

Analyses of the composite yield per recruit model CYPR14 for inferring plausible fishing mortality targets of fish in the tropics

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Abstract – Stocks' yield and size per recruit are widely used to provide fisheries management guidance. This study provides details for analyzing the composite (i.e. age-aggregated or stage-structured) yield per recruit (CYPR) model CYPR14, and proposes CYPR14 as a management tool for tropical fisheries. The fishing mortality rates maximizing CYPR (F_{CYPR}) and associated with the marginal increase in CYPR ($F_{0.1}$) and a target composite spawning potential ratio (CSPR; $F_{35\%CSPR}$ or $F_{40\%CSPR}$) were suggested as candidate fishing mortality targets, provided assessments employ the delay-differential model underlying CYPR14. Using Monte Carlo (MC) simulations relying on growth parameters and natural mortality of Lake Tanganyika's *Lates stappersii* and Lake Victoria's *Lates niloticus*, CYPR14 analyses involving maximum survivorship or declining survivorship were carried out to show how F_{CYPR} , $F_{0.1}$, $F_{35\%CSPR}$, and $F_{40\%CSPR}$ could be generated, given an age of knife-edge recruitment (r). Baseline MC employed $r=1$ year and yielded mean annual rates of $F_{CYPR}=0.52$, $F_{0.1}=0.33$, and $F_{35\%CSPR}=0.51$ for *L. stappersii* and $F_{CYPR}=0.23$, $F_{0.1}=0.14$, and $F_{40\%CSPR}=0.16$ for *L. niloticus*. CYPR14 with maximum survivorship produced CYPR isopleths such that the CYPR maximized at an infinite r and finite, higher F . For CYPR14 involving a declining survivorship, the CYPR declined with increased r and maximized with innermost closed-loop contours at lower F and an optimal age. The CSPR isopleths from both types of CYPR14 analyses were first concave down, and the optimal age served as their inflection point. In terms of benchmarks based on the maximum sustainable yield and of proxies thereof, CYPR14 should be for its underlying delay-differential model what the age-structured pool models are for age-structured assessment models.

Keywords: Data-poor stocks / stock status / *Lates stappersii* / *Lates niloticus* / Monte Carlo simulations

1 Introduction

Since the 1980s, the status of tropical fisheries has often been assessed through length data analyses, essentially using the software called FiSAT II (Gayani et al., 2005). The status determination chiefly relied on two approaches. With the first approach, analysts sequentially (i) estimated growth parameters, (ii) calculated the rates of natural mortality (M) with Pauly's (1980) estimators, (iii) derived the rates of total mortality (Z) usually through length-converted catch curves (Pauly, 1983), (iv) subtracted natural mortality from total mortality to obtain the fishing mortality rates (F), and (v) derived the exploitation fractions as the ratios of fishing mortality to total mortality (F/Z). The results from (iv) and (v)

were treated as indicators of, respectively, the fishing pressure and stock status for the time periods under review: analysts invariably concluded that the stocks were lightly (synonymized with weakly or under), optimally (synonymized with sustainably), or strongly (synonymized with over) exploited if the exploitation fractions were, respectively, less than 0.5, equal to 0.5, and greater than 0.5. In doing so, M was implicitly made equivalent to the fishing mortality producing the maximum sustainable yield (MSY), F_{MSY} : the stock status was evaluated by comparing $F=Z-M$ with M . Thus, the stocks were judged to be lightly, optimally, or strongly exploited if F was less than M , equal to M , or greater than M .

The second approach simulated the relative yield per recruit (YPR) and the relative biomass per recruit (Pauly and Soriano, 1986). The biological reference points based on this approach include (i) the exploitation fraction maximizing the

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relative YPR, (ii) the exploitation fraction at which the marginal increase in the relative YPR is 10% of the marginal increase when the exploitation fraction is zero, and (iii) the exploitation fraction achieving 50% of the unfished relative biomass per recruit. To determine the stock status, scientists treated the exploitation fractions derived with the second method as targets (i.e. desirable levels) against which the exploitation fractions from the first approach were compared to determine whether the stocks were healthy (e.g. [Bannerman and Cowx, 2002](#); [Montcho et al., 2015](#)).

Another type of analysis of potential management interest for tropical fisheries, and in general, for fisheries without age data irrespective of the fishery jurisdiction, may deal with composite (i.e. age-aggregated or stage-structured) yield per recruit (CYPR) models. CYPR models are derived from the governing equations of, and inherit assumptions associated with, delay-difference production models and delay-differential production models under equilibrium ([Munyandorero, 2012, 2015](#)). Analyses employing CYPR models involve (i) an equation calculating the composite spawning-stock per recruit (CSSR) and (ii) an equation calculating the CYPR as the product of the fishing mortality rate, average recruit during a stable fishing regime, and CSSR. Thus, unlike the age- and length-structured YPR and spawning-stock biomass per recruit, for which the selectivity and maturity schedules are often different, CYPR and CSSR are interrelated. The interrelation between CYPR and CSSR is due to the assumption that, consistent with the underlying delay-difference or delay-differential production model, animals in the harvested population, including recruits, all are fully selected and equally reproductively mature, and the selectivity and maturity schedules are identical. CYPR models infer the reference points in terms of fishing mortality rates. But, like the age- or length-structured spawning-stock biomass per recruit, the absolute CSSRs are not typically used; the related fishing mortality rates must, if need be, be derived from the composite spawning potential ratios (CSPRs, i.e. the fished CSSRs divided by the unfished CSSRs).

This study is based on the CYPR model CYPR14. In fact, of the CYPR models identified by [Munyandorero \(2015\)](#), CYPR14 was recommended for use because (i) it integrates more growth parameters, (ii) it has a yield-like curve (i.e. such a curve has a maximum whatever the age of recruitment lower than or equal to the maximum age in the population), (iii) the related maximizing fishing mortality corresponds to its counterpart derived from conventional surplus-production models, and (iv) its maximizing fishing mortality was the most accurate estimator of F_{MSY} and proxy thereof as prescribed through single-species, nominally data-rich stock assessments. CYPR14 is rooted in a continuous delay-differential model (CDDM) that was developed by [Walters \(2011, 2020\)](#); see applications by [Liao et al. \(2016a and b\)](#) and [Liao and Karim \(2021\)](#). Like most CYPR models and consistent with the assumptions associated with the underlying delay-difference models and delay-differential models (e.g. [Quinn and Deriso, 1999](#)), CYPR14 assumes (i) knife-edge selection or, equivalently, knife-edge recruitment to stable fishing regimes (because the ages of recruitment and selectivity are similar, these processes are henceforth used interchangeably), (ii) constant growth and natural mortality rates, and (iii) knife-edge maturity identical to the knife-edge selectivity. The latter assumption implies that in the CDDM and similar models, if spawning occurs early in this time step (e.g. this year) prior to the fishery and natural mortality, the total biomass of individuals at

Table 1. Notations used in the CYPR14 analysis.

Symbols	Description
a	Index for age
F	Fishing-regime-specific nominal fishing mortality rate (year^{-1} , $F \geq 0$)
r_p	Age (years) of knife-edge recruitment to the population ($r_p = 1$ year)
r	Age (years) of knife-edge recruitment to a fishing regime or of knife-edge selectivity ($r \geq 0$); r is also the age of knife-edge maturity (animals of age $< r$ are immature)
M	Constant natural mortality rate (year^{-1} , $M > 0$)
l_r	Natural survivorship, i.e. the probability to survive from r_p to r in the absence of fishing ($0 \leq l_r \leq 1$)
w_r	Average weight (kg) of a recruit
W_∞	Asymptotic mean weight (kg)
μ	Rate of metabolic loss of body mass (year^{-1} , $\mu > 0$)
$\bar{R}$	An average recruit (number) during a fishing regime

the start of this time step constitutes both the harvestable biomass and the spawning biomass, and comprises the biomass of this time step's recruits and the total biomass of adults that survive the previous time step: adults and recruits this time step all are fully selected and equally (100%) mature. Likewise, in CYPR14, the biomass of a recruit that enters a stable fishing regime represents the harvestable biomass and the spawning biomass.

The objective of this study was two-fold. The first objective was to provide the CYPR14 details needed for analyses employing this model. The second objective was to propose a rationale of using CYPR14-based fishing mortality targets (i.e. the fishing mortality rates that may potentially be desired by the fishery stakeholders for controlling perpetually the fishing effort in order to prevent overfishing and recruitment impairment). As illustration, stochastic analyses of CYPR14 were carried out and the plausible, candidate fishing mortality targets were generated for two fish species inhabiting each a different great lake in East Tropical Africa.

2 Methods

This section presents (i) the CYPR14 model (assumptions and deterministic equations, input requirements, and variations of the CYPR, CSSR, and CSPR with F) and (ii) CYPR14-based fishing mortality targets (rationale for fisheries management and estimation), and (iii) stochastic illustrations of (i) and (ii) using life-history variables of two latid species of the African great lakes. [Tables 1 and 2](#) provide, respectively, the notations and equations pertaining to CYPR14. The value of F maximizing the CYPR is denoted by F_{CYPR} .

2.1 The CYPR14 model

2.1.1 Assumptions and basic equations

For a single-species stock, consider a sequence of nominal F values (i.e. F values for fully selected fish) summarizing annual steps of piecewise stable fishing regimes: F (year^{-1}) = 0, By convention, each annual step begins at time 0, on 1 January, and

Table 2. The CYPR14 model (equations without source are developed in this study).

Equation	Description	Number	Source
$\Phi(F) = \frac{(F+M)w_r + \mu W_\infty}{(F+M)(F+M+\mu)}$	Function for the CSSR ⁽¹⁾	(1)	Walters (2011, 2020) and Munyandorero (2015)
$\gamma(F) = \frac{F}{F+M} R \{1 - \exp[-(F+M)]\} \Phi(F)$, where R is the number of recruits ($R = 1$); equivalently,	Function for the CYPR ⁽²⁾ .	(2a)	Munyandorero (2015)
$\gamma(F) = F\bar{R}(F)\Phi(F)$, where	Function for the CYPR	(2b)	Munyandorero (2015)
$\bar{R}(F) = \frac{\{1 - \exp[-(F+M)]\}}{F+M}$	Function for the average recruit ⁽²⁾	(3)	
$\gamma' = \bar{R}\Phi + F\bar{R}'\Phi + F\bar{R}\Phi'$	First derivative of γ with respect to F ⁽³⁾	(4a)	
where $\Phi' = -\frac{1}{[(F+M)(F+M+\mu)]^2}$		(4b)	
$[(F+M)^2 w_r + \mu W_\infty (2F + 2M + \mu)]$; and			
$\bar{R}' = \frac{(F+M+1)e^{-(F+M)} - 1}{(F+M)^2}$		(4c)	
$\Phi(F) = l_r \frac{(F+M)w_r + \mu W_\infty}{(F+M)(F+M+\mu)}$, where $l_r = \exp[-(r-1)M]$	Function for the CSSR involving (natural) survivorship from age r_p to age r (l_r ; see Tab. 1 for the description of r_p and r) ⁽⁴⁾	(5)	

(1) Walters (2011, 2020) developed the CDDM given the rate equations for number and biomass, respectively: $\frac{dN_t}{dt} = R_t - (F_t + M)N_t$ and $\frac{dB_t}{dt} = w_r R_t + \mu W_\infty N_t - [F_t + M + \mu]B_t$, where R_t , N_t , B_t , and F_t are the recruitment, number, biomass, and fishing mortality for time step t (see Tab. 1 for the parameters w_r , W_∞ , M , and μ). Under equilibrium, i.e. assuming constant recruitment ($R_t = R$) and constant fishing mortality ($F_t = F$), setting $\frac{dN}{dt} = 0$ and $\frac{dB}{dt} = 0$ leads to $N = R/(F+M)$ and $B = (w_r R + \mu W_\infty N)/(F+M+\mu)$. In the latter equation, replacing N by $R/(F+M)$ gives $B = \frac{(F+M)w_r + \mu W_\infty}{(F+M)(F+M+\mu)} R$; hence, $\frac{B}{R} = \frac{(F+M)w_r + \mu W_\infty}{(F+M)(F+M+\mu)}$, which is herein represented by $\Phi(F)$.

