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Abstract: Biological reference points are key quantities provided by stock assessments and used in fishery management for evaluating fishery status and setting future catch levels. For many fisheries worldwide, biological reference points are based on the spawning potential ratio (SPR), which measures per-recruit reproductive output as a function of the fishing rate relative to that when fishing is absent. SPR depends on the biological characteristics of the stock, which in turn can be influenced by the environment. A fishing rate based on SPR is often used as a proxy for the fishing rate that provides maximum sustainable yield. Here, we evaluate variability in the fishing rate (F_{40}) that provides an SPR of 40%, a commonly used limit reference point, given plausible variability in biological characteristics. Using eight case-study species from marine waters off the southeast United States, we consider both simple random variability and directional variability, both of which might result from climate change. We test the sensitivity of F_{40} to various life-history traits and compute distributions of F_{40}, given the expected variability in those traits. Based on those distributions, we evaluate the probabilities of overfishing given a target fishing rate (here, 75%F_{40}) that is based on prevailing conditions without considering future variability in F_{40}, consistent with common, current practice. Analyses also considered an SPR of 30% and 50% to evaluate the generality of conclusions. Results support that SPR-reference points are generally robust to plausible levels of variability in life-history traits that might be induced by environmental nonstationarity and that associated target fishing rates can provide meaningful buffers to prevent overfishing.

Keywords: biological reference points; nonstationarity; reef-associated fishes; spawning potential ratio

Key Contribution: This study demonstrates that limit reference points based on spawning potential ratio can be robust to plausible levels of variability in life-history traits and that, even with such variability, associated target reference points could prevent frequent overfishing.

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1. Introduction

Stock assessment models quantify the effects of fisheries on fish populations. Although a wide range of mathematical and statistical modeling approaches exist, stock assessments generally all share the common goal of providing scientific advice to fishery managers. In addition to advice on future catch, stock assessments can provide estimates of current stock status and fishery status, where the former measures stock size relative to a biological reference point (BRP) and the latter measures the fishing rate relative to its corresponding BRP [1]. A pressing challenge for the field of stock assessment and fishery management lies in how best to address environmental nonstationarity and climate change [2,3].

BRPs based on maximum sustainable yield (MSY) have an extensive history of use in fishery management [4,5]. For example, the current rate of fishing relative to the fishing rate at MSY (F_{MSY}) is often used to measure whether overfishing is occurring. When a

spawner-recruit model exists, MSY-based reference points can be derived directly. In particular, the slope of the spawner-recruit model, often described by the so-called "steepness" parameter, determines a stock's resilience to fishing and thus heavily influences the value of F_{MSY}. Unfortunately, steepness is notoriously difficult to estimate with precision from available data [6,7]. In such cases, an analyst must either assume a value of steepness, perhaps derived from a meta-analysis of similar species, or use an alternative approach. For example, in the southeast region of the United States (US), many assessments utilize the null recruitment model, which assumes no particular relationship between spawners and recruits and, consequently, is not suitable for the direct derivation of MSY [8]. When MSY-based reference points cannot be derived directly or are otherwise not used for management, a common proxy is based on the concept of spawning potential ratio (SPR) [9,10].

SPR is defined as the spawning output at a given fishing rate relative to that of an unfished stock. It can be expressed as a ratio or as a percentage, but, in either case, it is a declining function of the fishing rate (F) with a peak value at $F = 0$. A fishing rate of $F = F_X$ corresponds to SPR = X%, i.e., SPR that is X% of the unfished stock. When SPR reference points are used as proxies for MSY reference points, the current rate of fishing is compared to a pre-specified F_X to measure whether overfishing is occurring.

Whether using MSY, SPR, or some other metric, central to BRPs is the concept of limits and targets [1,11]. Limits represent the perceived maximum degree of sustainable exploitation, whereas targets represent the degree of exploitation aimed for by management. Limits should rarely be exceeded, which implies that when reference points are measured in F, the target should be no greater than the limit. In U.S. fishery management, F_{MSY} is treated as a limit, and considerable attention has been devoted to evaluating appropriate proxies for F_{MSY}, with a particular focus on SPR [12–15]. A common proxy for F_{MSY} is F_{40}, although the ideal level varies depending on life-history and fishery characteristics [10,13]. The target F would then be set at some value less than F_{MSY} or its proxy to provide a buffer to prevent frequent overfishing. This could be accomplished using a fixed percentage of the limit, such as $F_{TARGET} = 75\%F_{40}$, or it could be based on achieving pre-specified probabilities of overfishing [16,17].

Reference points are conditional on the selectivity of the fishery, where selectivity in stock assessments generally represents a relative vulnerability to capture at size or age. It combines the concepts of gear selectivity and the availability of the animals to the gear. For example, gear selectivity would be affected by such specifications as hook, mesh, or trap size, and availability would be affected by whether the animals are present where and when the gear is placed. Fishery selectivity is known to influence BRPs; in particular, populations can generally sustain higher fishing rates when selectivity allows spawning to occur prior to capture, and vice versa.

Nonstationarity in the environment can affect fish populations in a multitude of ways [2]. For example, climate change can affect home range [18] or depth distributions [19], both of which could subsequently affect the availability of fish to the fishery. Environmental variability, with or without direction, can also affect recruitment [20], growth, age at maturity, and natural mortality [17]. All of these sources of variability can affect the estimation of BRPs, including those based on SPR [21].

Life-history traits can vary in response to environmental conditions, but the underlying energetic constraints and evolutionary trade-offs that shape these traits remain in effect. Life-history theory treats the entire life cycle as a characteristic that can be optimized in an evolutionary sense for maximum fitness [22,23]. As such, the underlying trade-offs result in ecologically consistent scaling patterns among traits, referred to as life-history invariants [24–26]. For example, natural mortality scales inversely with age at maturity, and it scales positively with somatic growth rate [25]. In fisheries applications, life-history invariants have been used as a basis for computing SPR, both for informing data-limited fisheries [27–29] and for evaluating SPR as a proxy for MSY-based reference points [30].

