. Bimodal length distributions from Little Cayman and Cayman Brac for the years 2017 through 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).

Figure 7. Estimated spawning potential ratio (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).

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 maximum likelihood estimates 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 F were fixed at 0 for years without points.

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 maximum likelihood estimates 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).

955 Table 1. Summary of the types, years, and locations of data used to fit each model. Island/FSA abbreviations: Little Cayman (LC),
956 Cayman Brac (CB), Grand Cayman (GC), Pickle Bank (PB). “Pre/post” refers to FSA protection status (FSAs were protected in
957 2003). Prior to protection, length data was collected from fishery catch, and after protection, length data was collected *in situ* via
958 diver-operated laser calipers. *Age-length data (1988-92) were used in the LIME-integrated model to fit the growth parameters, but
959 these data did not contribute to the likelihood of the population length composition (model years: 1999-2019). ^Lengths of 25 un-aged
960 fish known to be 1 year old were recorded in 2012 on Little Cayman from a large recruitment event from 2011 spawning (Camp et al.
961 2013; Semmens et al. 2013).

Model	Estimates			Data type				Result
	Quantity	On island(s)	Pre/post-protection	Length	Index	Catch	Age	
Growth	L_{∞} , a_0 , and K	LC, CB, GC	Pre	1988-1992, 2012^			1988-1992	Tables 2, 3 Figures 3, 6
Catch curve	M	PB	Pre	2000				Tables 4, 5
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*	2005-2018	2001-2002	1988-1992*	Figure 8

963 Table 2. Hierarchical von Bertalanffy growth models for Cayman Islands Nassau Grouper, where
964 $\hat{L}[a] = L_{\infty j} \left[1 - e^{-K_j(a-a_{0j})} \right]$ for island j . Model m2, with island-specific K_j and shared L_{∞} and
965 a_0 , had the lowest AIC.

Model	Island-specific parameters	No. fixed effect parameters	Converged and pos. def. Hessian	AIC	Δ AIC
m1	---	4	Yes	3112.8	34.4
m2	K	5	Yes	3078.4	0
m3	L_{∞}	5	Yes	3082.2	3.8
m4	a_0	5	Yes	3087.9	9.5
m5	K, L_{∞}	7	No	3090.7	12.3
m6	L_{∞}, a_0	7	No	3086.4	8.0
m7	K, a_0	7	No	3088.7	10.3
m8	K, L_{∞}, a_0	10	No	---	---

966

967 Table 3. Estimated von Bertalanffy growth function parameters from model m2, which allowed
968 K_j to vary by island, i.e. $\hat{L}[a] = L_\infty[1 - e^{-K_j(a-a_0)}]$ for island j . 95% confidence interval limits
969 are given in parentheses.

Parameter	Overall / mean	Little Cayman	Cayman Brac	Grand Cayman
L_∞ (cm)	80.2 (76.8, 83.7)			
K_j (yr ⁻¹)	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

970

971

972 Table 4. Parameters used to fit the LBSPR model. Island abbreviations: LC = Little Cayman, CB
 973 = Cayman Brac, GC = Grand Cayman, and PB = Pickle Bank. Length-weight parameters were
 974 fit to the log-linear model, $\log(W_i) = \alpha + \beta \log(L_i)$, with weight in kg and length in cm.

Parameter		LC	CB	GC	PB	Source
L_∞	Asymptotic length (cm)	80.2	80.2	80.2	80.2	this study (Table 3, Fig. 3)
K	Growth coefficient (yr^{-1})	0.140	0.160	0.164	0.155	this study (Table 3, Fig. 3)
M	Natural mortality (yr^{-1})		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 (Fig. S8)
	Bin width (cm)		1			
	Maximum length (cm)		100			
	Minimum length (cm)		1			

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976

977 Table 5. 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	*81.2 (77.9, 84.3)	this study (Table 3, Fig. 3)
K	von Bertalanffy growth coefficient (yr ⁻¹)	0.140	*0.141 (0.126, 0.156)	this study (Table 3, Fig. 3)
a_0	Age at zero length	-0.832	*-0.802 (-0.951, -0.654)	this study (Table 3, Fig. 3)
M	Natural mortality (yr ⁻¹)		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)	*61.9 (59.4, 64.4)	*61.8 (59.2, 64.4)	
S_{95}	Length at 95% selectivity (cm)	*66.1 (59.9, 72.4)	*66.0 (59.4, 72.6)	
α	Length-weight intercept		3.725 x 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 (Fig. S4)
σ_I	Abundance index observation error		0.175	sensitivity analysis (Fig. S4)
σ_R	Recruitment process error	*0.87 (0.60, 1.25)	*0.83 (0.57, 1.21)	
CV_L	Growth curve coefficient of variation		0.096	likelihood profile (Fig. 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	

978 *estimated in model (MLE with 95% CI in parentheses). Otherwise fixed at specified value.

979

980 Table 6. LIME model estimates of min/max depletion, 2011 recruitment pulse, and growth
 981 parameters for the Little Cayman FSA, assuming different amounts of uncertainty in the growth
 982 parameters and length composition data. LIME-integrated included uncertainty in growth
 983 parameters while LIME-fixed-K did not. Francis data weighting included more uncertainty in the
 984 length composition data than using the Dirichlet-multinomial likelihood. Values are MLE with
 985 95% CI in parentheses.

	LIME-integrated		LIME-fixed-K	
	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*	80.2*
k	0.141 (0.126, 0.156)	0.146 (0.135, 0.158)	0.140*	0.140*
a_0	-0.80 (-0.95, -0.65)	-0.78 (-0.90, -0.66)	-0.83*	-0.83*

986 *fixed in model, not estimated.
 987