(2) In equation (2a), $\exp[-(F+M)]$ measures the number of individuals surviving, from one recruit, at the end of a fishing regime. Equation (3) can therefore also be interpreted as the average number of individuals available during a fishing regime, given a recruit of one (1) individual that entered the very fishing regime. That recruit of 1 individual is implicit in equation (1).

(3) Setting $\gamma' = 0$ reduces to $\zeta + M = F\eta$, with $\zeta = [(F+M)F - M]e^{-(F+M)}$ and $\eta = \frac{[1 - e^{-(F+M)}][(F+M)^2 w_r + 2(F+M)\mu W_\infty + \mu^2 W_\infty]}{(F+M+\mu)[(F+M)w_r + \mu W_\infty]}$. An equivalent simplification of $\gamma' = 0$ found in Munyandorero (2015) is such that $F = M + \lambda$, where

$\lambda = [(F+M)F + F - M]e^{-(F+M)} - \frac{F(F+M)[1 - e^{-(F+M)}]\mu(W_\infty - w_r)}{(F+M+\mu)[(F+M)w_r + \mu W_\infty]}$. Thus, F_{CYPR} is such that $M = F\eta - \zeta = F - \lambda$. Note that, following $F = M + \lambda$, (i) the nontrivial solution for F (i.e. $F > 0$) is conditional on M 's being $> -\lambda$, (ii) F_{CYPR} is less than M if $\lambda < 0$ and is $> M$ otherwise, and (iii) F_{CYPR} is equal to M if $\lambda = 0$. But this last outcome is trivial because it entails (i) that $F_{CYPR} = M = 0$ (yet F_{CYPR} must be > 0 and $M > 0$; hence F_{CYPR} can never equal M) and (ii) that $\mu = 0$ (yet $\mu > 0$), $w_r = W_\infty$ (a situation corresponding to catching all animals at the end of their lifespan), or both.

(4) The CYPR is calculated using equations (2a) or (2b). Based on equation (2b), it is easy to show (i) that, in γ' , the first derivative of equation (5) with respect to F is equation (4b) multiplied by l_r and (ii) that the reduced form of $\gamma' = 0$ is as in footnote 3 and, hence, is independent of l_r .

ends at time 1, on 31 December. The age of knife-edge selection and the age of knife-edge maturity are equal for all stable fishing regimes, but each stable fishing regime is characterized by a unique nominal fishing mortality, assumed to be constant throughout the year. For each fishing regime, the previous selectivity and maturity patterns determine and constrain the CSSR, in that the CSSR calculation cannot integrate alternative, eventually different selectivity and maturity schedules.

Given the above considerations, CYPR14 is a CYPR model in which the CSSR is hereinafter represented by the

function Φ of F , $\Phi(F)$ (Tab. 2, Eq. (1)) and the CYPR is described by the function γ of F , $\gamma(F)$ (Tab. 2, Eq. (2a) or Eq. (2b)). In short, the CYPR14 model is a system of equations (1) and (2a) or (2b).

Following equation (2a), the CYPR is the CSSR multiplied by the number of fish caught, from one recruit ($R = 1$), between time 0 when that recruit entered a fishing regime and time 1 when that regime ended. Equation (2a) can also be represented by equation (2b). Equation (2b) says that the CYPR results from the application of the fishing-regime-specific value of F

to the product of the average recruit $\bar{R}$ (Eq. (3)) and the CSSR; that product ($\bar{R}(F)\Phi(F)$) quantifies the average, harvestable and spawning biomass produced by one recruit during a fishing regime. Note that $\bar{R}$ is a function of F .

2.1.2 Input requirements

F is the only independent variable in the CYPR14 model. The CSSR, CYPR, average recruit, and their related quantities shown by equations (4a)–(4c) in Table 2 require natural mortality (M), asymptotic weight (W_∞), average weight of a recruit (w_r), and the rate of metabolic loss of body mass (μ) as defined by Walters (2011, 2020), but, whatever the fishing regime, these life-history variables are greater than zero, should be estimated externally, and are fixed.

Pauly's nonlinear empirical equation, without the variable temperature (Then et al., 2015), is herein used to estimate M : $M = 4.118K^{0.73}L_\infty^{-0.33}$, where L_∞ (cm) and K (year⁻¹) are the von Bertalanffy growth parameters; but note that M can be derived using any estimator that an analyst deems to be appropriate. The previous estimator of M is preferred over Pauly's (1980) estimators of M involving the variable temperature because recent studies found that the variable temperature was not statistically significant (e.g. Gislason et al., 2010; Then et al., 2015).

The asymptote weight is calculated as $W_\infty = AL_\infty^B$, where A is the scale and B is the exponent. Given the mean weight at age a (w_a) calculated as $w_a = W_\infty [1 - e^{-K(a-a_0)}]^B$, where a_0 is the age when the weight and length at age 0 are 0, the parameter μ is estimated using the nonlinear regression described by the equation derived by Huynh (2020): $w_{a+1} = W_\infty + (w_a - W_\infty)e^{-\mu}$.

The average weight of a recruit (w_r) is w_a for an age a treated both as the age of knife-edge selectivity and as the age of knife-edge maturity.

2.1.3 Variations of the CSSR, CSPR, and CYPR with F

Munyandorero (2015) showed that the function $\Phi(F)$ for the CSSR varies similarly as the age- and length-structured spawning stock biomass per recruit vary with F , and the composite spawning potential ratio (CSPR = the fished CSSR divided by the unfished CSSR) varies similarly as the static age- and length-structured spawning potential ratios (SPR) vary with F . Regarding the function $\gamma(F)$ for the CYPR, it exhibits a yield-like curve that, whatever the value of r less than or equal to the maximum age in the population, approaches zero as F approaches infinity and always peaks at an F value (F_{CYPR}). These patterns contrast $\gamma(F)$ with traditional age- and length-structured per recruit models, for which the YPR has no peak if the age or length of recruitment exceeds the optimal age or the optimal length, i.e. the age or the length at which growth rate and biomass are maximum for an unfished cohort (Laurec and Le Guen, 1981; Froese et al., 2008). The previous patterns of CYPR and CSPR are illustrated below with the application species.

2.2 CYPR14-based fishing mortality targets

2.2.1 Rationale for fisheries management

In fishery areas with data-rich stocks and catch control rules (e.g. some fishery areas of the U.S.A), an F level

associated with a target SPR (e.g. F at 40%SPR and denoted by $F_{40\%SPR}$) is commonly treated as an F_{MSY} proxy and a fishing mortality target (i.e. $F_{40\%SPR}$ is believed not to jeopardize the spawning stock and to impair recruitment). By analogy to this management paradigm, an F level associated with a target percent CSPR (e.g. F at 40%CSPR or $F_{40\%CSPR}$) can also be treated as a proxy of F_{MSY} that would be estimated once a CDDM is carried out, but the underlying SRR is untrustworthy, and the resulting MSY-based benchmarks are deemed unreliable for use. Such an F value can therefore be treated as a fishing mortality target to ensure healthy spawning stocks and avoid recruitment impairment in the tropics.

An F value maximizing the CYPR (F_{CYPR}) is also proposed as a candidate fishing mortality target for two reasons. First, such an F value theoretically corresponds to F_{MSY} as derived from conventional surplus-production models (Munyandorero, 2015). Second, comparisons of F_{CYPR} to the accepted F_{MSY} or F_{MSY} proxies from nominally data-rich stock assessments showed that F_{CYPR} has moderate to little bias (and, hence, moderate to high accuracy) vis-à-vis most of those F_{MSY} or F_{MSY} proxies (Munyandorero's (2015) Fig. 8a).

Another F level that can be set as a fishing mortality target is a value of F at which the marginal increase in CYPR is 10% of the marginal increase in CYPR when $F=0$. Such an F value is denoted by $F_{0.1}$ and, by definition, is such that $\frac{\Delta CYPR}{\Delta F}|_{F=F_{0.1}} = 0.1 \frac{\Delta CYPR}{\Delta F}|_{F=0}$. The application of $F_{0.1}$ may ensure the optimum economic (and perhaps social) returns, minimal loss in maximum yield (Gulland and Boerema, 1973), and, compared to F_{CYPR} , improved recruitment.

Although F_{CYPR} , $F_{0.1}$, and an F value producing a target CSPR ($F_{35\%CSPR}$ or $F_{40\%CSPR}$ in this study) are suggested as alternative F_{MSY} proxies, their levels can be seen as indicative of different signals. Like the traditional SPR, the CSPR measures the proportion of the spawning population that remains after fishing and, as such, indicates the impact of fishing on a stock's reproductive capacity and so emphasizes protecting the spawning stock rather than maximizing yield (e.g. Gulf of Mexico SPR Management Strategy Committee, 1996; Munyandorero, 2015). Thus, like for a percent SPR (Gabriel and Mace, 1999), a percent CSPR lower than a target CSPR signals recruitment-overfishing (i.e. a situation when the fishing mortality corresponding to that percent CSPR exceeds F at a target CSPR and reduced the biomass of mature individuals such that recruitment is impaired). There has also been a belief that $F_{0.1}$ is a conservative reference point for defining recruitment-overfishing (Mace and Sissenwine, 1993).

Nonetheless, $F_{0.1}$ and F maximizing the traditional YPR have been alternatively treated as indicative of the fisheries productivity: they are fishing mortality rates beyond which the optimum growth is hindered, thereby depressing the potential yield and catch value (as a result of being based on animals that have not reached the optimal age or the optimal size) and, consequently, causing growth-overfishing (e.g. Rivard and Maguire, 1993; Gabriel and Mace, 1999; Ben-Hasan et al., 2021). This paradigm is herein applied to F_{CYPR} and $F_{0.1}$ from CYPR14. Note that both recruitment-overfishing and growth-overfishing can happen simultaneously when the fishery is dealing with small and immature animals and the fishing mortality is high enough (Ben-Hasan et al., 2021).

