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Reproductive Biology and Early Life History Inform Steepness and the Productivity of Rockfishes (*Sebastes* spp., Scorpaenidae) in the California Current

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ABSTRACT

Steepness, a parameter derived from the stock-recruit relationship, is widely used in fishery stock assessments to scale the productivity of a population. Steepness is a highly influential parameter, but it is often unknown a priori and is typically difficult to estimate. Attempts to statistically estimate steepness, either within stock assessments or through meta-analyses, can lead to implausible results. We move beyond steepness as a statistical concept to emphasize that steepness is determined by life history traits and the early life survival of offspring of a population. We return to the original derivation of the Beverton-Holt stock-recruit relationship, and model recruitment to the population as a function of total egg production, rather than using spawning biomass as a proxy. We then demonstrate how to calculate steepness based on biology through a case study of rockfishes (*Sebastes* spp., Scorpaenidae) in the California Current, where steepness has been notoriously difficult to estimate. We leverage a wealth of reproductive ecology and early life history information (empirical data and associated life history parameters) to compute steepness values for four species of rockfishes, in order to illustrate how steepness varies by species based on differences in their life histories. We also show the sensitivity of steepness to the different life history traits. We conclude that steepness of a stock-recruit relationship is a real biological parameter and can be meaningfully informed with life history parameters including early life survival.

1 | Introduction

1.1 | General Introduction

Early in fisheries management, many scientists assumed essentially unlimited egg production in marine fish populations and that the recruitment of young individuals to the population was driven solely by environmental factors. The ‘oceans as cornucopia’ metaphor of T.H. Huxley (Lyons 1999; Smith 1994) developed because the fecundity of females in marine fish populations is generally very high, on the order of

hundreds-of-thousands to millions of eggs produced per female per year (Rothschild 1986). It is now well understood that although fish may have many propagules, no fish can produce an infinite number of offspring; Rothschild (1986) suggested that it is helpful to analogize fish to plants rather than vertebrates. Furthermore, the assumption of unlimited egg production is non-precautionary at best and potentially catastrophic at worst (Hutchings and Reynolds 2004).

Beverton and Holt (1957) and Ricker (1954) pioneered the development of stock-recruitment relationships (SRRs) to model the

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connection between the reproductive output of mature individuals (spawners) in a population and the subsequent recruitment of individuals to that population. Mace & Doonan (1988, 13) proposed reparametrizing SRRs in terms of steepness, commonly denoted by h , and defined as the fraction of recruits expected when spawning biomass is 20% of the steady state unfished level (Mace and Doonan 1988). Because steepness scales the productivity of a population allowing comparison of productivity across stocks, it became widely used in stock assessments (Mangel et al. 2013). The value of steepness is often highly influential in stock assessments, both on the perception of the productivity of the stock and biological reference points and on the recommendations for fisheries management. Thus, understanding the biological basis for steepness and being able to accurately estimate it is essential to modelling population dynamics and forecasting for the sustainable management of fisheries.

Although Mace and Doonan (1988) used biomass in their definition of steepness, a more biologically sound definition replaces biomass by reproductive output, so that steepness of the SRR is the number of propagules surviving to join the population (recruits) when reproductive output is reduced to 20% of its unfished value. Since information on fecundity is often not available to determine reproductive output, spawning stock biomass is commonly used as a proxy, with the implicit assumption that reproductive output is proportional to spawning biomass. However, this assumption is not true for many marine fishes because larger/older females commonly produce disproportionately more eggs than an increase in body weight suggests (Barneche et al. 2018; Dick et al. 2017; Marshall et al. 2021).

Over the last decades, determining steepness has mainly been viewed as a statistical question when fitting SRR models and has proven problematic for a variety of reasons (Lee et al. 2012). The required time series information of recruits over a range in stock size is typically lacking. Recruitment is often highly variable in response to climate and oceanographic conditions (Cury et al. 2014; Szuwalski et al. 2015; Vert-pre et al. 2013), which can mask the underlying relationship (Zimmermann et al. 2021). Furthermore, stock size and recruit information are generally outputs of a stock assessment model, and are thus statistical model outputs (rather than empirical data) that are influenced by all of the other model assumptions (Lee et al. 2012; Maunder and Thorson 2019; Zimmermann et al. 2021). Despite the uncertainty and challenges associated with identifying a statistical relationship between spawning stock biomass and recruitment, most stock assessments assume some form of a SRR (Methot et al. 2025). Some internationally managed fisheries, such as those for highly migratory species in the Pacific Ocean, are moving toward ensemble modelling approaches to encompass a suite of steepness assumptions due to the high uncertainty associated with this parameter (Maunder 2024).

In this paper, we explore an alternative to statistical estimation with the computation of steepness on the basis of biology informed by life history traits and early life survival. We present data and life history parameters from both published and previously unpublished studies to compute steepness for four species

of rockfish (*Sebastes* spp., Scorpaenidae) as examples of how this can be done.

1.2 | Steepness of the West Coast Rockfishes

The rockfishes of the northeastern Pacific Ocean in the California Current along the continental west coast of the United States (hereafter West Coast rockfishes) provide an example of the challenges associated with estimating steepness. West Coast rockfishes are a diverse group of economically, ecologically and culturally important marine fishes. More than 65 species occur in the California Current, which is characterized by strong seasonal, interannual and interdecadal variability in oceanographic conditions (Checkley and Barth 2009; Hyde and Vetter 2007; Love et al. 2002; Parker et al. 2000) and most are fished commercially and recreationally (Love et al. 2002). The life history traits of these rockfishes include longevity (up to 200+ years in some species), delayed maturation (up to 20+ years) and live-bearing (Love et al. 2002).

Because of these life history traits, rockfish populations were historically assumed to have low productivity but the enormous standing stocks in the middle of the 20th century masked low rates of natural mortality and led to overfishing (Francis 1986; Leaman 1991). After heavy exploitation through the 1970s into the 1990s, both commercially and recreationally fished shelf species declined considerably. In the early 2000s, seven species were declared overfished with spawning biomass estimated to be at <25% of the estimated unfished level (Parker et al. 2000; Ralston 1998). The overfished status led to coastwide fisheries closures of shelf habitat, large economic losses due to the inability to target robust populations, and the development of rebuilding plans that initially suggested a range of 8–59 years to rebuild the various species even with no fishing mortality (Berkeley et al. 2004).

The successful recovery of these stocks more rapidly than expected (NMFS 2019; PFMC 2018) led to greater access to fishing grounds on the West Coast shelf and slope, along with some recognition that many nearshore rockfish populations, which occupy habitats that had remained open during the shelf closures, had also been subject to increasing fishing mortality and conservation impacts (Cope et al. 2011; Dick and MacCall 2010; Gunderson et al. 2008). A lack of adequate life history data and monitoring programs for many of these nearshore species and for the many species of rockfish, in general, continues to challenge the sustainable management for the diverse West Coast rockfish stocks (PFMC 2018). For example, estimates of sustainable yield and the biomass giving the greatest productivity can vary considerably depending on the steepness of the SRR assumed in a stock assessment (Hilborn 2010).

For the Beverton-Holt SRR (BH-SRR), steepness ranges from 0.2, which corresponds to no productivity beyond the replacement of spawning individuals, to 1.0, which corresponds to a constant productivity regardless of the abundance of spawners. Dorn (2002) initiated the statistical approach to determine plausible probability distributions of steepness for unobserved rockfish stocks through a meta-analysis and suggested 0.65 as

an appropriate value; subsequent updates of this meta-analysis between 2007 and 2017 led to estimates ranging from 0.58 to 0.78 and the currently used value for West Coast rockfishes of 0.72 (Thorson et al. 2019). Other statistical approaches to inform steepness for rockfish populations include a phylogenetic analysis correlating steepness with other population parameters that produced a steepness value of 0.72 for the subfamily Sebastinae and 0.61 for the genus *Sebastes* (Thorson 2020).

The most recent update of the meta-analysis in 2018 estimated steepness in rockfish stocks to be 0.93, suggesting that perhaps productivity had dramatically increased in more recent years (PFMC 2019). However, given the slower life history of many of these species, the updated estimate was ultimately rejected for use within groundfish stock assessments (PFMC 2019). As of 2025, there have been no further analytical advancements to the approach for informing steepness. Thus, the designated prior for West Coast rockfish stock assessments remains at 0.72 (PFMC 2025), with a recognized need to better understand the dramatic increase in estimated steepness in the most recent meta-analysis (PFMC 2019), as well as to develop alternative approaches for informing steepness in stock assessment models. Here we show an alternative approach to compute steepness based on biology and life history traits to better inform stock assessments.

1.3 | Overview of the Paper

The original derivations of SRRs (Beverton and Holt 1957; Ricker 1954) explicitly modelled spawning output as total egg production, with the survival of offspring from the spawning of propagules (eggs or larvae) to recruitment to the population having density-independent and density-dependent components. Using a slightly different form of the BH-SRR, and following the tradition started by Mace and Doonan (1988), Mangel et al. (2010, 2013) derived steepness in terms of (1) the maximum, per-capita, density-independent early life survival of individuals to recruitment to the population, (2) the expected lifetime female spawning biomass and (3) the sex ratio at birth. This derivation showed that steepness is a function of individual reproductive traits and early life history.

We move beyond Mangel et al. (2010, 2013) by explicitly modelling total offspring (eggs or larvae) production by females. This advancement of the method explicitly accounts for maternal size- and age- effects on reproduction, which are not accounted for when using spawning biomass as a proxy for spawning output. This is because spawning biomass often does not scale proportionately with reproductive output for many marine fish species (Barneche et al. 2018). In particular, we leverage an immense amount of empirical data on the reproductive biology of rockfishes to explicitly incorporate known maternal size- and age- effects on the reproductive traits of brood fecundity and spawning frequency. We also update knowledge of early life dynamics in the pelagic environment to estimate the survival of offspring to recruit to the population.

To model early life survival, we first estimate the value of steepness consistent with the persistence of the population, which is achieved through the replacement of individuals from one generation to the next. Effectively, this is the minimum value of steepness

(i.e., 0.2 for BH-SRR model) for a specific stock. Considering the effects of stochasticity on persistence (He et al. 2006), we expect it to rarely be observed in nature. We then develop a method for the computation of steepness that applies weight- and stage-based natural mortality rates for larvae and pelagic juveniles (McGurk 1986) over the duration of the early life pelagic phase to estimate early life survival from empirical observations of early life growth. For these calculations, we assume that growth, in mass per day, is exponential in the early life phase, as is shown for other species (Buckley et al. 2006; Shoji et al. 2005; Kaji et al. 1996).

We illustrate our method using data on four focal species of rockfishes: Yellowtail rockfish (*S. flavidus*), Widow rockfish (*S. entomelas*), Chilipepper (*S. goodei*) and Bocaccio (*S. paucispinis*). Henceforth, we refer to them as Yellowtail, Widow, Chilipepper and Bocaccio. Among West Coast rockfishes, these species support some of the largest fisheries by volume in the California Current and have some of the best-informed stock assessments. Even so, questions remain regarding the productivity of their populations and the appropriate species-specific value of steepness to use for population modelling and management. Currently, steepness for each species is treated as a fixed input parameter in the stock assessment model. The most recent stock assessments at the time of our analysis fixed steepness at 0.72 from the meta-analysis for Yellowtail, Widow and Bocaccio, and at 0.57 for Chilipepper (Adams et al. 2019; Field et al. 2015; He and Field 2017; Stephens and Taylor 2018).

Each of our four focal species has a slightly different life history and reproductive pattern, as well as distributions and habitat associations, which suggests differences in population productivity and steepness across the stocks. Female Yellowtail and Widow are limited to only a single brood of larvae each year, the most common reproductive pattern in the *Sebastes*. Female Chilipepper and Bocaccio are capable of more than one brood each year, depending on maternal size, which is a different reproductive pattern within *Sebastes*. We present case studies for populations in coastal waters of the West Coast of the continental United States (U.S.) for Widow (California, Oregon and Washington), Chilipepper (U.S.- Mexico border to Oregon-Washington border), Bocaccio (U.S.-Mexico border to Cape Blanco, Oregon) and the southern stock of Yellowtail (California south of Cape Mendocino), for which the most reproductive information exists. Our methods and results show how reproductive ecology and early life history information influence the characterization of productivity of the stocks and thus help to inform steepness of the stock-recruit relationship.