Life-history invariants have a firm foundation in evolutionary principles, and they describe fundamental relationships among life-history traits. Empirical estimates of invariants rely on average relationships across species. However, these relationships are highly variable among species, such that an average may describe general patterns, but not the traits of any single species particularly well. An alternative approach models life-history traits hierarchically based on taxonomic structure, as implemented in the R package *FishLife* [31,32]. *FishLife* is similarly backed by evolutionary principles, describing empirically derived relationships among life-history traits, but it does so while accounting for taxonomy. The *FishLife* approach effectively uses data from a large database (*FishBase*, [33]) to predict life-history traits at multiple taxonomic levels, including the species level.

We used *FishLife* to define mean values and covariability of life-history traits at the species level, in the form of plausible multivariate distributions of those traits. We then used those distributions to evaluate the effects of nonstationarity on SPR values. We focused on F_{40}, given its common use in fishery management, as a limit reference point (e.g., [13]), but the general patterns in results would also apply to other values of F_x. As case studies, we focused on eight reef-associated fishes found in US Atlantic, Caribbean, and Gulf of Mexico waters. The species we included are from five families (Carangidae, Haemulidae, Lutjanidae, Serranidae, Sparidae) and eight genera, such that our suite of analyses encompass a wide range of life histories: red snapper (*Lutjanus campechanus*), vermilion snapper (*Rhomboplites aurorubens*), red grouper (*Epinephelus morio*), gag grouper (*Mycteroperca microlepis*), black sea bass (*Centropristis striata*), red porgy (*Pagrus pagrus*), greater amberjack (*Seriola dumerili*), and white grunt (*Haemulon plumierii*). Four of these species (the groupers, black sea bass, and red porgy) are known to be protogynous hermaphrodites, which may increase their susceptibility to overexploitation. Relative abundances of the eight species vary spatially by latitude, longitude, and depth [34,35]. However, they generally co-occur and support multispecies commercial and recreational fisheries [36,37].

Using our case-study species, we had three primary objectives. The first was to evaluate the sensitivity of F_{40} to multiple life-history traits. Some traits demonstrate more plasticity than others, and if those same traits highly influence SPR, we would expect more variability in F_x than we would if those traits have little influence on SPR. The second objective was to evaluate the variability of F_{40}, given plausible levels of plasticity in life-histories. We did so under various assumptions about patterns in nonstationarity (i.e., simple random or directional) in the life-history parameters and about patterns in the fishery (i.e., selectivity). We interpret the magnitude of variability in the reference points to be a measure of robustness to nonstationarity, in the sense that lower variability indicates greater resilience. The third objective was to evaluate the probability of overfishing, given the variability in F_{40} and a target fishing rate of $75\%F_{40}$ [38]. We selected 75% because it is used in our region of study, but the approach could apply to any percentage. These objectives are intended to shed light on how environmental nonstationarity might affect the utility of SPR-based targets and limit reference points.

2. Materials and Methods

The Materials and Methods section is organized as follows. First, we briefly review the computation of SPR and F_x. We then describe eight case-study species and the derivation of parameter values, followed by a methodological description of sensitivity analysis. The section concludes with a description of approaches to include nonstationarity in life-history characteristics, both with and without direction. All analyses were done using R [39].

2.1. Model

Spawning potential ratio (SPR) is computed as the equilibrium spawners per recruit (ϕ) at fishing rate F divided by the unfished spawners per recruit:

$$\mathrm{SPR}_F = \phi_F / \phi_{F=0} \quad (1)$$

which can be multiplied by 100 to be expressed as a percentage. Because calculations are on a per-recruit basis, the expected spawning output of each recruit over its lifetime can be computed by summing across ages (a):

$$\phi_F = \sum_{a=1}^{A} w_a \mu_a N_a \tag{2}$$

where A is the maximum age, w_a is the weight at age, μ_a is the maturity at age, and N_a is the relative abundance at age, starting with $N_a = 1$ and decremented over ages as $N_{a+1} = N_a e^{-Z_a}$, with Z_a representing total mortality rate at age. This computation makes two simplifying assumptions, both of which could easily be modified if needed for any particular application. The first is that reproductive output is proportional to body weight; if other measures of output are available, such as egg production at age, they could be used in place of w_a. The second assumption is that spawning output depends only on females; if that assumption is invalid, Equation (2) could be extended to include both males and females.

Weight at age in Equation (2) is computed as an allometric function of length at age (L_a):

$$w_a = \beta_1 L_a^{\beta_2} \tag{3}$$

in which parameters β_1 and β_2 are constants. In general, weight tends to scale with body volume, which implies $\beta_2 \approx 3$. Length at age is modeled with the standard von Bertalanffy growth function:

$$L_a = L_\infty \left(1 - e^{-K(a-a_0)}\right) \tag{4}$$

where L_∞ is the asymptotic length, K is the growth coefficient, and a_0 is the theoretical age at length zero.

Maturity at age in Equation (2) is computed as an increasing logistic function of age:

$$\mu_a = 1 / \left(1 + e^{-\gamma_m (a-\tau_m)}\right) \tag{5}$$

with slope parameter γ_m and location parameter τ_m defining the age at 50% maturity. Mortality at age combines the mortality that occurs from natural causes (M) with the mortality that occurs from fishing (F_a):

$$Z_a = M + F_a. \tag{6}$$

For simplicity, we assumed that natural mortality is independent of age, but one could readily include age-dependent M in the application of Equation (6). Fishing rate at age is the product of selectivity at age (s_a) and an overall fishing rate (F), such that $F_a = s_a F$. We assumed that selectivity follows a logistic function, as in Equation (5), but with slope parameter γ_s and location parameter τ_s defining the age at 50% selectivity.

We computed SPR as a declining function of F using a range of values from $F = 0$ to $F = 2$. The value of F that provides SPR = 0.4 (or 40%) is, by definition, F_{40}.