2.2.2 Estimation of F_{CYPR} , $F_{0.1}$, and F associated with a target CSPR

F_{CYPR} , $F_{0.1}$, and F associated with a target CSPR can be obtained through numerical search. F_{CYPR} can also be obtained either (i) through an optimization method of γ or (ii) by solving the zero-derivative of γ ($\gamma' = 0$) for F ; γ' is given by equations (4a)–(4c).

3 Application of CYPR14 to two fish species of the African great lakes

3.1 Application species and input parameters

The equations found in Table 2 were applied to two latid species: (i) *Lates stappersii* exploited in Lake Tanganyika (3° 20'–8° 48' S, 29° 05'–31° 15' E (<http://www.fao.org/fi/oldsite/ltr/gen.htm>)) and (ii) *Lates niloticus* exploited in Lake Victoria (0° 20' N–3° S, 31° 39'–4° 53' E (Njiru et al., 2008)). These species were chosen solely because of the availability of life-history variables needed to address uncertainty in (hence to calculate plausible values of) various quantities, especially in the proposed fishing mortality targets, and because of their economic importance (Sarvala et al., 2006; Marshall and Mkumbo, 2011).

To analyze CYPR14 and infer plausible fishing mortality targets for Lake Tanganyika's *L. stappersii* and Lake Victoria's *L. niloticus*, the basic inputs were (i) the von Bertalanffy growth parameters L_∞ and K (note: $a_0 = 0$ because the growth parameters were derived using the electronic length–frequency analysis (ELEFAN) algorithm of the software FiSAT II, a method that precludes the estimation of a_0), (ii) the weight–length scales (A) and exponents (B), and (iii) the nominal fishing mortality rate F ($F = 0, \dots, 2$). L_∞ , K , A , and B came from the literature and were treated as observed data (Supplementary Tabs. 1 and 2).

3.2 Characterizing uncertainty and stochasticity

Uncertainty was characterized under program R, version 4.1.0 (R Core Team, 2021), by performing random draws of L_∞ , K , A , B , and M . Uncertainty in these parameters was propagated into other quantities (W_∞ , w_a , w_r , μ , $\bar{R}$, CYPR, CSSR, CSPR, and fishing mortality targets) also using program R. As in Munyandorero (2018, 2020), it was considered (i) that the variability of the observed growth parameters reflected scientific uncertainty in their estimations and (ii) that no unique pairs (L_∞ , K) and (A , B) were better than other such pairs for proper CYPR14 analyses. In other words, all compiled pairs (L_∞ , K) and (A , B) were assumed to be equally reliable.

To incorporate growth parameters uncertainty, the values of L_∞ and K on the one hand and of A and B on the other, were jointly resampled with replacement (5000 replicates) given each parameter's mean and without assuming a probability distribution error. The resampled parameter values were negatively related, strongly for B against A , and their boxplot distributions were approximately symmetrical (Supplementary Figs. 1a–d).

Uncertainty in M (Supplementary Figs. 2a, b) was introduced by sampling M values from a lognormal distribution error with a coefficient of variation (CV) of 0.5 and a

mean, on log scale, obtained by inputting the random draws of L_∞ and K in the equation $M = 4.118K^{0.73}L_\infty^{-0.33}$. A CV of 0.5 was suggested by MacCall (2009) as a minimal default value for the variability of M on log scale.

Given the random realizations of L_∞ , K , A , B , and M , 5000 Monte Carlo (MC) simulations were run employing various equations. For each MC sequence, a set of random values of L_∞ , K , A , B , and M was used to derive: (i) asymptotic weight, (ii) mean weight at age, (iii) the parameter μ , (iv) the CSSR, CSPR, and $F_{35\% \text{CSPR}}$ for *L. stappersii* and $F_{40\% \text{CSPR}}$ for *L. niloticus* based on their presumed longevities (see below), (v) average recruitment, and (vi) CYPR, F_{CYPR} , and $F_{0.1}$. This way, the 5000 MC simulations generated different random values of W_∞ (Supplementary Figs. 2c, d), w_r (Supplementary Figs. 2e, f), μ (Supplementary Figs. 2g, h), CYPR, F_{CYPR} , $F_{0.1}$, CSPR, $F_{35\% \text{CSPR}}$, and $F_{40\% \text{CSPR}}$. In the end, it was possible to describe uncertainty in various quantities.

3.2.1 Baseline analyses

Baseline MC runs employed the age of knife-edge recruitment and maturity r of 1 year for both species. Thus, baseline w_r was the mean weight at age 1 (Supplementary Figs. 2e, f). This assumption stemmed from the following facts. First, the *L. stappersii* fishery in Lake Tanganyika has operated with a variety of small mesh-sized and non-selective fishing gears and methods and has never been regulated in terms of size limits (Munyandorero, 2002, 2018). Second, even though the *L. niloticus* fishery in Lake Victoria has been regulated in terms of slot limits, it persistently operated with multiple, non-selective gear types and methods and compliance with slot limits may have been inefficient (Njiru et al., 2009; Munubi and Nyakibinda, 2020). Such fishery characteristics and management histories suggest that fishermen have always caught all available sizes and ages of Lake Tanganyika's *L. stappersii* and of Lake Victoria's *L. niloticus*. It should be noted that the age at 50% maturity for both species is attained in the first or second year; so, the assumption of knife-edge maturity at one year is slightly violated in baseline analyses.

3.2.2 Responses of CYPR and CSPR to various ages of knife-edge recruitment

In addition to age 1 used as the default age of knife-edge recruitment and maturity, sensitivity analyses involving different ages of recruitment ($r = 0, \dots, 10$ for *L. stappersii*, and $r = 0, \dots, 16$ for *L. niloticus*) were performed to evaluate the effects of r on CYPR14 results. The maximum lifespan of 10 years for *L. stappersii* came from Munyandorero (2002). The maximum lifespan of 16 years for *L. niloticus* was the mean of the ratios $2.996/K$. The ratio $2.996/K$ as estimator of maximum lifespan is due to Taylor (1958).

Explicit in the evaluations of equation (1) and equations (2a) or (2b) by age r were (i) that $w_r = w_a$ and (ii) that, for $r > 1$, the age of maturity became r . Implicit in those evaluations was that a recruit had a maximum survivorship to age r (i.e. the probability is 1 for that recruit to survive to age r in the absence of fishing). Because of this constraint of maximum survivorship to age r , technically due to defining the recruitment at age r , analyses and results were hereinafter referred to as CYPR14 analyses with maximum survivorship (CYPR14 m.s.), CYPR m.s., and CSPR m.s., etc.

In the end, sensitivity analysis results were displayed through isopleths of the summary statistics (mean, median, and the 2.5% and 97.5% percentiles, and hence, the 95% uncertainty envelop, UE) of CYPR and CSPR as functions of F and r , constructed with the R package *akima* (Akima and Gebhardt, 2021). The curves of fishing at candidate fishing mortality targets were superimposed on those isopleths to show how those mortality rates varied with r . In the CYPR isopleths thus constructed, the topographies to the right of the fishing curve at each fishing mortality target were treated as areas of growth-overfishing. For the CSPR isopleths, such topographies were treated as areas of recruitment-overfishing.

3.2.3 Responses of CYPR and CSPR to declining survivorships to age r

A relatively meaningful sensitivity analysis of the effects of r on CYPR and CSPR would be (i) to consider that all members of a cohort graduate to the population at age r_p (the cohort size is herein 1 individual) but are not necessarily vulnerable and 100% reproductively mature and (ii) to calculate the CSSR. at successive values of r given that, from age r_p to age $r - 1$, the cohort endures natural mortality only and, at age r , also fishing mortality on top of natural mortality. Thus, there is a time-lag between age r_p and age r ($r - r_p$ years), during which the cohort is affected by natural survivorship, i.e. the probability that it will survive from r_p to r in the absence of fishing.

Denoting the survivorship at age r_p by $l_{r_p} = 1$ (here, $r_p = 1$ year consistent with baseline analyses), the one-individual cohort of age r_p is ultimately affected by its survivorship l_r to age r when it becomes fully-selected and 100% reproductively mature: $l_r = \exp[-(r - 1)M]$ (in fact, at age $r_p = 1$, l_{r_p} is rewritten as $l_1 = \exp(-0M) = 1$; if $r = 2$, $l_2 = \exp(-0M) \exp(-M) = \exp(-M)$; if $r = 3$, $l_3 = \exp(-M) \exp(-M) = \exp(-2M)$ and so on until when r = the maximum age in the population). Note that l_r can be obtained recursively using age-specific values of M : $l_r = l_{r-1} \exp(-M_{r-1})$, but, for illustration purposes, M_{r-1} is set to M . In short, this approach initializes the recruitment of size 1, age r_p , and $l_{r_p} = 1$ at the population level. When that recruit will enter a fishing regime at age r , it will, from age to age, have been cumulatively decremented by M such that the CSSR is represented by equation (5); because l_r decreases as r increases, it was hereinafter referred to as declining survivorship. The CYPR is calculated as usual using equations (2a) or (2b), but, in this case, employs equation (5) for the CSSR. Note (i) that if $r = r_p$ (i.e. the youngest cohort in the population becomes 100% mature and fully selected), CYPR14 analyses reduce to baseline analyses, (ii) that the CSSR and CYPR involving the declining survivorship preclude use of ages $r < r_p$, because l_r cannot be greater than 1, and (iii) that l_r propagates additional uncertainty in the CSSR, CYPR, and CSPR.

4 Results

4.1 Baseline outcomes

In this section and Sections 4.2. and 4.3, the results relate to CYPR14 m.s. As expected, the curves of γ were dome-shaped and varied asymmetrically with F (Figs. 1a, b). They peaked at mean $F_{CYPR} = 0.52 \text{ year}^{-1}$ (CV = 0.22) for Lake Tanganyika's *L. stappersii* and at mean $F_{CYPR} = 0.23 \text{ year}^{-1}$ (CV = 0.09) for Lake Victoria's *L. niloticus* (Tab. 3). The CSPR declined as F

increased (Figs. 1c, d). Mean $F_{35\%CSPR}$ for *L. stappersii* was 0.51 year^{-1} (CV = 0.29) and mean $F_{40\%CSPR}$ for *L. niloticus* was 0.16 year^{-1} (CV = 0.10).

Figure 1 and Table 3 provide other statistics of F_{CYPR} , $F_{0.1}$, $F_{35\%CSPR}$, and $F_{40\%CSPR}$. Mean F_{CYPR} and mean $F_{35\%CSPR}$ for *L. stappersii* were close, and both estimates were substantially greater than mean $F_{0.1}$ of 0.33 year^{-1} (CV = 0.23). For *L. niloticus*, mean $F_{40\%CSPR} < \text{mean } F_{CYPR}$ and was slightly greater than mean $F_{0.1} = 0.14 \text{ year}^{-1}$ (CV = 0.09). Note (i) that the CYPR and CSPR as well as F_{CYPR} , $F_{0.1}$, and $F_{40\%CSPR}$ for *L. niloticus* were more precise (narrower 95% uncertainty envelopes, UEs, and interquartile ranges as well as lower CVs) than the CYPR, CSPR, F_{CYPR} , $F_{0.1}$, and $F_{35\%CSPR}$ for *L. stappersii*, (ii) that, for some reasons in *L. stappersii*, CYPR's 97.5% percentile peaked at a lower F than did CYPR's mean and lower percentiles, but various summary statistics peaked at almost the same F level for *L. niloticus*, (iii) that F_{CYPR} and $F_{0.1}$ in *L. stappersii* were comparably precise but were more precise than $F_{35\%CSPR}$, and (iv) that the precisions of *L. niloticus*' F_{CYPR} , $F_{0.1}$, and $F_{40\%CSPR}$ were comparable.

