

Food for Thought

Conflicting perceptions on the life-history covariates of density-dependent recruitment based on information-generating equations

Joseph Munyandorero  *

Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, Stock Assessment Group, 100 8th Avenue SE, St. Petersburg, FL 33701, USA

*Corresponding author: tel: + 1 727 896 8626; fax: + 1 727 823 3704; e-mail: Joseph.Munyandorero@MyFwc.com.

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The stock–recruit steepness (h) and compensation ratio are alternative measures of the degree of density-dependent recruitment. They relate similarly to the longevity-related life-history traits (LRLHTs), but studies using information-generating equations and describing such relationships convey three conflicting perceptions. Perception 1 is that h and the compensation ratio decrease as longevity increases and are highest in short-lived, high-productivity species. This perception, usually believed to be inherent in the definition of steepness, is not substantiated by the very definition and, hence, theoretically is wrong. Perception 2 is that h and the compensation ratio increase with longevity and are highest in long-lived, low-productivity species; this perception may occur when the relationships between natural mortality and other LRLHTs are strong, and is most likely correct. Perception 3 is that h and the compensation ratio are independent of LRLHTs; this perception may be caused by the lack of the relationships between natural mortality and other LRLHTs, and is a distortion of perception 2.

Keywords: conflicting perceptions, density-dependent recruitment, life-history traits, longevity

Introduction

Contemporary fisheries management ideally relies on two alternative, interconvertible stock–recruit parameters measuring the strength of density-dependent recruitment (recruitment compensation). First is steepness, which is the ratio of (i) the unexploited recruitment produced by 20% of the unexploited parental stock to (ii) the unexploited recruitment produced by the entire unexploited parental stock (Mace and Doonan, 1988; Francis, 1992). Second is the Goodyear recruitment compensation ratio (Goodyear, 1980), hereinafter referred to as compensation ratio; this parameter has also been called maximum lifetime reproductive rate (Myers *et al.*, 1999, 2002) and maximum recruits per recruit (Goodwin *et al.*, 2006) at low spawner abundance. The terms density-dependent recruitment, recruitment compensation, and compensatory recruitment are herein used interchangeably to refer to steepness, the compensation ratio, or both.

The compensation ratio in its strict sense is the change in egg-to-recruit mortality when a stock is reduced from an unfished level to a near-zero level (Walters and Martell, 2004; van Poorten *et al.*, 2018). The change in question may result from mechanisms such as food supply, competition among juveniles, juvenile predation, cannibalism, and reduced abundance through factors like fishing. C. Walters (pers. comm.) holds that no relationships exist between the compensation ratio thus defined and the usual adult life-history traits such as absolute fecundity, natural mortality, and longevity [however, through this opinion, the alleged impact of fishing on the compensation ratio is *ipso facto* cancelled if it is agreed that (i) fishing deals with the recruited, adult stages; (ii) fishing truncates the age and size structures and contributes to reducing stock abundance and maximum age; and (iii) fishing can induce density-dependent fecundity and, perhaps, density-dependent natural mortality]. However, under Walters and Martell's (2004) and van

Poorten *et al.*'s (2018) definition of the compensation ratio, higher recruitment compensation can be expected for some of the long-lived demersal species whose juveniles can hide more efficiently from predation risk than can juveniles of small pelagic fish that are at high risk no matter how they behave (C. Walters, pers. comm.). Studies that so far calculated steepness (using information-generating equations described below) by incorporating some input requirements of the abovementioned definition of the compensation ratio include Mangel *et al.* (2010), Simon *et al.* (2012), Brodziak *et al.* (2015), and Kai and Fujinami (2018), but, overall, the data requirements on the temporal variation in food density, the feeding behaviour, and the dynamics of pre-recruited stages for calculating the compensation ratio as defined by Walters and Martell (2004) and van Poorten *et al.* (2018) may be seldom available for most exploited populations.

Perhaps due to the paucity in the data needed to calculate the compensation ratio based on the feeding ecology and the dynamics of early life stages, stock–recruit model outputs of annual spawning stock biomass and recruitment as well as the unfished spawning biomass per-recruit (computed using annual vital rates) have been the basis for obtaining a snapshot of the compensation ratio as defined by Walters and Martell (2004) and van Poorten *et al.* (2018). Thus, the compensation ratio has often been calculated as the unfished spawning biomass per-recruit multiplied by the slope at the origin of a stock–recruit curve; the slope in question usually refers to annual recruitment and has been called maximum annual recruit production (e.g. Shepherd, 1982; Goodwin *et al.*, 2006) and an indicator of the compensatory reserve (Rose *et al.*, 2001). This article is mainly based on the compensation ratio thus calculated because such a parameter has been widely used (e.g. Myers *et al.*, 2002; Goodwin *et al.*, 2006; Munyandorero, 2020).

Compensation ratio and steepness have been used in two ways. First, compensation ratio and steepness were substituted for the traditional parameters of stock–recruit relationships (SRRs) in stock assessment and simulation models of exploited population dynamics (e.g. Martell *et al.*, 2008a; Allen *et al.*, 2013; Wiedenmann *et al.*, 2013; Methot *et al.*, 2019). Second, steepness was expressed as functions of the compensation ratio for developing informative prior distributions of steepness (e.g. Myers *et al.*, 2002; Mangel *et al.*, 2010; Munyandorero, 2020). This is the reason why such equations are herein referred to as information-generating equations.

Unfortunately, studies that used information-generating equations yielded results or were the basis of postulates supporting differing perceptions on the life-history covariates of recruitment compensation. The simultaneous validity of those perceptions may be questionable, but each perception appears to have instilled a sense of belief and reasoning which, in turn, have influenced analysis setups, especially in simulation testing models, depending on the schools of thought researchers belonged to. For example, Coggins *et al.* (2007, p. 200 and Table 1) assumed that recruitment compensation was strongest in long-lived species based on meta-analysis results in Myers *et al.* (1999) and Goodwin *et al.* (2006). Similarly, Allen *et al.* (2009, p. 262 and Table 1) assigned a high compensation ratio of 30 to Murray cod (*Maccullochella peelii peelii*) and Gwinn and Allen (2010, p. 628) assigned a moderate compensation ratio of 15 to largemouth bass (*Micropterus salmoides*), considering that these species were, respectively, long-lived and short-lived predators. In contrast, Wiedenmann *et al.* (2013, Table 2) also made the use of Myers

et al.'s (1999) results but were rather consistent with a perception advocated by Mangel *et al.* (2010) according to which recruitment compensation would be strongest in short-lived species.

The first objective of this study is to point out that the literature that relied on information-generating equations has produced results and theories that convey three conflicting perceptions on the life-history covariates of recruitment compensation. That is, recruitment compensation (i) was postulated to be increasing with life-history variables negatively related to longevity (e.g. Mangel *et al.*, 2010, p. 92) and, hence, would be expected to be highest in short-lived, high-productivity species; (ii) was found to be increasing with life-history variables positively related to longevity and to be highest in long-lived, low-productivity species (e.g. Goodwin *et al.*, 2006, Figure 4c and d); and (iii) was found to be independent of life-history traits related to longevity (Shertzer and Conn, 2012) and, hence, would be similar across life histories. Furthermore, if one contemplates that only one perception must be correct and that the other two perceptions are questionable, then the second objective of the study is to comment on the perceptions in question to elucidate the reasons why a perception is likely correct or otherwise is wrong or is distorted. Before documenting and commenting on those perceptions, the commonly used expressions of steepness in relation to the compensation ratio and their properties are presented. These properties are meant to be preliminaries for gaining insight of the comments made and, especially, to show that adult natural mortality is the main determinant of compensatory recruitment inferred from information-generating equations.