2 | Methods

2.1 | Steepness in Terms of Reproductive Output and Life History Parameters

In Material S1, we derive steepness, h as a function of (1) the maximum, per-capita, density-independent survival of propagules (eggs or larvae) to recruitment to the population α , (2) the expected lifetime egg production of a female at birth for a population in the steady state $\overline{LEP}_0$, and (3) the sex ratio at birth where r is the fraction of males and $(1 - r)$ the fraction of females (Table 1)

TABLE 1 | Description of the terms in Equation (1) for steepness.

Expression	Interpretation
$h = \frac{\alpha(1-r)\overline{\text{LEP}}_0}{4+\alpha(1-r)\overline{\text{LEP}}_0}$	Biological definition of steepness, h
α	Maximum, per-capita, density-independent survival of propagules (eggs or larvae) to recruitment to the population
r	Fraction of males at birth
$\overline{\text{LEP}}_0 = \sum_{a=0}^A S(a)p_{f,m}(a)\phi(a)(1+v(a))$	Expected lifetime egg production in the absence of fishing
A	Maximum age of adults
$S(a) = e^{-M(0)-M(1)\dots-M(a-1)}$	Survival of an individual to age a
$M(a)$	Annual rate of mortality at age a
$p_{f,m}(a)$	Probability that a female of age a is mature
$\phi(a)$	Batch fecundity at age a
$v(a)$	The probability that a female of age a has a second brood in the current breeding season ^a

^aWhen females are capable of more than two broods per season, we replace $1 + v(a)$ by $\sum_{j=1}^J j\psi(j, a)$ where J is the maximum number of broods per season and $\psi(j, a)$ is probability that a female of age a has j broods in the current season.

$$h = \frac{\alpha(1-r)\overline{\text{LEP}}_0}{4+\alpha(1-r)\overline{\text{LEP}}_0} \quad (1)$$

The relevant parameters in Table 1 can be estimated empirically. To do so, we use life history information from stock assessments, reproductive ecology and early life history studies. This information allows us to estimate a point estimate for steepness (and estimate the associated uncertainty) for each of the four focal species of rockfish based on their own reproductive ecology and early life history.

2.2 | Specifications for Live Bearing Rockfish

As noted, all species of *Sebastes* are livebearers: females mate with males and internally fertilize eggs. The gestation period of embryos lasts from a few weeks to months, depending on the species and temperature (Love et al. 2002). The brood of larvae is released at a single time, called the time of parturition. In a majority of rockfish, females release only a single brood each year. However, in at least 15 species, females are capable of more than a single brood per year (Lefebvre et al. 2018). Holder and Field (2019) describe the species that are capable of multiple broods per year and discuss the likely environmental factors associated with multiple brooding species, which are more common in species with more southern distributions in the California Current such as Chilipepper and Bocaccio. Beyer et al. (2021) showed that some Rosy rockfish (*Sebastes rosenblatti*) are capable of 4–5 broods in a single reproductive season given optimal conditions in the laboratory. However, up to two broods during the spawning season is the most common for Bocaccio and Chilipepper, the two multiple brooding capable species in our study, depending on size (Lefebvre et al. 2018; Ralston and MacFarlane 2010). Up to three broods have been observed in these species but are rare. Less than 3% of multiple

brooding Chilipepper females produced three broods in the wild during a period of favourable conditions (Lefebvre et al. 2018). Because two broods are the most common pattern, and more than two are rare, we assume two broods a year are possible for Chilipepper and Bocaccio, depending on female size and age. For single brooding Yellowtail and Widow, the probability of a second brood is zero. We assume a 50:50 sex ratio of males to females at birth.

2.3 | Rockfish Life History Information

We use life history information from the most recent fishery stock assessments at the time of our analysis (Adams et al. 2019; Field et al. 2015; He and Field 2017; Stephens and Taylor 2018), and research studies on the reproductive ecology and early life history of rockfishes to inform the parameters to compute steepness (see Table 2). We separately consider growth, natural mortality, maturity, brood fecundity and spawning frequency.

2.3.1 | Growth

We model post-recruitment growth using the von Bertalanffy growth function (vBGF) to determine female fork length L [cm] at age a [year]

$$L(a) = L_{\infty} \left(1 - e^{-k(a-a_0)} \right) \quad (2)$$

where L_{∞} , k and a_0 are the asymptotic length, the vBGF growth rate and the hypothetical age at zero length, respectively. Since many life history traits are correlated with body size and reported in terms of length, we invert length-at-age, $L(a)$ from Equation (2) to convert length-based life history traits to an equivalent trait-at-age.

TABLE 2 | Life history parameters and their values.

Variable	Short description	Yellowtail	Widow	Chilipepper	Bocaccio
Relative life history pattern within the genus <i>Sebastes</i>		'slower'	'slower'	'faster'	'faster'
Length [cm] at age [years], Equation (2)					
A [year]	Maximum age	64	54	35	40
a_0 [year]	Theoretical age at zero length	-2.01	-0.10	-0.62	-0.87
L_∞ [cm]	Asymptotic length	52.1	50.4	48.3	67.7
k [1/year]	von Bertalanffy growth rate	0.11	0.17	0.20	0.23
Weight [kg] – length [cm] allometry, Equation (3)					
a_w [unitless]	Scaling factor	1.18×10^{-5}	1.74×10^{-5}	4.05×10^{-5}	7.36×10^{-5}
b_w [unitless]	Exponent	3.07	2.96	3.20	3.11
Survival, Equation (4)					
M [1/year]	Rate of natural mortality	0.18	0.14	0.16	0.18
Probability of maturity at length [unitless], Equation (5)					
L_{50} [cm]	Length at which 50% of females are mature	34.9	30.1 ^a	24.4	37.7
b_m [cm]	Dispersion parameter	0.401	NA ^a	0.270	0.334
A_{50} [year]	Age at which 50% of females are mature	8.1 ^a	5.5	2.9 ^a	2.7 ^a
Brood fecundity [larvae] at length, Equation (6)					
a_ϕ [larvae]	Scaling factor	1.382×10^{-2}	1.063×10^{-2}	1.383×10^{-1}	1.210×10^{-1}
b_ϕ [larvae]	Exponent	4.571	4.623	3.767	3.820
Spawning frequency at length, Equation (7)					
a_{MB} [unitless]	Length independent factor	NA	NA	-3.899	-7.983
b_{MB} [1/cm]	Length dependent factor	NA	NA	0.1139	0.1196

^aSee text for explanation.

We assume that length $L(a)$ [cm] and weight $W(a)$ [kg] follow the allometry

$$W(a) = a_w L(a)^{b_w} \quad (3)$$

where a_w and b_w are the scaling and exponent parameters of the allometry, respectively. We obtained the parameters for Equations (2) and (3) from recent stock assessments of Widow, Chilipepper and Bocaccio West Coast populations and for the southern stock of Yellowtail. The stock assessments use the Schnute growth equation (Schnute 1981; Schnute and Fournier 1980) so we obtained L_∞ and a_0 by conversion of the parameters L_1 and L_2 of the Schnute growth equation (Methot and Wetzel 2013, Appendix A).

2.3.2 | Maximum Age and Natural Mortality

Expected lifetime egg production is calculated from the age at recruitment to the maximum possible age of adults. We assumed recruitment at age 0 and a maximum age from the literature

of 64years for Yellowtail (Shaw and Archibald 1981), 54years for Widow (Adams et al. 2019), 35years for Chilipepper (Love et al. 2002) and 40years for Bocaccio (Love et al. 2002; Table 2).

Consistent with the stock assessments, we used a constant rate of natural mortality M after recruitment to the population for our study species. However, alternative age- and size- based assumptions of M can be applied for other species (Brodziak et al. 2011). When natural mortality is constant in the absence of fishing, the probability of survival $S(a)$ to age a is

$$S(a) = e^{-Ma} \quad (4)$$

2.3.3 | Maturity

We model the probability of female maturity-at-age, $p_{f,m}(a)$ as a logistic function of length-at-age depending on the shape parameter, b_m and the length, L_{50} at which 50% of females in the population are mature (by convention the length at maturity in a population)

$$p_{f,m}(a) = \frac{e^{(L(a)-L_{50})/b_m}}{1 + e^{(L(a)-L_{50})/b_m}} \quad (5)$$

We obtained female maturity-at-length parameters from recent stock assessments, except for Yellowtail, where we used the estimate of L_{50} specific to California (Wyllie Echeverria 1987) converted from total length to fork length (Echeverria and Lenarz 1984), which better characterized the life history of the southern stock. When maturity was reported by length, we found the age at which 50% of the females in the population are mature by converting L_{50} to the age, a_{50} at which 50% of the females are mature by using the length-at-age relationship in Equation (2).

The stock assessment for Widow fitted age-at-maturity directly, with 50% of individuals mature at the age of 5.47 years. For comparison to the other species, we determined the value for L_{50} from the vBGF. The analogue of b_m is the dispersion parameter in a logistic model of maturity-at-age, which for Widow was $b_m = 0.775$.

2.3.4 | Fecundity

We model brood fecundity-at-age $\phi(a)$ as a power function of maternal length-at-age (Dick et al. 2017)

$$\phi(a) = a_\phi L(a)^{b_\phi} \quad (6)$$

where the scaling constant, a_ϕ and the exponent, b_ϕ are the result of a Bayesian hierarchical meta-analysis of fecundity-length parameters for *Sebastes* species by sub-genera (Dick et al. 2017). Dick et al. (2017) reported parameters in terms of total length, which we converted to fork length through a species-specific length conversion (Echeverria and Lenarz 1984).

2.3.5 | Spawning Frequency

We set the probability of multiple brooding-at-age to zero for species that have only been observed as single brooders (Yellowtail and Widow). For species observed as multiple brooders (Chilipepper and Bocaccio), we modelled the probability of producing two broods a year, $v(a)$, as a logistic function of maternal length-at-age $L(a)$ following Lefebvre et al. (2018)

$$v(a) = \frac{e^{a_{MB} + b_{MB}L(a)}}{1 + e^{a_{MB} + b_{MB}L(a)}} \quad (7)$$

We determined the parameters a_{MB} and b_{MB} by fitting a logistic regression to data on multiple brooding females collected by the NOAA Southwest Fisheries Science Center (NOAA SWFSC) from 2009 to 2020 in central and southern California (Lefebvre et al. 2018). Multiple brooding is more prevalent for Chilipepper in southern California but also occurs in central California in some years. We updated Lefebvre et al. (2018) to pool data across regions for Chilipepper to represent the coastwide population and to model unpublished multiple brooding information on Bocaccio from that study.

2.4 | Early Life History (ELH)

In the following we use ELH as an acronym for Early Life History and the associated mathematical quantities, such as the duration of the pre-recruitment period in days (D_{ELH}), weight during the ELH (W_{ELH}) and the probability of survival to each day during the ELH (S_{ELH}). These quantities are used to estimate α .

We now show how α can be computed in two ways. The first method is based on evolutionary principles for persistence of the population and provides a lower bound for α . The second is an empirical method that uses weight- and stage- based daily natural mortality rates from a meta-analysis (McGurk 1986) to calculate survival during the ELH period. For the empirical method, we assume that ELH growth in mass is exponential prior to recruiting to the population (Buckley et al. 2006; Kaji et al. 1996; Shoji et al. 2005).

The ELH growth information used to inform early life survival and α comes from reproductive ecology studies of rockfish, including the NOAA SWFSC's annual Rockfish Recruitment and Ecosystem Assessment Survey (RREAS) and other surveys of benthic juveniles in early settlement (Field et al. 2010; Laidig 2010; Ralston et al. 2013; Woodbury and Ralston 1991). The methods to model ELH growth and specific data sources are described below and in Material S2.

2.4.1 | Weight at Birth

We used the initial weight of larvae at birth to inform early life growth (Table 3). To obtain the species-specific weight of a larva at birth W_B [g] (or weight of a hydrated egg for egg-releasing species), we sampled late-stage larvae from rockfish ovaries when the brood was close to parturition. We divided the fresh weight of a subsample [g] by the count of larvae to estimate an individual larva weight. The inverse of these subsample counts (i.e., larvae per g of gonad and total gonad weight) was used to calculate fecundity in Beyer et al. (2015), Lefebvre et al. (2018) and Beyer et al. (2024).