4.2 Effects of r on the CYPR

For both application species, CYPR's summary statistics increased with F and mainly with r (Fig. 2). CYPR isopleths show (i) that CYPR medians and means were comparable, but CYPRs' 95% UEs were wide (e.g. at $r = 10$ years in *L. stappersii*, the 95% UE of CYPR ranged from >0.19 to $>0.4 \text{ kg}$; at $r = 16$ years in *L. niloticus*, the 95% UE of CYPR was about 28–60 kg) and (ii) that CYPRs' summary statistics were highest at the maximum age and were associated with some finite and relatively higher levels of F .

The variations of the candidate fishing mortality targets with r indicate that those mortality targets increased gradually from age 0 to age 4 in *L. stappersii* and to age 9 in *L. niloticus*, and then leveled off. For *L. niloticus*, the means, medians, and 2.5% and 97.5% percentiles of $F_{40\%CSPR}$ and $F_{0.1}$ were marginally different, especially at lower values of r ; all these summary statistics were lower than their F_{CYPR} counterparts and so were equally conservative (in terms of effort reduction), presenting less risk of growth-overfishing irrespective of r . For *L. stappersii*, (i) all summary statistics of $F_{0.1}$ were less than the corresponding statistics of F_{CYPR} and $F_{35\%CSPR}$ and so were more conservative in terms of less risk to fishery yield, (ii) only the 2.5% percentile of $F_{35\%CSPR}$ was less than the 2.5% percentile of F_{CYPR} for all r values, (iii) the 97.5% percentile of $F_{35\%CSPR}$ was greater than the 97.5% percentile of F_{CYPR} whatever r , and (iv) the means and medians of $F_{35\%CSPR}$ and F_{CYPR} were similar from age 0 to age 4; for $r > 4$, mean and median $F_{35\%CSPR}$ exceeded mean and median F_{CYPR} . Thus, for $r > 4$ in *L. stappersii*, F_{CYPR} on average presented less risk of growth-overfishing than $F_{35\%CSPR}$.

4.3 Effects of r on the CSPR

At lower F s, isopleths of the CSPR summary statistics were high and parallel to the y -axis, and, therefore, were insensitive to r (Fig. 3). With higher F s, their isopleths were first concave down, increasing (up to age 4 in *L. stappersii* and age 9 in *L. niloticus*), then they suddenly became concave up,

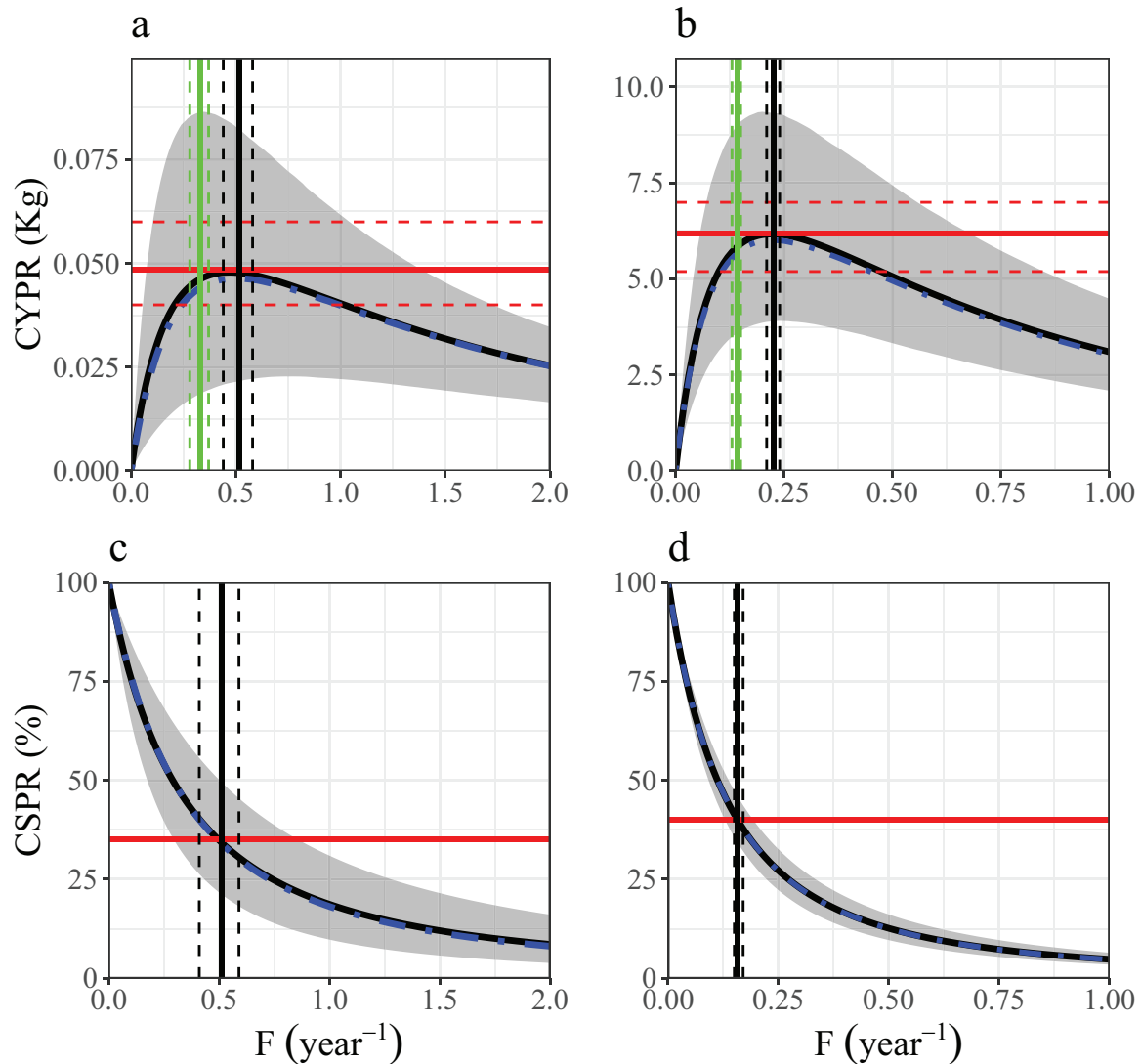


Fig. 1. Variations, against fishing mortality (F), of mean (black solid line), median (blue dash-dotted line), and the 95% uncertainty envelopes (gray area) of (a) and (b) the composite yield per recruit (CYPR) and (c) and (d) the composite spawning potential ratio (CSPR) based on baseline CYPR14 analyses (age of knife-edge recruitment = 1 year) for *L. stappersii* in Lake Tanganyika (left panels) and *L. niloticus* in Lake Victoria (right panels). The vertical, black dashed line, solid line, and dashed line represent, from left to right, the 25% percentile, mean, and 75% percentile of F_{CYPR} and $F_{35\%CSPR}$ (*L. stappersii*) or $F_{40\%CSPR}$ (*L. niloticus*); the vertical, green dashed line, solid line, and dashed line represent, from left to right, the 25% percentile, mean, and 75% percentile of $F_{0.1}$; the horizontal red dashed line, solid line, and dashed line on the CYPR plots represent, from bottom to top, the 25% percentile, mean, and 75% percentile of MSY per recruit; the horizontal red and solid line on the CSPR plots locate the levels of 35% CSPR and 40% CSPR.

increasing. Furthermore, the CSPR response surfaces were precise, having similar means and medians; for *L. stappersii*, however, the lower and upper limits of mean CSPRs' 95% UEs were 5% lower and 10% greater, respectively, than mean CSPRs. No value of r in the F - r planes avoided CSPRs less than 35% for *L. stappersii* and less than 40% for *L. niloticus*.

The curves of the points (F_{CYPR}, r) , $(F_{0.1}, r)$, $(F_{35\%CSPR}, r)$, and $(F_{40\%CSPR}, r)$ were also superimposed on the CSPR isopleths (Fig. 3). They were described along with CYPR isopleths (Fig. 2). They noticeably vary similarly as the CSPR isopleths, suggesting that the CSSR may be their main determinant. The coordinates $(F_{35\%CSPR}, r)$ for *L. stappersii* and $(F_{40\%CSPR}, r)$ for *L. niloticus* lay perfectly on the 35% and 40% contours, except in the isopleth of mean

CSPR of *L. stappersii* when $r > 4$ years, perhaps due to interpolation issues.

While the performance of F_{CYPR} , $F_{0.1}$, $F_{35\%CSPR}$, and $F_{40\%CSPR}$ in CYPR isopleths was judged with respect to their risk to fishery yield, their performance in CSPR isopleths should deal with their risk to the spawning stock biomass. In this context, means and medians of F_{CYPR} and $F_{35\%CSPR}$ for *L. stappersii* would equally avoid recruitment-overfishing if $r \leq 4$ years; for $r > 4$, F_{CYPR} would best protect the spawning biomass. Whatever the value of r of *L. stappersii*, mean and median $F_{0.1}$ would outperform mean F_{CYPR} and mean $F_{35\%CSPR}$ in avoiding recruitment-overfishing in that $F_{0.1}$ summary statistics were associated with CSPR between 45% and 50%. For *L. niloticus*, the spawning stock biomass would be at risk at

Table 3. Summary statistics of candidate fishing mortality targets for *L. stappersii* in Lake Tanganyika and *L. niloticus* in Lake Victoria as obtained from base CYPR14 analyses (UI=uncertainty interval, CV=coefficient of variation).

Parameter	Median	Mean	Lower–Upper 95% UI	CV
<i>L. stappersii</i>				
F_{CYPR}	0.50	0.52	0.33–0.77	0.22
$F_{0.1}$	0.32	0.33	0.21–0.50	0.23
$F_{35\%CSPR}$	0.49	0.51	0.29–0.86	0.29
<i>L. niloticus</i>				
F_{CYPR}	0.22	0.23	0.19–0.27	0.09
$F_{0.1}$	0.14	0.14	0.12–0.17	0.09
$F_{40\%CSPR}$	0.16	0.16	0.13–0.19	0.10

mean or median F_{CYPR} whatever the age of knife-edge recruitment, but fishing at mean or median $F_{40\%CSPR}$ and, better, at mean and median $F_{0.1}$, would avoid recruitment-overfishing.

4.4 Effects of declining survivorship to r on the CYPR

In this section and Section 4.5, the assumption of equal selectivity and maturity remains as in CYPR14 m.s., but one individual recruited to the population at age 1 and to fishing regimes at successive r values after being affected by the declining survivorship to age r (l_r).