Equations of steepness as functions of the compensation ratio

The unfished spawning biomass per-recruit Φ_0 (see Table 1 for other notations used) is considered to have been calculated using appropriate age- or stage-structured life-history variables. The maximum annual recruit production a must have been estimated using annual time series of spawning stock biomass and recruits generated with stock assessment models, independently of SRRs parameterized in terms of steepness (h) or the compensation ratio (a.k.a. lifetime reproductive rate) calculated as a multiplied by Φ_0 . It should be noted that the parameter a represents the number of recruits per unit of spawning stock biomass and is a proxy of egg-to-recruit survival for the near-zero number of eggs produced. It should also be noted that the compensation ratio is the ratio of (i) maximum annual recruit production at near-zero spawning stock biomass (a) to (ii) the annual recruit production at the unfished spawning stock biomass ($1/\Phi_0$). The quantity $1/\Phi_0$ is the slope of the unfished replacement line of a stock–recruit curve and is a proxy of egg-to-recruit survival for an unfished state.

For two-parameter SRRs, steepness as functions of the compensation ratio can be generically written as $h = f(a\Phi_0)$. Such functions have been often expanded on the Beverton–Holt SRR (BH–SRR) of the form $R = aS/(1 + bS)$ and on the Ricker SRR (R–SRR) of the form $R = aS \exp(-bS)$, where R is recruitment, S is spawning stock biomass, and a and b are parameters (e.g. Myers *et al.*, 2002; Brooks and Powers, 2007). The functions are:

$$h = f(a\Phi_0) = \frac{a\Phi_0}{4 + a\Phi_0} \text{ for the BH – SRR,} \quad (1)$$

and

Table 1. Notations used in this article.

Symbols	Description
M	Adult constant natural mortality, herein assumed to be similar for all ages
a^*	Slope at the origin of a stock–recruit curve, also called maximum annual recruit production if the parental stock is in mass unit and the recruitment is in number— a is used along with the parameter b in various stock–recruit relationships
Φ_0^*	The unfished spawning biomass per-recruit
R	Recruitment
S	Spawning stock biomass
h	Parameter of a stock–recruit relationship
n	A shape parameter of a three-parameter stock–recruit relationship
B	Total stock biomass (= spawning stock biomass) in Mangel <i>et al.</i> 's (2010, 2013) production models
N	Total stock size in number (= number of spawners) in Kindsvater <i>et al.</i> 's (2016) production model
τ	Index for time
F	Fishing mortality
t	Index for age
T_{\max}	Maximum observed age
T_{∞}	An age greater than T_{\max}
l_t	Survivorship (i.e. the probability that a recruit will survive to age t) in the absence of fishing
Ψ_t	The probability of maturation at age t multiplied by the weight at age t
E_0	Total number of eggs produced at the unfished state
E_{low}	The low number of total eggs produced (typically, this number approaches zero)
M_0	Egg-to-recruit total mortality rate for E_0
M_{low}	Egg-to-recruit total mortality rate for E_{low}
R_{low}	Recruitment produced by E_{low}
R_0	Unfished recruitment produced by E_0
ϵ_t	Total number of eggs produced at age t
S_0	Unfished spawning stock biomass
r_0	Unfished recruitment produced by S_0
r_0^*	Unfished recruitment produced by 20% of S_0
K	Growth rate for following the von Bertalanffy growth function
L_{∞}	Asymptotic length following the von Bertalanffy growth function

*The compensation ratio is given by a multiplied by Φ_0 .

$$h = f(a\Phi_0) = 0.2(a\Phi_0)^{0.8} \text{ for the R-SRR.} \quad (2)$$

A generic function for three-parameter SRRs (Punt and Cope, 2019) can be represented by $h = f(a\Phi_0, n)$, where n is the shape parameter. For the original Shepherd SRR (S-SRR) as written by Mangel *et al.* (2013), i.e. $R = aS/[1 + (bS)^{1/n}]$,

$$h = f(a\Phi_0, n) = \frac{0.2a\Phi_0}{1 + 0.2^{1/n}(a\Phi_0 - 1)}. \quad (3)$$

When n is particularly equal to 1, (3) reduces to (1).

In Mangel *et al.* (2013), the steepness equation expanding on their production model, where recruitment is governed by the S-SRR (B1.1 and B1.2), is an analogue of (3). In fact, in (B1.2), the ratio $1/M$ (M is natural mortality), which has usually been used to measure the mean life-span of a species (Mangel, 1996), corresponds to Φ_0 inherent in their production model

(Munyandorero, 2015). Throughout this article, the ratio $1/M$ or $(1-r)/M$ in (1)–(3) (r is the fraction of females in the population), as shown in (B1.2) and (B1.5)–(B1.6) (Box 1), should be thought of as Φ_0 , keeping in mind that such an Φ_0 is inversely related to natural mortality (see Box 1 about when that ratio would be meaningful in terms of mass unit per-recruit). The product of a and $1/M$ or $(1-r)/M$ gives what Mangel *et al.* (2010) call the Beverton number, and these authors noted that that number is exactly the compensation ratio.

Properties of steepness as functions of the compensation ratio

The functions $h = f(a\Phi_0)$ and $h = f(a\Phi_0, n)$, particularly (1)–(3), can be described as information-generating equations because they have often been used to construct informative prior distributions of h and the compensation ratio (e.g. Myers *et al.*, 2002; Mangel *et al.*, 2010; Munyandorero, 2020). Information-generating equations show that:

- (i) For a population characterized by a set of life-history variables, all candidate parametric SRRs involve a unique compensation ratio ($a\Phi_0$). In those SRRs, the value of $a\Phi_0$ must be >1 for a population to persist even in the absence of fishing (Martell *et al.*, 2008a). Thus, h must be >0.2 . For the BH-SRR, h is always <1 because in (1), the numerator is smaller than the denominator; setting h to 1 (i.e. $4 = 0$) would be a fallacy.
- (ii) The dependent variable h and its predictor $a\Phi_0$ (both of which measure density-dependent recruitment) are predicted and confounded by the density-independent parameter a .
- (iii) For three-parameter SRRs, the parameter n also predicts h .

According to Mangel *et al.* (2013), the functions $h = f(a\Phi_0)$ and $h = f(a\Phi_0, n)$ help in understanding the steepness connection with life-history traits incorporated into Φ_0 , so they can indeed be suitable for investigating how longevity-related life-history traits (LRLHTs) covary with steepness. At first, h is a monotonically increasing, saturating function of the compensation ratio for the BH-SRR and a non-saturating function of the compensation ratio for the R-SRR (Figure 1). This property is fundamental. It has three major corollaries: (i) that steepness and the compensation ratio vary similarly with the same variables; (ii) that, at stock level, density-dependent factors inducing increase in compensatory response elevate steepness; and (iii) that populations whose LRLHTs are conducive to high compensation ratios have high steepness.

Upon expanding the expression of the compensation ratio, it is possible to gain insight on the connection between steepness and LRLHTs and, specifically, to note that adult natural mortality likely is the main predictor of the compensation ratio (Box 2).

On the life-history covariates of steepness and compensation ratio

There is a wealth of literature describing empirical and theorized relationships (i) between steepness h or the compensation ratio and maximum annual recruit production a (e.g. Goodwin *et al.*, 2006; Mangel *et al.*, 2010, 2013; Kindsvater *et al.*, 2016; Munyandorero, 2020) and (ii) between h or the compensation

Box 1. Mangel *et al.*'s production model variants and their associated life-history traits

The production model of Mangel *et al.* (2013) is a differential equation describing the biomass change at time τ as follows:

$$\frac{dB}{d\tau} = \frac{aB}{1 + (bB)^{1/n}} - (M + F)B, \tag{B1.1}$$

where B is the total biomass, M is the natural mortality, and F is the fishing mortality; a , b , and n are parameters of the Shepherd SRR (S-SRR), $\frac{aB}{1 + (bB)^{1/n}}$. Mangel *et al.* (2013) showed that the stock–recruit steepness parameter (h) expanding on (B1.1) is

$$h = \frac{0.2a\frac{1}{M}}{1 + 0.2^{1/n}\left(a\frac{1}{M} - 1\right)}. \tag{B1.2}$$

The S-SRR reduces to the BH-SRR when $n = 1$.