2.4.2 | α Determined by Persistence of the Population

At the minimum, α must be sufficiently large, denoted by $\alpha_{\text{persistence}}$, for the population to remain in a deterministic steady state (He et al. 2006). In the steady state with a 50:50 sex ratio at birth, a female must produce enough offspring over a lifetime to replace the spawning female and its male mate in the next generation. Thus, the survival of offspring for a population to remain in the steady state is two individuals surviving from the total eggs produced by a female over a lifetime so that

$$\alpha_{\text{persistence}} = \frac{2}{LEP_0} \quad (8)$$

This is a hard floor for α in the sense that a population subject to fluctuations will go extinct at the persistence value of α (see He et al. (2006) for more discussion).

TABLE 3 | Early life history parameters and their values.

Variable	Short description	Yellowtail	Widow	Chilipepper	Bocaccio
W_B [g]	Weight at birth	4.8×10^{-4}	5.7×10^{-4}	10.4×10^{-4}	6.8×10^{-4}
PLD [d]	Pelagic Larval Duration	103	105	138	100
Weight [g] – length [cm] allometry, Equation (13)					
$a_{w_{ELH}}$	Scaling factor	8.36×10^{-3}	8.36×10^{-3}	8.36×10^{-3}	8.36×10^{-3}
$b_{w_{ELH}}$	Exponent	3.403	3.403	3.403	3.403
Weight [g] at age [d], Equation (14)					
$a_{\text{empirical}}$	Scaling factor	3.03×10^{-8}	3.96×10^{-9}	3.40×10^{-9}	1.07×10^{-9}
$b_{\text{empirical}}$	Exponent	3.763	4.283	4.245	4.608

2.4.3 | α Determined From ELH Growth and Weight- and Stage- Based Daily Natural Mortality Rates

Time dependent growth in mass during the ELH can be used to estimate survival using the McGurk (1986) meta-analysis of daily natural mortality rates to find mortality rates at pre- and post- transitional stages for fish eggs, larvae and pelagic juveniles from their dry weight. Hsu et al. (2024) recently compared McGurk's allometry with empirical measurements of the rate of mortality for Pacific saury (*Cololabis saira*, Scomberesocidae) and found good agreement.

Following McGurk (1986) we assume dry weight [g], denoted by W_{dry} , is 20% of the wet weight. Based on dry weight, the instantaneous daily natural mortality rate for pelagic larvae with a dry weight less than $5.04 \cdot 10^{-3}$ g is

$$M_{\text{larva}} = 2.2 \cdot 10^{-4} W_{\text{dry}}^{-0.85} \quad (9)$$

For pelagic juveniles heavier than the transitional dry weight, the instantaneous daily natural mortality rate is

$$M_{\text{juvenile}} = 5.26 \cdot 10^{-3} W_{\text{dry}}^{-0.25} \quad (10)$$

We denote the probability of an individual surviving to day d of the ELH period by $S_{\text{ELH}}(d)$ so that $S_{\text{ELH}}(0) = 1$ and for subsequent days

$$S_{\text{ELH}}(d) = S_{\text{ELH}}(d-1)e^{-M_{\text{ELH}}(W_{\text{ELH}}(d))} \quad (11)$$

where $M_{\text{ELH}}(W_{\text{ELH}}(d))$ is the rate of mortality on day d determined from either Equations (9) or (10), according to $W_{\text{dry}} = 0.2W_{\text{ELH}}(d)$.

We then set

$$\alpha = S_{\text{ELH}}(D_{\text{ELH}}) \quad (12)$$

which is survival to the final day of the ELH period, D_{ELH} . To operationalize Equation (12) using empirical observations of young-of-year (YOY) size-at-age and estimates of pelagic larval duration (PLD), we relied mainly on data from the NOAA SWFSC annual RREAS mentioned above, which is a mid-water trawl survey that targets pelagic juvenile rockfish along the

West Coast in the months prior to settlement to develop pre-recruitment indices of abundance (Ralston et al. 2013). The survey has sampled a core area off of central California each year since 1983, generating a 42-year time series. Furthermore, since 2001 the survey expanded in scale and combined with other surveys to cover the entire West Coast (Field et al. 2021). Almost all pelagic juvenile rockfish caught in the survey are measured for length and a subset of individuals are measured for weight. Otoliths were extracted to estimate age in days since birth (Woodbury and Ralston 1991).

Using YOY length-at-age information from the RREAS for the focal species we developed linear ELH length-at-age relationships to model species-specific ELH growth (Material S2, Figure SM2-1). The paired length and age data included 378 Yellowtail, 749 Widow, 620 Chilipepper and 631 Bocaccio. Weight information is generally sparse for most species in the survey. This is due to the challenges associated with equipping oceanographic vessels with scales accurate to 0.1 g or less on a moving vessel. We were unable to fit species-specific ELH weight-at-age relationships with such limited weight data. Instead, we converted the robust YOY length-at-age dataset to the weight-at-age information needed to apply the weight- and stage- based daily natural mortality rates to estimate α by developing and applying a general ELH weight-length relationship to convert the data (Material S2, Figure SM2-2).

We fit the ELH weight-length relationship to data from three sources. The first data source included the subset of pelagic juveniles collected by the RREAS that had paired length and weight information, with sample sizes of 10 Yellowtail, 25 Widow, 37 Chilipepper and 21 Bocaccio. The YOY pelagic juvenile lengths ranged from 1.22 cm to 7.06 cm. We supplemented weight information from a second set of unpublished length and weight measurements from newly settled juvenile rockfish in nearshore kelp forests in central California, also collected by the NOAA SWFSC (Laidig 2010; Laidig T. unpublished), which sampled Yellowtail ($n=9$) but none of the other study species. The lengths of newly settled Yellowtail juveniles ranged from 4.29 to 6.01 cm. We also included weight information from juveniles of the study species that became trapped in the San Onofre, California nuclear power plant seawater intake and cooling system (Field et al. 2010). This third dataset sampled near shore juveniles. We restricted the dataset to juveniles less than 10 cm, assuming that these were the most

recently settled. This resulted in a sample size of 9 Bocaccio juveniles, with a range in length between 4.9 and 9.7 cm.

We used the allometric form.

$$W_{\text{ELH}} = a_{W_{\text{ELH}}} L_{\text{ELH}}^{b_{W_{\text{ELH}}}} \quad (13)$$

to model the ELH weight (W_{ELH} , wet weight, [g]) and length (L_{ELH} , standard length, [cm]) relationship, where $a_{W_{\text{ELH}}}$ is the scaling factor and $b_{W_{\text{ELH}}}$ the exponent of the power function. We pooled species information due to a lack of weight data and found the parameters of Equation (13) by fitting a generalized linear mixed effects model (GLMM) to the natural log transformed ELH length and weight data, with individual species modelled as random effects (Gelman and Hill 2007). The intercept parameter was back-transformed from log-space using a bias-correction multiplier of $\exp(\sigma^2/2)$. We used the fixed effect parameters to apply a single, 'general' ELH weight-at-length relationship to all four focal species (Table 3).

The general ELH weight-at-length relationship allowed us to then estimate species-specific weight-at-age during the ELH period by converting the robust ELH length-at-age data to weight-at-age and assuming that growth in weight during the ELH period is exponential. Once the length-at-age data were converted to weight-at-age, we fit a linear least squares regression to the natural log transformed converted weight and age data specific to each species (Material S2, Figure SM2-3) to model ELH weight each day during the ELH period.

$$W_{\text{ELH}}(d) = a_{\text{empirical}} d^{b_{\text{empirical}}}. \quad (14)$$

Similar to above, $a_{\text{empirical}}$ is the scaling factor that was back-transformed using the bias-correction above, and $b_{\text{empirical}}$ the exponent of the power function. We needed this relationship to apply the daily weight- and stage- based natural mortality estimates to estimate α . In some cases, shortly after birth, the weight predicted by Equation (14) fell below the empirical weight at birth, in which case we replaced the predicted weight by the empirical weight at birth.

The empirical computation of α also requires the duration of the ELH period, commonly called the pelagic larval duration (PLD), which includes both larvae and pre-recruit pelagic juveniles in our study. To estimate the PLD for Bocaccio, we used direct observations of settlement from D'Souza (1998). We did not have direct observations for the other three species so we used the age (in days) at which 50% of pelagic young-of-year (YOY) settle based on declining age frequency information from the RREAS pelagic juvenile rockfish survey (Figure SM2-4). In Material S2 we estimate the lengths of the PLDs to be 103 d for Yellowtail, 105 d for Widow and 138 d for Chilipepper. We assume a PLD of 100 d for Bocaccio from D'Souza (1998).

We used the species-specific ELH weight-at-age, corrected for values falling below the weight-at-birth and the PLD to estimate the probability of survival in the ELH phase by applying the McGurk (1986) daily natural mortality rates (Equations 9 and 10) to estimate daily survival (Equation 11) so that

$$\alpha_{\text{empirical}} = S_{\text{ELH}}(\text{PLD}) \quad (15)$$

Because direct estimates of the early life survival of pre-recruits is generally lacking, our two methods complement one another to allow assessment of the adequacy of the model-based values of α . For example, the persistence method can be used to obtain the lower bound of α to ensure that the estimate from the empirical data is not lower than survival at persistence.

2.5 | Sensitivity of Steepness to Parameters

We used an elasticity analysis to better understand the influence of each life history parameter, generically denoted by p , on steepness, generically denoted by $h(p)$. For this analysis we held all but one parameter constant, varied the focal parameter by +20% or -20% (denoted by Δp) of its baseline value and calculated steepness at each of the perturbed values ($h(p + \Delta p)$ or $h(p - \Delta p)$). We report the proportional change in steepness due to varying the parameter, that is, $\frac{1}{h(p)}(h(p + \Delta p) - h(p))$ or $\frac{1}{h(p)}(h(p) - h(p - \Delta p))$.

We also explore other assumptions of life history traits in Material S3. These include a sensitivity to multiple brooding in Chilipepper and Bocaccio where the number of broods is restricted to one per year and a sensitivity to an alternative assumption for post-recruit natural mortality that uses a size- and age- based M , rather than a constant M , to model higher rates of post-recruit natural mortality prior to maturation. The supplemental also shows how our calculation of steepness for each of the four focal species is sensitive to differences in the calculated expected lifetime egg production and the sex ratio at birth. The sensitivity of steepness to different values assumed for early life survival α , the pelagic larval duration (PLD) and constant post-recruit natural mortality M are shown in the main text.

In Material S4 we present simulation methods to estimate a distribution for steepness to generate priors that incorporate the variability and uncertainty in the life history parameters.

3 | Results

3.1 | Lifetime Egg Production

In Figure 1, we show the life history traits that are required for the computation of lifetime egg production in the absence of fishing, $\overline{\text{LEP}}_0$. We show $\overline{\text{LEP}}_0$ for the focal species in Table 4. Bocaccio had the highest $\overline{\text{LEP}}_0$, followed by Widow, Chilipepper and Yellowtail with the lowest.