2.2. Case-Study Species and Parameter Values

As case-study examples, we chose eight reef-associated marine species that support important fisheries in southeast US federal waters. We deliberately chose species from eight different genera and five different families to span a range of life histories. From the family *Lutjanidae*, we included red snapper and vermilion snapper; from *Serranidae*, red grouper, gag grouper, and black sea bass; from *Sparidae*, red porgy; from *Carangidae*, greater amberjack; and from *Haemulidae*, white grunt.

For each species, we used the R package *FishLife* to obtain values for most life-history parameters described above, including L_∞, K, τ_m, and M [31,32]. In addition, *FishLife* provided values for the weight at asymptotic size, W_∞, which was used indirectly to

compute the length-weight coefficient β_2. Specifically, we estimated β_2 by inserting weight W_∞ and length L_∞ into Equation (3), taking logarithms, and then rearranging:

$$\beta_2 = (\log(W_\infty) - \log(\beta_1))/\log(L_\infty). \quad (7)$$

We obtained species-specific estimates of β_1 from *FishBase* [33,40] for use in Equation (7).

We assumed for all species that the theoretical age at size zero was $a_0 = -0.5$, the slope parameter of maturity was $\gamma_m = 3$, the slope parameter of selectivity was $\gamma_s = 1$, and the age at 50% selection equal to that of maturity $\tau_s = \tau_m$. This latter assumption follows the justification described by Williams and Shertzer [30], who noted that the availability of fish to the fishing gear often relates to maturity through migration patterns or size-at-age distributions. However, as in Williams and Shertzer [30], we also examined cases where selectivity occurs before maturity ($\tau_s = 0.75\tau_m$) or after maturity ($\tau_s = 1.25\tau_m$), as selectivity relative to maturity is known to be an important component of SPR.

Using parameter values described above, including mean values of life-history traits from *FishLife*, we computed the mean value of $\overline{F_{40}}$. We consider this value to represent prevailing conditions, as might be estimated by a stock assessment. We computed the target fishing rate as $F_{\text{TARGET}} = 75\%\overline{F_{40}}$.

2.3. Sensitivity Analysis

We computed sensitivity (Z_i) of $\overline{F_{40}}$ to life-history parameters using local perturbation analysis [21], adopting the approach defined by Ellner and Guckenheimer [41]:

$$Z_i = \frac{Y(1.05p_i) - Y(0.95p_i)}{0.1Y(p_i)} \quad (8)$$

where Y represents the response variable $\overline{F_{40}}$ as a function of the mean value of each parameter (p_i) obtained from *FishLife*. Typically, the approach applies 5% or 10% perturbations to compute a local response (Equation (8) uses 5%), with smaller values being more localized, linear approximations of the proportional sensitivity [41]. The analysis varies one life-history parameter at a time to isolate the effect of that particular input on model output (i.e., $\overline{F_{40}}$). A positive value of Z_i shows that an increase in the life-history parameter p_i leads to an increase in $\overline{F_{40}}$, and a negative value shows the opposite effect. A value of $|Z_i| \geq 1.0$ indicates that a 10% change in parameter p_i (5% increase and 5% decrease) results in a larger than 10% change in $\overline{F_{40}}$. For this analysis, we included only those parameters obtained from *FishLife* (L_∞, W_∞, K, τ_m, M). We excluded the length-weight parameter β_1, because as a simple multiplier in spawners per recruit (Equation (2)), it cancels from the computation of SPR (Equation (1)), and therefore $\overline{F_{40}}$ is not influenced by this parameter. We also excluded the length-weight parameter β_2, because it is a function of the other parameters (Equation (7)).

2.4. Nonstationarity and Probability of Overfishing

In addition to mean values of life-history characteristics, *FishLife* provides the variance-covariance matrix of trait values in log space, $\mathbf{\Sigma}$. We used $\mathbf{\Sigma}$ to define the range of plasticity in life-history characteristics at the species level that a given stock might experience due to nonstationarity in the environment or other causes. In addition, the covariance terms of $\mathbf{\Sigma}$ maintain life-history tradeoffs that occur due to energetic or evolutionary constraints, as documented by a large body of literature on life-history theory (e.g., [22,23]) and invariants (e.g., [24–26]).

We evaluated the effects of variability in life-history characteristics on estimation of F_{40} under two basic assumptions about nonstationarity. The first represents a case of increased variance but without a change in mean values, which we refer to as *nondirectional*. The

second adds a shift in mean values, which we refer to as *directional*. For nondirectional variability, we drew parameter values at random from a multivariate normal distribution:

$$\boldsymbol{x} \sim \text{MVN}(\boldsymbol{\mu}, \boldsymbol{\Sigma}) \tag{9}$$

where $\boldsymbol{x}$ is the vector of characteristics (in log space) and $\boldsymbol{\mu}$ is the vector of mean values (in log space) for the five parameters obtained from *FishLife*. We truncated the distribution to 95% confidence intervals to avoid random draws of extreme outliers. Given a random draw, we exponentiated components of vector $\boldsymbol{x}$ to obtain values of L_∞, W_∞, K, τ_m, and M in arithmetic space. We additionally included the corresponding variability in the length-weight relationship of Equation (7). Nondirectional variability simulates the case where life-history traits change over time but without any discernable trend.

