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Original Article

Length-based risk analysis for assessing sustainability of data-limited tropical reef fisheries

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This study extended a "data-limited" length-based stock assessment approach to a risk analysis context. The estimation-simulation method used length frequencies as the principal data in lieu of catch and effort. Key developments were to: (i) incorporate probabilistic mortality and growth dynamics into a numerical cohort model; (ii) employ a precautionary approach for setting sustainability reference points for fishing mortality (F_{REF}) and stock reproductive biomass (B_{REF}); (iii) define sustainability risks in terms of probability distributions; and, (iv) evaluate exploitation status in terms of expected length frequencies, the main "observable" population metric. This refined length-based approach was applied to six principal exploited reef fish species in the Florida Keys region, consisting of three groupers (black grouper, red grouper, and coney), two snappers (mutton snapper and yellowtail snapper), and one wrasse (hogfish). The estimated sustainability risks for coney were low (<35%) in terms of benchmarks for fishing mortality rate and stock reproductive biomass. The other five species had estimated sustainability risks of greater than 95% for both benchmarks. The data-limited risk analysis methodology allowed for a fairly comprehensive probabilistic evaluation of sustainability status from species and community perspectives, and also a frame of reference for exploring management options balancing sustainability risks and fishery production.

Keywords: average length mortality estimation, snappers, stock assessment, tropical groupers

Introduction

The ecological and economic importance of tropical multispecies coral reef fisheries makes their sustainability a key conservation concern. Sustainability is defined as the ability of exploited stocks to produce goods and services, while maintaining sufficient reproductive capacity to ensure this production into the indefinite future (Ault *et al.*, 2014). Commercial tropical reef fisheries are mostly artisanal, characterized by numerous small fishing vessels landing catches at many ports widely distributed in space (Gallucci *et al.*, 1996). This is also the situation for recreational reef fisheries (c.f. Ault *et al.*, 2005a). Keeping track of total landings and the associated fishing effort for recreational fisheries is substantially more complex than industrial fisheries that are

characterized by a relatively small number of large vessels that land their catches at a few major ports. Evaluating the sustainability of tropical reef fisheries is often not possible by traditional stock assessment methods (e.g. statistical catch at age, stock synthesis, and biomass dynamic models) because these require long time series of reliable age-structured catches and fishing effort by fleets and gears that do not exist (Ault and Olson, 1996; Quinn and Deriso, 1999; Walters and Martell, 2004; Haddon, 2011).

An alternative "data-limited" approach using length frequency data in lieu of catch and effort for evaluating the sustainability status of coral reef fishes was described in Ault *et al.* (1998). A numerical cohort length-structured population model was parameterized using fishery-dependent and independent length

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composition data, along with basic life history demographic information on lifespan, age-and-growth and sexual maturity. Their population model was then used to compute sustainability benchmarks (e.g. spawning potential ratio, SPR). A key aspect of the approach was that it employed a length-based estimation model for total mortality rate (Ehrhardt and Ault, 1992; Ault *et al.*, 2005b, 2014).

More recently there has been a trend in stock assessment to incorporate uncertainty in fishery data and demographic processes to evaluate sustainability metrics from a probabilistic perspective, i.e. typically posing questions such as "what is the likelihood that a given stock is being fished sustainably?" (Francis, 1992; Hilborn and Walters, 1992; Smith et al., 1999; Sainsbury et al., 2000; Patterson et al., 2001; Mangel et al., 2010; Shertzer et al., 2010; Methot and Wetzel, 2013; Punt et al., 2016; Link, 2018; Munyandorero, 2018). In this study, we extend the length-based approach of Ault et al. (1998), which produced deterministic point estimates of sustainability metrics, to a stochastic risk analysis context (Wagner, 1975; Keeney and Raiffa, 1976; Hertz and Thomas, 1983; Law and Kelton, 2000). Key developments were to: (i) incorporate probabilistic mortality and growth dynamics into the numerical cohort model; (ii) employ a precautionary approach for setting sustainability reference points for fishing mortality (F_{REF}) and stock reproductive biomass (B_{REF}); (iii) define sustainability risks in terms of probability distributions; and, (iv) evaluate exploitation status in terms of expected length frequencies, the main "observable" population metric. This refined length-based approach was applied to six key example species of the exploited snapper-grouper complex in the Florida Keys coral reef ecosystem.

Material and methods

Demographic parameters for length-based approach

The "data-limited" assessment approach of Ault *et al.* (1998) requires some basic species-specific life history demographic parameters: (i) the von Bertalanffy length dependent on age growth function [Table 1, Equation (T-1)]; (ii) the allometric weight–length relationship [Table 1, Equation (T-2)]; (iii) the oldest age (a_{λ}) ; and, (iv) the length at which 50% of individuals attain sexual maturity $(L_{\rm m})$ (c.f. Table 1). The principal sampling data required for a given fish population are abundance-at-length compositions, which are used to estimate the indicator variable \overline{L} , average length in the exploited phase of the population (i.e. the mean length of individuals $> L_{\rm c}$, the minimum length of first capture regulated by the fishery). This information was then used to estimate population instantaneous total (Z), natural (M), and fishing (F) mortality rates.

Total mortality Z was estimated based on the following theoretical definition of \overline{L} following the "truncated model" of Ehrhardt and Ault (1992),

$$\overline{L}(t) = \frac{F(t) \int\limits_{a_c}^{a_{\lambda}} N(a, t) L(a, t) da}{F(t) \int\limits_{a_c}^{a_{\lambda}} N(a, t) da},$$
(1)

where N(a, t) is abundance at age a and time t, L(a, t) is length at a and t, F(t) is fishing mortality rate at time t, and a_c is the age

at first capture. For exploited populations, $\overline{L}(t)$ in Equation (1) directly reflects the total mortality Z(t) or population loss due to fishing manifested through changes in the observed size composition (Beverton and Holt,1957; Ehrhardt and Ault, 1992; Quinn and Deriso, 1999). Substituting the von Bertalanffy model for L(a,t) and the exponential mortality model for N(a,t) [Table 1, Equation (T-3)] in Equation (1), along with a little algebra, gives the total mortality $\hat{Z}(t)$ estimation formula derived by Ehrhardt and Ault (1992),

$$\left[\frac{L_{\infty} - L_{\lambda}}{L_{\infty} - L_{c}}\right]^{\frac{\hat{Z}(t)}{K}} = \frac{\hat{Z}(t)(L_{c} - \overline{L}(t)) + K(L_{\infty} - \overline{L}(t))}{\hat{Z}(t)(L_{\lambda} - \overline{L}(t)) + K(L_{\infty} - \overline{L}(t))},$$
(2)

where K and L_{∞} are parameters of the von Bertalanffy growth equation, $L_{\rm c}$ is length at first capture, and L_{λ} is average length at age a_{λ} [Table 1, Equation (T-4)]. Estimation of Z was carried out using the numerical algorithm LBAR (Ault *et al.*, 1996; FAO, 2003). Equations (1) and (2) are based on the assumption of a finite lifespan (maximum age $= a_{\lambda}$), in contrast to length-based mortality models that assume an infinite lifespan (maximum age $= a_{\infty}$; Beverton and Holt, 1957), to potentially guard against bias in estimates of Z for shorter-lived species (Ehrhardt and Ault, 1992).

Natural mortality rate M was estimated from lifespan (*sensu* Alagaraja 1984; Hewitt and Hoenig, 2005) based on survivorship to age a_{λ} ,

$$S(a_{\lambda}) = \frac{N(a_{\lambda})}{N(a_r)} = e^{-M(a_{\lambda} - a_r)}, \tag{3}$$

i.e. the fraction of initial cohort numbers surviving from age of recruitment $a_{\rm r}$ to the maximum age a_{λ} . Setting $a_{\rm r}=0$ in Equation (3) and solving for M yields an estimator for natural mortality rate,

$$\hat{M} = \frac{-\ln[S(\hat{a}_{\lambda})]}{\hat{a}_{\lambda}},\tag{4}$$

where \hat{a}_{λ} is the observed maximum age. Following a heuristic for exploited populations (e.g. Hewitt and Hoenig, 2005), computations of \hat{M} utilized a lifespan survivorship of 5%, i.e. $S(\hat{a}_{\lambda}) = 0.05$ [in contrast to perhaps 1% for unexploited populations (Quinn and Deriso, 1999)]. Given estimates for Z and M, fishing mortality rate was estimated by $\hat{F} = \hat{Z} - \hat{M}$.