For *L. stappersii*, the combination of l_r and r did not change the magnitude of F_{CYPR} , $F_{0.1}$, and $F_{35\%CSPR}$ and their variations with r . But that combination shifted the CYPR m.s. response surfaces from the top-open-ended orientations and increasing trends seen in Figure 2, to concave-down shapes at higher r values; those shapes became progressively vertical or oblique, with leftward orientations at lower r values (Fig. 4). The CYPR means and calculated percentiles increased toward innermost contours, whereby the topographies of higher CYPRs extended horizontally up to $F=2$ year⁻¹ and vertically up to $r=4$ years. The highest CYPR was lower than the CYPR m.s. (Fig. 2), but contrary to the latter result, maximum CYPR occurred at low F s and $r=1$ –4 years. For example, the greatest mean CYPR contour spanned $r=1$ and $r=2$ and was achieved by the lowest values of all candidate fishing mortality targets. In this context, it may be appropriate to apply $F_{0.1}$ because it entails less fishing pressure while producing the highest yield.

The combination of l_r and r in *L. niloticus* also reshuffled the CYPR response surfaces and the patterns of F_{CYPR} , $F_{0.1}$, and $F_{40\%CSPR}$ versus r (Fig. 4). Use of l_r led to CYPR isopleths with leftward horizontal shapes and well-defined closed-loop contours of maximum CYPR; the CYPR maximizing contours were centered at $r=5$ –9 years across narrow ranges of F . The highest CYPR was achieved by F_{CYPR} only, while the next highest CYPR was achieved by $F_{40\%CSPR}$ and $F_{0.1}$. The curves of the points (F_{CYPR} , r), ($F_{0.1}$, r), and ($F_{40\%CSPR}$, r) peaked at $r \approx 7$ years; F_{CYPR} , $F_{0.1}$, and $F_{40\%CSPR}$ were comparatively lower than their counterparts derived using CYPR14 m.s. Finally, the topographies of higher CYPRs did not stretch horizontally beyond $F \approx 1.2$ year⁻¹ but extended vertically up to $r=16$ years.

4.5 Effects of declining survivorship to r on the CSPR

For *L. stappersii*, the CSPR isopleths and the variations of F_{CYPR} , $F_{35\%CSPR}$, and $F_{0.1}$ with r were insensitive to l_r (Fig. 5)

in that they showed patterns and management performance comparable to those obtained with CSPR m.s. (Fig. 3). For *L. niloticus*, the CSPR isopleths were first concave down, then turned shortly upward (Fig. 5). Instead of showing vertical orientations seen with CSPR m.s. isopleths. (Fig. 3), CSPR isopleths involving the declining survivorship were parallel with the curves of F_{CYPR} , $F_{40\%CSPR}$, and $F_{0.1}$ against r , and, like them, peaked between $r=5$ –9 years before trending leftward.

4.6 On the trade-offs between CYPR and CSPR

It may be useful to plot and read CYPR and CSPR isopleths together to determine management trade-offs between CYPR and CSPR. Figure 6 presents mean CYPR and mean CSPR isopleths jointly, considering that the fisheries (hypothetically) operated at any candidate mean fishing mortality targets obtained from baseline analyses. Unlike in Schmalz et al. (2016), these fishing mortality targets were superimposed on isopleths because the application species lacked stock assessment results that may otherwise help judge the performance of CYPR14 results.

In the F – r dimensions of *L. stappersii*'s CYPR and CSPR, higher F for any value of r reduced CSPR irrespective of whether the calculations used the maximum or the declining survivorship (Fig. 6). For a given $F > 0$, the reduction of CSPR at $F=0$ (i.e. 100%) was lesser as r was increased. For example, the CSPR associated with $r=2$ years was reduced from 100% at $F=0$ to 40–45% at F_{CYPR} , whereas at $r=6$ years, the CSPR of 100% at $F=0$ was reduced to 60–65% at F_{CYPR} . The same reduction pattern can be seen for *L. niloticus*' CSPR m.s. When, in *L. niloticus*, the calculations used the declining survivorship, the reduction of CSPR at $F=0$ to a given $F > 0$ was highest for r associated with the inflection point of CSPR isopleths.

At any candidate fishing mortality target, higher r increased the CYPR m.s. and the CSPR m.s. for both application species (Fig. 6). But when the declining survivorship was accounted for in *L. stappersii*, the CYPR declined and the CSPR increased with higher r . Interestingly for this species, use of the declining survivorship suggested the possibility of achieving both maximum CYPR and CSPR > 40% at F_{CYPR} or $F_{35\%CSPR}$. In *L. niloticus*, the CYPR involving the declining survivorship was maximum between $r=5$ –9 years, years below and above which the CYPR declined; the CSPR associated with F_{CYPR} , $F_{0.1}$, and $F_{40\%CSPR}$ varied little with r .

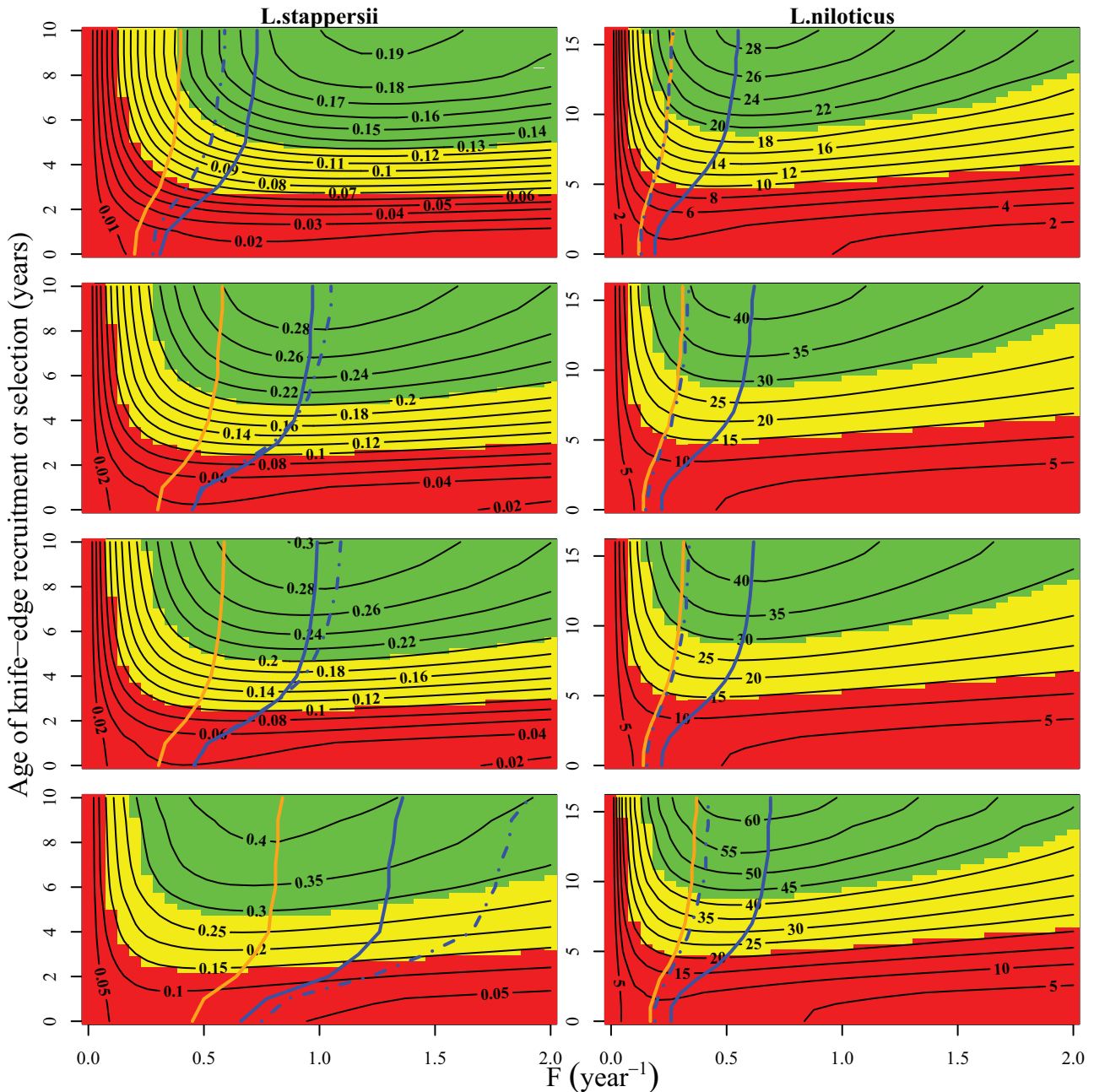


Fig. 2. Isopleths of, from top to bottom, the 2.5% percentile, median, mean, and 97.5% percentile of CYPR m.s. (kg) as a function of fishing mortality (F) and the age of knife-edge recruitment or of knife-edge selection for *L. stappersii* in Lake Tanganyika (left panels) and *L. niloticus* in Lake Victoria (right panels). The plots also show the eumetric fishing curves of the 2.5% percentile, median, mean, and 97.5% percentile of F_{CYPR} (blue solid line), $F_{0.1}$ (orange solid line), as well as $F_{35\%\text{CSPR}}$ for *L. stappersii* and $F_{40\%\text{CSPR}}$ for *L. niloticus* (blue dash-dotted line) against the age of knife-edge recruitment. Areas shaded by the red color, yellow color, and green color are, respectively, topographies of low CYPR, intermediate CYPR, and high CYPR. If F_{CYPR} , $F_{0.1}$, or F at a target CSPP is treated as the fishing mortality target, the region below and to the right of the corresponding lines represents growth-overfishing.

5 Discussion

The present study described details on the CYPR14 model and its analyses, with the goal to propose inclusion of CYPR14 in the tropical fisheries management toolkit. The populations of Lake Tanganyika's *L. stappersii* and Lake Victoria's *L. niloticus* were used to illustrate analyses that incorporated uncertainty in growth and natural mortality. CYPR14 may be

suitable for data-poor stocks because it only requires growth parameters and natural mortality. CYPR14 can be the basis of various biological reference points (Munyandorero, 2015), but the focus herein was on potential fishing mortality targets in terms of CYPR14-based F_{CYPR} and $F_{0.1}$ and of an F value associated with a target CSPP.