For directional variability, we assumed that the mean (in log space) of one life-history parameter ($\mu_i^{'} = \mu_i \pm \sigma_i$) increased or decreased by one standard deviation (σ, square root of variance term from $\boldsymbol{\Sigma}$), for example, in response to a shift in environmental conditions. Variability in life-history traits should be expected, given the phenotypic plasticity in response to exploitation or environmental conditions [42,43]. However, to our knowledge, there is no single measure of expected variability for a given group of latitudinally overlapping species. Therefore, one standard deviation was selected as an exploratory value to quantify direction and magnitude of change in the results. We then generated life-history traits using a two-step approach. First, for the trait (i) responding directly to the environmental shift, we applied a univariate normal distribution, such that $x_i \sim \text{N}\left(\mu_i^{'}, \sigma_i\right)$. Second, for the four other traits, we maintained the covariance structure described above and conditioned on the new mean of the ith trait:

$$\boldsymbol{x}_{\forall \text{j} \neq \text{i}} \middle| x_i = \mu_i^{'} \sim \text{MVN}(\boldsymbol{\mu}, \boldsymbol{\Sigma}). \tag{10}$$

Although we varied one trait at a time, this analysis differs from the sensitivity analysis (Section 2.3) in that covariance among traits was maintained, as would be expected from life-history theory. For example, mortality rate tends to be negatively correlated with age at maturity [26]. Directional variability simulates the case where we have a reasonable understanding of prevailing conditions, but those conditions have recently changed or will change in the future as a result of trends in the environment. We focused this analysis of directional variability on natural mortality and growth rate, as these life-history traits appear to be the most directly affected by climate change [44–46].

For each species and each analysis described above, we generated new sets of life-history traits and recomputed $\overline{F_{40}}$ as described by Equations (1)–(7). To obtain distributions of F_{40}, we repeated each procedure 2000 times, which was more than sufficient for the means and variances to stabilize. Given that distribution for each species, we computed the probability (P) of overfishing if $F = F_{\text{TARGET}} = 75\%\overline{F_{40}}$, where P is the probability mass for which F_{TARGET} exceeds F_{40}. We interpret this probability to be a measure of resilience to unaccounted variability in F_{40}, in the sense that the target is based on prevailing conditions, but the new limit may have shifted. To evaluate generality of conclusions, these nondirectional analyses were repeated for SPR of 30% ($\overline{F_{30}}$) and 50% ($\overline{F_{50}}$).

3. Results

Mean values of parameters obtained from *FishLife* (L_∞, W_∞, K, τ_m, M) varied substantially across our eight species, reflecting the wide range of life-histories (Table 1). The length-weight coefficients (β_1) were all near 0.01, and the length-weight exponents (β_2) were all near 3.0, close to a priori expectation [40].

Table 1. Species-specific parameter values. Asymptotic length (L_∞), asymptotic weight (W_∞), growth coefficient (K), age at maturity (τ_m), and natural mortality (M) are mean values from *FishLife* [31,32]; the length-weight coefficient (β_1) is from *FishBase* [33]; and the length-weight exponent (β_2) was derived from Equation (7).

Species	L_∞ (cm)	W_∞ (g)	K (y^{-1})	τ_m (y)	M (y^{-1})	β_1 (g $cm^{-\beta_2}$)	β_2
Red snapper	91.56	10,795	0.17	3.29	0.25	0.014	2.99
Vermilion snapper	60.45	2889	0.19	3.09	0.28	0.015	2.97
Red grouper	89.38	9601	0.14	7.73	0.23	0.014	2.98
Gag grouper	119.59	26,041	0.14	7.87	0.30	0.010	3.10
Black sea bass	28.60	200	0.32	2.93	0.59	0.011	2.91
Red porgy	58.27	3180	0.16	3.98	0.31	0.013	3.05
Greater amberjack	151.52	48,879	0.23	2.69	0.55	0.016	2.97
White grunt	40.36	1033	0.27	2.95	0.81	0.014	3.03

The sensitivity analysis revealed consistent patterns across species (Table 2). Values of $\overline{F_{40}}$ (Supplementary Figure S1) were most sensitive to natural mortality, in which higher M resulted in higher $\overline{F_{40}}$. The growth coefficient and age at maturity were also influential and in the same direction as natural mortality, but with values that ranged from about 30–48% of those for M. Values of L_∞ and W_∞ were relatively unimportant, with W_∞ being the only parameter where higher values resulted in lower $\overline{F_{40}}$.

Table 2. Sensitivity of $\overline{F_{40}}$ to life-history parameters (Z_i of Equation (8)). Values greater than 1.0 indicate that 10% change in the parameter resulted in a greater than 10% change in $\overline{F_{40}}$.

Species	L_∞ (cm)	W_∞ (g)	K (y^{-1})	τ_m (y)	M (y^{-1})
Red snapper	0.14	−0.05	0.50	0.37	1.05
Vermilion snapper	0.16	−0.08	0.48	0.32	1.04
Red grouper	0.08	−0.04	0.38	0.46	1.11
Gag grouper	0.06	−0.03	0.34	0.43	1.09
Black sea bass	0.10	−0.04	0.35	0.14	1.03
Red porgy	0.14	−0.03	0.45	0.42	1.14
Greater amberjack	0.11	−0.04	0.36	0.27	1.12
White grunt	0.10	−0.03	0.28	0.11	1.03

In addition to life-history parameters, the age at selection relative to that of maturity affected $\overline{F_{40}}$ (Table 3). For all species, selectivity occurring prior to maturity resulted in decreased $\overline{F_{40}}$ (range 16–46% decrease), and selectivity occurring after maturity resulted in increased $\overline{F_{40}}$ (range 27–169% increase). The two species where $\overline{F_{40}}$ was most affected by selectivity relative to maturity were red grouper and gag grouper. These groupers have an older age at maturity than the other species in our analysis (Table 1), therefore setting the offset of selectivity as a proportion of that age resulted in more ages being selected before or after maturity, as compared to species with younger age at maturity.

With nondirectional variability in life-history traits and selectivity that coincided with maturity, the distributions of F_{40} had coefficients of variation (CVs) that ranged from 0.18–0.34 (Table 3, Figure 1, Supplementary Figures S2–S9). Given the level of variance in the distributions, the probabilities of overfishing if $F = 75\%\overline{F_{40}}$ ranged from 0.04 to 0.20 across species (Figure 1). Those probabilities were generally lower when selectivity occurred prior to maturity, ranging from 0.01 to 0.20, and they were generally higher when selectivity occurred after maturity, ranging from 0.09 to 0.33 (Table 3). The shifts in overfishing probabilities were a direct result of decreased or increased variance in the distributions of F_{40}, as indicated by CVs (Table 3). With lower variance, the distribution is "narrower" and therefore has less probability mass below the target of $75\%\overline{F_{40}}$. For each species-selectivity combination, values of $\overline{F_{30}}$ were higher than those of $\overline{F_{40}}$, and values of $\overline{F_{50}}$ were lower, as expected; however, CVs and consequently overfishing probabilities were relatively unaffected by the choice of SPR (Supplementary Tables S1 and S2).