For application to reef fishes in the Florida Keys, life history demographic parameters for grouper and snapper species were obtained from a comprehensive literature synthesis. Length composition data were obtained from NOAA's Southeast Fisheries Science Center from the following statistical sampling programs: (1) the reef fish visual census (RVC), a fishery independent *in situ* diver survey (Smith *et al.*, 2011); (2) the Trip Interview Program (TIP), a dockside intercept survey of the commercial fleet; (3) the marine recreational information program (MRIP), an intercept survey of sportfishers fishing from private/rental boats, small charter boats, and the shoreline (NMFS, 2017); and, (4) the head boat (HB) program, a dockside intercept survey of sportfishers from large charter boats (Dixon and Huntsman, 1992; Bohnsack *et al.*, 1994). Estimates of \overline{L} were computed using a survey design ratio-of-means estimator (Cochran, 1977; Lohr, 2010),

Table 1. Parameters, variables, and equations for population demographic relationships used in the estimation-simulation risk analysis of Florida reef fish population dynamics.

Symbol	Definition	Computational formula	Units	Equation no.
а	Cohort age class $(a=0,\ldots,a_{\lambda})$		Months	
Δ a	Model age step		Months	
Δt	Model time step		Months	
L(a,t)	Length at age a and time t	$L(a,t) = L_{\infty}(1 - e^{-K(a-a_0)})$	mm FL	T-1
L_∞	Asymptotic length		mm FL	
K	Brody growth coefficient		Per year	
a_0	Age at which length equals zero		Years	
W(a,t)	Weight at age a and time t	$W(a,t) = \alpha(L(a,t))^{\beta}$	kg	T-2
α	Scalar coefficient of weight-length function		Dimensionless	
β	Power coefficient of weight-length function		Dimensionless	
a_{λ}	Maximum age (under exploitation)		Years	
L _m	Length at 50% maturity		mm FL	
a _r	Age at recruitment to population (= age 0)		Months	
L_{r}	Length at recruitment to population	$L_r = L_{\infty} \left(1 - e^{-K(a_r - a_0)} \right) \tag{(4.6)}$	mm FL	
N(a,t)	Numbers (abundance) at age $a + \Delta a$ at time $t + \Delta t$	$N(a + \Delta a, t + \Delta t) = N(a, t)e^{-(M(a,t)+F(a,t))}$	Number of fish	T-3
F(a,t)	Fishing mortality rate at age a at time t		Per year	
M(a,t)	Natural mortality rate at age a at time t		Per year	
Z(a,t)	Total mortality rate at age a at time t	Z(a,t) = M(a,t) + F(a,t)	Per year	
		$\hat{z}_{t-1} = \hat{z}_{K}^{(t)} = \hat{z}_{t}(t) + \kappa (1 - \bar{I}_{t}(t))$,	
$\hat{Z}(t)$	Total mortality rate estimated from L	$\begin{bmatrix} \frac{L_{\infty} - L_{\lambda}}{L_{\infty} - L_{c}} \end{bmatrix}^{\frac{2(\kappa)}{K}} = \frac{\hat{z}(t) \left(L_{c} - \overline{L}(t) \right) + K \left(L_{\infty} - \overline{L}(t) \right)}{\hat{z}(t) \left(L_{1} - \overline{I}(t) \right) + K \left(L_{\infty} - \overline{I}(t) \right)}$	Per year	(2)
$\overline{L}(t)$	Average length in the exploited phase at time t	[] 2(0)(2x 2(0))+N(230 2(0))		
Lc	Minimum length at first capture	(mm FL	
$\frac{L_{\lambda}}{L}$	Mean length at maximum age	$L_{\lambda} = L_{\infty} (1 - e^{-K(a_{\lambda} - a_0)})$	mm FL	T-4
L	Composite \overline{L} from empirical sampling surveys	M()	mm FL	
S(a)	Survivorship to age a	$S(a) = \frac{N(a)}{N(a_r)} = e^{-Z(a - a_r)}$ $\hat{M} = -\ln(0.05)/\hat{a}_{\lambda}$	Dimensionless	(3)
Ŵ	Natural mortality rate estimated from \hat{a}_{λ}	$\hat{M} = -\hat{\ln}(0.05)/\hat{a}_{\lambda}$	Per year	(4)
\hat{a}_{λ}	Observed maximum age		Years	
\tilde{a}_{λ}	Theoretical maximum age			
Ê	Fishing mortality rate estimated from \hat{Z} and \hat{M}	$\hat{F} = \hat{Z} - \hat{M}$	Per year	
F_{med}	Median of distribution of F	$t{+}\Delta t$	Per year	
N(L)	Theoretical length-based population model	$N(L) = \int\limits_{t}^{t+\Delta t} \int_{a_{r}}^{a_{\lambda}} R(\tau - a)S(a)\theta(a)p(L a)dadt$	Numbers	T-5
$R(\tau - a)$	Recruits lagged back to birth	t	Numbers	
$\theta(a)$	Sex ratio at age a	$\theta(a) = 1$	Dimensionless	
$\overline{L}(a)$	Mean length at midpoint of age interval $a+\Delta a$	$\overline{L}(a) = L_{\infty} \left(1 - e^{-K((a+0.5\Delta a) - a_0)} \right)$	mm FL	
(11.)	5 1 199 CL 1 1 1 1 1 1	$(c,\overline{L}(a))$ $= (d-\overline{L}(a))$ $= (c-\overline{L}(a))$	5' ' 1	T.
p(L a)	Probability of being length <i>L</i> given age <i>a</i>	$p(c \leq \overline{L}(a) \leq d) = \Phi\left(\frac{d - \overline{L}(a)}{\sigma(a)}\right) - \Phi\left(\frac{c - \overline{L}(a)}{\sigma(a)}\right)$	Dimensionless	T-6
С	Lower bound of length distribution at age a			
d	Upper bound of length distribution at age <i>a</i>			
$\Phi(\cdot)$	Cumulative normal distribution	— · · · /= · · › β		
$\overrightarrow{W}(a)$	Mean weight at midpoint of age interval $a+\Delta a$	$\overline{W}(a) = \alpha(\overline{L}(a))^{\beta}$	kg	
$\phi(L)$	Selectivity at length L	$\phi(L) = 1$	Dimensionless	
	sciectivity at length 2	41 A4 =	Difficisioniess	
$\overline{N}(t)$	Average population abundance at time t	$\overline{N}(t) = \int_{0}^{t+\Delta t} \int_{0}^{a_{\lambda}} N(a,t) (1 - e^{-Z(a,t)}) / Z(a,t) dadt$	Numbers	
		$B_{\text{EX}}(L_{\text{c}},t) = \int_{L_{x}}^{a_{\text{f}}} N(L a,t)W(L a,t)\phi(L)dL$		
$B_{EX}(L_c,t)$	Exploitable population biomass	$B_{\text{FX}}(L_c, t) = \int_{0}^{\infty} N(L a, t)W(L a, t)\phi(L)dL$		(9)
- (()		L _c		(-)
N (1 - 1)		$\overline{\mathbf{a}}_{\lambda}$ $(1 - \epsilon)\overline{\mathbf{a}}_{\lambda}$	N. 1	- -
$\overline{N}(L,t)$	Average abundance (numbers) at length at time t	$\overline{N}(L,t) = \sum_{a_{r}}^{a_{\lambda}} p(L a,t) \overline{N}(a,t)$	Numbers	T-7
$\overline{B}(t)$	Average population biomass at time t	$\overline{B}(t) = \int\limits_{t}^{t+\Delta t} \int\limits_{a_{r}}^{a_{\lambda}} \overline{N}(a,t) \overline{W}(a,t) dadt$		
- (-)	0.1.1			
$Y_w(F, L_c, t)$	Yield in weight at time t	$Y_{w}(F, L_{c}, t) = F(t)B_{EX}(L_{c}, t)$		(10)
		L		
SSB	Spawning (mature) stock biomass	$SSB(t) = \int_{L_m}^{L_{\lambda}} B(L a,t) dL$	mt	(11)
CDD	Construction of the state of th		D:il	(12)
SPR	Spawning potential ratio	$SPR = SSB_{\hat{F}}/SSB_{F=0}$	Dimensionless	(12)
F_{REF}	Fishing mortality rate at reference SPR	f = c	Per year	
		$\int_{C} N(L,t)LdL$	·	
Ê	Model projected \overline{L}	$\hat{\overline{L}} = \frac{\int_{C}^{\hat{T}} \overline{N}(L,t)LdL}{\int_{\hat{T}}^{\hat{L}_{\lambda}} \overline{N}(L,t)dL}$	mm FL	T-8
		$\int \overline{N}(L,t)dL$		
F/F_{REF}	Current to reference F (overfishing limit, OFL)	L _C	Dimensionless	
B/B_{REF}	Current to reference spawning biomass		Dimensionless	(13)