3.2 | Early Life Survival

In Table 5 we show the resulting values of $\alpha_{\text{empirical}}$ for the focal species, all of which are greater than $\alpha_{\text{persistence}}$. Chilipepper had the highest estimated early life survival of pre-recruit larvae and

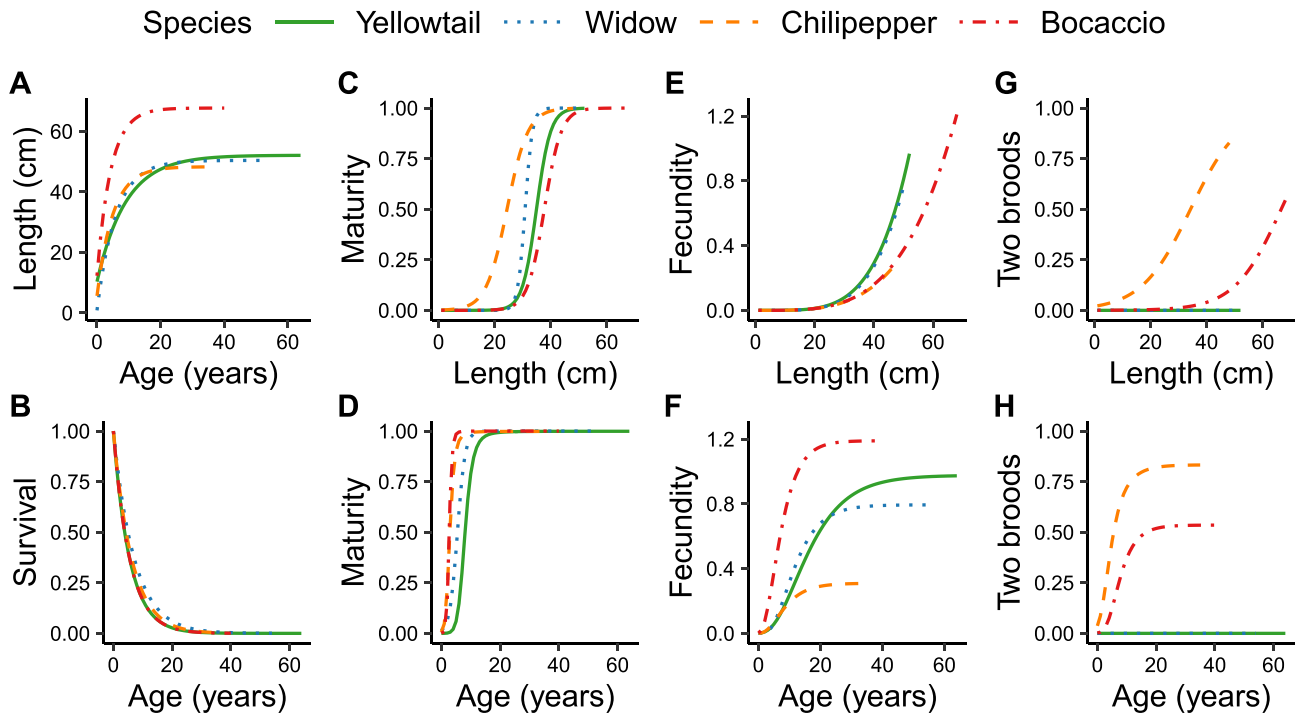


FIGURE 1 | Life history patterns as a function of age or size for the four focal species (green solid: Yellowtail; blue dotted: Widow; orange dashed: Chilipepper; red dot and dash: Bocaccio). A) Female length-at-age is determined from the von Bertalanffy growth function (vBGF); (B) the probability of survival to age is $S(a) = e^{-Ma}$ where M is the species-specific constant rate of natural mortality; (C, D) the probability of maturity-at-length from a fitted logistic regression converted using the length-at-age relationship to a probability of maturity-at-age; (E, F) brood fecundity-at-length (in millions of larvae) converted to brood fecundity-at-age using the length-at-age relationship; (G, H) and the fitted logistic regression for the probability of a female producing two broods-at-length converted to two broods-at-age using the length-at-age relationship. In panels (G) and (H) the two horizontal lines refer to Yellowtail and Widow, for which the probability of two broods is 0.

TABLE 4 | Expected lifetime egg production, $\overline{LEP}_0$ in the absence of fishing for the four focal species.

Species	$\overline{LEP}_0$
Yellowtail	4.71×10^5
Widow	1.22×10^6
Chilipepper	9.24×10^5
Bocaccio	2.69×10^6

TABLE 5 | Point values for early life survival, α calculated for population persistence, $\alpha_{\text{persistence}}$ and estimated from early life history data $\alpha_{\text{empirical}}$.

Species	$\alpha_{\text{persistence}}$	$\alpha_{\text{empirical}}$
Yellowtail	4.25×10^{-6}	1.63×10^{-5}
Widow	1.64×10^{-6}	1.49×10^{-5}
Chilipepper	2.17×10^{-6}	1.99×10^{-4}
Bocaccio	7.44×10^{-7}	2.54×10^{-5}

pelagic juveniles estimated from the ELH growth data, followed by Bocaccio, Yellowtail and Widow with the lowest early life survival.

TABLE 6 | Point values for steepness, h using the two different methods to estimate early life survival, α .

Species	$h_{\text{persistence}}$	$h_{\text{empirical}}$
Yellowtail	0.2	0.49
Widow	0.2	0.69
Chilipepper	0.2	0.96
Bocaccio	0.2	0.90

3.3 | Steepness

In Table 6 and Figure 2, we show the point values for steepness computed using the two methods for α . A value of $\alpha < \alpha_{\text{persistence}} = 0.2$ cannot persist in nature. For all four species, the empirical method produces a value of steepness consistent with persistence of the population. The empirical estimate of steepness is highest for Chilipepper, followed by Bocaccio, Widow and Yellowtail with the lowest estimate of steepness.

3.3.1 | Sensitivity to Variation in Parameter Values

In Figure 3, we show the sensitivity of steepness to a 20% increase or decrease in each life history parameter. This elasticity

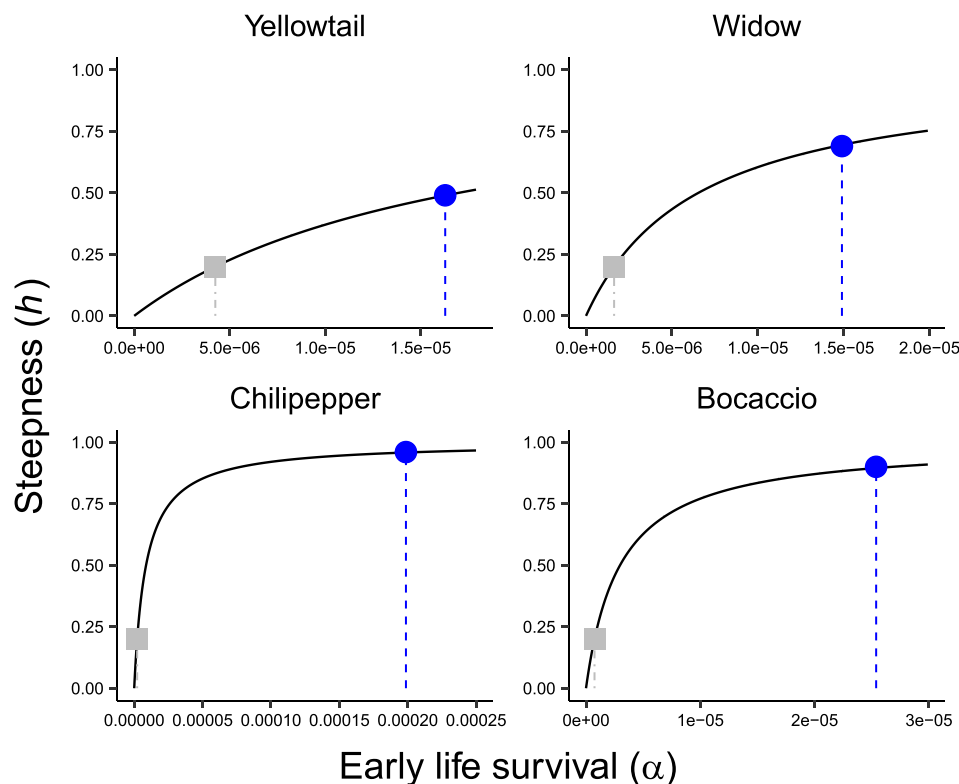


FIGURE 2 | Point values of steepness (h) for the four focal species as a function of α (black line). The grey dashed line and square indicates the estimate using $\alpha_{\text{persistence}}$, the minimum early life survival for population persistence and the blue dashed line and circle the estimate using $\alpha_{\text{empirical}}$.

analysis shows the corresponding proportional increase or decrease in steepness. For all four species, the calculation of steepness using the empirical method for α was most sensitive to (1) the vBGF asymptotic length, (2) the exponent of the brood fecundity-at-length relationship and (3) the weight of larvae at birth. The effects are asymmetric for either the increase or decrease in the parameter. The first two of these parameters influence the calculation of LEP_0 . In particular, the exponent of the fecundity relationship scales the strength of maternal size effects on brood fecundity. Changes in this parameter have a corresponding disproportional effect on steepness. The weight of larvae at birth is used to replace any values of predicted weight from the ELH weight-at-age model that fall below the weight at birth in the very early days of life. The number of days replaced with the birth weight was 14 d for Yellowtail, 17 d for Widow, 20 d for Chilipepper and 19 d for Bocaccio. This ELH growth information is then used to estimate early life survival α . Yellowtail and Widow were also sensitive to the rate of post-recruit natural mortality, the rate of growth and the pelagic larval duration. Steepness for Yellowtail was sensitive to the age at maturation.

In Material S3 we show that steepness is somewhat sensitive to multiple brooding in Chilipepper and Bocaccio. When second broods were prohibited, steepness for Chilipepper dropped from 0.96 to 0.93 and for Bocaccio from 0.90 to 0.87. Female Yellowtail and Widow produce only a single brood per year so were not included in that sensitivity analysis.

Steepness was less sensitive to an alternative pattern of post-recruit natural mortality M for Chilipepper and Bocaccio but was more sensitive for Yellowtail and Widow (Material S3). The

alternative M sensitivity analysis explored a higher post-recruit natural mortality rate prior to maturation with the same constant M for adults post-maturation. Steepness for Chilipepper dropped from 0.96 to 0.95 and for Bocaccio from 0.90 to 0.88 using the alternative age- and sized- based assumption for M . Steepness for Yellowtail dropped from 0.49 to 0.33 and for Widow from 0.69 to 0.55.

Simulations for distributions of steepness in Material S4 (Figure SM4-1) show wider distributions for Yellowtail and Widow relative to Chilipepper and Bocaccio.

4 | Discussion

We have shown how to use reproductive biology and early life history parameters to compute steepness, and illustrated the methodology with four species of rockfish. Our results show how differences in life history traits among species, even closely related ones such as rockfishes, influence steepness. For our focal species, steepness is informed by a wealth of life history information. This highlights the value of empirical studies of reproductive ecology, growth and early life history to better inform estimates of steepness and knowledge of stock productivity.

Our method for computing steepness from life history parameters can be adapted for species other than rockfish that have different patterns in life history traits with age or size. Since life history traits can be modelled as general and flexible functions of age, alternative assumptions are straightforward to implement. For example, instead of assuming a constant

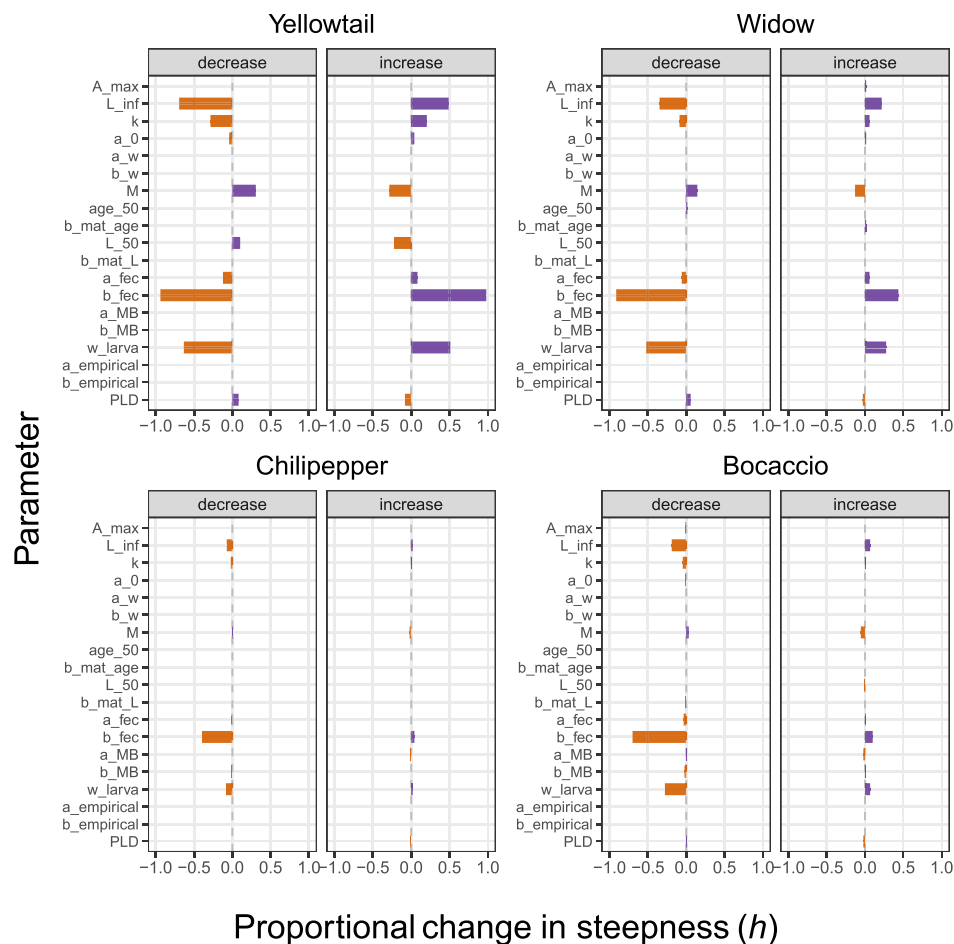


FIGURE 3 | Proportional change in steepness (h) using $\alpha_{\text{empirical}}$ when all but one parameter is held constant and the focal parameter is increased by 20% or decreased by 20%.

post-recruit natural mortality rate with age, which we chose for consistency with stock assessments, one could assume an age- or size-dependent rate (Brodziak et al. 2011) as we show in a sensitivity analysis in Material S3. Analysts should carefully consider the life history traits, relationships with age and the data available for their population of interest prior to implementing the method.