Mangel *et al.* (2010) used a model like (B1.1), but the recruitment was described by the BH-SRR based on females:

$$\frac{dB}{d\tau} = \frac{a(1 - r)B}{1 + b(1 - r)B} - (M + F)B, \tag{B1.3}$$

where a and b are parameters and r is the fraction of females in the population. Kindsvater *et al.* (2016) focused on the number (N) change at time τ as

$$\frac{dB}{d\tau} = \frac{aN}{1 + bN} - (M + F)N. \tag{B1.4}$$

The equations of h expanding on (B1.3) and (B1.4) are, respectively,

$$h = \frac{a\frac{(1 - r)}{M}}{4 + a\frac{(1 - r)}{M}} \tag{B1.5}$$

and

$$h = \frac{a\frac{1}{M}}{4 + a\frac{1}{M}}. \tag{B1.6}$$

It should be noted that (B1.6) is a reduced form of (B1.2) when $n = 1$.

Before Mangel *et al.*'s (2010, 2013) and Kindsvater *et al.*'s (2016) studies, Martell *et al.* (2008b) had integrated (B1.1) involving the BH-SRR and Martell and Walters (2008) had integrated (B1.4) to produce time-dynamics equations with the recruitment stage and the adult stage. The produced equations were indeed delay-difference (or stage-structured) models.

Munyanorero (2015) used a variety of delay-difference models to develop the composite (i.e. age-aggregated or stage-structured) yield per-recruit models and the related composite spawning stock per-recruit (CSSR) models. He showed that the ratio $1/M$ in (B1.2) and (B1.6) and the ratio $(1 - r)/M$ in (B1.5) are the unfished CSSR and are analogues of the unfished spawning stock biomass per-recruit calculated through age-structured models [the unfished CSSRs $1/M$ and $(1 - r)/M$ are not intuitive because they are not in mass units; they usually follow from the fact that both the parental stock, and recruits in a delay-difference model are in number or biomass. They would be in mass unit if the parental stock was in biomass and the recruits were in number but were associated with a mean weight w_r . In that case, the previous unfished CSSRs would become w_r/M and $(1 - r)w_r/M$. Therefore, in the context of SRRs used in (B1.1), (B1.3), and (B1.4), $(1 - r)M$ and M represent the slopes of the unfished replacement lines of the stock–recruit curves used in Mangel *et al.*'s production model variants.

ratio and LRLHTs, especially the unfished spawning biomass per-recruit Φ_0 and its arguments, i.e. growth, natural mortality, and reproduction rates (e.g. Goodwin *et al.*, 2006; Shertzer and Conn, 2012; Brodziak *et al.*, 2015; Munyanorero, 2020). In the previous literature, h has been often calculated using (1), whether Φ_0 was based on age- or stage-structured variables [the types of (1) involving stage-structured variables are (B1.5)–(B1.6)]. Regardless, those studies show three conflicting perceptions (henceforth called perceptions 1, 2, and 3) on how h and the compensation ratio vary with LRLHTs.

The expected patterns of steepness and the compensation ratio in relation to longevity (T_{\max}) are shown in Figure 2. The plots are constructed using (i) the compensation ratio values ranging from 1.01 to 200.01, by the step of 0.1, and (ii) 200 maximum ages T_{\max} from age 1 by the step of 0.025 year. Then, if need be for plotting purposes, M , Φ_0 , and a can be calculated, respectively, as $M = 1/T_{\max}$, $\Phi_0 = 0.0013T_{\max}^{3.77}$ (Goodwin *et al.*, 2006; the generation time is used as a proxy of T_{\max}), and $a = 4h/\Phi_0(1 - h)$. For Figure 2e and f, h and the compensation ratio are set, respectively, to the means of 0.75 and 12 in Shertzer and Conn (2012).

Box 2. Expanding the compensation ratio for gaining insight on its predictors

The connection of density-dependent recruitment with LRLHTs can be comprehended by expanding the expression of the compensation ratio such that

$$a\Phi_0 = a \sum_{t=0}^{T_{\infty}} l_t \Psi_t, \tag{B2.1}$$

where T_{∞} is an age greater than the maximum age (T_{\max}) of a species, l_t is the age-specific survivorship (i.e. the probability that a recruit will survive to age t) in the absence of fishing [$l_t = 1$ for $t = 0$ and $l_t = l_{t-1} \exp(-M)$ for $t > 0$; equivalently, $l_t = \exp(-Mt)$ for any age], and Ψ_t is the probability of maturation at age t multiplied by the weight at age t (itself a function of growth variables). $\Phi_0 = \sum_{t=0}^{T_{\infty}} l_t \Psi_t$ clearly is an incidence function where l_t (hence M) directly controls the reduction levels of a recruitment of size 1 (for which $l_t = 1$; for a recruiting age group, which is herein age 0, initializing the recruitment at 1 is equivalent to assuming that the survivorship at that age is 1) to successive ages. Therefore, via l_t , the compensation ratio is confounded with the cumulative, exponentially decrementing effects of M on a recruit during its lifetime in an unexploited population, l_t having a as global, outer weight and Ψ_t as age-specific, inner weight. Thus, the main predictor of the compensation ratio in information-generating equations appears to be M , keeping in mind that, for a given species, M and T_{\max} theoretically are inversely proportional ($MT_{\max} = 1$) and, across the continuum of life histories, vary inversely.

The previous arguments hold for the compensation ratio as defined in [Walters and Martell \(2004\)](#) and [van Poorten et al. \(2018\)](#), i.e. the compensation ratio is equal to $e^{(M_0 - M_{\text{low}})}$ where M_0 is egg-to-recruit total mortality rate for the unfisher state, E_0 , and M_{low} is egg-to-recruit total mortality rate for the near-zero number of eggs produced, E_{low} (i.e. the parental stock in terms of total eggs produced is severely depleted). In fact, with reference to the BH-SRR geometry, for example, $e^{(M_0 - M_{\text{low}})}$ can be rewritten in the form of the compensation ratio used in this article, considering (i) that the egg-to-recruit survival components (e.g. survivals from starvation, predation, diseases) for E_{low} are lumped into the ratio $R_{\text{low}}/E_{\text{low}}$:

$$e^{-M_{\text{low}}} = \frac{R_{\text{low}}}{E_{\text{low}}} = a \text{ (i.e. the slope at the origin of the stock-recruit curve),} \tag{B2.2}$$

where R_{low} is recruitment at E_{low} and (ii) that the egg-to-recruit survival components for E_0 are lumped into the ratio R_0/E_0 :

$$e^{-M_0} = \frac{R_0}{E_0} = \frac{1}{\Phi_0} \text{ (i.e. the slope of the unfisher replacement line of the stock-recruit curve),} \tag{B2.3}$$

where R_0 is recruitment at E_0 and Φ_0 is the unfisher number of eggs per-recruit. Here, Φ_0 can be expanded as $\Phi_0 = \sum_{t=0}^{T_{\infty}} l_t \epsilon_t$, where ϵ_t is total eggs produced at age t ; l_t follows from M applicable to the recruited females and can be calculated as above. Thus, in the context of the BH-SRR geometry, the compensation ratio in [Walters and Martell \(2004\)](#) and [van Poorten et al. \(2018\)](#), $e^{(M_0 - M_{\text{low}})}$, can be lumped into the ratio of (B2.2)–(B2.3) (i.e. the ratio of recruit production at the near-zero number of eggs produced to recruit production in the unfisher state). Because M_0 is equal to $-\ln(R_0/E_0) = \ln(\Phi_0)$, it is a function of M endured by spawners among post-recruits in the unfisher state (Φ_0 is basically predicted by both M and ϵ_t). Because the compensation ratio is predicted by M through Φ_0 , steepness is also predicted by M .

Perception 1

Perception 1 was advocated by [Mangel et al. \(2010, p. 92, 2013, p. 935\)](#) and [Kindsvater et al. \(2016, Table 1 and p. 5 of Appendix S1\)](#), who postulated that h increases as the maximum annual recruit production (a) increases ([Figure 2a and b](#)). The postulate “ h increases with a ” was based on theoretical analyses employing the following information-generating equations: equation (13) in [Mangel et al. \(2010\)](#), equations (6) and (11) in [Mangel et al. \(2013\)](#), and equation (S1.18) in [Kindsvater et al. \(2016\)](#). It concurs with the comment by [Shertzer and Conn \(2012\)](#): “A higher value of steepness translates into higher expected productivity, particularly at low levels of spawning stock biomass ([Figure 1](#))”. Under this perception, SRRs of short-lived, highly productive species [characterized by high M , a , and unexploited number of recruits r_0 (produced by the unfisher spawning stock biomass S_0), small Φ_0 , as well as short reproductive span and generation time] would have higher steepness.