$$\overline{L}(t) = \frac{\overline{y}}{\overline{x}} = \frac{\sum_{i} y_{i}}{\sum_{i} x_{i}},$$

following the formal definition of population average length [Equation (1); Beverton and Holt, 1957], where x_i is the number of fish measured in sample unit i (e.g. fishing trip), y_i is the summed lengths of measured fish in unit i, and n is number of sample units. Computations for variance of \overline{L} followed Lohr (2010).

Numerical length-based cohort model

The numerical length-based cohort population model described in Ault *et al.* (1998), tailored for data-limited situations, was extended here to incorporate stochastic mortality and growth. The original model was based on the following conservation law for population abundance,

$$\frac{dN(a,t)}{dt} = \frac{\partial N(a,t)}{\partial a} + \frac{\partial N(a,t)}{\partial t} = -Z(a,t)N(a,t),\tag{5}$$

in which the partial differential equation expresses population age structure in terms of average number of fish by age over time. This formulation allowed for incorporation of population demographic processes characteristic of tropical marine fishes, including quasi-continuous growth, protracted spawning-recruitment seasons, and competition-based population dynamics (Ault and Fox, 1989; Sparre and Venema, 1992; Ault and Olson, 1996; Ault et al., 1999). The numerical model tracked cohort numbers-at-size (length and weight) over age and time. Model parameters and equations are given in Table 1. For application in this study, the model time step Δt was monthly (12 equal periods for 1 year). Adapted for data-limited fisheries, model assumptions were: (i) average annual constant recruitment, apportioned evenly for each model time step; (ii) knife-edged length at sexual maturity L_m ; and, (iii) knife-edged gear selectivity at length L_c .

Probabilistic mortality rates

Probabilistic total mortality (Z) was described using the statistical properties of the survey design average length estimates (i.e. normally distributed; Lohr, 2010). A normal $N(\mu, \sigma^2)$ probability density function was parameterized by setting $\mu = \overline{L}(t)$ and $\sigma^2 = \left[\text{SE} \left(\overline{L}(t) \right) \right]^2$, and then used to generate random deviates of average length. Random deviates of Z were computed from the average length deviates using Equation (2).

In a similar manner, probability distributions of natural mortality M were computed from corresponding probability distributions for maximum age a_{λ} [Equation (4)]. As demographic information has become more complete for Florida reef fishes over the past 20 or so years, the maximum observed age for many species has also increased, sometimes doubling or tripling in value (e.g. Claro, 1981; Mason and Manooch, 1985; O'Hop *et al.*, 2015). Thus, we considered the reported \hat{a}_{λ} a minimum value with the uncertainty extending in one direction, i.e. to older ages. The exponential probability density function (expo(β), Law and Kelton, 2000) was selected as a simple distribution for describing random deviates of a_{λ} matching these characteristics. Estimation of the rate parameter $1/\beta$ for the expo(β) distribution was carried out in several steps. First, an estimate of \hat{M} [Equation (4)] for the

observed maximum age \hat{a}_{λ} was used to compute the theoretical maximum age \tilde{a}_{λ} following a rearrangement of Equation (4),

$$\tilde{a}_{\lambda} = \frac{-\ln(S(\tilde{a}_{\lambda}))}{\hat{M}},\tag{6}$$

and presuming survivorship S to age \tilde{a}_{λ} was 0.1% (i.e. $S(\tilde{a}_{\lambda})=0.001$). Next, the age interval Δa_{λ} from the observed maximum age \hat{a}_{λ} to the theoretical maximum age \tilde{a}_{λ} was computed as

$$\Delta a_{\lambda} = \tilde{a}_{\lambda} - \hat{a}_{\lambda}. \tag{7}$$

Random deviates for the $\exp(\beta)$ distribution range from 0 to ∞ ; correspondingly, the random deviates for maximum age were defined as ages beyond the observed maximum age (i.e. where $0 = \hat{a}_{\lambda}$). The exponential rate parameter $1/\beta$ was estimated in an analogous manner to \hat{M} [Equation (4)] using

$$\frac{1}{\beta} = \frac{-\ln(0.001)}{\Delta a_{\lambda}},\tag{8}$$

that specifies an $\exp o(\beta)$ distribution with 99.9% of the random deviates occurring over the Δa_{λ} range. Each generated $\exp o(\beta)$ random deviate was converted to actual age by adding the observed maximum age \hat{a}_{λ} , and then input to Equation (4) to compute a random deviate of M.

The above procedures were used to generate a pair of Z and M random deviates, from which a random deviate for fishing mortality F was computed (F = Z - M). This provided the input mortality rates for a single run of the numerical population model. In our applications, to achieve the asymptotic properties of the selected probability distributions, $n = 90\,000$ runs were carried out for a given species.

Probabilistic length-at-age

Variation in length-at-age around the von Bertalanffy growth function was modelled as normally distributed with a constant coefficient of variation of 7% (CV, standard deviation divided by the mean), following general characteristics observed in lengthage growth studies for a wide variety of fish species (*inter alia* Then *et al.*, 2015). This variation was incorporated into the numerical cohort model by the following procedure. For each model age a, a normal $N(\mu, \sigma^2)$ probability density function was parameterized by setting $\mu = \overline{L}(a,t)$ predicted by the growth function and $\sigma^2 = \left[0.07\overline{L}(a,t)\right]^2$. Then, the lengths at age L(a,t) for N(a,t) individuals were generated by the random normal distribution with the cut-off at 3σ in both positive and negative directions. The frequency distribution of the lengths was generated by a histogram with 15 bins above and below the mean $\overline{L}(a,t)$ resulting in a total of 31 length sub-cohorts.