With sufficient data, such as what we showed here for the four focal species, steepness can be computed from the life history parameters as an alternative method to statistically estimating steepness in a stock assessment. However, our method is not meant to replace the traditional estimation methods of steepness for stock assessments but rather as a complement to them. For example, our life history based computation of steepness could be used to develop a prior on steepness to improve estimation in a stock assessment (described in more detail below) or to confirm that the estimate of steepness from a stock assessment or meta-analysis is plausible, based on the life history traits of that population. Importantly, for rockfish we showed that large differences in steepness are possible; in fact, they should be considered likely among species due to different life history traits.

Our calculation of steepness is sensitive to early life history survival, for which empirical observations are often lacking. Thus, we showed two methods to inform estimates of early life survival,

α . Each method provides different information. The persistence criterion that each female replaces itself and its mate in the next generation is a clear minimum value for α , but we should never expect to see it in nature because small fluctuations will rapidly lead to extinction of a population with the persistence value of α . The calculation of α at persistence should be used as a hard floor for early life survival and a check to ensure that the empirical method estimates early life survival higher than the value at persistence.

Early life history growth information is important to apply the ELH daily weight- and stage-based natural mortality rates to estimate early life survival and to compute steepness. However, ELH weight data are often lacking for fish larvae and pelagic juveniles due to the difficulties of collecting accurate weights at sea for very small organisms. We combined the sparse ELH weight data for rockfish to convert a robust length-at-age dataset to weight-at-age using a pooled species weight-length key. It is preferable to use species-specific weight-at-age data or, at least, a species-specific weight-length relationship when sufficient data exist; however, we did not have the data to do so. Our method is sensitive to estimates of early life growth and shows the importance of collecting these data as part of future research to improve estimates of early life survival.

It is also important to consider intra-specific variation in life history traits, which could influence differences in productivity

among stocks of a particular species. One should not expect that the values of steepness in Table 6 to apply across the entire range of any of the species in our study because there will typically be biogeographic variation in the life history parameters. Several studies have shown that body sizes are generally larger and lifespans longer at greater depths and higher latitudes (Atkinson and Sibly 1997; Gertseva et al. 2017; Kapur et al. 2020; Munch and Salinas 2009). For example, the Canadian stock of Bocaccio appears to have a far lower estimated rate of natural mortality (0.07–0.09 per year) than the California stock (0.18 per year), a considerably slower growth rate (female von-Bertalanffy growth coefficient of about 0.15 compared to 0.23 for California), a larger asymptotic size (L_{∞} of 78 cm compared to 67.7 cm in California) and a later age-at-maturity (age at 50% maturity approximately 6 years rather than 2.7 years) compared to the California stock (DFO 2024; He and Field 2017). Given this variation, our point estimates of steepness can be used as the starting point for developing priors for steepness of each of the study species outside of California, from where most of our data were drawn and by using simulation methods. We emphasize that steepness is likely to be stock-specific, in addition to species-specific.

In Material S4: Simulation to Generate Priors for Steepness we show how to generate distributions for steepness by assigning distributions to the life history parameters. Similarly, because life history parameters for a species in a given location may vary over time, either because of simple stochastic variation or because of shifting climate (Hsu et al. 2024; McClure et al. 2023), one should not think of the value we computed as the value of steepness fixed forever. For example, for the four focal species one could update both adult life history parameters and ELH information to explore variation in steepness through time, with shifts in productivity or oceanographic conditions, or by region for specific stocks where life history traits differ due to regional differences in the environment.

4.1 | Steepness and Life Histories

We more closely examine the connection between steepness and life histories that is captured in Equation (1). To begin, if we let $x = \alpha(1-r)\overline{LEP}_0$, then Equation (1) becomes written as $h(x) = \frac{x}{4+x}$ from which we draw two conclusions. First, if two species have the same product $\alpha(1-r)\overline{LEP}_0$, they will have the same steepness, regardless of the particular values of α , r and $\overline{LEP}_0$. Second, since $h(x)$ always increases with x ($\frac{dh}{dx} > 0$ for all $x > 0$), if two species, indicated by subscript 1 and 2, have the relationship that $\alpha_1(1-r_1)\overline{LEP}_{0,1} < \alpha_2(1-r_2)\overline{LEP}_{0,2}$ then the steepness of species 2 will be greater than the steepness of species 1, again regardless of the individual values of α , r and $\overline{LEP}_0$. For example, a less fecund species could have a higher steepness than a more fecund one because the survival during the early life history is greater for its offspring than for the more fecund species (see Kai and Fujinami (2018) for one example). These simple mathematical facts shed important insight on biology.

In the case of constant natural mortality, steepness is determined by twelve life history parameters $\alpha, r, M, L_{50}, b_m, a_\phi, b_\phi, a_{MB}, b_{MB}, L_{\infty}, k$ and a_0 . This has three related implications. First, if one looks for simple correlations, such as plotting steepness against α (which is also the slope of

the BH-SRR at the origin), M , or age at maturity, the resulting plots will likely have enormous scatter because of plotting a function in 2 dimensions that also depends on 10 other parameters. Second, sophisticated methods are required to parse out the relationships from data alone (Horswill et al. 2025; Thorson 2020; Thorson et al. 2014, 2019). Third, and most important, Equation (1) constrains the relationship between steepness and the life history parameters. For example, specifying both steepness and natural mortality in a stock assessment may result in apparent statistical inconsistency when it is, in fact, biological inconsistency (Grunloh 2024; Mangel et al. 2013).

The elasticity analysis allowed us to identify specific biological parameters where a proportional change in the parameter may have a disproportional effect on the calculation of steepness. We showed that steepness for our four focal species is most sensitive to differences in asymptotic length from the vBGF, the strength of maternal size effects on brood fecundity (fecundity-length exponent) and the weight of larvae at birth, which is used to inform ELH growth and survival. The asymptotic size and fecundity are related in that fecundity increases disproportionately with maternal size in these species. The maternal size effects on brood fecundity are stronger for Yellowtail and Widow compared to Chilipepper and Bocaccio, shown by the fecundity exponent. Yellowtail and Widow were also sensitive to other parameters, such as the rate of natural mortality, growth and the pelagic larval duration. This sensitivity analysis provides guidance for areas of future research to better understand variability in these life history parameters and influence on steepness.

In Figure 4, we show all the panels in Figure 2 on a single graph. For a given value of α , the values of steepness are organized according to Yellowtail < Chilipepper $\approx$ Widow < Bocaccio. The shapes of these curves are determined by the variables influencing expected lifetime egg production (i.e., growth, adult survival, maturity, fecundity and spawning frequency). Bocaccio, which are comparatively fast growing, obtain a large size and mature early, have the highest expected lifetime egg production (Table 4). Yellowtail, which are comparatively slower growing, obtain a smaller asymptotic size than Bocaccio but similar to

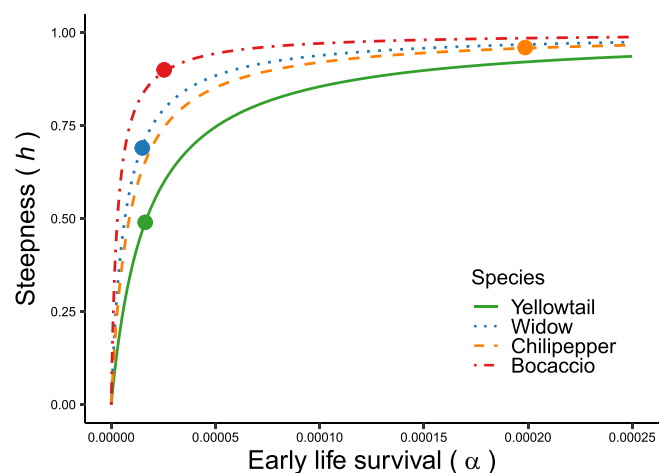


FIGURE 4 | Sensitivity of steepness (h) to early life survival α for the four focal species, colour and texture coded in the legend. The coloured circles are the point estimates of steepness using $\alpha_{\text{empirical}}$.

Chilipepper and Widow and are comparatively slower to mature and have the lowest expected lifetime egg production.

Species with similar expected lifetime egg production will have similar shaped curves, however, α can still vary dramatically among species based on the ELH dynamics and can result in very different values of steepness. For example, one possible reason for the higher early life survival of Chilipepper larvae is that the weight at birth is nearly double the weight at birth of the other three species, which may confer a survival advantage. Chilipepper generally release larvae earlier in the winter season, with a peak release in January in central California, compared to a later peak in larval release of February for the other three species (Love et al. 2002). It is possible that Chilipepper evolved larger larvae to cope with the poorer feeding conditions earlier in the winter compared to larvae released later in the year (Stafford et al. 2014). This hypothesis for differences in early life survival among rockfishes based on birth weight and larval growth is testable as part of future research to improve our understanding of recruitment dynamics.

Other researchers applying the Mangel et al. (2010) approach found estimates of steepness to be even more sensitive to some life history parameters. For example, Kolody et al. (2019, 228) applied the methods of Mangel et al. (2010) to southern bluefin tuna and found that letting larval survival range from 0.935 to 0.949 per day lead to steepness $0.25 \leq h \leq 0.95$. We note that the method of Mangel et al. (2010) uses spawning biomass rather than egg production to estimate steepness and is agnostic on the determination of α . Our deeper focus on early life history in the

current analysis allows us to explore specific early life history questions related to early life survival, such as 'How does pelagic larval duration affect steepness?'. In Figure 5, we show the single parameter sensitivity across a wide range of possible values for ELH duration. It is expected that the estimated steepness will decline as PLD increases because early life survival declines, but in our example the rate of decline for each of the focal species is very different. Both this sensitivity and our elasticity analysis do not indicate such a high level of sensitivity to early life history parameters as reported in Kolody et al. (2019), at least not for rockfishes, but this can be explored with the collection of additional ELH information and comparison of different methods to estimate early life survival.