Beside the simplest CYPR14 analyses, this study expanded on analyses of the stochastic response surfaces of CYPR and

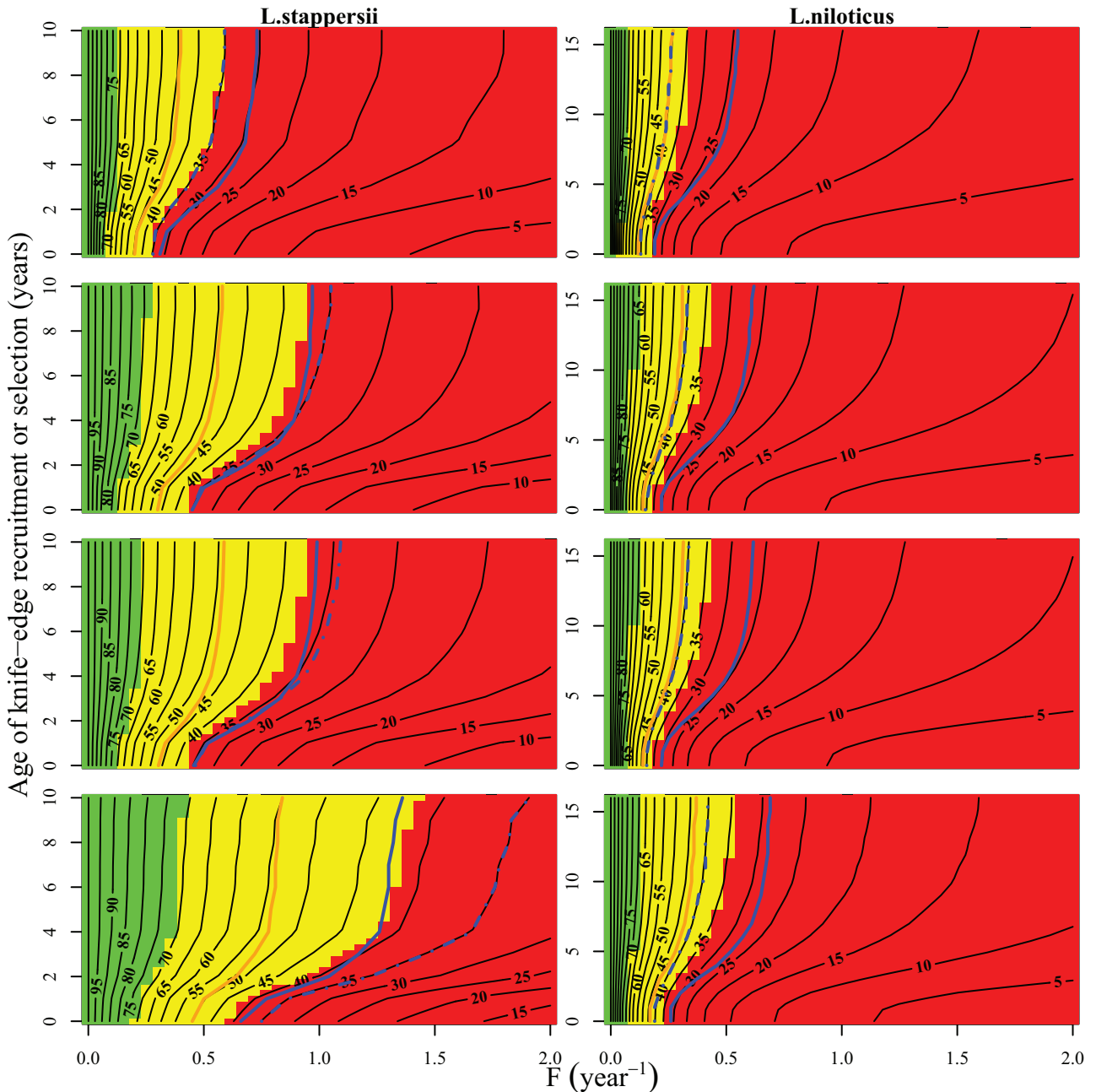


Fig. 3. Isopleths of, from top to bottom, the 2.5% percentile, median, mean, and 97.5% percentile of CSRP m.s. (%) as a function of fishing mortality (F) and the age of knife-edge recruitment or the age of knife-edge selection for *L. stappersii* in Lake Tanganyika (left panels) and *L. niloticus* in Lake Victoria (right panels). The plots also show the variations of the 2.5% percentile, median, and 97.5% percentile of F_{CYPYR} (blue solid line), $F_{0.1}$ (orange solid line), as well as $F_{35\% \text{CSRP}}$ for *L. stappersii* and $F_{40\% \text{CSRP}}$ for *L. niloticus* (blue dash-dotted line) against the age of knife-edge recruitment. Areas shaded by the red color, yellow color, and green color are, respectively, topographies of low CSRP, intermediate CSRP, and high CSRP. If F_{CYPYR} , $F_{0.1}$, or F at a target CSRP is treated as the fishing mortality target, the region below and to the right of the corresponding lines represents recruitment-overfishing.

CSRP in F - r dimensions, whereby the calculated CSRP followed from CYPYR14 m.s. or involved a declining survivorship. The latter analyses showed features that contrast CYPYR and CSRP isopleths with isopleths of traditional length- and age-based YPR and SPR or relative fecundity per recruit, RFR (i.e. isopleths of YPR and SPR or RFR as functions of F on the x-axis and of the length L_c or age t_c at first capture on the y-axis,

assuming no fishing-induced mortality of animals below L_c or t_c). Likewise, the eumetric fishing curves associated with these two types of yield isopleths trended differently.

To grasp the differences between the YPR and CYPYR and between the SPR or RFR and CSRP, first recall that the classical YPR isopleths tend to be horizontally U-shaped, opening at the right side; the YPR increases from the outer

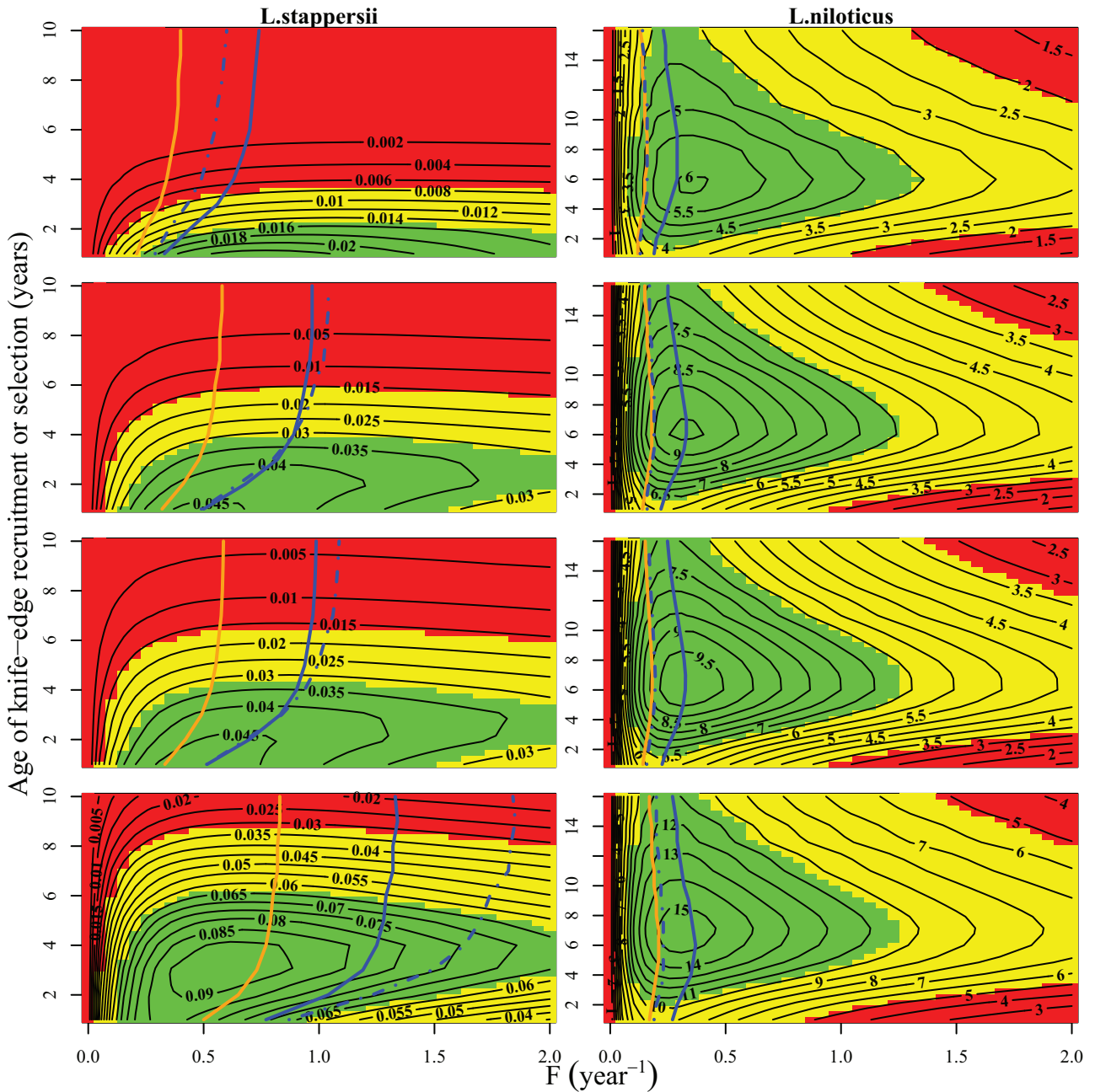


Fig. 4. Isoleths of, from top to bottom, the 2.5% percentile, median, mean, and 97.5% percentile of CYPR involving a declining survivorship (kg) as a function of fishing mortality (F) and the age of knife-edge recruitment or of knife-edge selection for *L. stappersii* in Lake Tanganyika (left panels) and *L. niloticus* in Lake Victoria (right panels). The plots also show the eumetric fishing curves of the 2.5% percentile, median, mean, and 97.5% percentile of F_{CYPR} (blue solid line), $F_{0.1}$ (orange solid line), as well as $F_{35\%\text{CSPR}}$ for *L. stappersii* and $F_{40\%\text{CSPR}}$ for *L. niloticus* (blue dash-dotted line) against the age of knife-edge recruitment. Areas shaded by the red color, yellow color, and green color are, respectively, topographies of low CYPR, intermediate CYPR, and high CYPR. If F_{CYPR} , $F_{0.1}$, or F at a target CSPR is treated as the fishing mortality target, the region below and to the right of the corresponding lines represents growth-overfishing.

contours to the inner ones and maximizes at an infinite F level with the innermost, far right horizontal or oblique contour associated with the optimal age or the optimal length (e.g. Laurec and Le Guen, 1981; Annala and Breen, 1989; Goodyear, 1993; Froese et al., 2008; Schmalz et al., 2016; Mildemberger et al., 2017). Furthermore, the eumetric fishing curves (i) of the points (F_{max} , L_c) or (F_{max} , t_c) where F_{max} is the

fishing mortality rate that maximizes the YPR for a given value of L_c or t_c , and (ii) of the points (F , L_{max}) or (F , t_{max}) where L_{max} or t_{max} is the length or the age that maximizes the YPR for a fixed value of F , have commonly been superimposed on the YPR isopleths (e.g. Laurec and Le Guen, 1981; Ault et al., 2019). Such curves increase and are concave down. On the other hand, the SPR or RFR isopleths increase with a