Sustainability analyses

The numerical cohort model was used to conduct sustainability analyses for exploited reef fish species. This involved comparisons of various population metrics at current levels of fishing mortality F(t) relative to management limit reference points. Three principal population metrics were exploitable population biomass $(B_{\rm EX})$, yield in weight $(Y_{\rm w})$, and spawning stock biomass (SSB). For all three metrics, biomass B(a, t) at age a and time t was

estimated as numbers N(a, t) times weight W(a, t). Exploitable biomass $B_{\rm EX}$ was calculated by integrating over the exploited length range at a particular time t,

$$B_{\rm EX}(L_{\rm c},t) = \int_{L_{\rm c}}^{L_{\lambda}} B(L|a,t) \phi(L) dL = \int_{L_{\rm c}}^{L_{\lambda}} N(L|a,t) W(L|a,t) \phi(L) dL,$$
(9)

where L|a,t was length conditioned on age a and time t (i.e. the distribution of lengths at a given age-time), and $\phi(L)$ was gear selectivity at length. Note that L_{λ} refers to the distribution of lengths at age a_{λ} . Yield in weight $Y_{\rm w}$ at time t was calculated by multiplying F at t by the exploitable biomass $B_{\rm EX}$ at t,

$$Y_{\rm w}(F, L_{\rm c}, t) = F(t)B_{\rm EX}(L_{\rm c}, t).$$
 (10)

Similarly, SSB at a given level of fishing mortality at time t was obtained by integrating over sexually mature individuals in the population,

$$SSB(t) = \int_{L_{-}}^{L_{\lambda}} B(L|a,t) dL.$$
 (11)

In the integrations of Equations (9)–(11), all lengths above L_c or L_m were included. SPR, a management benchmark that defines stock reproductive capacity (c.f. Ault *et al.*, 2014), was computed as the ratio of SSB(t) at current F(t) relative to that of an unexploited stock (F=0),

$$SPR = \frac{SSB_{F(t)}}{SSB_{F=0}} . {12}$$

A new procedure was developed to establish limit reference points for population sustainability risk. This method employed three precautionary demographic principles: (1) setting $L_{\rm c}=L_{\rm m}$, which assured that exploitation was directed only toward mature adults and not juveniles, giving fish at least one chance to spawn in their lifetime on average (Beverton and Holt, 1957; Ricker, 1975); (2) setting F = M as a proxy for $F_{\rm MSY}$, that is, the fishing mortality rate that achieves maximum sustainable yield (Mace, 2001); and, (3) considering MSY as a hard limit to the associated exploitation rate F_{MSY} , not to be exceeded (as opposed to a target; c.f. Caddy and McGarvey, 1996; Caddy, 2004). The numerical cohort model was then used to calculate the SPR at $F_{\rm MSY}$ for a suite of Florida grouper (Epinephelidae) and snapper (Lutjanidae) species. For each family, the species' average SPR at MSY was rounded to the nearest 5% increment and defined as the "reference" %SPR point. The sustainability risk reference point for fishing mortality, F_{REF} , was defined as the F generating the reference %SPR. The sustainability risk reference point for population biomass, B_{REF} , was defined as the spawning biomass at F_{REF} , where

$$\frac{B}{B_{\text{REF}}} = \frac{\text{SSB}_{F(t)}}{\text{SSB}_{F_{\text{REF}}}} \tag{13}$$

The distribution of random deviates of F and the sustainability reference points were used in the numerical model to compute

probability distributions for several sustainability benchmarks: SPR, F/F_{REF} (commonly termed the overfishing limit, OFL), and B/B_{REF} . The proportion of the distribution of SPR less than the reference %SPR was the estimated probability risk to sustainability in terms of remaining stock reproductive capacity. The proportion of the distribution of F/F_{REF} greater than 1.0 was the estimated probability risk to sustainability in terms of fishing mortality rate and fleet overcapitalization. The proportion of the distribution of B/B_{REF} less than 1.0 was the estimated probability risk to sustainability in terms of spawning population biomass. Lastly, the numerical cohort model was configured to compute Y_w and SPR for the full range of feasible combinations of L_c and F, i.e. "isopleth" surfaces (e.g. Beverton and Holt, 1957), to help put in context current exploitation rates in terms of sustainability risks and fishery production, and to aid exploration of feasible future management options for species with currently high levels of sustainability risk.

Results

Model parameters

The sustainability risk analysis methodology was applied to six principal exploited reef fish species in the Florida Keys region, consisting of three groupers [Epinephelidae; black grouper (Mycteroperca bonaci), red grouper (Epinephelus morio), coney (Cephalopholis fulva)], two snappers [Lutjanidae; mutton snapper (Lutjanus analis), yellowtail snapper (Ocyurus chrysurus)], and one wrasse [Labridae; hogfish (Lachnolaimus maximus), also commonly referred to as the "hog snapper"]. The life history demographic parameters for these example species are provided in Table 2. Average length in the exploited phase was estimated from length composition data for the recent period 2012-2016 for each of the four statistical sampling programs (Table 3). Annual survey estimates of mean and variance of \overline{L} were weighted by annual sample size to produce the time period values. Although the four sampling programs collected information from reef habitats in the Florida Keys, no single survey encompassed the full range of habitats for the six species: the fishery independent diving survey was restricted to depths <33 m, and commercial and recreational fishing was off-limits within a network of 23 no-take marine reserves (Smith et al., 2011). To obtain representative population values, composite $\overline{\overline{L}}$ and $SE(\overline{\overline{L}})$ were estimated for each species by taking the respective arithmetic means of \overline{L} and $var(\overline{L})$ from the data sources. The composite \overline{L} was then used to compute total mortality rate \hat{Z} (Table 3) and subsequent estimates of fishing mortality rate \hat{F} (Table 4).

Probabilistic mortality rates

The process for generating probabilistic mortality rates is illustrated for black grouper in Figures 1–3. A normal distribution for \overline{L} was generated from the composite estimates \overline{L} and $SE(\overline{L})$ (Figure 1a). The random deviates of \overline{L} were used to compute random deviates of Z using Equation (2) (Figure 1b). An exponential distribution for a_{λ} was developed from the observed maximum age \hat{a}_{λ} and Equations (4)–(8) (Figure 2a). The highest probability occurred at the observed \hat{a}_{λ} , 33 years for black grouper, and the mean of the exponential distribution was $\beta + \hat{a}_{\lambda} = 39.2$ years. The random deviates of a_{λ} were used to compute random deviates of M using Equation (4) (Figure 2b). The resulting distribution of F was obtained by subtracting a random value of M from

Table 2. Population life history demographic parameters for six exploited reef fishes in the southern Florida coral reef ecosystem used in length-based sustainability risk assessments.

Family	Species	\hat{a}_{λ}	\hat{M}	K	L_{∞}	a_0	α	β	$L_{\rm m}$	$L_{\rm c}$	L_{λ}	References
Groupers	Black Grouper		0.09078	0.1432	1299.8	-0.9028	8.7475E-06	3.0843	834	600	1290	SEDAR (2010)
(Epinephelidae)	(Mycteroperca bonaci)											
	Coney		0.15767	0.2000	377.0	-3.5300	1.4487E-05	3.0300	220	200	373	Trott (2006),
	(Cephalopholis fulva)											Burton <i>et al.</i> (2015)
	Red grouper	29	0.10330	0.1251	829.0	-1.2022	5.4600E-06	3.1800	292	500	810	SEDAR (2015)
	(Epinephelus morio)											
Snappers	Mutton snapper	40	0.07489	0.1650	799.0	-1.230	1.4771E-05	3.0275	323	400	811	O'Hop et al. (2015)
(Lutjanidae)	(Lutjanus analis)											
	Yellowtail snapper	23	0.13025	0.1330	489.3	-3.132	6.1400E-05	2.7790	232	260	474	O'Hop et al. (2012)
	(Ocyurus chrysurus)											
Wrasses	Hogfish	23	0.13025	0.1058	849.0	-1.329	9.5000E-05	2.7452	177	300	784	Cooper et al. (2013)
(Labridae)	(Lachnolaimus maximus)											

Parameter definitions and units are given in Table 1.

Table 3. Mean length (\overline{L}) and standard error (SE (\overline{L})) for six reef-fish species for the period 2012–2016 from four primary data sources: RVC, reef fish visual census; TIP, commercial trip information program; MRIP, marine recreational information program; and, HB, headboat survey.