Our focus on reproductive biology also allows us to explore counter-factual thought experiments (Pearl and MacKenzie 2019) related to different life history patterns. As described above, most female *Sebastes* produce only a single brood of larvae each year (single brooding); however, at least fifteen species are capable of multiple broods during a reproductive season, including two of our study species, Chilipepper and Bocaccio (Lefebvre et al. 2018). Multiple brooding is more common in larger females than smaller females (Ralston and MacFarlane (2010) for Bocaccio, Lefebvre et al. (2018) for Chilipepper). We found there is little change in estimated steepness if the second brood is prohibited: for Chilipepper, steepness dropped from 0.96 to 0.93; for Bocaccio the corresponding drop was from 0.90 to 0.87. Limiting these species to only a single brood is equivalent to assuming an extreme of zero survival of larvae from the second brood. Thus, the high steepness of these species is not simply a matter of the

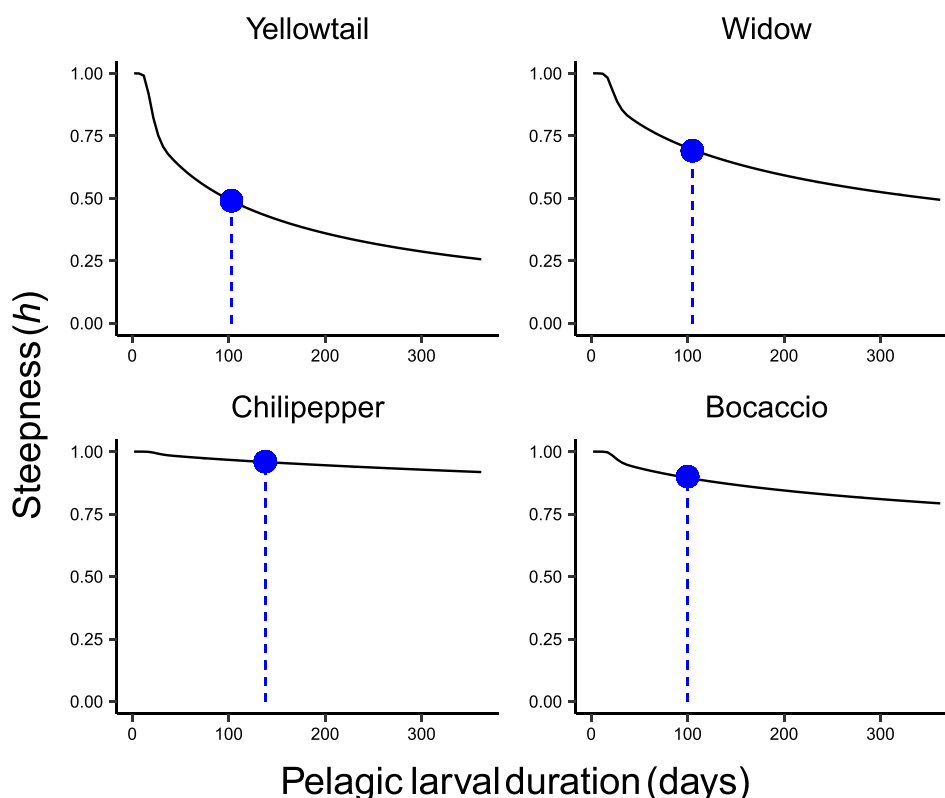


FIGURE 5 | Sensitivity of steepness (h) to the pelagic larval duration (PLD) for the four focal species. The blue dashed line and blue circle are the empirical PLD and corresponding estimate of steepness, respectively.

capability of females of these species to produce two broods a year. However, to better understand the importance of multiple brooding in rockfishes, future research should focus on potential differences in larval survival rates between first and subsequent secondary broods to better understand the evolution of this reproductive pattern in *Sebastes*.

The sensitivity analysis of steepness to an alternative, higher post-recruit natural mortality pattern based on size and age prior to maturation slightly lowered the estimate of steepness for Chilipepper and Bocaccio relative to the assumption of constant, post-recruit M in our base model, but was much lower for Yellowtail and Widow. This was due, in part, to the earlier age at maturation of Chilipepper and Bocaccio, which correspond to fewer years of higher natural mortality in the sensitivity when compared to Yellowtail and Widow, which mature at considerably older ages. West Coast rockfish stock assessments currently assume a constant M post-recruitment however future studies should explore possible size- or age- based assumptions for M , which can be compared to these sensitivities to better understand stock productivity.

4.2 | Comparison of Steepness From the Stock Assessments With That Determined by Reproductive Biology

In the stock assessments for Yellowtail and Chilipepper both steepness and natural mortality were fixed, whereas natural mortality was estimated in the stock assessment of Widow and Bocaccio, with steepness fixed. In Figure 6, we compare the value of steepness that was assumed in the stock assessments with the value that emerges when one uses reproductive biology. For Widow, the assumed value of steepness is close to the one predicted by reproductive biology. For Yellowtail, the assumed value for steepness was above that predicted by reproductive biology. For Chilipepper and Bocaccio—the species with multiple broods—the assumed values of steepness were much less than those predicted using reproductive biology. These differences should be explored to better understand differences in productivity among stocks and how to model steepness that better aligns with the species biology.

For reasons explained in Mangel et al. (2013) we recommend not specifying both the rate of natural mortality and steepness in a

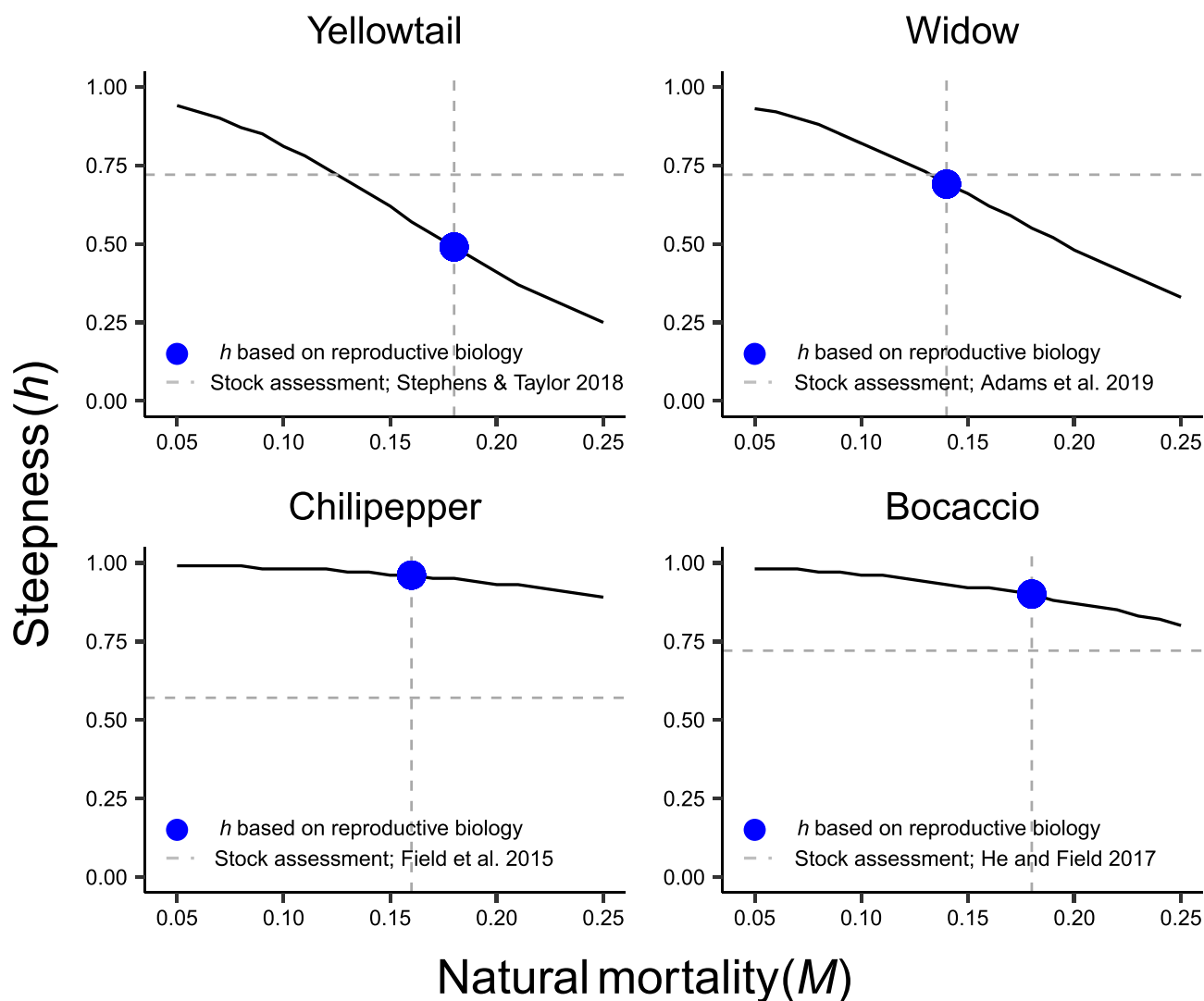


FIGURE 6 | Sensitivity of steepness (h) to the post-recruit rate of natural mortality for the four focal species (black line) compared to the values of natural mortality and steepness assumed in the stock assessments (vertical and horizontal dotted lines respectively) and the value of steepness predicted by using reproductive biology (blue circle).

stock assessment, but if one insists on doing so then we recommend using reproductive biology to confirm that the specifications of steepness and the rate of natural mortality are consistent with the life history of the stock being assessed.

4.3 | The Meaning of Steepness Approaching 1

It is clear from Equation (1) that $h = 1$ only occurs in the limit of $\alpha(1-r)\overline{LEP}_0 \rightarrow \infty$. Since both α and $1-r$ are less than 1, this limit requires that lifetime egg production in the absence of fishing approaches infinity. Although infinite egg production is not possible it may be argued that $h = 0.96$, as for Chilipepper, is close enough to 1 that one can set steepness equal to 1 in the stock assessment and thereby lower the burden of the work. If one does so, then it is helpful to clarify what is being assumed. For example, Kolody et al. (2019, pg. 228) noted that setting steepness equal to 1 is the most optimistic prediction for recruitment possible and has a high risk of overfishing. They note, as we have, that the assumption that steepness is 1 is contrary to a precautionary approach and contradicts fundamental biology.

To explore exactly what replacing a value of steepness less than 1 by a value that is very close to but less than 1 in terms of the reproductive biology, we return to Equation (1) and imagine that h is specified (say between 0.9 and 0.999), focus on Chilipepper and assume that $\alpha(1-r)$ is known. For computations we use $\alpha_{\text{empirical}}$ for Chilipepper from Table 5. We let $\overline{LEP}_0(h)$ denote the lifetime egg production in the absence of fishing required to produce a particular value of steepness from Equation (1). Elementary manipulations show that

$$\overline{LEP}_0(h) = \frac{4h}{\alpha(1-r)(1-h)} \quad (16)$$

This is an algebraic restatement that setting steepness equal to 1 requires infinite productivity. For values of $h < 1$ but different than 0.96 (our point estimate for steepness for Chilipepper using $\alpha_{\text{empirical}}$), we define relative lifetime egg production as the ratio of $\overline{LEP}_0(h)$ to the value for Chilipepper in Table 4. We show this ratio in Figure 7 for different values of steepness. Replacing the empirical point estimate $h = 0.96$ by $h = 0.999$ requires a greater than 40-fold increase in the current estimate of lifetime egg production in the absence of fishing. We are prompted to ask how frequently such an increase in $\overline{LEP}_0$ occurs, but this is beyond the scope of the current paper.