Table 3. Values of $\overline{F_{40}}$ conditional on mean life-history traits from *FishLife*. Also shown is the probability of overfishing (P) given the target fishing rate of $F = 75\%\overline{F_{40}}$ and the coefficient of variation (CV) in the probability density of F_{40}, assuming nondirectional variation in life-history parameters. Each value is shown for selectivity that occurs before maturity ($\tau_s = 0.75\tau_m$), coincides with maturity ($\tau_s = \tau_m$), or occurs after ($\tau_s = 1.25\tau_m$).

Species	τ_s=0.75τ_m			τ_s=τ_m			τ_s=1.25τ_m		
	$\overline{F_{40}}$	P	CV	$\overline{F_{40}}$	P	CV	$\overline{F_{40}}$	P	CV
Red snapper	0.18	0.01	0.15	0.22	0.04	0.18	0.28	0.09	0.25
Vermilion snapper	0.21	0.11	0.24	0.25	0.14	0.27	0.32	0.16	0.38
Red grouper	0.16	0.02	0.14	0.26	0.09	0.21	0.57	0.29	0.62
Gag grouper	0.19	0.03	0.14	0.35	0.09	0.20	0.94	0.33	0.52
Black sea bass	0.50	0.17	0.30	0.69	0.18	0.30	1.05	0.21	0.35
Red porgy	0.22	0.07	0.19	0.29	0.11	0.24	0.42	0.19	0.42
Greater amberjack	0.42	0.20	0.35	0.55	0.20	0.34	0.78	0.21	0.40
White grunt	0.62	0.10	0.23	0.90	0.10	0.22	1.45	0.16	0.25

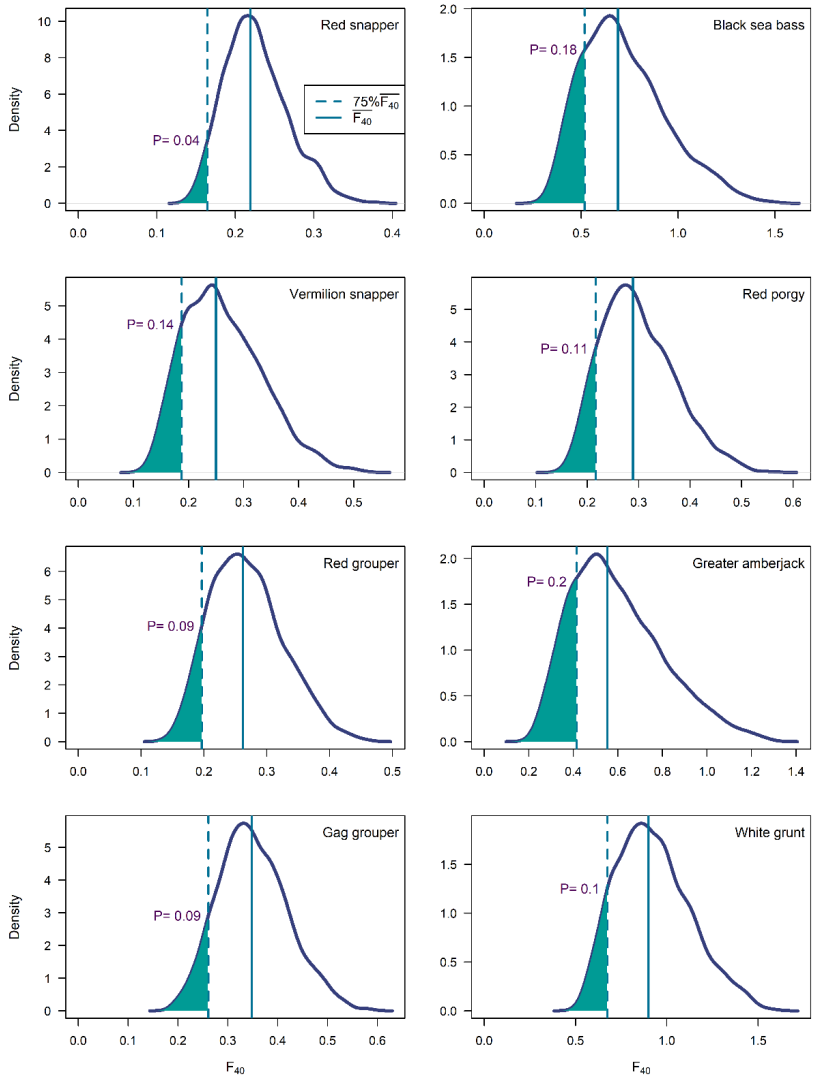

Figure 1. Probability density of F_{40} for reef-associated species conditional on nondirectional variability in life-history traits. The value $\overline{F_{40}}$ from prevailing conditions (mean traits) is represented by a solid vertical line, and the corresponding value $75\%\overline{F_{40}}$ is represented by a dashed line, as indicated in the top-left panel. The shaded region represents the probability of overfishing (P) if $F = 75\%\overline{F_{40}}$. Note variations in the scales of X- and Y-axes.

Directional variability shifted the distributions of F_{40} in a manner consistent with the sensitivity analysis. An increase in the growth coefficient shifted the distributions toward higher values of F_{40}, and a decrease in the growth coefficient shifted them toward lower values (Figure 2, Supplementary Figure S10). Consequently, if the target fishing rate remained constant, the probability of overfishing would be lower given an increase in the growth coefficient, and it would be higher given a decrease in the growth coefficient (Figure 2). Similarly, an increase in the natural mortality rate shifted the distributions of F_{40} toward higher values, and a decrease in the mortality rate toward lower values, with the probability of overfishing changing in accordance with the distributional shifts (Figure 3, Supplementary Figure S11).