	RVC		TIP		MRIP		НВ		Composite			
Species	$\overline{\overline{L}}$	$SE(\overline{L})$	$\overline{\overline{L}}$	$SE(\overline{L})$	$\overline{\overline{L}}$	$SE(\overline{L})$	$\overline{\overline{L}}$	$SE(\overline{L})$	$\overline{\overline{L}}$	$\operatorname{SE}(\overline{\overline{L}})$	$\hat{m{Z}}$	
Black grouper	684.6	24.3	708.3	11.5	734.6	22.7	759.6	18.5	721.8	19.9	0.6793	
Coney	272.7	6.8					291.1	23.3	281.9	17.2	0.2253	
Red grouper	594.1	20.0	579.5	16.8	572.2	11.2	590.2	8.5	584.0	14.8	0.3645	
Mutton snapper	494.5	10.4	549.7	27.0	548.4	12.8	554.9	9.8	536.9	16.6	0.3213	
Yellowtail snapper	304.5	5.1	312.4	2.9	312.7	3.0	301.7	2.7	307.8	3.5	0.5051	
Hogfish	333.2	3.6	353.3	11.9	358.3	4.8	345.4	13.3	347.6	9.4	1.1157	

Composite is the average of the four data sources, and was used to estimate total mortality rate \hat{Z} .

Table 4. Reef fish sustainability analysis metrics for six south Florida stocks.

Species	Ê	F _{med}	F _{REF}	$\hat{\overline{L}}_{\hat{F}}$	$\hat{\overline{L}}_{F=0}$	$\hat{\overline{L}}_{F_{\text{REF}}}$	$\hat{\pmb{F}}/\pmb{F}_{REF}$	$B_{\hat{F}}/B_{REF}$	SPR
Black grouper	0.5885	0.6015	0.0770	714.5	1005.2	914.9	7.64	0.037	0.015
Coney	0.0677	0.0898	0.1450	280.3	293.5	268.3	0.47	1.557	0.624
Red grouper	0.2612	0.2770	0.1420	571.4	657.3	599.1	1.84	0.665	0.266
Mutton snapper	0.2464	0.2564	0.0781	532.7	664.8	604.4	3.15	0.339	0.136
Yellowtail snapper	0.3748	0.3922	0.1491	306.2	366.9	332.1	2.51	0.489	0.196
Hogfish	0.9855	0.9938	0.1220	345.4	524.0	458.4	8.08	0.161	0.064

Symbols are defined in Table 1. Sustainability conditions: $\frac{F}{F_{BFF}} < 1$, $\frac{B}{B_{BFF}} > 1$, and SPR > 0.4.

a random value of Z drawn as pairs for each of 90 000 simulation runs (Figure 3). The distribution of F random deviates was somewhat asymmetrical; hence, the median of the distribution, $F_{\rm med}$, was used as the expected value for F (Table 4).

Probabilistic length-at-age and model verification

The incorporation of probabilistic lengths-at-ages into the numerical cohort model is illustrated for mutton snapper in Figure 4a and b. The variation in length-at-age with respect to the mean growth function $\overline{L}(a,t)$ for a constant CV of 7% is shown in Figure 4a. The light lines represent 15 length sub-cohorts above and below the mean length-age relationship (black solid line). For mutton snapper, a total of 14 880 length-age vector elements (= 40 years \times 12 time-steps per year \times 31 length sub-cohorts) were used to

generate the graphs (Figure 4a and b). The constant CV assumption resulted in an increasing magnitude of variation in length-atage with increasing age, a commonly observed characteristic of fish length-age studies (*inter alia* Then *et al.*, 2015). The corresponding model-predicted numbers at length and age for the unexploited case (F = 0; Z = M) are illustrated in Figure 4b.

A key aspect of the numerical cohort model was computation of population numbers-at-length [Table 1, Equations (T-5–T-7)], the main "observable" data from a fish population for the length-based approach. The model-predicted length composition for the exploited life stage of mutton snapper when F=0 is illustrated in Figure 4c (i.e. the $L>L_{\rm c}$ portion of the graph shown in Figure 4a). Incorporation of variation in length-at-age facilitated the production of realistic length frequency distributions, as illustrated by the correspondence between the observed length

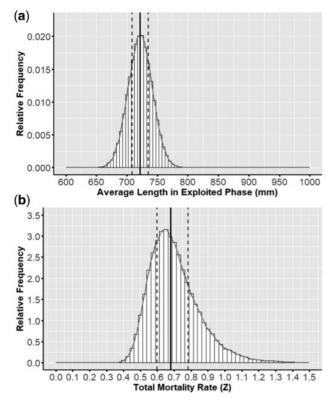


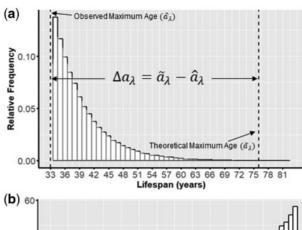
Figure 1. Generation of stochastic total mortality rates for black grouper (*Mycteroperca bonaci*): (a) A normal distribution for \overline{L} , average length in the exploited phase, was generated from the composite estimates \overline{L} and $SE(\overline{L})$ from sampling surveys (Table 3). (b) The random deviates ($n=90\,000$) of \overline{L} were used to compute random deviates of Z using Equation (2). Vertical solid lines denote the median values, and left and right dashed lines denote the first and third quartiles of the respective distributions.

composition for mutton snapper and the model-predicted length composition at \hat{F} (Figure 4d). The comparison graph of Figure 4d, and the corresponding comparison of model-predicted versus observed average length estimates, were subsequently built-in to the modelling procedure as a basic verification check for the simulated population dynamics.

Sustainability analyses

Our procedure for establishing sustainability risk reference points was applied to Florida grouper and snapper species, utilizing the life history synthesis of Ault *et al.* (2005b, 2008). The numerical cohort model was used to compute the SPR at $F_{\rm MSY}$ (i.e. $F=\hat{M}$) for each species (Figure 5). The average SPR at MSY for groupers was 39.8%, and the average for snappers was 38.4%. These were rounded to the nearest 5% increment, resulting in a reference SPR of 40% for both families. Thus, the limit reference point for fishing mortality rate was established as $F_{REF} = F_{40}\%_{SPR}$ for the six example species (Table 4), and the corresponding model-predicted exploitable population biomass at F_{REF} was defined as B_{REF} .

The basis for reference point evaluation is illustrated in Figure 6 for black grouper. Model-predicted population metrics $(Y_w, B_{iX}, SSB, \overline{L})$ were scaled to their respective maximum values. In this representation, *SSB* and *SPR* are synonymous. The



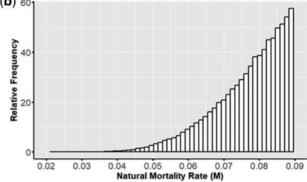


Figure 2. Generation of stochastic natural mortality rates for black grouper (*Mycterperca bonaci*): (a) An exponential distribution for maximum age a_{λ} was developed from the observed maximum age \hat{a}_{λ} and Equations (4), (6), (7), and (8). (b) The random deviates ($n = 90\ 000$) of a_{λ} were used to compute random deviates of M using Equation (4).

relationships among population metrics, fishing mortality rates, and limit reference points show the inherent trade-offs between fishery yield production and population sustainability: the projected yield of black grouper at $F_{\rm REF}$ was about 10–15% lower than maximum yield, but the projected SPR at maximum yield was less than 20% compared to the sustainability threshold of 40%SPR at $F_{\rm REF}$. Likewise, the projected exploitable biomass ($B_{\rm EX}$) was about 45% of its maximum value at $F_{\rm REF}$ and about 25% at maximum yield. For black grouper, the estimated current $F(\hat{F}, F_{\rm med})$ far exceeded the fishing mortality rate for achieving maximum yield or maintaining sustainable levels of reproductive capacity and exploitable biomass.

As shown in Figure 6, average length \overline{L} declines with increasing F in a similar manner as $B_{\rm EX}$ and SSB. This property was the basis for the average length estimator of mortality rate [Equations (1) and (2)], but was also utilized to evaluate sustainability reference points in terms of \overline{L} and the associated length frequencies, the main "observable" for a population in length-based assessments (Figure 7). Model-projected \widehat{L} [Table 1, Equation (T-8)] and associated length frequencies for hogfish at F=0, $F_{\rm REF}$, and the current \widehat{F} (Figure 7a and b) show how the process of increasing exploitation rate leads to "juvenescence", i.e. making the population younger, smaller, and less fecund (Ault *et al.*, 1998; Anderson *et al.*, 2008). Time-series plots of average length estimates for the four sampling programs (Figure 7c) indicate that hogfish \overline{L} has been well below sustainability reference levels (the shaded area between F=0 and $F=F_{\rm REF}$) since at least 1979.