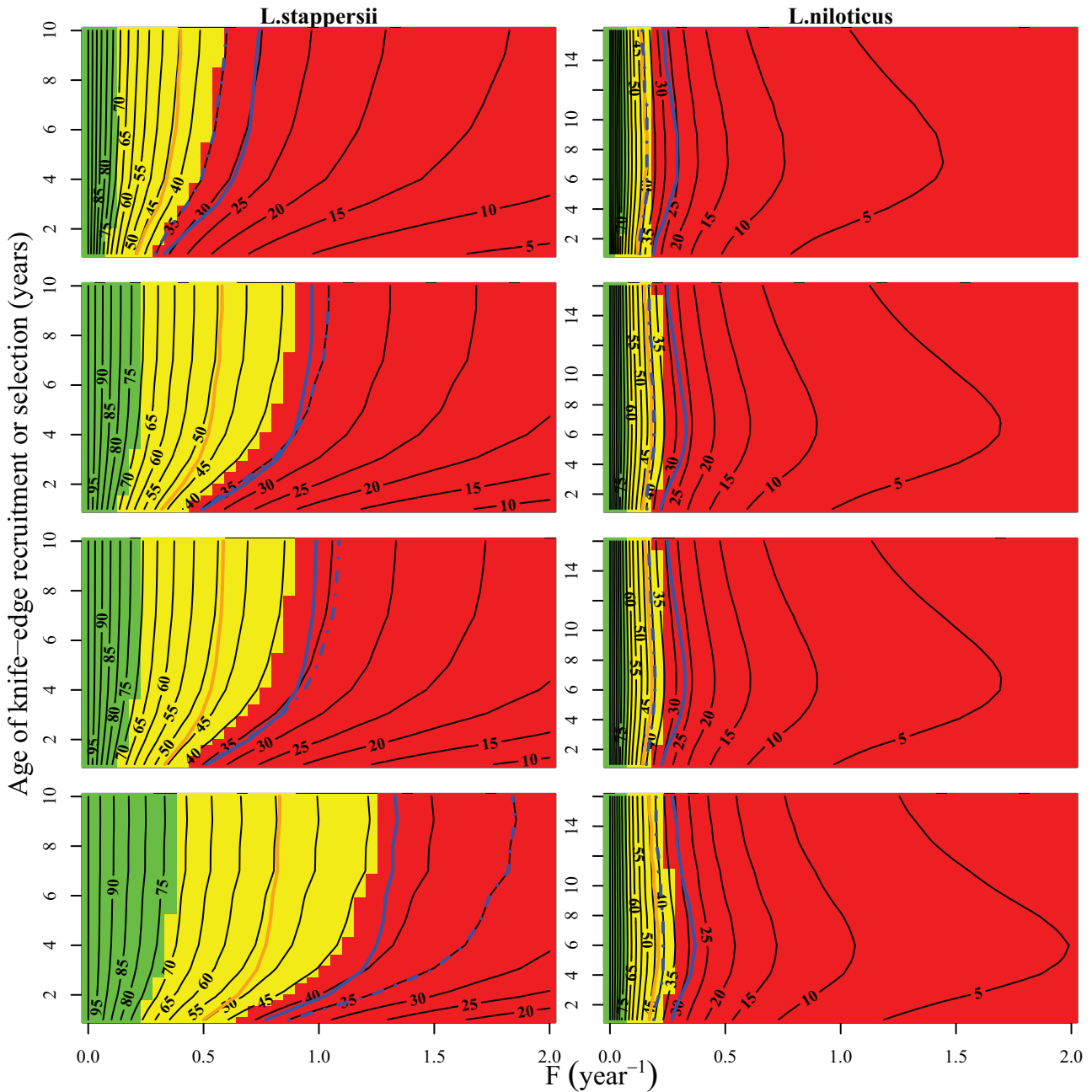


Fig. 5. Isoleths of, from top to bottom, the 2.5% percentile, median, mean, and 97.5% percentile of CSpr involving a declining survivorship (%) as a function of fishing mortality (F) and the age of knife-edge recruitment or the age of knife-edge selection for *L. stappersii* in Lake Tanganyika (left panels) and *L. niloticus* in Lake Victoria (right panels). The plots also show the variations of the 2.5% percentile, median, mean, and 97.5% percentile of F_{CYP} (blue solid line), $F_{0.1}$ (orange solid line), as well as $F_{35\%CSpr}$ for *L. stappersii* and $F_{40\%CSpr}$ for *L. niloticus* (blue dash-dotted line) against the age of knife-edge recruitment. Areas shaded by the red color, yellow color, and green color are, respectively, topographies of low CSpr, intermediate CSpr, and high CSpr. If F_{CYP} , $F_{0.1}$, or F at a target CSpr is treated as the fishing mortality target, the region below and to the right of the corresponding lines represents recruitment-overfishing.

downward concavity, trending asymptotically against F ; the SPR or RFR is lowest at the inner and rightward contours, typically for small and young spawners, and highest otherwise, typically for large and old spawners (e.g. [Laurec and Le Guen, 1981](#); [Goodyear 1993](#); [Froese et al., 2008](#); [Schmalz et al., 2016](#); [Munyandorero, 2018](#), [Ault et al., 2019](#)). While a contour of the target SPR or RFR can appear on the SPR or RFR

isoleths, no literature describing such plots with eumetric fishing curves was found.

In contrast, CYP m.s. isopleths are concave up with a bottom-up increase of the CYP that maximizes with an infinite r value at the innermost vertical contour associated with a finite F value. The reasons for the bottom-up increase of the CYP are that, following equations (1) and (2a) or (2b) and

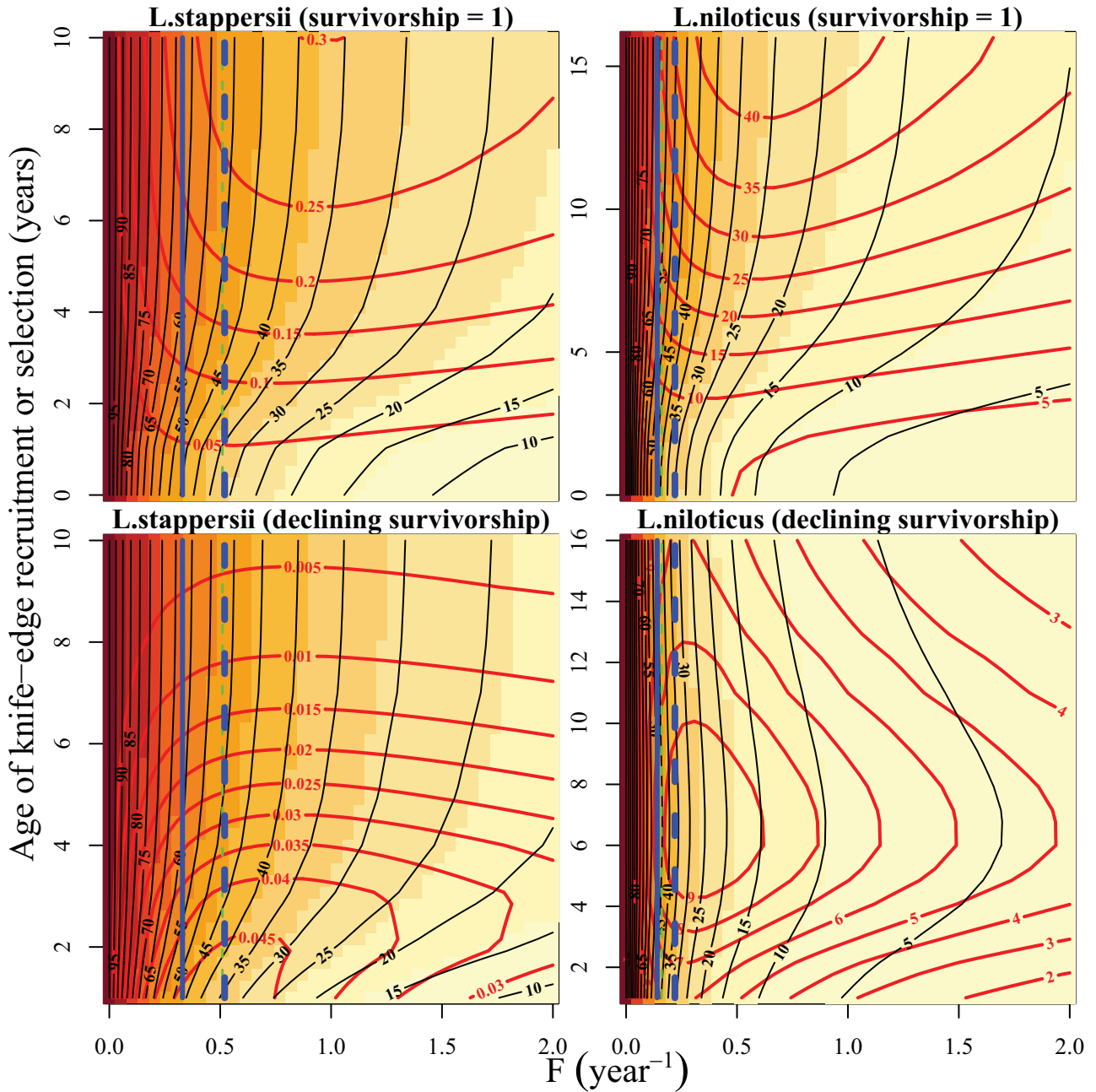


Fig. 6. Simultaneous presentation of trade-offs between mean CYPR (red contours and figures) and mean CSPR (black contours and figures) as a function of fishing mortality (F) and the age of knife-edge recruitment or the age of knife-edge selection for *L. stappersii* in Lake Tanganyika (left panels) and *L. niloticus* in Lake Victoria (right panels), considering that the fisheries operate at mean F_{CYPR} (vertical, blue solid dash line), mean $F_{0.1}$ (vertical, blue solid line), or mean $F_{35\%CSPR}$ for *L. stappersii* and mean $F_{40\%CSPR}$ for *L. niloticus* (vertical and light green dash line) as estimated from baseline analyses (Tab. 3).

given a set of L_{∞} , K , A , and B , the values of W_{∞} , w_{as} and μ do not change. As a result, higher r values drive up w_r , the CSSR, and CYPR so that, for $F > 0$, the CYPR is highest at the largest r value considered in the isopleth construction. Since, for a given value of $F > 0$, the age r maximizing CYPR (r_{max}) is unique, it may be superfluous to superimpose the eumetric fishing curves of the points (F, r_{max}) on CYPR isopleths. Regarding the curves of the points (F_{CYPR}, r) , $(F_{0.1}, r)$, $(F_{35\%CSPR}, r)$ for *L. stappersii*, and $(F_{40\%CSPR}, r)$ for

L. niloticus, they increase and are concave up, varying similarly as the CSPR isopleths.

On the other hand, CYPR isopleths involving the declining survivorship, as well as the curves of the points (F_{CYPR}, r) , $(F_{0.1}, r)$, $(F_{35\%CSPR}, r)$, and $(F_{40\%CSPR}, r)$, show unique patterns that differ between the applications species, perhaps due to the differences in their longevity and other input parameters. Overall, the declining survivorship reduced the CYPR, such that, in *L. stappersii* (a relatively short-lived and

small-bodied species), higher r values were associated with the lowest CYPR, and the points (F_{CYPR}, r) , $(F_{0.1}, r)$, and $(F_{35\% \text{CSPR}}, r)$ varied similarly as in CYPR m.s. isopleths. Thus, unlike in CYPR m.s. isopleths, higher F_{CYPR} , $F_{0.1}$, and $F_{35\% \text{CSPR}}$ generated using the declining survivorship produced lower CYPR. In *L. niloticus* (a relatively long-lived and large-bodied species), the effects of the declining survivorship appear to be offset by the magnitude of w_r because higher CYPR can be seen at higher r values. For this species, not only F_{CYPR} , $F_{0.1}$, $F_{40\% \text{CSPR}}$ were low and spanned the topography of high CYPR across the r range, but also the curves of the points (F_{CYPR}, r) , $(F_{0.1}, r)$, and $(F_{40\% \text{CSPR}}, r)$ varied little.