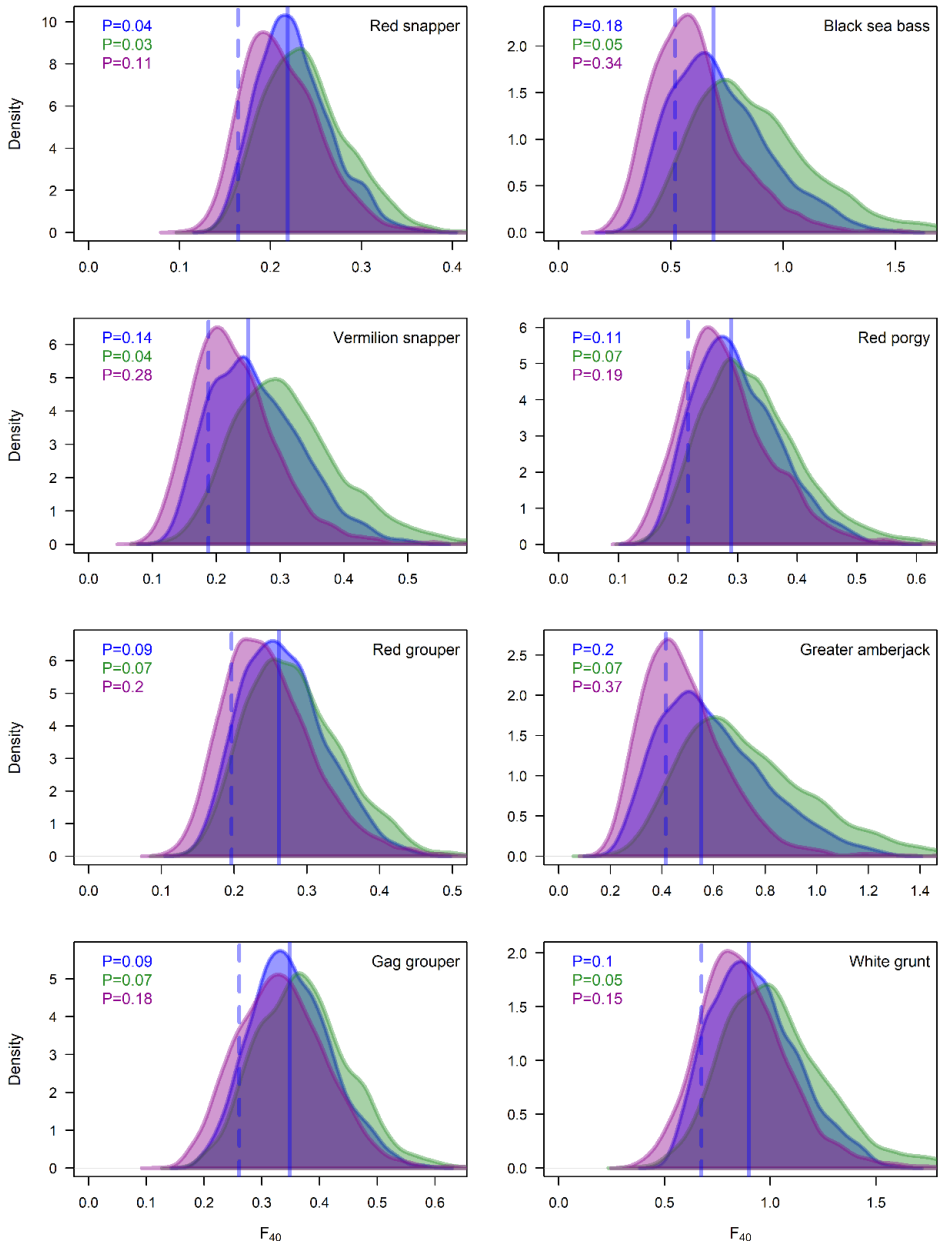

Figure 2. Probability densities of F_{40} for reef-associated species conditional on directional variability (± 1 standard deviation) in the growth coefficient. A decreased growth coefficient shifts the density of F_{40} toward lower values (**magenta**), whereas an increased growth coefficient shifts the density toward higher values (**green**), relative to the density with nondirectional variability (**blue**). The vertical lines correspond to $F = \overline{F_{40}}$ (**solid**) and $F = 75\%\overline{F_{40}}$ (**dashed**) from prevailing conditions, with the probability of overfishing (P) for each distribution indicated in each panel.