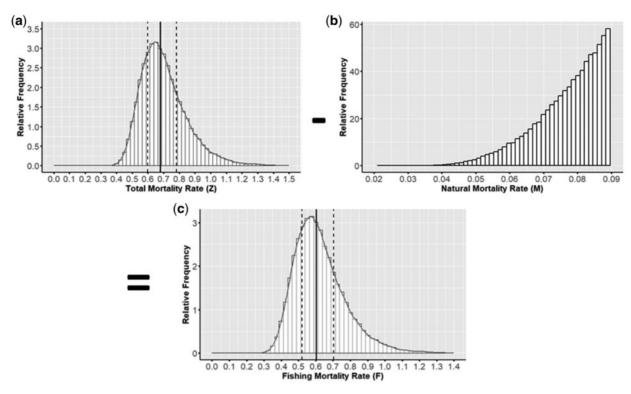


Figure 3. Generation of stochastic fishing mortality rates for black grouper (*Mycterperca bonaci*). The distribution of *F* was obtained by subtracting a random value of *M* from a random value of *Z* drawn as pairs for each of 90 000 simulation runs. Vertical solid lines denote the median values, and left and right dashed lines denote the first and third quartiles of the respective distributions.

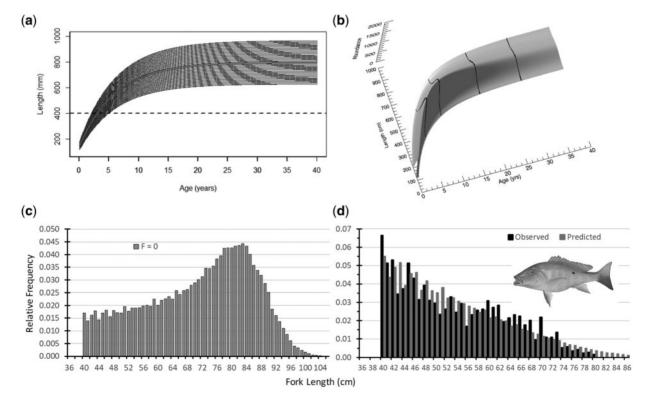


Figure 4. Incorporation of probabilistic growth into the numerical cohort model, illustrated for mutton snapper (*Lutjanus analis*): (a) Variation in length-at-age with respect to the mean growth function for a constant CV of 7%; the light lines represent 15 length sub-cohorts above and below the mean length-age (black solid line); the dashed line shows the minimum length of capture L_c . (b) The corresponding model-predicted numbers at length and age for the unexploited case (F = 0; Z = M), utilizing the probability of length at a given age, p(L|a) [Table 1, Equation (T-6)]. (c) Model projections of the length frequency distribution from panel (b) for the exploited life stage (lengths $> L_c$). (d) Comparison of observed (black bars) versus model-predicted (shaded bars) length frequencies at current F for verification check.

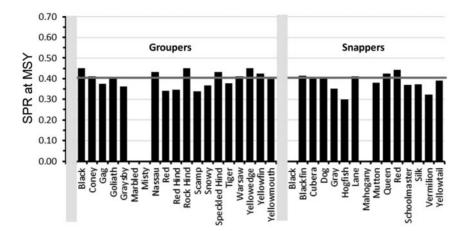


Figure 5. Estimates of SPR at maximum sustainable yield (MSY) for Florida groupers (17 species) and snappers (13 species). Generation of SPR was carried out for each species using life history demography parameters, and setting $F_{MSY} = M$ and $L_c = L_m$ in the numerical cohort model. Species in the fishery lacking histograms had insufficient demographic data. The horizontal line is the estimated community limit reference point or overfishing threshold (i.e. 40%SPR).

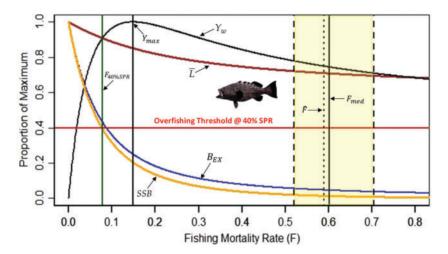


Figure 6. Illustration of the inter-relationship between population metrics yield in weight (Y_w , solid black line), exploitable biomass (B_{EX} , solid blue line), SSB (solid gold line), and average length (-L, solid brown line) dependent on fishing mortality rate F for black grouper ($Mycteroperca\ bonaci$) at $L_c=600\$ mm. Population metrics were scaled to their respective maximum values. The horizontal red line depicts the sustainability limit of 40% SPR (i.e. SSB in this representation), and the vertical green line denotes the corresponding fishing mortality limit reference point of $F_{40\%SPR}=F_{REF}$. The yellow shaded region encompasses the respective first and third quartiles and median value (F_{med}) for the distribution of the current estimated \hat{F} .

Estimates of \hat{F} , $F_{\rm med}$, model-projected \bar{L} at \hat{F} , and associated reference points and sustainability benchmarks are given in Table 4 for the six example species. A model verification check showed good correspondence between the model-predicted \hat{L} (Table 4) and the composite \bar{L} estimated from the sampling data (Table 3) for each species. Evaluations of sustainability benchmarks at \hat{F} indicated a sustainable condition for one species, coney. Probability distributions for $F/F_{\rm REF}$ and SPR for the six species are shown in Figure 8. The estimated sustainability risks for coney were less than 35% for both $F/F_{\rm REF}$ and SPR. The other five species had estimated sustainability risks of greater than 95% for both benchmarks. Distributions of F were based on the joint probabilities of F and $F/F_{\rm REF}$ and some probabilities of $F/F_{\rm REF$

F=Z-M). This situation occurred in simulation runs for one out of the six species, coney (Figure 8e and f), resulting in $F/F_{\rm REF}$ < 0 for 15.6% of the cases and SPR > 1 in 15.9% of the cases. Although not shown on the graphs, these cases were considered to reflect the condition of a very low fishing mortality rate near 0 and were included in computations of risk.

A "Kobe control rule plot" of $F/F_{\rm REF}$ against $B/B_{\rm REF}$ (Figure 9) suggested a wide range of sustainability status for the six species. The bivariate probability ellipses around the species' point estimates exhibited an interesting pattern: at low exploitation levels, the uncertainty was high with respect to $B/B_{\rm REF}$, but low with respect to $F/F_{\rm REF}$ (coney), while the converse was true at high levels of exploitation (black grouper, hogfish). As discussed in Ault *et al.* (2005b), this was likely attributed to the properties of the $\overline{L} = f(F)$ relationship shown in Figure 7a. At high levels of F in the

