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Embracing uncertainty, continual spawning, estimation of the stock–recruit steepness, and size-limit designs with length–based per-recruit analyses for African tropical fisheries

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ABSTRACT

Per-recruit analysts of African tropical fish mostly applied deterministic and sex-aggregated length–based Beverton–Holt per-recruit models, but rarely examined the spawning biomass per-recruit (SBPR), spawning potential ratio (SPR), size-limit regulations, and stock–recruit steepness (*h*). To relax the restrictive assumptions of the previous models, this study outlines a framework of using length–based per-recruit models accounting for continual spawning and incorporating uncertainty in sex-specific and total yield per-recruit (YPR), SPR, *h*, equilibrium yield (Y_e), and biological reference points, especially those based on fishing mortality, *F* (F_{BRP}s). Continual spawning is incorporated through weighting SBPR with monthly proportions of the spawning-capable stage. Uncertainty is introduced into life-history parameters through the resampling with replacement and with bivariate normal distributions, and into various metrics through Monte Carlo simulations. The Beverton–Holt and Ricker stock–recruit relationships are assumed in yield functions. The approach is illustrated with the Bukabuka (*Lates stappersii* Boulenger, 1914) fishery in southern Lake Tanganyika, for which the potential effects of alternative minimum length limits (L_{min}) and catch-and-release values on various metrics are examined. Females Bukabuka represent 63% of the combined YPR and SBPR because they predominate in large sizes; *h* is greater if recruitment were dependent on both sexes than on females; the most imprecise metrics are the YPR, Y_e, and MSY benchmarks; cryptic mortalities of sublegal individuals would exacerbate growth-overfishing; higher L_{min} and discard survivals would lead to higher F_{BRP}s, but can prevent recruitment-overfishing; in the F–L_{min} planes, the contours maximizing YPR and Y_e can be the basis for optimal L_{min} designs. Strategies most likely to benefit the Bukabuka fishery would apply L_{min} = 250–300 mm fork length and promote full compliance with releases and ways to reduce post-discard mortality.

1. Introduction

The yield-per-recruit (YPR), spawning biomass per-recruit (SBPR), and egg production per-recruit (EPR) are widely used to provide management guidance of fishery resources. They are useful in jurisdictions with harvest control rules, but with unknown or unreliable stock–recruit relationships (Booth, 2004; Weil et al., 2005a,b; Legault and Brooks, 2013). YPR is the expected equilibrium lifetime yield (landings and dead discards) from a recruit passing through an exploited population, assuming absence of density-dependent growth and recruitment. Management goals based on YPR may maximize the yield a cohort can produce (Beverton and Holt, 1957) or optimize economic returns (Gulland and Boerema, 1973); the latter goal favors resource conservation (Goodyear, 1993). One approach for calculating YPR requires (i) the age or size of recruitment to the fishing ground; (ii) a growth function relating age with length and weight; (iii) schedules of fishery selectivity (probability of being caught for any fish available in the fishing ground) and natural mortality; and (iv) equilibrium fishing mortality rates characterizing successive piecewise time intervals of stable fishing regimes.

SBPR and EPR represent the equilibrium reproductive potential of a recruit over its lifespan. Their calculation also requires fishery selectivity, mortality rates, and growth parameters, and includes the reproductive information of the cohort spawning segment (maturity, sex-ratio, weight or fecundity schedules and, occasionally, the spawning offset, i.e., the fraction of a year representing the time between the start of the year and the month of peak spawning), assuming absence of density-dependent suppression of maturation or fecundity-at-size/age. The absolute values of SBPR and EPR are not typically used; instead, SBPR and EPR are expressed relative to their unfished amounts (Beverton and Holt, 1957; Goodyear, 1977, 1993; Laurec and Le Guen, 1981). This procedure generates the spawning potential ratio, SPR

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(Goodyear, 1993), which measures the proportional reduction in total potential productivity attributable to a fully selected fishing mortality, conditional on a given selectivity pattern. As such, SPR indicates the impact of fishing on a stock's reproductive capacity and so emphasizes protecting the spawning stock. SPR can also be used as a measure of fishing mortality (Martell et al., 2015) or an index of the compensatory capacity (Kindsvater et al., 2016).

YPR, SBPR, and EPR are commonly based on annual vital rates (e.g., natural mortality, growth parameters) and biological or exploitation events (e.g., spawning offsets, size of first capture) assuming they are constant from year to year. As such, YPR and SBPR (or EPR) are equilibrium metrics during one annual time-step but, for management scales, are static and asymptotic over time.

Because the age determination of exploited populations in temperate regions is relatively easy and because those populations usually have single, short spawning seasons per year, scientists preferred age–structured per-recruit models and the related biological reference points (BRPs), eventually accounting for single spawning offsets (Gabriel et al., 1989). In tropical Africa, the age determination of fish is difficult even impossible. Spawning there is protracted and often occurs year-round, with variable peaks and sizes at maturity that can change from year to year (Chapman and van Well, 1978; Ellis, 1978; Duponchelle and Legendre, 2000; Smith, 2000; Ekanem et al., 2004; Panfili et al., 2004; Guèye et al., 2012; Ba et al., 2016). Because of the aging difficulties and unique reproductive dynamics of fish in tropical Africa, analyses of fishery performances relied chiefly on length–based per-recruit models and, except a few studies (Munyandorero, 2001; Booth, 2004; Weil et al., 2005a,b; Thiaw et al., 2011), did not include the standard SBPRs or EPRs and SPR.