4.4 | Recommendations for West Coast Rockfishes

Our results show that we can give a detailed biological basis for steepness, and that our method has the potential to be used in support of stock assessments that provide management advice for West Coast fisheries. Since the ideal approach for estimating steepness should be within an assessment model itself, we recommend that our estimates be used to develop diffuse priors, rather than fixed estimates, which is consistent with the intention of using priors for steepness to inform West Coast rockfish over the past two decades (Dorn 2002; Thorson et al. 2019). While the meta-analysis approach enabled a degree of stability in addressing productivity estimates for this important assemblage of fishes, there has been a

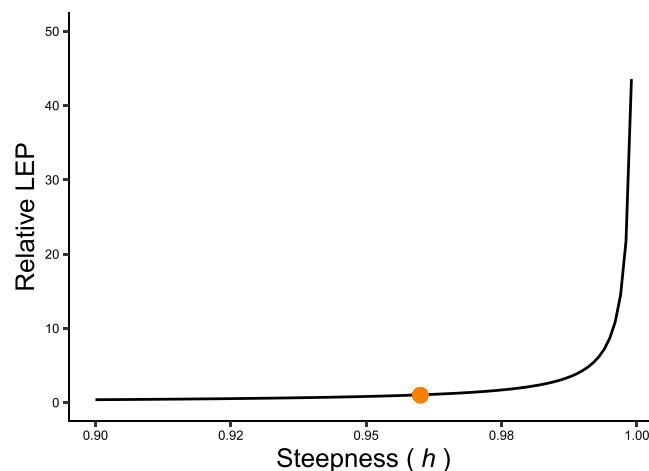


FIGURE 7 | Relative lifetime egg production, $\overline{LEP}_0(h)$ for Chilipepper needed to achieve a specified value of steepness (h) ranging from 0.9 to 0.999. Relative $\overline{LEP}_0(h)$ is the calculated value of $\overline{LEP}_0$ for a given value of steepness divided by the empirical $\overline{LEP}_0$ for Chilipepper in Table 4 in the absence of fishing. The orange dot shows the relative value of 1 at our point estimate.

growing level of discomfort with results of the meta-analysis, particularly as associated with the degree of variability in the results based on the assessments included for any given update (Thorson et al. 2019), concerns over the potential for bias in the priors to propagate across multiple meta-analyses (He and Field 2019) and the drift toward higher estimates of steepness in more recent years. We highlight four key points regarding how our results provide the basis for developing a new approach for informing steepness:

- First, our results indicate that high values of steepness for rockfish are plausible, particularly for species such as Chilipepper and Bocaccio that have relatively fast life histories. Chilipepper and Bocaccio have faster growth, earlier age of maturity, greater spawning frequency and shorter expected lifespans relative to Yellowtail and Widow (Table 2). This is an important finding considering the most recently estimated values from the meta-analysis (ranging from 0.932 to 0.943) were considerably greater than all previous estimates of steepness for rockfish. The higher values were rejected for use in management at the time, and the previously estimated prior of 0.72 has continued to be used for rockfish stock assessments more recently through at least 2025 (PFMC 2025). Our analysis has shown how reproductive biology and early life history survival can lead to steepness values greater than 0.9 for at least some rockfish species.
- Second, our results indicate that lower values of steepness are equally plausible for rockfish, as suggested by our estimates for Yellowtail and Widow (0.49 and 0.69, respectively). These species have considerably slower life histories and more northern distributions relative to Chilipepper and Bocaccio. The lower estimates of steepness for these two species are closer to the boundaries of the range of the distribution of prior values developed for West Coast rockfish over the past two decades (0.58–0.78) and suggest that for such stocks, early estimates from the meta-analysis were likely associated with reasonable and useful estimates of productivity.

- Third, we emphasize that the contrast in our results for the higher productivity stocks (Chilipepper and Bocaccio) relative to the lower productivity stocks (Yellowtail and Widow) clearly demonstrates that a single value applied across this diverse and species-rich genus is likely to be inappropriate. Species with even slower life histories, such as Yelloweye rockfish (*S. ruberrimus*) or Rougheye rockfish (*S. aleutianus*), which have considerably slower growth as adults and later ages at maturity relative to our study species, are likely to be associated with even more disparate estimates of steepness and stock productivity. Although the current practice using the meta-analysis to develop a single prior for all West Coast rockfishes has the benefit of providing a level of parsimony among assessment results when data are insufficient to estimate it, our results indicate that the relative productivity among stocks is likely to vary considerably in response to the different life history characteristics of each stock.
- Fourth, our results clearly indicate that there is, and will remain, considerable uncertainty in both steepness and how to use the results of either priors or point estimates for steepness meaningfully. Many rockfish stock assessments are well informed by age data via biological sampling of adult stages and by a fairly large body of literature on early life history dynamics. Despite this, we show that modest changes in the estimates of growth, egg production and early life history parameters, such as ELH weight-at-age, weight of larvae at birth and pelagic larval duration, can influence point estimates of steepness and warrant further study.

Despite no shortage of uncertainty and challenges in any meaningful approach to informing steepness within assessment models, the approach described in this paper provides a more robust, life history-based foundation with which to develop steepness and productivity estimates for West Coast rockfish. Our recommendation is thus to refine uncertainty estimates in a manner consistent with the application of species-specific priors to use in assessment models, while simultaneously resolving the existing data gaps for these and other groundfish species that might constrain or bias such estimates.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

This study did not generate original data. Catch data from the NOAA Southwest Fisheries Science Center Rockfish Recruitment and Ecosystem Assessment Survey (RREAS) are available at https://coastwatch.pfeg.noaa.gov/erddap/tabledap/FED_Rockfish_Catch.html and are also accessible through the R package 'RREAS' (<https://github.com/tanyalrogers/RREAS>).

Endnotes

¹Since *Sebastes* give birth to live young, it would be appropriate to use $\overline{LLP}_0$ to denote lifetime larval production in an unfished population. We keep the notation $\overline{LEP}_0$ because of the preponderance of egg production in fishes that are spawners and not livebearers.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Material S1.** Computing steepness as a function of reproductive output. **Material S2.** Early life history (ELH) growth and pelagic larval duration (PLD). **Material S3.** Deterministic sensitivities. **Material S4.** Simulation to generate priors.

Supplementary Materials 1: Computing steepness as a function of reproductive output

We use the Beverton-Holt Stock-Recruitment Relationship (BH-SRR, Beverton & Holt [1957]) to model expected recruitment of young individuals to a population given the total reproductive output produced by spawning females in a given year, and an age-structured population model for the dynamics of individuals who successfully recruited to the population. Rockfish (*Sebastes* spp.) are live-bearing but most fish are not, so in this section we refer to eggs with the understanding that the analysis applies to larvae and pups as well. In deference to the predomination of eggs in reproduction by fish, we use LEP to denote lifetime offspring production, understanding that E could refer to eggs, larvae, or pups. The BH-SRR is based on the assumption that individuals in the recruitment class experience per-capita mortality with density independent and density dependent components (Mangel, 2006, 2021). We let $E(s)$ denote the number of individuals in the recruitment class at time s in the recruitment period and assume (following Beverton & Holt, 1957)

$$\frac{dE}{ds} = -m_1E - m_2E^2 \quad (\text{SM1.1})$$

where m_1 and m_2 are the rates of density independent and density dependent mortality respectively, in the sense that per-capita rates of mortality are m_1 and m_2E . We specify the initial number of eggs to Equation SM1.1.

The solution of Equation SM1.1 (see Mangel 2006, pg. 213) is

$$E(s) = \frac{e^{-m_1 s} E(0)}{1 + \left(\frac{m_2}{m_1}\right) (1 - e^{-m_1 s}) E(0)} \quad (\text{SM1.2})$$

19 If the time from offspring production to recruitment to the population is s_r , then $E(s_r)$ is
 20 the number of individuals in the recruitment class at the time of recruitment.

21 In light of the form of Equation SM1.2, we introduce the parameters $\alpha = e^{-m_1 s_r}$ and β
 22 $= (m_2/m_1)(1 - e^{-m_1 s_r})$ so that

$$E(s_r) = \frac{\alpha E(0)}{1 + \beta E(0)} \quad (\text{SM1.3})$$

23 and also denote the right side by $\bar{R}_0$.

24 With this parametrization, α is both the maximum (i.e., before density dependence acts)
 25 probability that an individual survives to time s_r and the slope of the BH-SRR as $E(0) \rightarrow 0$. When
 26 $E(0) = 1/\beta$ survival of an offspring propagule to recruitment is $\frac{\alpha}{2}$. The right side of Equation
 27 SM1.3 differs from the way Beverton and Holt (1957) wrote it (Mangel, 2021). When computing
 28 steepness, however, this form has two distinct advantages. First, steepness is independent of β
 29 (Mangel et al., 2010). Second, α only depends on the strength of density independent mortality
 30 m_1 .

31 To calculate the total number of offspring $E(t)$ produced by mature females in year t , we
 32 sum over age the number of females of each age and individual female reproductive traits at each
 33 age. The reproductive traits that vary by age include maturity (the fraction of mature females in
 34 each age group), batch or brood fecundity (the number of offspring [eggs, larvae or pups] a
 35 female releases at each spawning event by age) and spawning frequency (the number of batches

or broods released by a female by age). The total number of offspring also depends on the fraction of females at birth in the population, which we denote by $1 - r$.

In symbols, $E(t)$ is the summation over age a to the maximum age A of the number of females of age a at time t , determined by the sex ratio r and the total number of individuals of age a at time t denoted by $N(a, t)$, the probability that a female of age a is mature, $p_{f,m}(a)$, the batch fecundity at age a , $\phi(a)$, the probability that a female of age a has j batches in the current season, $\psi(j, a)$

$$E(t) = (1 - r) \sum_{a=0}^A N(a, t) p_{f,m}(a) \phi(a) \sum_{j=1}^J j \psi(j, a) \quad (\text{SM1.4})$$

Since our focal species have at most one or two broods per year (Lefebvre et al., 2018; Ralston & MacFarlane, 2010), we can simplify Equation SM1.4. In these species the probability of two broods increases with maternal size and age; we let $v(a)$ denote the probability that a female of age a has a second brood and replace Equation SM1.4 by

$$E(t) = (1 - r) \sum_{a=0}^A N(a, t) p_{f,m}(a) \phi(a) (1 + v(a)) \quad (\text{SM1.5})$$

This equation (SM1.5) assumes that the fecundity and the survival of larvae from second broods are identical to first broods. It may be necessary to modify the equation for other species.

Equations SM1.4 and SM1.5 require the number of individuals $N(a, t)$ in each age class at each time. We assume that individuals recruit to the population at age $a = 0$ and experience a rate of natural mortality $M(a)$ at age a so that, for $a > 0$ and $N(0, t-1)$ given by Equation SM1.3

$$N(a, t) = N(a - 1, t - 1)e^{-M(a-1)} \text{ (SM1.6)}$$

In stock assessments of West Coast rockfishes it is common to set $M(a) = M$, a constant, for post-recruitment stages. This is how we apply M to the study species but the method is flexible to different patterns in M by age (Brodziak et al., 2011). We keep the rate of mortality age dependent for the rest of this supplement.

Steepness is the ratio of recruits in the steady state when total offspring production is 20% of the steady state reproductive output to the steady state recruits in the absence of fishing.

$$\text{The latter is } \bar{R}_0 = \frac{\alpha \bar{E}_0}{1 + \beta \bar{E}_0} \text{ and the former is } \frac{0.2\alpha \bar{E}_0}{1 + 0.2\beta \bar{E}_0}.$$

In the steady state, the number of individuals depends only on age and not time so we denote them by $\bar{N}(a)$, and identify $\bar{N}(0) = \bar{R}_0$. Thus,

$$\bar{E}_0 = (1 - r) \sum_{a=0}^A \bar{N}(a) p_{f,m}(a) \phi(a) (1 + v(a)) \text{ (SM1.7)}$$

Iterating Equation SM1.6

$$\bar{N}(a) = \bar{N}(0) [e^{-M(0)-M(1)\cdots-M(a-1)}] \text{ (SM1.8)}$$

To simplify notation, we let $S(a) = e^{-M(0)-M(1)\cdots-M(a-1)}$ denote the probability an individual propagule survives to age a , and let $\overline{LEP}_0$ denote the expected lifetime offspring production of a female in the absence of fishing so that

$$\overline{LEP}_0 = \sum_{a=0}^A S(a) p_{f,m}(a) \phi(a) (1 + v(a)) \text{ (SM1.9)}$$

Since $\bar{N}(0)$ is constant, Equation SM1.7 becomes

$$\bar{E}_0 = (1 - r)\bar{N}(0)\bar{LEP}_0 \text{ (SM1.10)}$$

Recruitment in the steady state is then

$$\bar{R}_0 = \frac{\alpha(1 - r)\bar{N}(0)\bar{LEP}_0}{1 + \beta(1 - r)\bar{N}(0)\bar{LEP}_0} \text{ (SM1.11)}$$

Recruitment when offspring production is 20% of $\bar{LEP}_0$ is

$$\bar{R}_{0.2} = \frac{0.2\alpha(1 - r)\bar{N}(0)\bar{LEP}_0}{1 + \beta 0.2(1 - r)\bar{N}(0)\bar{LEP}_0} \text{ (SM1.12)}$$

so that steepness is

$$h = \frac{\bar{R}_{0.2}}{\bar{R}_0} = \frac{\frac{0.2\alpha(1 - r)\bar{N}(0)\bar{LEP}_0}{1 + \beta 0.2(1 - r)\bar{N}(0)\bar{LEP}_0}}{\frac{\alpha(1 - r)\bar{N}(0)\bar{LEP}_0}{1 + \beta(1 - r)\bar{N}(0)\bar{LEP}_0}} \text{ (SM1.13)}$$