Perception 1 has been a paradigm often used to guide analyses of, or to characterize beliefs about, stocks’ productivity and

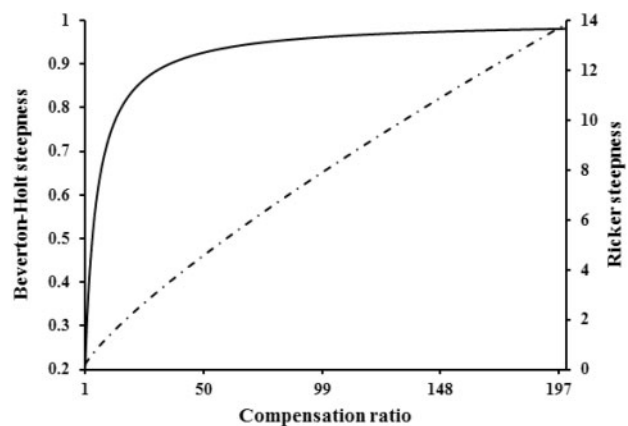


Figure 1. The variations of steepness as functions of the compensation ratio. These functions are given by (1) for the Beverton–Holt stock–recruit relationship (solid line) and by (2) for the Ricker stock–recruit relationship (dash-dotted line).

resilience to fishing. That is, in simulation testing analyses in particular, SRRs of short-lived, highly productive species have been *a priori* assumed to have high steepness and the opposite has been assumed for long-lived, low-productivity species; SRRs of medium-lived and medium-productivity species have been assigned some intermediate steepness values (e.g. [Wiedenmann et al., 2013](#), Table 2; [Wetzel and Punt, 2015](#), Table 1, 2016, Table 2). Before these studies, [Myers et al. \(2002, Figure 1\)](#) appear to have been contradicted by their results for the species of domain 1 (short-lived and early-maturing species) and to have faced the dilemma of treating steepness of the population of ayu *Plecoglossus altivelis* from Lake Biwa, Japan, as an “outlier” but “very reliable” estimate. This dilemma suggests their bias towards perception 1.

Perception 2

Empirical and simulation-based relationships between the compensation ratio or steepness (h) and LRLHTs indicated that h and the compensation ratio tended to be highest in long-lived, low-productivity species (characterized by low M , a , and r_0 , high Φ_0 , as well as long reproductive span and generation time), a pattern

herein termed perception 2 ([Figure 2c and d](#)). Examples of empirical results conveying perception 2 can be found in [Rose et al. \(2001, pp. 300–301\)](#), [Myers et al. \(2002, pp. 356–360\)](#), [Goodwin et al. \(2006, Figure 4c and d\)](#), and [Forrest et al. \(2010, Figure 8c and d\)](#).

On the other hand, simulation models that were developed to examine the effects of contrasting life histories and of changing life-history parameters (sensitivity analyses) on the calculations of h and the compensation ratio indicated that:

- (i) Tendency statistics of h increased with asymptotic length ([Brodziak et al., 2015, Figure 3a](#); [Cortés, 2016, Tables 1 and 2](#)) or, equivalently, decreased as M was increased ([Brodziak et al., 2015, Figure 5c](#); [Munyanadorero, 2020](#)).
- (ii) h decreased with increased unfished replacement lines of an SRR curve, i.e. when Φ_0 decreased ([Brooks, 2013, Figure 3](#); [Munyanadorero, 2020](#)).

[Hillary et al. \(2012, p. 73\)](#) also noted that the compensation ratio correlates positively with Φ_0 , but they did not indicate whether their observation was based on empirical or simulation analyses.

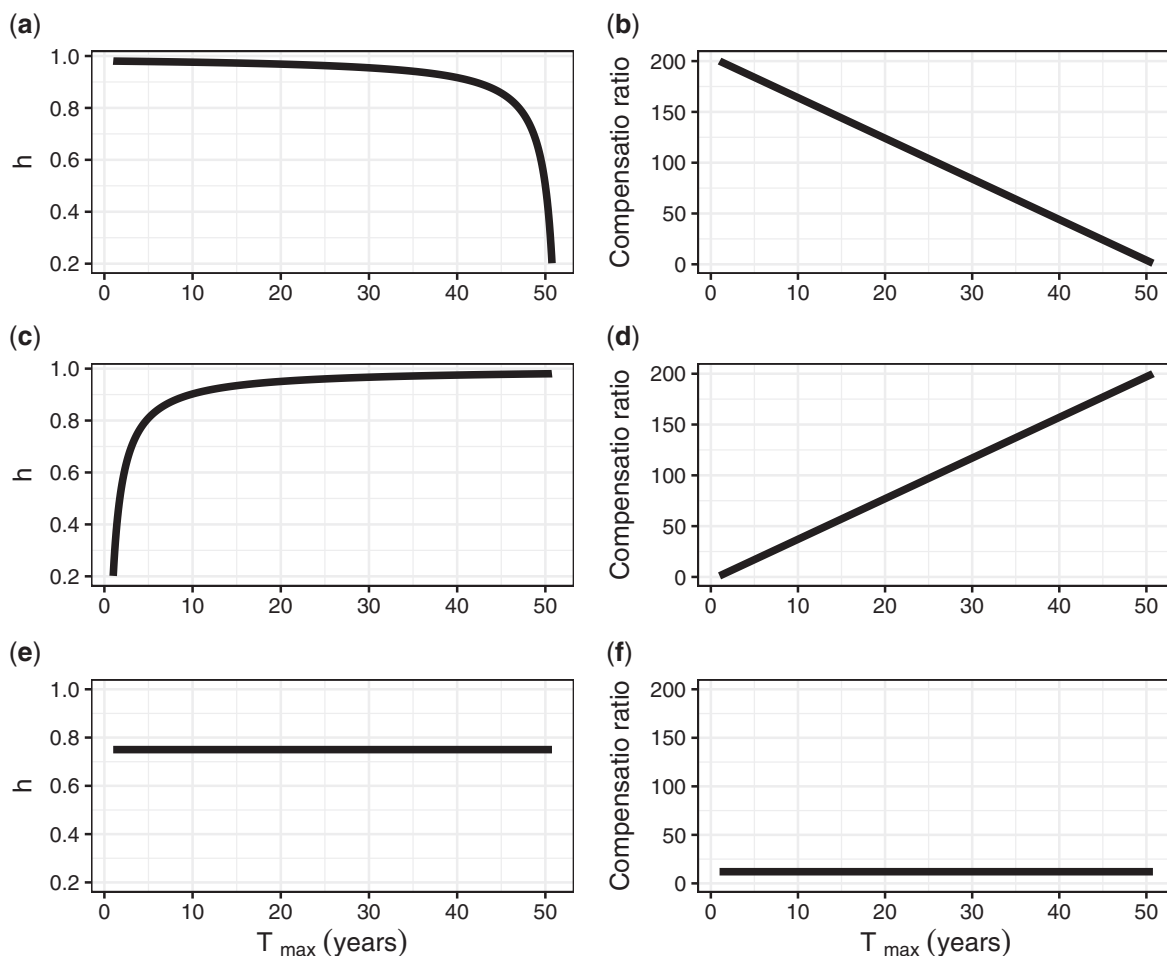


Figure 2. Schematic patterns of the BH-SRR steepness (h , left panels) and compensation ratio (right panels) in relation to longevity (T_{max}) according to (a and b) perception 1, (c and d) perception 2, and (e and f) perception 3. Note: perception 1 usually follows from the relationship between h and the parameter a (e.g. [Mangel et al., 2010](#)), which is theoretically correlated negatively with T_{max} , and perceptions 2 (e.g. [Goodwin et al. 2006](#); [Brodziak et al., 2015](#)) and 3 (e.g. [Goodwin et al., 2006](#); [Shertzer and Conn, 2012](#)) usually follow from the relationships between h or the compensation ratio and the parameters positively or negatively related to T_{max} .