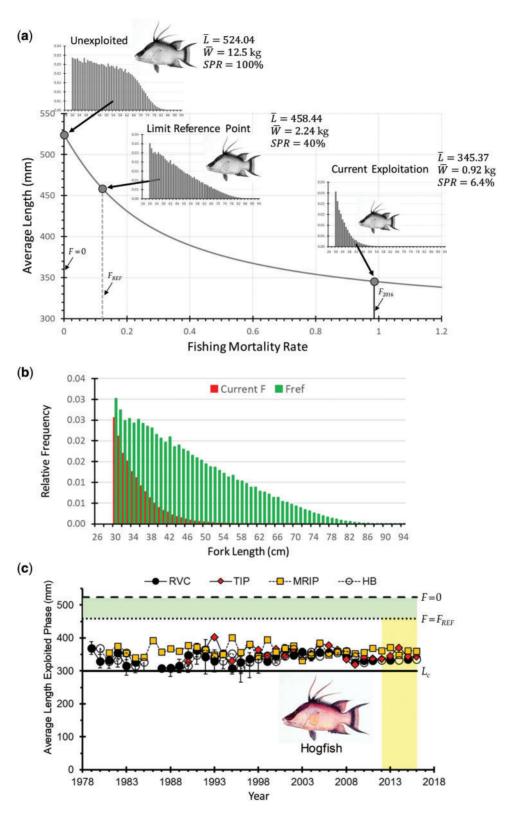


Figure 7. Illustration of length-based population metrics and reference points for hogfish (*Lachnolaimus maximus*). (a) Model projections of average length dependent on fishing mortality rate, and the corresponding changes in length composition and population metrics (mean length, mean weight, and SPR) at F = 0, $F = F_{REF}$, and current \hat{F} . (b) Comparison of model projections of length frequency distributions at current \hat{F} (dark bars) and F_{REF} (light bars). (c) Time series (1979–2016) estimates of average length in the exploited phase (\bar{L}) from sampling surveys; SEs are plotted for the RVC to give a sense of error variance; post-2000 these are less than the diameter of the symbol (black circle) reflecting improvements in survey precision; the vertical shaded bar is the 5-year region where estimates were pooled to generate \bar{L} and SE(\bar{L}) (see Table 3). Lower solid line indicates regulated minimum size at first capture (i.e. L_c); the horizontal shaded band indicates the region for \bar{L} under sustainable exploitation levels (i.e. between $F = F_{REF}$ and F = 0).

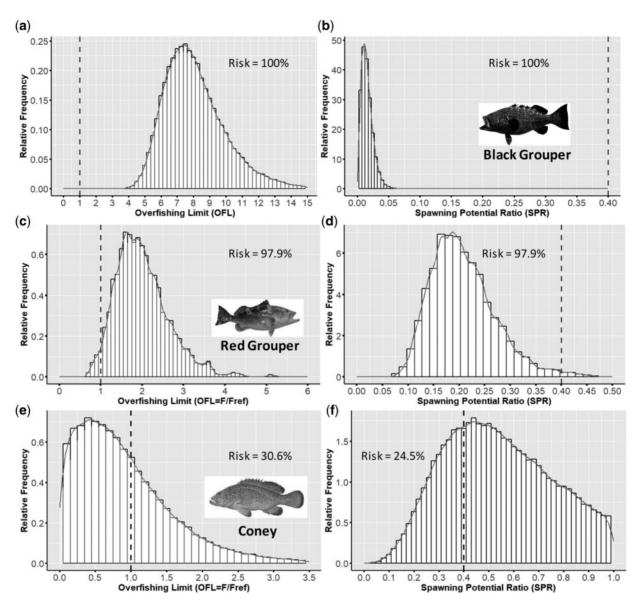


Figure 8. Sustainability risk analysis in terms of overfishing limits $(F/F_{REF}, left panels)$ and SPRs (right panels) for six reef-fish species: (a, b) black grouper; (c, d) red grouper; (e, f) coney; (g, h) hogfish; (i, j) mutton snapper; and, (k, l) yellowtail snapper. For OFL, sustainability risk is the percentage of the distribution above 1.0; for SPR, sustainability risk is the percentage of the distribution below 0.40.

asymptotic region of the curve, small variations in average length (vertical direction) lead to a wide range of possible F values (horizontal direction). Length distributions are highly truncated along this entire region of the curve, translating to a low range of possible biomass values. At low levels of F between F=0 and $F=F_{\rm REF}$, variations in average length result in a narrow range of possible F values. There are high numbers of larger and older animals in the population in this region of the curve, translating to a wider range of possible biomass values.

The model-projected SSB (i.e. SPR) and yield over a range of fishing mortality rates was shown in Figure 6 for black grouper at the current regulated minimum size of $L_{\rm c}=600$ mm. The isopleth graphs for SPR and yield of Figure 10 expand this view to include the full range of $L_{\rm c}$ values in addition to F. In this case, the current estimated stock condition with respect to fishing mortality, depicted as a probable range of \hat{F} , and minimum size of capture

 $(L_{\rm c})$ appears to be far from optimal in terms of minimizing sustainability risks (*SPR*) of black grouper in the Florida Keys, or optimizing fishery production. These isopleth surfaces provide the basis for evaluating future management options to increase $L_{\rm c}$, reduce $F_{\rm c}$, or some combination of both interventions.

Discussion

The length-based approach developed by Ault *et al.* (1998) was extended in this study and allowed for a fairly comprehensive evaluation of fishery sustainability status using length frequencies as the principal data. The requisite life history demographic parameters for age, growth, and reproduction were essentially the same as would be for any structured assessment approach (e.g. Quinn and Deriso, 1999). The numerical cohort model developed here was novel in that it computed population metrics by integrating over length, reflecting the actual fishing selectivity

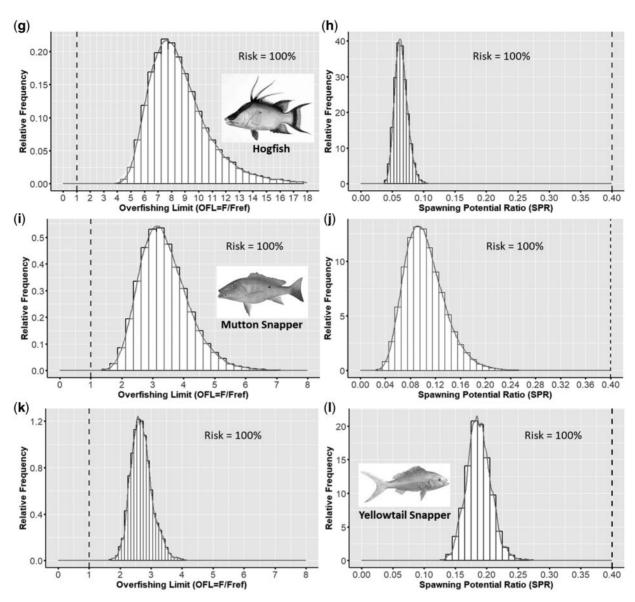


Figure 8. Continued.

process, which is based on length $(L > L_c)$ rather than age $(a > a_c)$. The main distinction of the length-based assessment presented here is that estimation of mortality rates did not require estimates of total catch and total effort by fleet-gear, which can be extremely challenging to obtain reliably for small-scale artisanal-style fisheries (Gallucci et al., 1996). Rather, total mortality rate was estimated from the average length in the exploited phase following Ehrhardt and Ault (1992). This approach has been most useful for situations where reliable length frequency data were available, but reliable catch-effort data were either not available (Ault et al., 2008; Nadon et al., 2015) or only available for a short period of time (Ault et al., 1998, 2005b). The approach differed from other length frequency methods that evaluate sustainability (Hordyk et al., 2014, 2015, 2016), but do not explicitly estimate mortality rates. The Ehrhardt-Ault model assumes that a stock has experienced a constant mortality rate for a number of years preceding the estimate of Z(t) in year t. As shown here for hogfish (Figure 7c) and in previous analyses for other reef-fish species in the Florida Keys (Ault *et al.*, 1998, 2005b; Smith *et al.*, 2011), time series of average length have been remarkably constant for the past 20 or more years. In addition, there have been no changes in size regulations for our six example species in the Florida Keys region from the mid- to late-1990s through 2016. Thus, our application of the Ehrhardt–Ault model appeared to be in line with the constant mortality rate assumption, and did not require a length-based estimator for non-constant mortality conditions (e.g. Gedamke and Hoenig, 2006).