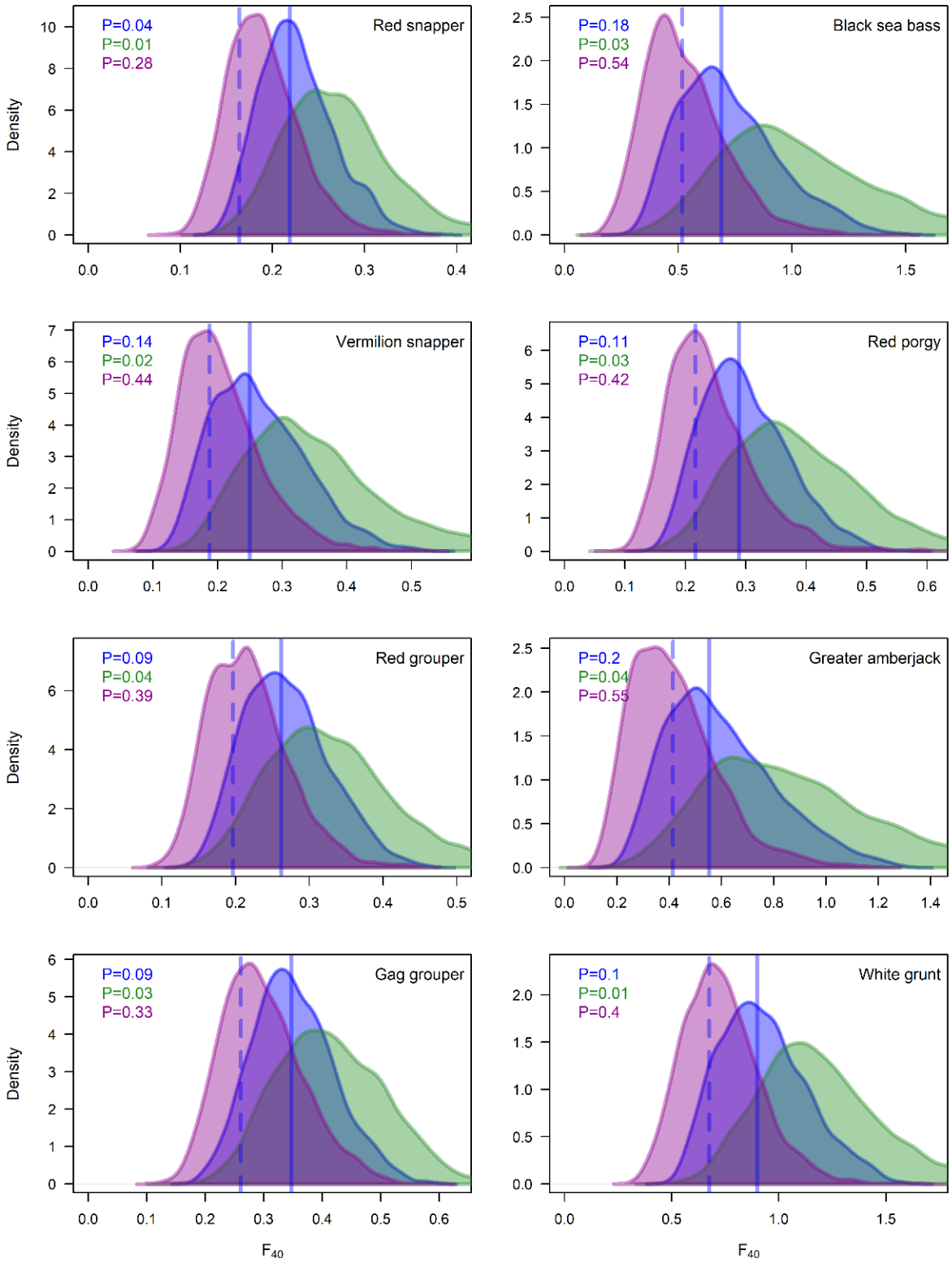

Figure 3. Probability densities of F_{40} for reef-associated species conditional on directional variability ($\pm$1 standard deviation) in the natural mortality rate. A decreased mortality rate shifts the density of F_{40} toward lower values (**magenta**), whereas an increased mortality rate shifts the density toward higher values (**green**), relative to the density with nondirectional variability (**blue**). The vertical lines correspond to $F = \overline{F_{40}}$ (**solid**) and $F = 75\%\overline{F_{40}}$ (**dashed**) from prevailing conditions, with the probability of overfishing (P) for each distribution indicated in each panel.

4. Discussion

Using mean values and covariances of life-history parameters from *FishLife* [31,32], we evaluated variability in SPR-based reference points for eight reef-associated species found in marine waters of the southeast US. These species comprised five families and eight genera. We found that values of F_{40} were most sensitive to natural mortality and, to a lesser degree, the growth coefficient and age at maturity. Values of F_{40} were relatively insensitive to asymptotic length and asymptotic weight, with the latter parameter being the only one that showed a negative relationship (i.e., an increase in asymptotic weight led to a decrease in F_{40}). Given plausible levels of variability in these life-history traits, we found that the resulting distributions of F_{40} had low to moderate levels of deviation from the prevailing mean, with CVs ranging from 0.20 to 0.34. Species-specific CVs were generally smaller when selectivity occurred prior to maturity and larger when selectivity occurred after maturity. Although we focused on F_{40}, the general patterns in our results held true for other values of SPR (Supplementary Tables S1 and S2).

Given those levels of variability in F_{40}, setting the target fishing rate at $F_{\text{TARGET}} = 75\%\overline{F_{40}}$ provided a buffer against overfishing, with the probability of overfishing ranging from 0.04 to 0.20, depending on the species. These probabilities were similar for other values of SPR (Supplementary Tables S1 and S2); however, we note that this result is conditional on the focal level of SPR being the appropriate limit reference point. For example, if the target were set to $F_{\text{TARGET}} = 75\%\overline{F_{30}}$, but the appropriate limit was actually $\overline{F_{50}}$, then for all our case-study species, the target would exceed the limit, which is nonsensical. The computed probabilities are fairly low, compared to the probabilities considered allowable by several U.S. fishery management councils in their control rules (generally 0.25–0.5), to the probabilities evaluated by Ralston et al. (also 0.25–0.5, [47]), and to the range recommended by Mildenberger et al. (0.25–0.45, [48]). Ultimately, the acceptable probability of overfishing is a policy decision. The yield per recruit when fishing at F_{TARGET} was 82–85% of the yield per recruit when fishing at $\overline{F_{40}}$, which suggests that the overfishing buffer can be achieved without much sacrifice to catch levels. Although we focused on the constant fishing rate of $F_{\text{TARGET}} = 75\%\overline{F_{40}}$, a similar control rule could also include a ramp or step function that reduces the target F at low biomass [49]. With directional variability toward a lower growth coefficient, the probabilities of overfishing increased (range 0.11–0.37), and with directional variability toward a higher growth coefficient, the probabilities of overfishing decreased (range 0.03–0.07). Similarly, with directional variability toward lower natural mortality, the probabilities of overfishing increased (range 0.28–0.55), and with directional variability toward higher natural mortality, the probabilities of overfishing decreased (range 0.01–0.04).