In fine, perception 2 is opposite of perception 1 (Figure 2a–d), conveying interpretations that contrast with those of Shertzer and Conn (2012) through their Figure 1. With empirical relationships, however, estimates of h for medium-lived and large-bodied species can be higher than estimates of h for long-lived and medium-bodied species, but short-lived species have the lowest steepness (e.g. Thorson *et al.*, 2015, Figure 1a).

Based on meta-analysis results in Myers *et al.* (1999) and Goodwin *et al.* (2006), Coggins *et al.* (2007, p. 200 and Table 1), Allen *et al.* (2013, Table 1), and Gwinn *et al.* (2015, pp. 265–266 and Table 1) adopted perception 2 by assigning smaller compensation ratios to short-lived, high-productivity species and higher compensation ratios to long-lived, low-productivity species. Input values in equations (8)–(13) of Thorson *et al.* (2015) were also taken from Myers *et al.* (1999) and conform to this paradigm.

Perception 3

Perception 3 (Figure 2e and f) suggests that steepness (h) would be independent of LRLHTs (Shertzer and Conn, 2012, pp. 39 and 46–48) or that LRLHTs would explain the compensation ratio (hence h) very little, except for Φ_0 , with which the compensation ratio correlates positively (Goodwin *et al.*, 2006). There were also no relationships between the compensation ratio or h and LRLHTs in Forrest (2008) as well as between h and LRLHTs in Wiff *et al.* (2018).

It is not clear if, following perception 3, a single value or probability distribution of steepness and compensation ratio should be assigned to all exploited populations worldwide. The works of Shertzer and Conn (2012) and Wiff *et al.* (2018) were developed for generating prior distributions and tendency statistics of steepness applicable in stock assessments of, for the former study, the southeastern United States’ demersal fishes (Atlantic, Caribbean, and Gulf of Mexico waters) and, for the latter, fish resources in Chilean waters.

Comments on perceptions 1–3

One may be wondering whether the various relationships (positive, negative, and none) between h or the compensation ratio and life-history variables, as prescribed or obtained using information-generating equations, are simultaneously correct.

On perception 1

The postulate “ h increases as a increases” or a comment favouring it (i.e. steepness by definition is positively correlated with the maximum annual recruit production in any case where recruitment monotonically increases with spawning capacity beyond 20% of the virgin level) was deemed to be a truism (*sensu* a reviewer). Thus, the postulate in question and the perception it conveys (perception 1, i.e. steepness and the compensation ratio are highest in short-lived species) may be widely accepted, even via applications not explicitly using information-generating equations (e.g. Porch and Laretta, 2016), in which high steepness was perceived as an indicator of high productivity at low spawning stock biomass. Yet that postulate fundamentally departs from the recruitment compensation expectations of life-history theory of Rose *et al.* (2001), through which these authors proposed and demonstrated empirically a pattern of density-dependent recruitment consistent with perception 2 (i.e. steepness was highest in long-lived species,

therein aggregated into an endpoint of periodic life-history strategy). Moreover, in comparison with the postulate under review, other empirical and simulation-based relationships are quite otherwise (e.g. Goodwin *et al.*, 2006, Figure 3c–d; Munyandorero, 2020, Table 3).

Because the recruitment compensation expectations of life-history theory and other empirical and simulation-based evidence on recruitment compensation challenge the postulate “ h increases as a increases” (conceptually seen as inherent in the definition of steepness according to its advocates), the focus herein is on determining, using first principles of the definition of steepness, whether that postulate is substantiated by the very definition and, hence, whether perception 1 theoretically is correct or wrong. To start, consider the BH-SRR of the form $R = aS/(1 + bS)$. It is also considered that, for a given stock, the previous equation for the BH-SRR provided a trustworthy fit to the stock–recruit pairs generated with an assessment model conditional on a set of fishery data and life-history parameters. Under a stable age-structure, the definition of steepness involves Φ_0 , the recruitment r_0 produced by the unfished spawning stock biomass S_0 ($S_0 = r_0\Phi_0$), and the recruitment r_0^* produced by 20% of S_0 (Francis, 1992; Haddon, 2001)—in the context of Mangel *et al.*’s production model variants (Box 1), it is worth keeping in mind that $\Phi_0 = 1/M$ or $\Phi_0 = (1 - r)/M$ because both the parental stock and recruits are in number or in biomass (Munyandorero, 2015). The values of r_0 and r_0^* then can be predicted by

$$r_0 = \frac{aS_0}{1 + bS_0} \iff r_0 = \frac{(a\Phi_0 - 1)}{b\Phi_0}, \tag{4.1}$$

$$r_0^* = \frac{0.2aS_0}{1 + 0.2bS_0}. \tag{4.2}$$

For the abovementioned form of the BH-SRR, steepness h is, by definition, given by the ratio $\frac{r_0^*}{r_0}$ which simplifies as

$$h = \frac{0.2(1 + bS_0)}{1 + 0.2bS_0} = \frac{0.2(1 + br_0\Phi_0)}{1 + 0.2br_0\Phi_0} = \frac{a\Phi_0}{4 + a\Phi_0}. \tag{5a}$$

Likewise, for the R-SRR $R = aS \exp(-bS)$ with $r_0 = \frac{\ln(a\Phi_0)}{b\Phi_0}$ and $r_0^* = 0.2aS_0 \exp(-0.2bS_0)$ and for the S-SRR $R = aS/[1 + (bS)^{1/n}]$ with $r_0 = \frac{(a\Phi_0 - 1)^n}{b\Phi_0}$ and $r_0^* = \frac{0.2aS_0}{1 + (0.2bS_0)^{1/n}}$, the equations defining steepness simplify, respectively, as

$$h = \frac{0.2e^{-0.2bS_0}}{e^{-bS_0}} = \frac{0.2e^{-0.2br_0\Phi_0}}{e^{-br_0\Phi_0}} = 0.2(a\Phi_0)^{0.8}, \tag{5b}$$

$$h = \frac{0.2 \left[1 + (bS_0)^{\frac{1}{n}} \right]}{1 + (0.2 bS_0)^{\frac{1}{n}}} = \frac{0.2 \left[1 + (br_0\Phi_0)^{\frac{1}{n}} \right]}{1 + (0.2 br_0\Phi_0)^{\frac{1}{n}}} = \frac{0.2a\Phi_0}{1 + 0.2^{\frac{1}{n}}(a\Phi_0 - 1)}. \tag{5c}$$

In (5a)–(5c), the quantity $bS_0 = br_0\Phi_0$ is a simple transformation of the compensation ratio: $bS_0 = a\Phi_0 - 1$, $bS_0 = \ln(a\Phi_0)$, and $bS_0 = (a\Phi_0 - 1)^n$ for the BH-SRR, R-SRR, and S-SRR, respectively. It follows that bS_0 is also a measure of density-dependent recruitment, which is positively correlated perfectly