Furthermore, unlike elsewhere where uncertainty has been recognized and incorporated into per-recruit analyses (e.g., Chiang et al., 2008; Lin et al., 2015), per-recruit analyses for African tropical fisheries have often been implemented deterministically. The latter analyses overwhelmingly relied on length–based Beverton–Holt per-recruit models applying constant parameter values (e.g., Munyandorero, 2001; Bannerman and Cowx, 2002). A few studies employed "age"–based per-recruit models and addressed uncertainty via stochastic parameters and sensitivity analyses based on variable natural mortality or variable recruitment (Moreau, 1980; Moreau et al., 1984; Booth, 2004; Weil et al., 2005a,b; Thiaw et al., 2011). Regardless, these analyses assumed (i) age-independent natural mortality, (ii) knife-edge selectivity, and (iii) spawning occurring in a pulse, at the start of the year, and encompassing males and females that all were considered spawning-capable (Brown-Peterson et al., 2011).

Per-recruit analysts of African tropical fisheries also overlooked two other issues of management interest. First, they have not yet investigated the potential benefits of size-limit regulations although size-limit designs/experiments exist or are conceivable (Njiru et al., 2009; Jamu et al., 2011; Ghambi and Mzengereza, 2016; Kolding et al., 2016). Second, the lack of stringent management requirements involving nominally modern assessment techniques impeded the estimation of stocks' productivity in terms of stock–recruit parameters; but see Booth (2004), Linhoss et al. (2012), Munyandorero (2012), and Kolding et al. (2016) for exceptions. Yet Chevaillier and Laurec (1990), Martell et al. (2008, 2015), and Pine III et al. (2008) showed that, by combining SBPR, YPR, a plausible level of the compensatory recruitment, and an amount of the unfished recruitment for a given stock, one can develop the equilibrium yield, eventually on a per-recruit basis, and derive the benchmarks based on the maximum sustainable yield (MSY).

With emphasis on African tropical fisheries, this study outlines a framework for analyzing uncertainty in sex-specific and combined length-based YPR, SBPR, SPR, stock–recruit steepness (the fraction of the unexploited recruitment produced by 20% of the unexploited parental stock, thus a measure of compensatory recruitment), equilibrium yield, and BRPs, including the benchmarks based on MSY. Length–based per-recruit models with continual spawning (LBPRMCS) in SBPR are employed to relax the assumptions associated with the length-based Beverton–Holt per-recruit models. The following aspects are considered: (i) introducing uncertainty through the variability in the von Bertalanffy growth function (VBGF) parameters (asymptotic length and growth rate) and in weight-length scales and exponents; (ii) weighting YPR and SBPR by length-specific sex ratios; and (iii) for SBPR, accounting for sex-specific maturity schedules and monthly proportions of the spawning-capable stage within a year.

To characterize uncertainty, the pairs of the above-mentioned VBGF and weight-length parameters are resampled first with replacement and then with bivariate error distributions. The random realizations of the VBGF parameters are used to derive constant natural mortality following Pauly's nonlinear empirical equation (Then et al., 2015). Using Monte Carlo (MC) simulations, uncertainty in VBGF and weight-length parameters as well as in constant natural mortality is propagated into the times of cohort growth from length to length, length-specific natural mortality, per-recruit metrics, steepness, equilibrium yield, and BRPs. The steepness is derived owing to two aspects. First, stock–recruit metadata indicate linear relationships (on log scales) between the slopes at the origin of spawner–recruit curves and asymptotic sizes (Denney et al., 2002; Goodwin et al., 2006; Hall et al., 2006). Therefore, empirical estimates of slopes at the origin of spawner–recruit curves are conceivable given asymptotic sizes in the range of the above-mentioned relationships. Second, the combination of the unfished SBPR and the slope at the origin of a spawner–recruit curve produces the steepness (e.g., Mangel et al., 2013). Given the steepness, YPR, SBPR, and an amount of the unfished recruitment, the equilibrium yield functions of fishing mortality are developed and two measures related to the sustainable yield, F_{MSY} and MSY, are obtained as in Martell et al. (2008, 2015). Uncertainty in various metrics is described by empirical distributions, 95% uncertainty intervals (UIs), and coefficients of variation (CVs).

The proposed approach is illustrated with the Bukabuka (*Lates stappersii* Boulenger, 1914) fishery in southern Lake Tanganyika (SLT; 8°28′ 9°02′S and 30°08′ 30°44′E; Tanzanian and Zambian sectors) that has essentially been an open access, unregulated fishery. No catch-and-release and size-limit regulations have yet been imposed on this fishery. To promote well-informed designs of optimal size-limit strategies, simulations are conducted with alternative scenarios of the discarding behavior and discards survival rates to explore how the catch-and-release and size-limit regulations, if they were imposed, would affect the Bukabuka fishery performance in SLT. In comparison with the unregulated conditions in terms of a fishery operating without size-based and catch-and-release regulations, the goal of this exercise is determining a combination of size-limits and discards survival rates that would result in yield increase or, at least, in minimum yield loss while improving the spawning potential.

2. Methods

2.1. Schedules of inputs

For Bukabuka in SLT, a vector of low bounds for fork-length (FL) classes i (L_i), each with 10 mm of width (Δl), is created: L_i = 20–440 mm. L_i = 20 mm FL is the smallest length which has been historically recorded in biological samples of landings. Li = 440 mm FL is the low bound of the largest length class for which reproductive data have been collected.

The length-based schedules used include mean weight, time of cohort growth from length to length, sex-ratio, proportion of mature individuals, fishery selectivity, and natural mortality. Males and females share the selectivity and natural mortality schedules, as well as the growth pattern, whereby length-at-age is described by the VBGF. Table 1 provides details on the previous schedules and on other parameters and metrics developed below.

Mean weight-at-length is given by