Average length and catch-effort indicator variables for determining mortality rates both arise from the same fundamental mathematical theory, respond to increasing fishing mortality in a similar manner (e.g. Figure 6), and should produce exactly the same mortality estimates for a stock provided that sampled length frequency and catch-effort data were representative of the actual fish population (Ault *et al.*, 2014). Thus, when length frequency and catch-effort data are both available, the average length approach can serve as a cross-check against more traditional

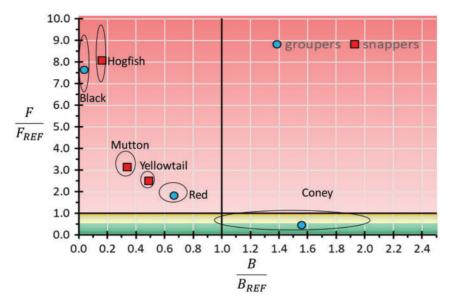


Figure 9. Limit control rule or "Kobe diagram" for six Florida exploited reef fishes. Note that the limit reference point is where $F/F_{REF} = B/B_{REF} = 1$. Point values were evaluated at \hat{F} for each species, and the associated probability ellipses were the first and third quartiles of the bivariate distribution.

methods for estimating mortality rates (Prager,1994; Methot and Wetzel, 2013), or against other data-limited approaches (Carruthers *et al.*, 2014; Newman *et al.*, 2015; Carruthers and Agnew, 2016).

This study extended length-based stock assessment to a risk analysis context by incorporating probabilistic mortality rates and length-at-age. Using the statistical properties of sampling survey average length estimates (Lohr, 2010), generation of normally distributed average length random deviates and subsequent conversion to total mortality (Z) random deviates via Equation (2) was relatively straightforward (Figure 1). Less straightforward was the procedure for generating a probability distribution for natural mortality (M) from assumptions about lifespan. For Florida reef fishes, as life history information has become more complete over time, the observed maximum age (a_{λ}) has generally increased, sometimes in quite dramatic fashion. For example, an early growth study for hogfish recorded a_{λ} at 11 years (Claro et al., 1989), and a subsequent study recorded a_{λ} at 23 years (McBride and Richardson, 2007). Likewise, maximum observed age has increased for mutton snapper from 9 years (Claro, 1981) to 14 years (Mason and Manooch, 1985) to 40 years (O'Hop et al., 2015). Hence our use of an exponential probability distribution for a_{λ} (Figure 2), with the observed maximum age as the starting point of maximum probability and the random deviates exponentially decreasing in one direction (i.e. longer lifespans). The resulting distribution of fishing mortality rates (F = Z - M)was asymmetrical, prompting our choice of F_{med} as the expected value (Figure 3).

Since the procedure for developing probability distributions of F was based on the joint probability distributions of Z and M, the combination of a high value for a random deviate of M and a low value for a random deviate of Z could result in a negative random deviate for F. This situation occurred in approximately 16% of the simulation runs for one of our example species, coney. Contributing factors for coney were a relatively low exploitation

rate as reflected by $F/F_{\rm REF}$ (Figure 8) and relatively high uncertainty in estimates of average length (Table 3) compared with the other species. From a theoretical perspective, simulation runs with $F/F_{\rm REF} < 0$ or SPR > 1 could be treated as infeasible and excluded from risk computations. Our perspective was that these cases reflected the uncertainty in the mortality estimates, representing the general condition of a very low fishing mortality rate near 0, and were thus included in computations of risk.

Variation in length-at-age was modelled as a constant CV of 7% above and below the expected length from the length-age growth function (Figure 4a), emulating both the pattern of increasing variation in length with increasing age and the magnitude observed in a wide range of fish species (Then et al., 2015; Nadon and Ault, 2016). While the ideal approach for describing variation in length-at-age might be to use an individual-based population model and incorporate uncertainty into the population dynamic rate functions (c.f. Ault et al., 1999), the information requirements for application generally far exceed what is typically available in a "data-limited" situation. In contrast, the constant CV approach was much simpler to implement in the numerical population model, and resulted in realistic predictions of length frequencies, the main "observable" from the fishery. These model-predicted length frequencies also facilitated verification checks (Figure 4d) and the evaluation of expected length compositions under various levels of exploitation (Figures 4c, 7a and b).

Our use of the numerical population model to investigate precautionary reference points for species-specific fishing mortality ($F_{\rm REF}$) was based on several criteria. First, the exploited population was assumed to be the full mature adult lifestage (i.e. $L_{\rm c}=L_{\rm m}$), such that individuals landed had at least some chance of spawning before capture. Second, maximum sustainable yield was considered as a limit rather than a target, with F=M used as a proxy for $F_{\rm MSY}$. Third, model-predicted SPR at $F_{\rm MSY}$ was considered to be the minimum limit for sustainability. Application to Florida grouper and snapper species resulted in average family

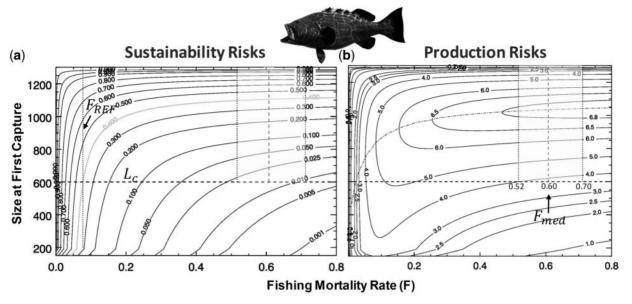


Figure 10. Black grouper (*Mycteroperca bonaci*) isopleth diagrams for (a) SPR and (b) fishery yields with respect to fishing mortality rate (x-axis) and regulated minimum size (y-axis), showing the relationship between risks to sustainability (SPR) and fishery production (yields). The horizontal dashed line is the current L_c . In panel (a), the leftmost vertical dotted line is F_{REF} , and the light contour line is 40%SPR. The curved dashed red line in panel (b) is the "eumetric line" (i.e. maximum yield at each combination of L_c and F). The rectangles show the range of estimated current fishing mortality rate (middle is median F_{med} , and left and right bounds are the first and third quartiles, respectively).

SPRs at $F_{\rm MSY}$ for groupers and snappers of 39.8% and 38.4%, respectively (Figure 5); thus, the basis of our choice of $F_{40\% SPR}$ to be a reasonably precautionary $F_{\rm REF}$ in our applications. Notably in the region, the South Atlantic Fishery Management Council has stated that an MSY proxy was 30% static SPR (SEDAR 19, 1999), but that the OY (optimal yield) proxy was 45% SPR. The Gulf of Mexico Fishery Management Council has set the maximum fishing mortality threshold (limit) at $F_{30\% SPR}$ for most reef fish stocks. It is apparent that these benchmarks have been set too liberally by the Councils, based on the current condition of the reef fishery resources.

Application of a risk analysis methodology for length-based assessment allowed for probabilistic evaluations of sustainability status from species (Figure 8) and community (Figure 9) perspectives, and also a frame of reference for exploring management options balancing sustainability risks (e.g. SPR, Figure 10a) and fishery production (Figure 10b). Results for the six example species showed varying degrees of sustainability status with respect to overfishing limits (Figure 8, left panels), SPR (Figure 8, right panels), and the combination of F/F_{REF} and B/B_{REF} (Figure 9). For coney, over 50% of the respective probability distributions for the overfishing limit and SPR were within the sustainable range (Figure 8e and f). The opposite occurred for the other five species. While the focus of this study was to develop a lengthbased risk analysis methodology appropriate for data-limited fisheries, our results are in line with previous analyses for exploited reef fishes in the Florida Keys (Ault et al., 1998, 2005b) and surrounding regions (Cooper et al., 2013; O'Hop et al., 2015).

The scientific challenge in the coming years will be to evaluate the sustainability status for the full exploited Florida reef-fish community, which is comprised of over 50 principal species (NOAA TIP) from a wide range of families, including snappers, groupers, wrasses, grunts (Haemulidae), porgies (Sparidae),

triggerfishes (Balistidae), barracudas (Sphyraenidae), and squirrelfishes (Holocentridae). At present, most of these species have not undergone stock assessments as part of NOAA's SouthEast Data, Assessment, and Review (SEDAR) program, largely due to data limitations. Understanding sustainability status from a more comprehensive community perspective, e.g. the percentage of species with high sustainability risks, will circumscribe the extent of the challenges facing resource managers to reduce risks via effort and size controls (Figure 10), seasonal and spatial restrictions, or other measures (Bohnsack and Ault, 1996; Bohnsack, 1998; Bohnsack *et al.*, 2004; Meester *et al.*, 2004; Ault *et al.*, 2005a, 2013).

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