Of the greater interest for CYPR isopleths involving the declining survivorship is the fact that maximum CYPR occurs at innermost contours across narrow ranges of low values of r and F . Because CYPR assumes, like the traditional YPR, that there is no fishing-induced mortality below r , and because the traditional YPR maximizes at the optimal age and the optimal length (Laurec and Le Guen, 1981; Froese et al., 2008), an analysis of biomass against age for an unfished cohort was carried out *post hoc* to check if the highest CYPR occurred at optimal ages. This analysis revealed that the optimal age associated with mean CYPR was 3 years for *L. stappersii* and 7 years for *L. niloticus* (Supplementary Fig. 3). Therefore, the declining survivorship caused CYPRs to maximize at r values in the vicinity of those optimal ages.

The patterns of CSPR m.s. isopleths and of CSPR and CYPR isopleths involving the declining survivorship were at glance puzzling. There was no *a priori* expected behavior of those CYPR isopleths. As for both types of CSPR isopleths, they were expected to resemble the traditional SPR or RFR isopleths, considering that the assumption of ages r of knife-edge selection implies that all fish below r and available in the fishing ground would not be vulnerable. Technically, this assumption is equivalent to a situation of a fishery in which various size or age limits have been imposed and fish below those limits, once caught, all have been released and have experienced zero fishing-induced mortality (100% post-release survival). Yet the above-mentioned CYPR and CSPR isopleths to some extent resemble the YPR and SPR isopleths found, for example, in Coggins et al. (2007), Goodyear (1993), and Munyandorero (2018) when species were subjected to catch-and-release and size limit regulations and to post-release survival rates.

Regardless, a close examination of equations (1) and (5) along with their evaluation at each age r reveals that the r -specific CSSR is analogous to the age-specific biomass for an unfished cohort (Supplementary Fig. 3). In fact, in equations (1) and (5), the one-individual cohort is affected by the natural survivorship to age $r-1$ (l_{r-1}) only and, at age r , also by fishing and natural mortalities on top of l_r . It is worth recalling that, for equation (1), $l_r=1$ to each age r ; for equation (5), l_r decreases as r is higher (Tab. 2). In addition to l_r , another parameter varying with r is the mean weight w_r . It follows that, for each nominal F , the curve of the CSSR against r has an optimal age, acting as the inflection point for the curve in question (Supplementary Fig. 4 for the CSSR response surfaces). With the CSSR involving the declining survivorship, that inflection point is, irrespective of F , well defined at $r=2-3$ years for *L. stappersii*'s mean CSSR and at $r=6$ or 7 years for *L. niloticus*'s mean CSSR isopleths. The CSPR isopleths based on both types of survivorships and the CYPR

isopleths involving the declining survivorship inherit the patterns of CSSR isopleths, including the inflection points at optimal ages, beyond and around which the CSPR and CYPR contours are reshuffled, taking various orientations and shapes apparently determined by the balance between l_r and w_r .

CYPR14 analyses involving the declining survivorship were primarily developed as sensitivity analyses. But they may be more realistic in evaluating the effects of r on CYPR and CSPR, for three reasons. First, the declining survivorship adjusts the CSSR m.s., through which it is counterintuitive that, in a multi-age population, the yield from a cohort increases continually with r , owing to the implicit, strong assumption that, from age to age, the cohort experienced zero natural mortality since it recruited to the population. Second, the declining survivorship causes the CYPR to maximize at an optimal age, which is coherent with the traditional YPR analyses. Finally, for a fixed rate of F , higher r may be associated with lower CYPR and higher CSPR.

On a social note, and if the management goal is, for example, the maximization of yield, maximum CYPR based on the declining survivorship may be preferable over maximum CYPR m.s. In fact, stakeholders may be worried by the cost of high fishing pressure necessary for achieving the latter type of CYPR, whereas they would be relatively comfortable with the maximum CYPR calculated using the declining survivorship, because such an CYPR implies lesser fishing pressure.

A reviewer requested a sensitivity analysis on the impact of the assumption of equal (and differing) ages of maturity and selectivity on CSPR. The assumption of equal maturity and selectivity, which is typical of two-stage-structured models of exploited population dynamics, is rigid; it strictly applies to a baseline analysis conditional on that assumption being justified. Exploring various ages r of recruitment/selectivity, which also are the ages of 100% maturity, implies a strong assumption that the schedules in question are shifted to and coincide at the explored values of r , because CYPR14 only considers the CSSR and the resulting CYPR and CSPR at an assumed age of knife-edge selectivity. In comparison to results employing the true age of maturity (typically in a baseline analysis), the previous paragraphs indicate (i) that greater r values in calculations with maximum survivorship inflate the CSSR and CYPR and (ii) that the combination of r and l_r brings about species-specific patterns of CSSR and CYPR. Regarding the effects of differing ages of maturity and selectivity on CSPR, they may be impossible to evaluate in the context of two-stage-structured models.

The status of the stocks of Lake Tanganyika's *L. stappersii* and Lake Victoria's *L. niloticus* was not determined because this study was not accompanied with stock assessments aimed at such a task. The calculated values of F_{CYPR} , $F_{0.1}$, $F_{35\% \text{CSPR}}$ (for *L. stappersii*) and $F_{40\% \text{CSPR}}$ (for *L. niloticus*) were instead suggested as candidate fishing mortality targets, provided stock assessments or simulations (e.g. through management strategy evaluations) of Lake Tanganyika's *L. stappersii* and Lake Victoria's *L. niloticus* relied on CDDMs—this comment on the restrictive, joint use of CYPR14 and CDDM is fundamental in that it guards one against comparisons of CYPR14-based fishing mortality targets to results from delay-difference/differential formulations other than the CDDM, because CYPR models and reference points therefrom or involving them (typically MSY benchmarks) must be consistent with the equations governing the parent

stage-structured models (Munyandorero, 2015, Fig. 4 and Tab. 6). In that case, F_{CYPR} could serve in two ways. Like $F_{0.1}$ or an F value associated with a target CSPR, F_{CYPR} would first be treated as an F_{MSY} proxy if the SRR and F_{MSY} resulting from a CDDM-based assessment are untrustworthy (note: the preference between $F_{0.1}$, $F_{35\% \text{CSPR}}$ or $F_{40\% \text{CSPR}}$, and F_{CYPR} would depend on the management goal). In that case, for example, an estimate of F in the last year of the CDDM could be compared to F_{CYPR} to determine the stock status (provided this is the management objective). Second, since F_{CYPR} is a relatively accurate estimator of F_{MSY} (Munyandorero, 2015), it can be used to initialize the estimation of F_{MSY} in a CDDM-based assessment, consistent with the so-called management-oriented approach of exploited population dynamics (e.g. Martell et al., 2008).

6 Conclusions

Despite advances in developing CYPR models (Munyandorero, 2012, 2015), the present study may be the first one to provide detailed analyses specifically of CYPR14. The goal of the study was to propose CYR14 as a management tool for tropical fisheries, along with or alternatively to the commonly used length-based methods. More generally, it is useful to stress that, in terms of MSY-based benchmarks and proxies, CYPR14 is for CDDMs what the conventional age-structured pool models are for age-structured stock assessment models (e.g. Shepherd, 1982). Therefore, CYPR14, preferably involving the declining survivorship if the ages of recruitment to the population and to the fishery are different, would be fully useful if it were accompanied with CDDM-based stock assessments or simulations.

Although the previous goal and usefulness of CYPR14 were advocated for data-poor stocks in the tropics, they are valid for any data-poor stocks irrespective of the geographical area.

Conflict of interest

There are no known competing interests that could influence this study.

Data accessibility statement

The input parameters, tools (R scripts), and outputs that support this study are available at <https://doi.org/10.17882/90241> (Munyandorero, 2022).

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Supplementary Material

Table 1. Observed von Bertalanffy growth parameters used to analyze CYPR14.

Table 2. Observed weight–length scales (A) and exponents (B) used to analyze CYPR14 for *L. stappersii* in Lake Tanganyika (lengths were in mm and weight in g) and *L. niloticus* in Lake Victoria (lengths were in cm and weight in g).

Figure 1. Scatter plots and marginal boxplot distributions of the random draws of (a) and (b) the von Bertalanffy growth parameters and (c) and (d) weight–length scales and exponents for *L. stappersii* in Lake Tanganyika (left panels) and *L. niloticus* in Lake Victoria (right panels).

Figure 2. Frequency distributions of (a) and (b) natural mortality (M), (c) and (d) asymptotic weight (W_{∞}), (e) and (f) mass of the average recruit (w_r), and (g) and (h) the rate of metabolic loss of body mass (μ) for *L. stappersii* in Lake Tanganyika (left panels) and *L. niloticus* in Lake Victoria (right panels). The dashed blue line represents the mean of the distribution.

Figure 3. Variations, against age, of mean (black solid line), median (blue dash-dotted line), and the 95% uncertainty envelopes (gray area) of biomass for an unfished cohort of *L. stappersii* in Lake Tanganyika and *L. niloticus* in Lake Victoria. The age-specific biomass B_a was given by $B_a = l_a w_a$, where w_a (kg) is mean weight at age a and l_a is the survivorship to age a : $l_a = 1$ if $a = 0$ year and $l_a = l_a - 1 \exp(-M) = \exp(-aM)$ if $a > 0$; M is natural mortality. Mean biomass, median biomass, the 95% lower biomass limit, and the 95% upper biomass limit of *L. stappersii* peaked at ages 3, 3, 2, and 4 years. Such summaries statistics for *L. niloticus* peaked at ages 7, 7, 6, and 7 years.

Figure 4. Isopleths of the mean composite spawning-stock per recruit (CSSR) as a function of fishing mortality (F) and the age of knife-edge recruitment or the age of knife-edge selection r for *L. stappersii* in Lake Tanganyika (left panels) and *L. niloticus* in Lake Victoria (right panels). The CSSR of the top plots was calculated considering that the survivorship to each age r is 1 (Eq. (1), Tab. 2) and the CSSR of the bottom plots involved the declining survivorship to each age r (Eq. (5), Tab. 2).

The Supplementary Material is available at <https://www.alr-journal.org/10.1051/alr/2022016/olm>.

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