We chose to focus on F_{40} as a limit reference point because of its widespread use in fishery management. However, we did not evaluate whether F_{40} is optimal in terms of serving as a proxy for F_{MSY} or, more generally, for achieving management goals. The optimal level of SPR for any given stock would vary on a case-by-case basis, with good default values seemingly in the range of 40–50% [10,12,14,15]. Although we included the concept of environmental variability through inferred effects on life-history traits, the limit ($\overline{F_{40}}$) and target ($75\%\overline{F_{40}}$) reference points were treated as static. That was by design, such that those values would represent prevailing conditions, as might be estimated by a stock assessment. We were interested in evaluating the resilience of those static reference points under the reality of nonstationarity. In some cases, however, time-varying (i.e., dynamic) reference points can be informative [3,50]. Dynamic reference points may have intuitive appeal, but their application should be undertaken with caution as they do not necessarily improve management [51–53].

We did not examine the effect of the sex ratio. If constant across ages, sex ratio is unimportant for computing SPR because it occurs in both the numerator and denominator of SPR as a scalar and, therefore, cancels. We also did not examine the potential contribution of males toward spawning output. Several species in our study (red grouper, gag grouper, black sea bass, red porgy) are protogynous hermaphrodites, where the sex ratio shifts from

female to male with age. If fishing preferentially selects larger fish, it can deplete males at a higher rate than females, creating the potential for sperm limitation. Protogyny poses unique challenges to computing SPR, such as whether males should be included in the analysis and, if so, how to weigh their contribution toward spawners per recruit relative to that of females [54,55]. Because protogynous stocks can be particularly vulnerable to overfishing, they may require a higher level of SPR than a stock with an otherwise similar life-history [14].

For computing probabilities of overfishing, our analysis considered variability in life-history traits as the sole source of uncertainty in the limit reference point. Other potential sources of uncertainty include estimation error and implementation error. Estimation error of a limit reference point stems from fitting the estimation model (e.g., assessment model) to imprecise data [11]. Implementation uncertainty represents imprecise management, such that the actual fishing rate may not equal the target [56]. Our analyses, although simplified, allowed us to isolate the effects of variability in life-history traits.

It is not surprising that there is variability in F_x given variation in life-history parameters, as indicated by the scenario of nondirectional change. However, given plausible levels of variation provided by *FishLife*, the species-specific distributions of F_x were, in general, reasonably precise (based on CVs, Table 3). As a consequence, the target fishing rate of $F_{\text{TARGET}} = 75\%\overline{F_{40}}$ appears to be resilient to overfishing. In cases of directional change, the probabilities of overfishing increased if the growth coefficient or natural mortality were reduced, and the probabilities decreased if the growth coefficient or natural mortality were increased. Under the current regime of climate warming, Wang et al. [45] found that growth rate and natural mortality would likely increase. That result may differ across systems or species, but where it holds, F_{TARGET} would be more robust to overfishing, potentially at the cost of foregone yield relative to that of a dynamic target.

5. Conclusions

Our study explored the potential effects of environmental nonstationarity on the utility of SPR-based target and limit reference points, and we used *FishLife* to define plausible levels of variability in life-history parameters. In an actual stock assessment, it would be preferable to base reference points on life-history parameters and selectivity patterns specific to the stock in question. For data-limited stocks, *FishLife* seems a viable tool for obtaining life-history parameter values.

The focus here was on reference points related to the fishing rate. We did not consider variability in recruitment, because SPR is computed on a per-recruit basis, and it is therefore unaffected by the level of recruitment. However, nonstationarity in recruitment may be an important consideration for many fisheries [57]. With an assumption about the level of recruitment, SPR can provide reference points related to spawning output. Unfortunately, any such assumption may prove untenable, given the difficulty of recruitment forecasting under environmental nonstationarity or climate change [58,59]. Nonetheless, even without biomass reference points to gauge stock status, fishery managers have (at least partial) control over the fishing rate or exploitation rate, which can be robust to overfishing in a nonstationary world [60].

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/fishes9120497/s1, Table S1. Biological reference points, probabilities of overfishing, and coefficients of variation associated with $\overline{F_{30}}$. The values of $\overline{F_{30}}$ represent prevailing conditions, derived from mean life-history traits from *FishLife*. The probability of overfishing (P) is based in the target fishing rate of $F = 75\%\ \overline{F_{30}}$ and the coefficient of variation (CV) describes variability in the probability density of F_{30}, assuming nondirectional variation in life-history parameters. Each value is shown for selectivity that occurs before maturity ($\tau_s = 0.75\tau_m$), coincides with maturity ($\tau_s = \tau_m$), or occurs after ($\tau_s = 1.25\tau_m$); Table S2. Biological reference points, probabilities of overfishing, and coefficients of variation associated with $\overline{F_{50}}$. The values of $\overline{F_{50}}$ represent prevailing conditions, derived from mean life-history traits from *FishLife*. The probability of overfishing (P) is based in the target fishing rate of $F = 75\%\ \overline{F_{50}}$ and the coefficient of variation (CV) describes variability

in the probability density of F_{50}, assuming nondirectional variation in life-history parameters. Each value is shown for selectivity that occurs before maturity ($\tau_s = 0.75\tau_m$), coincides with maturity ($\tau_s = \tau_m$), or occurs after ($\tau_s = 1.25\tau_m$); Figure S1: Spawning potential ratio for case-study species; Figure S2: Relationships between life-history traits for red snapper; Figure S3: Relationships between life-history traits for vermilion snapper; Figure S4: Relationships between life-history traits for red grouper; Figure S5: Relationships between life-history traits for gag grouper; Figure S6: Relationships between life-history traits for black sea bass; Figure S7: Relationships between life-history traits for red porgy; Figure S8: Relationships between life-history traits for greater amberjack; Figure S9: Relationships between life-history traits for white grunt; Figure S10: Mean growth curves for case-study species based on the prevailing growth coefficient (K), a one standard-deviation increase in K, and a one standard-deviation decrease in K; Figure S11: Distributions of natural mortality (M) for case-study species based on prevailing conditions, a one standard-deviation increase in M, and a one standard-deviation decrease in M.

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