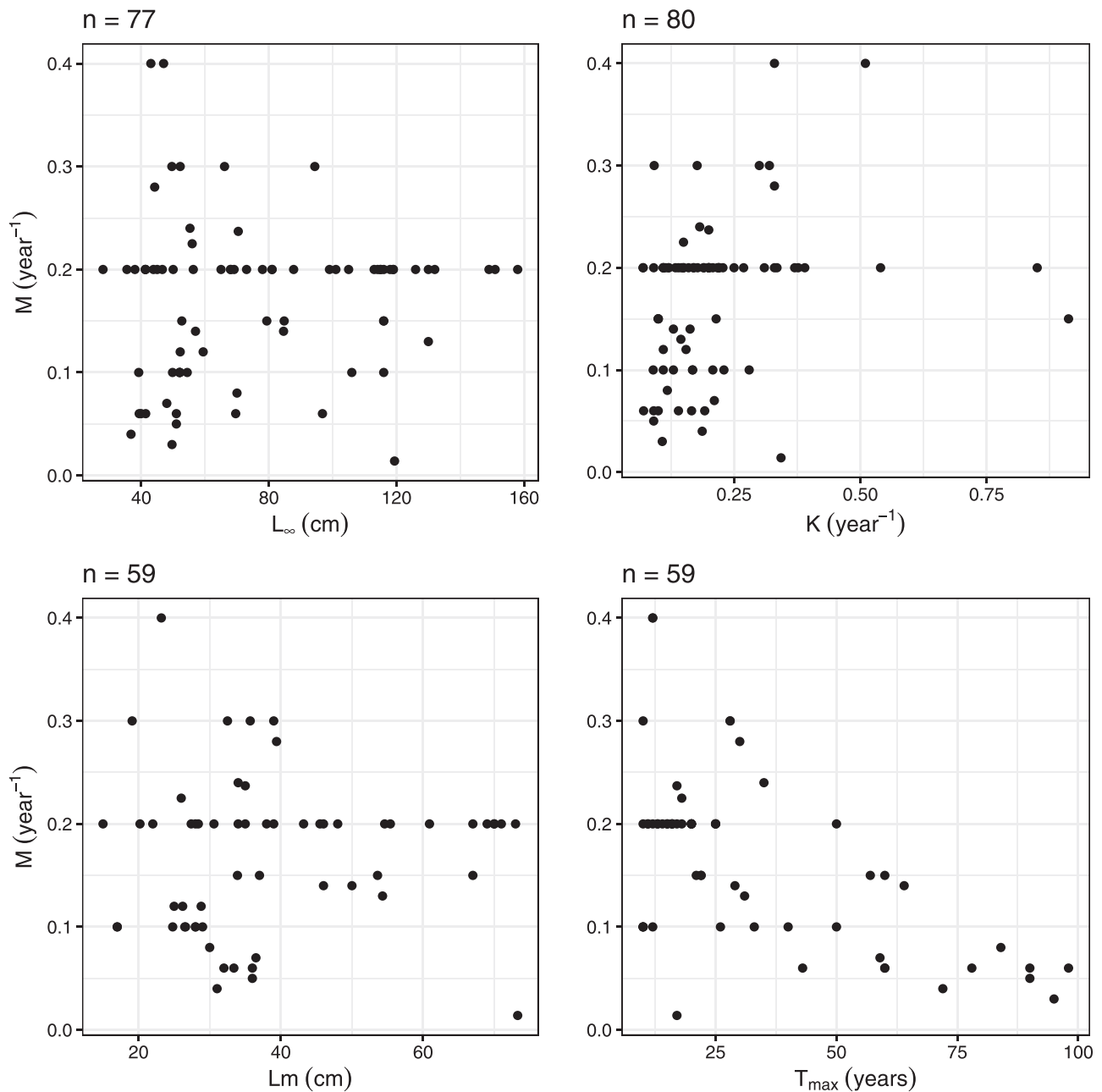


Figure 3. Scatterplots of natural mortality M against asymptotic length L_∞ , growth rate K , size at 50% maturity L_m , and observed maximum age T_{max} for demersal marine fishes analysed by Shertzer and Conn (2012, Table 1) [see also SEDAR 24-AW-06 available at <http://sedarweb.org/docs/wpapers/SEDAR24-AW06.pdf>; these results data consisted of a subset of a dataset used by Rose *et al.* (2001)]. Except for M , L_∞ , K , L_m , and T_{max} were not available in the metadata used by Shertzer and Conn (2012); the latter four parameters are assembled from various sources. Shertzer and Conn's (2012) metadata comprises 94 stocks; the value of n shown in the plots is the number of populations for which a parameter was obtain.

with $a\Phi_0$. Thus, bS_0 and $a\Phi_0$ must correlate similarly with a . Like for $a\Phi_0$, the quantity bS_0 and a are not necessarily independent, but stating that bS_0 increases with a would be equivalent to the postulate “ h increases as a increases”.

Equation (5a) shows the following three properties of the definition of steepness and helps in making various observations [such properties and observations hold for (5b) and (5c) as well as for equations defining steepness expanding on any parametric SRRs, such as those found in Punt and Cope (2019)]:

- (i) The far-right expression of h in (5a) is (1) but, importantly, is equivalent to the first two expressions of h in (5a) and, as such, is itself the definition of steepness.
- (ii) The far-right expression of h in (5a) may let one think that steepness is positively related to a , but this would not be the correct interpretation because steepness cannot be so by leaving Φ_0 out: steepness always involves the product of a and Φ_0 (Brooks and Powers, 2007), which is the compensation ratio. So, as detailed in the second and third sections

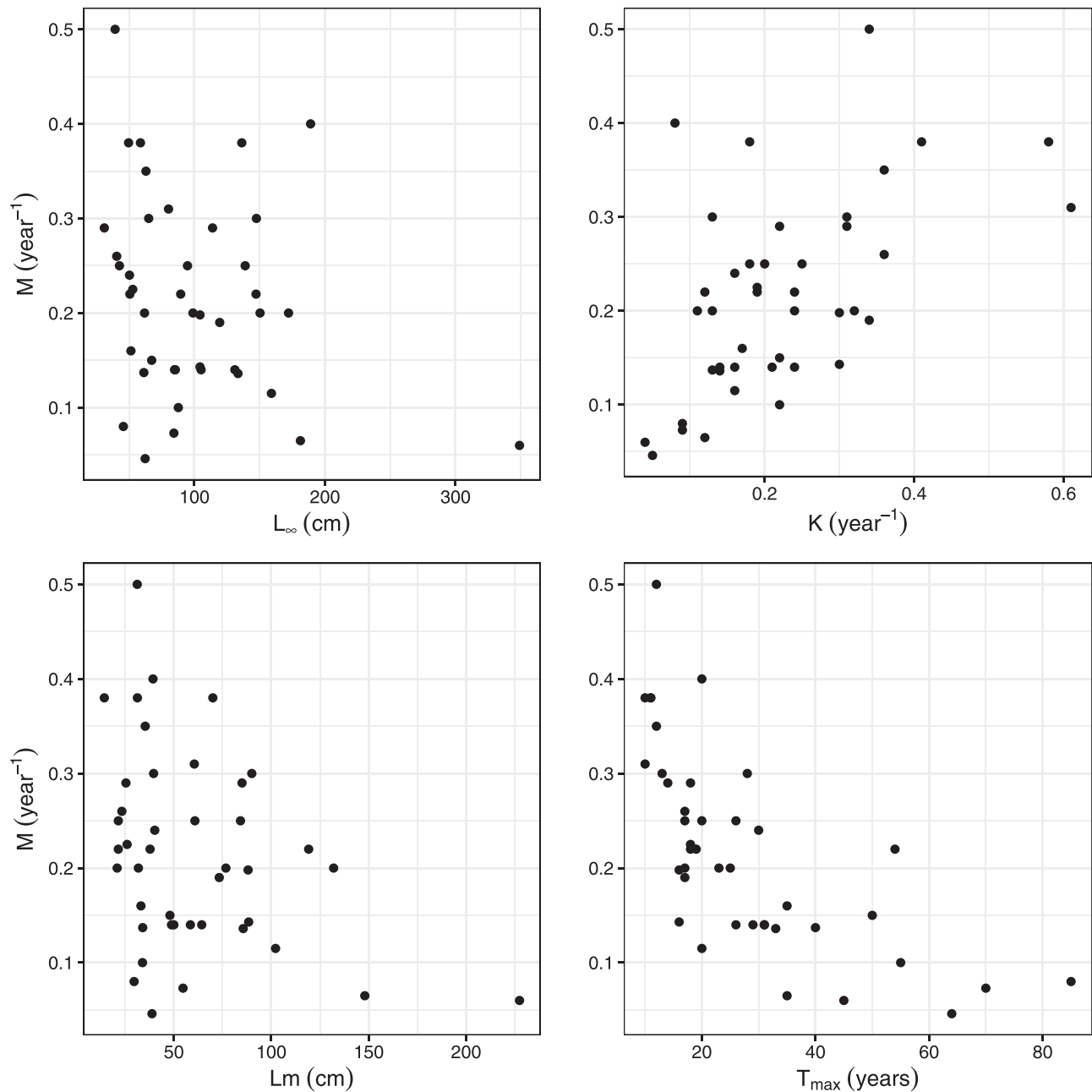


Figure 4. Scatterplots of natural mortality M against asymptotic length L_{∞} , growth rate K , size at 50% maturity L_m , and observed maximum age T_{\max} in supplementary data of Wiff *et al.* (2018). T_{\max} was not provided in those data; they are taken from Munyandorero (2015) and FishBase (www.fishbase.org/), but none was available for White marlin (*Tetrapturus albidus*).

above, steepness simply is a function of $a\Phi_0$ and not of a alone. This property that directly emerges from the definition of steepness rules out increase in steepness with $a\Phi_0$ (Figure 1). Thus, in the context of information-generating equations and to be consistent with the definition of steepness, one must say that steepness increases as the compensation ratio increases and that, for the BH-SRR, steepness approaches 1 when the compensation ratio approaches infinity. In this context, if stock-specific density-dependent factors induce increase in the compensatory response, then steepness increases; for an among-stock comparison, stocks

with the highest compensation ratios have the highest steepness.

- (iii) For the postulate “ h increases as a increases” to be true using the far-right expression of h in (5a), Φ_0 must, whatever the value of a , be a constant or, owing to a less restrictive assumption, Φ_0 and a must be independent of each other. Under such a circumstance, the postulate “ h increases as a increases” would rather be an exception to the rule (i.e. h increases with $a\Phi_0$), but constraining Φ_0 to a constant for any value of a , or assuming that Φ_0 and a are independent, would be unrealistic, nay wrong. Nor would it be supported

by empirical relationships: the parameter a has a strong negative correlation with Φ_0 (Denney *et al.*, 2002, Appendix A; Goodwin *et al.*, 2006, Figure a and b; Munyandorero, 2020, Table 3).

On perception 2

For perception 2, high steepness and compensation ratio for long-lived species has been observed in many studies. According to Rose *et al.* (2001, pp. 209–300) and Goodwin *et al.* (2006, p. 499), the patterns of steepness and compensation ratio seen across a range of fish life-spans are mediated by life-history traits. Most of those traits (Φ_0 , reproductive span, generation time, asymptotic size, etc.) are functions of or correlate with natural mortality M —the explanatory power of M on those traits or the correlations of M with them becomes stronger as, for each population, MT_{\max} approaches 1.

Although short-lived species tend to have higher maximum annual recruit production, M decrements drastically their population sizes and realized Φ_0 during a few early years of their shorter life spans (Munyandorero, 2020), when all vital rates (growth, reproduction, survival) appear to be completed. The resulting low compensation ratio suggests that compensatory recruitment processes may be beginning in early stages of life, when recruitment density-independent processes would be still operating. In contrast, long-lived species may have distinct life-history stages during which the previous processes may be overlapping very little. That way, perception 2 is consistent with the life-history continuum theory, in which weak density-dependent recruitment is typical of short-lived, “highly reproductive species”, while strong density-dependent recruitment characterizes long-lived, “survivor species” (Rose *et al.*, 2001, pp. 299–301; Goodwin *et al.*, 2006, p. 499). Forrest *et al.* (2010, p. 1620) agreed with the previous life-history theory, noting that populations with low M values tended to have higher steepness and that “stronger recruitment compensation are expected to be able to be sustained at lower levels of spawning biomass”.

On perception 3

For perception 3, the lack of statistical relationships between h and M as well as between h and age at maturity, led Shertzer and Conn (2012) to conclude that either this was a fact or the data were uninformative to detect the relationships [note that the dataset used by Shertzer and Conn (2012) was largely made by a subset of Rose *et al.*'s (2001) dataset]. Commenting on those lacking relationships, Mangel *et al.* (2013) said that steepness was a function of many life-history variables and that projecting a multidimensional space into two separate dimensions was guaranteed to generate considerable scatters that would obscure among-species biological relationships. But although Shertzer and Conn (2012) rightly said that M characterizes longevity, there were, in their study and in that of Goodwin *et al.* (2006), no relationships between M and other LRLHTs as predicted by the life-history theory [Figure 3; see, for example, the expected relationships between life-history variables in Adams (1980)]. In fact, most M values in Goodwin *et al.* (2006) and Shertzer and Conn (2012) have been set to 0.2 irrespective of longevity. In contrast, M values in the study of Wiff *et al.* (2018, Appendix A. Supplementary data) vary noisily, without trend against the von Bertalanffy growth parameter L_∞ and the size at maturity; they show

moderate patterning with the von Bertalanffy growth parameter K and maximum age (Figure 4).

Conclusion

Based on results obtained using information-generating equations, this article documents three conflicting perceptions on the observed and postulated directions (positive, negative, and none) of the relationships between steepness or the compensation ratio and life-history variables. These perceptions cannot be all simultaneously true. Their coexistence raises a theoretical question regarding the correct perception, wrong perception, and distorted perception. Deeper investigations into such an important topic for fishery science and management are warranted.

Meanwhile, the present study suggests that perception 1 (i.e. steepness and the compensation ratio are highest in short-lived, high-productivity species) theoretically is wrong because the underlying conceptual argument, the postulate “steepness increases as a increases”, is not substantiated by the definition of steepness. Moreover, that postulate has no support of empirical and simulation-based relationships, which suggest either the opposite (i.e. steepness or the compensation ratio decreases with a) or the lack of association between steepness or the compensation ratio and a . Thus, the definition of steepness via information-generating equations and the results that these equations generate suggest that the notion that high steepness or high compensation ratio reflects high productivity (at low spawning stock biomass) may be a fallacy. In this context, analysis assumptions made under perception 1 may be incorrect and the results therefrom may be misleading.

On the other hand, there may not be analytical derivations allowing the determination of whether perceptions 2 (i.e. steepness and the compensation ratio are highest in long-lived, low-productivity species) and 3 (i.e. steepness and the compensation ratio are independent of longevity) are wrong or true. However, numerical simulations supporting perceptions 2 (e.g. Brodziak *et al.*, 2015, Figure 5c; Munyandorero, 2020, Table 3; see also the comments above on this perception) and empirical relationships underpinning perception 3 (e.g. Figures 3 and 4) suggest that:

- (i) Perception 2 is evident when, in simulations and in metadata of spawning stock biomass and recruitment, the expected (positive or negative) patterns of M vs. other LRLHTs for the species under investigation are strong. Typical patterns of M can be found in Adams (1980): M is negatively correlated with asymptotic size, maximum length, longevity, and age and size at maturity and increases with the parameters K , a , and r_0 .
- (ii) The lack of the expected relationships between M and all or some LRLHTs blurs any relationships between h or the compensation ratio and other LRLHTs and, hence, results in perception 3. As such, those lacking patterns of M negate the previous suggestion and stand to make the metadata (of spawning stock biomass and recruitment) uninformative about significant relationships between h or the compensation ratio and some or all LRLHTs. It follows that perception 3 distorts perception 2, which may be the correct perception.

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References

- Adams, P. B. 1980. Life history patterns in marine fishes and their consequences for fisheries management. *Fishery Bulletin*, 78: 1–12.
- Allen, M. S., Brown, P., Douglas, J., Fulton, W., and Catalano, M. 2009. An assessment of recreational fishery harvest policies for Murray cod in southeast Australia. *Fisheries Research*, 95: 260–267.
- Allen, M. S., Ahrens, R. N. M., Hansen, M. J., and Arlinghaus, R. 2013. Dynamic angling effort influences the value of minimum-length limits to prevent recruitment overfishing. *Fisheries Management and Ecology*, 20: 247–257.
- Brodziak, J., Mangel, M., and Sun, C.-L. 2015. Stock–recruitment resilience of North Pacific striped marlin based on reproductive ecology. *Fisheries Research*, 166: 140–150.
- Brooks, E. N. 2013. Effects of variable reproductive potential on reference points for fisheries management. *Fisheries Research*, 138: 152–158.
- Brooks, E. N., and Powers, J. E. 2007. Generalized compensation in stock–recruit functions: properties and implications for management. *ICES Journal of Marine Science*, 64: 413–424.
- Coggins, L. G. Jr, Catalano, M. J., Allen, M. S., Pine, W. E. III, and Walters, C. J. 2007. Effects of cryptic mortality and the hidden costs of using length limits in fishery management. *Fish and Fisheries*, 8: 196–210.
- Cortés, E. 2016. Estimates of maximum population growth rate and steepness for blue sharks in the north and south Atlantic Ocean. *Collective Volume of Scientific Papers, International Commission for the Conservation of Atlantic Tunas*, 72: 1180–1185.
- Denney, H. H., Jennings, S., and Reynolds, J. D. 2002. Life-history correlates of maximum population growth rates in marine fishes. *Proceeding of the Royal Society of London B*, 269: 2229–2337.
- Forrest, R. E. 2008. Simulation models for estimating productivity and trade-offs in the data-limited fisheries of New South Wales, Australia. PhD thesis, The University of British Columbia, Vancouver, BC.
- Forrest, R. E., McAllister, M. K., Dorn, M. W., Martell, S. J. D., and Stanley, R. D. 2010. Hierarchical Bayesian estimation of recruitment parameters and reference points for Pacific rockfishes (*Sebastes* spp.) under alternative assumptions about the stock–recruit function. *Canadian Journal of Fisheries and Aquatic Science*, 67: 1611–1634.
- Francis, R. I. C. C. 1992. Use of risk analysis to assess fishery management strategies: a case study using orange roughy (*Hoplostethus atlanticus*) on the Chatham Rise, New Zealand. *Canadian Journal of Fisheries and Aquatic Science*, 49: 922–930.
- Goodwin, N. B., Grant, A., Perry, A. L., Dulvy, N. K., and Reynolds, J. D. 2006. Life history correlates of density-dependent recruitment in marine fishes. *Canadian Journal of Fisheries and Aquatic Science*, 63: 494–509.
- Goodyear, C. P. 1980. Compensation in fish populations. *In Biological Monitoring of Fish*. Ed. by C. H. Hocutt and J. R. Stauffer Jr. Lexington Books, pp. 253–280. DC Heath and Co., Lexington, MA.
- Gwinn, D. C., and Allen, M. S. 2010. Exploring population-level effects of fishery closures during spawning: an example using largemouth bass. *Transactions of the American Fisheries Society*, 139: 626–634.
- Gwinn, D. C., Allen, M. S., Johnston, F. D., Brown, P., Todd, C. R., and Arlinghaus, R. 2015. Rethinking length-based fisheries regulations: the value of protecting old and large fish with harvest slots. *Fish and Fisheries*, 16: 259–281.
- Haddon, M. 2001. *Modelling and Quantitative Methods in Fisheries*. CRC Press, Boca Raton, FL.
- Hillary, R. M., Levontin, P., Kuikka, S., Manteniemi, S., Mosqueira, I., and Kell, L. 2012. Multi-level stock–recruit analysis: beyond steepness and into model uncertainty. *Ecological Modelling*, 242: 69–80.
- Kai, M., and Fujinami, Y. 2018. Stock–recruitment relationships in elasmobranchs: application to the north Pacific blue shark. *Fisheries Research*, 200: 104–115.
- Kindsvater, H. K., Mangel, M., Reynolds, J. D., and Dulvy, N. K. 2016. Ten principles from evolutionary ecology essential for effective marine conservation. *Ecology and Evolution*, 6: 2125–2138.
- Mace, P. M., and Doonan, I. J. 1988. A generalised bioeconomic simulation model for fish population dynamics. *Research Document 88/4*. New Zealand Fishery Assessment, Wellington.
- Mangel, M. 1996. Life history invariants, age at maturity and the ferox trout. *Evolutionary Ecology*, 10: 249–263.
- Mangel, M., Brodziak, J., and DiNardo, G. 2010. Reproductive ecology and scientific inference of steepness a fundamental metric of population dynamics and strategic fisheries management. *Fish and Fisheries*, 11: 89–104.
- Mangel, M., MacCall, A. D., Brodziak, J., Dick, E. J., Forrest, R. E., Pourzand, R., and Ralston, S. 2013. A perspective on steepness, reference points, and stock assessment. *Canadian Journal of Fisheries and Aquatic Science*, 70: 930–940.
- Martell, S. J. D., and Walters, C. J. 2008. Experimental policies for rebuilding depleted stocks. *Canadian Journal of Fisheries and Aquatic Science*, 65: 1601–1609.
- Martell, S. J. D., Pine, W. E., and Walters, C. J. 2008a. Parameterizing age-structured models from a fisheries management perspective. *Canadian Journal of Fisheries and Aquatic Science*, 65: 1586–1600.
- Martell, S. J. D., Walters, C. J., and Sumaila, U. R. 2008b. Industry-funded fishing license reduction good for both profits and conservation. *Fish and Fisheries*, 9: 1–12.
- Methot, R. D., Wetzel, R., Taylor, I., and Doering, K. 2019. *Stock Synthesis User Manual, Version 3.30.14*. NOAA Fisheries, Seattle, WA.
- Munyandorero, J. 2015. Composite per-recruits: alternative metrics for deriving biological reference points of fishery resources. *Regional Studies in Marine Science*, 2: 35–55.
- Munyandorero, J. 2020. Inferring prior distributions of recruitment compensation metrics from life-history parameters and allometries. *Canadian Journal of Fisheries and Aquatic Sciences*, 77: 295–313.
- Myers, R. A., Barrowman, N. J., Hilborn, R., and Kehler, D. G. 2002. Inferring Bayesian priors with limited directed data: application to risk analysis. *North American Journal of Fisheries Management*, 22: 351–364.
- Myers, R. A., Bowen, K. G., and Barrowman, N. J. 1999. Maximum reproductive rate of fish at low population sizes. *Canadian Journal of Fisheries and Aquatic Science*, 56: 2404–2419.
- Porch, C. E., and Laretta, M. V. 2016. On making statistical inferences regarding the relationships between spawners and recruits and the irresolute case of western Atlantic bluefin tuna (*Thunnus thynnus*). *PLoS One*, 11: e0156767.
- Punt, A. E., and Cope, J. M. 2019. Extending integrated stock assessment models to use non–densatory three-parameter stock–recruitment relationships. *Fisheries Research*, 217: 46–57.
- Rose, K. A., Cowan, J. H. Jr, Winemiller, K. O., Myers, R. A., and Hilborn, R. 2001. Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. *Fish and Fisheries*, 2: 293–327.

- Shepherd, J. G. 1982. A versatile new stock-recruitment relationship for fisheries, and the construction of sustainable yield curves. *ICES Journal of Marine Science*, 40: 67–75.
- Shertzer, K. W., and Conn, P. B. 2012. Spawner–recruit relationships of demersal marine fishes: prior distribution of steepness. *Bulletin of Marine Science*, 88: 39–50.
- Simon, M., Fromentin, J.-M., Bonhommeau, S., Gaertner, D., Brodziak, J., and Etienne, M.-P. 2012. Effects of stochasticity in early life history on steepness and population growth rate estimates: an illustration on Atlantic bluefin tuna. *PLoS One*, 7: e48583–17.
- Thorson, J. T., Monnahan, C. C., and Cope, J. M. 2015. The potential impact of time-variation in vital rates on fisheries management targets for marine fishes. *Fisheries Research*, 169: 8–17.
- van Poorten, B., Korman, J., and Walters, C. 2018. Revisiting Beverton–Holt recruitment in the presence of variation in food availability. *Review of Fish Biology and Fisheries*, 28: 607–624.
- Walters, C. J., and Martell, S. J. D. 2004. *Fisheries Ecology and Management*. Princeton University Press, Princeton, NJ.
- Wetzel, C. R., and Punt, A. 2015. Evaluating the performance of data-poor moderate and catch-only assessment methods for U.S. west coast groundfish. *Fisheries Research*, 171: 170–187.
- Wetzel, C. R., and Punt, A. E. 2016. The impact of alternative rebuilding strategies to rebuild overfished stocks. *ICES Journal of Marine Science*, 73: 2190–2207.
- Wiedenmann, J., Wilberg, M. J., and Miller, T. J. 2013. An evaluation of harvest control rules for data-poor fisheries. *North American Journal of Fisheries Management*, 33: 845–860.
- Wiff, R., Flores, A., Neira, S., and Caneco, B. 2018. Estimating steepness of the stock-recruitment relationship in Chilean fish stocks using meta-analysis. *Fisheries Research*, 200: 61–67.

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