Simplifying Equation SM1.13 gives

$$h = \frac{0.2(1 + (1 - r)\beta\bar{N}(0)\bar{LEP}_0)}{1 + 0.2(1 - r)\beta\bar{N}(0)\bar{LEP}_0} \text{ (SM1.14)}$$

Since in Equation SM1.11, $\bar{R}_0$ (left side) and $\bar{N}(0)$ (right side) are the same they cancel

and Equation SM1.11 becomes

$$1 = \frac{\alpha(1 - r)\bar{LEP}_0}{1 + (1 - r)\bar{N}(0)\beta\bar{LEP}_0} \text{ (SM1.15)}$$

We rearrange this equation to obtain

$$1 + (1 - r)\bar{N}(0)\beta\bar{LEP}_0 = \alpha(1 - r)\bar{LEP}_0$$

so that

$$(1 - r)\bar{N}(0)\beta\bar{LEP}_0 = \alpha(1 - r)\bar{LEP}_0 - 1 \text{ (SM1.16)}$$

Using Equation SM1.16 the numerator and denominator of Equation SM1.14 become
 respectively $0.2\alpha(1-r)LEP_0$ and $0.8 + 0.2\alpha(1-r)LEP_0$ so that steepness is

$$h = \frac{0.2\alpha(1-r)LEP_0}{0.8 + 0.2\alpha(1-r)LEP_0} = \frac{\alpha(1-r)LEP_0}{4 + \alpha(1-r)LEP_0} \text{ (SM1.17)}$$

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116

117

118 Details for simplifying Equation SM1.13

119

$$\begin{aligned}
 h &= \frac{\bar{R}_{0.2}}{\bar{R}_0} \\
 &= \frac{\frac{0.2\alpha(1-r)\bar{N}(0)LEP_0}{1+0.2(1-r)\beta N(0)LEP_0}}{\frac{\alpha(1-r)\bar{N}(0)LEP_0}{1+(1-r)\beta N(0)LEP_0}} \\
 &= \frac{0.2\alpha(1-r)\bar{N}(0)LEP_0}{1+0.2(1-r)\beta N(0)LEP_0} \cdot \frac{1+(1-r)\beta N(0)LEP_0}{\alpha(1-r)\bar{N}(0)LEP_0} \\
 &= \frac{0.2(1+(1-r)\beta N(0)LEP_0)}{1+0.2(1-r)\beta N(0)LEP_0}
 \end{aligned}$$

Supplementary Materials 2: Early Life History (ELH)

growth and Pelagic Larval Duration (PLD)

These methods have not been reported before in the context of the computation of steepness, so we carefully show the intermediate steps.

Early Life History Growth

To determine the ELH growth curves, we first separated length-at-age data by focal species from the NOAA SWFSC Rockfish Recruitment and Ecosystem Assessment Survey (RREAS) (Fig. SM2-1). The RREAS survey samples Young-of-Year (YOY) rockfish in a mid-water trawl, and for a subset of fish, measures standard length (cm) and collects otoliths to interpret daily growth increments, reporting age in days (Ralston et al., 2013; Woodbury & Ralston, 1991).

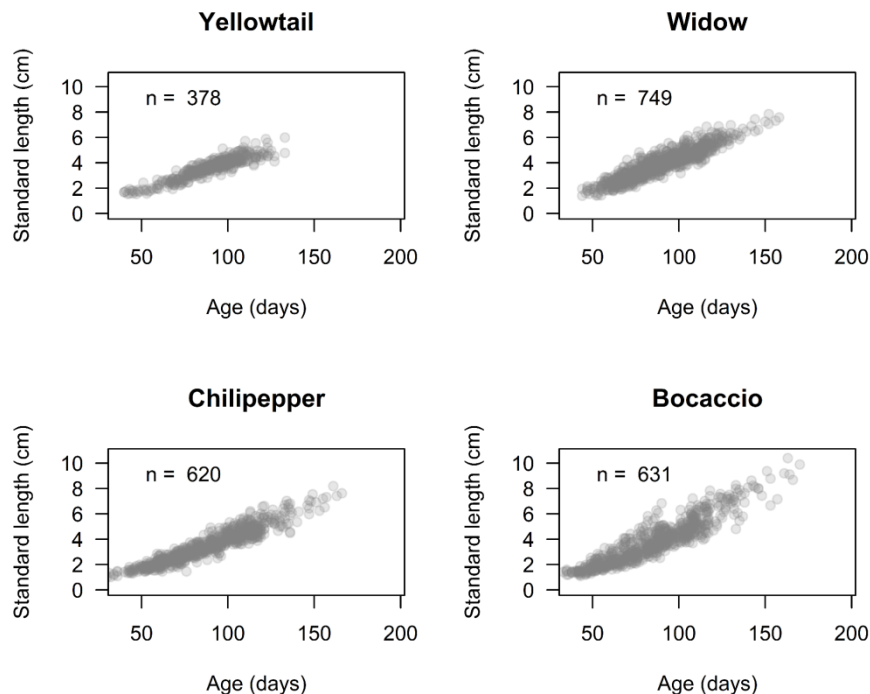


Figure SM2-1. Early life history length-at-age relationships for the four focal species based on data from the NOAA SWFSC Rockfish Recruitment and Ecosystem Assessment Survey (RREAS), a mid-water pelagic trawl survey that targets pelagic Young-of Year (YOY) rockfish in the months prior to settlement. Data are gray circles with sample size shown for each species shown.

Since our method for computing ELH survival requires weight, and paired length and weight data for larval rockfish is very limited, we pooled length (standard length, cm) and weight (grams) data for the four focal species. Length and weight data came from the RREAS (n = 93), Laidig (2010, n = 9), and the San Onofre power plant impingement dataset (Field et al., 2010, n = 9) to develop a general ELH weight-at-length relationship (Fig. SM2-2). There was not enough data to develop independent ELH weight-length curves for each of the study species, so we fit a

linear mixed effects model to leverage information sharing among the species to develop a single, general ELH weight-length relationship. To fit a linear model, we natural log transformed the ELH length and weight data. Weight was the response variable, length was the predictor variable (fixed effect), and species identity was modeled as a random effect.

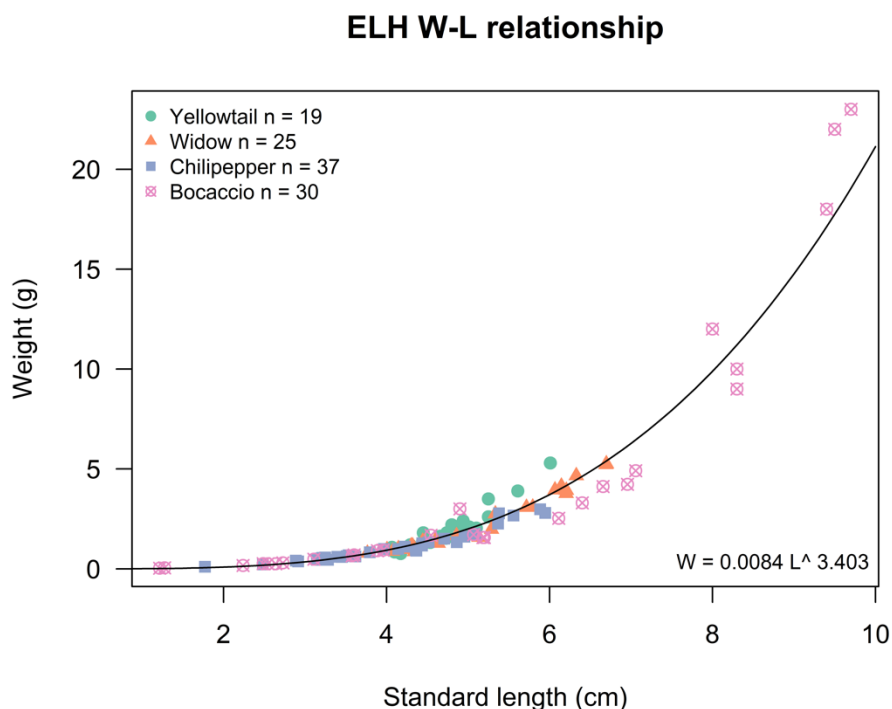
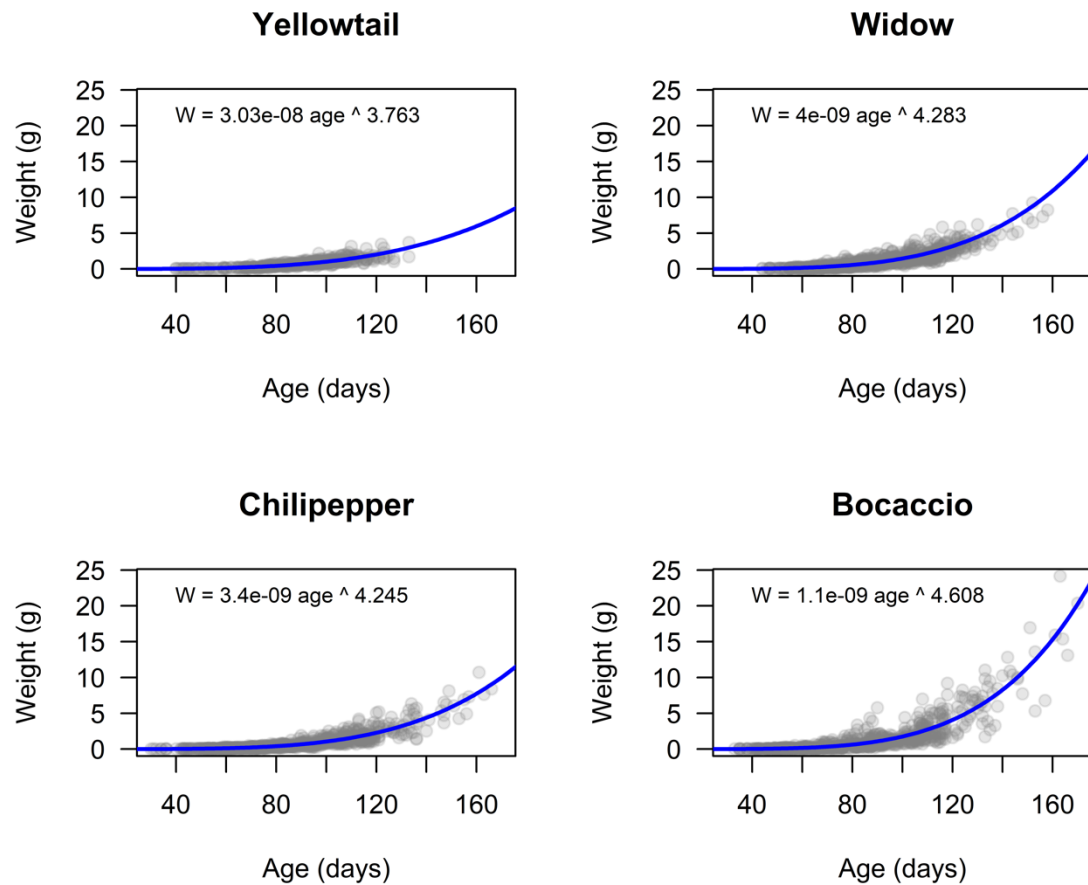


Figure SM2-2. The empirical ELH weight-length relationship. The data come from pooled study species information for pelagic juveniles collected by RREAS, newly settled juveniles collected from kelp forests in central California and nearshore small juveniles sampled at the San Onofre power plant for Yellowtail (green circles), Widow (orange triangles), Chilipepper (blue squares), and Bocaccio (purple open circle with x). A single curve is fitted to the ELH length and weight data, with species identification as a random effect.

We used the general ELH weight-at-length relationship in figure SM2-2 to convert the length-at-age data in figure SM2-1 to weight-at-age for each of the four focal species (SM2-3).

38



39

40 **Figure SM2-3.** Species-specific weight-at-age growth curves, determined by combining the data
 41 shown in figures SM2-1 and SM2-2. The gray circles are empirical ELH length-at-age
 42 observations converted to weight-at-age through the general ELH weight-length relationship.
 43 The curves correspond to exponential daily growth in mass.

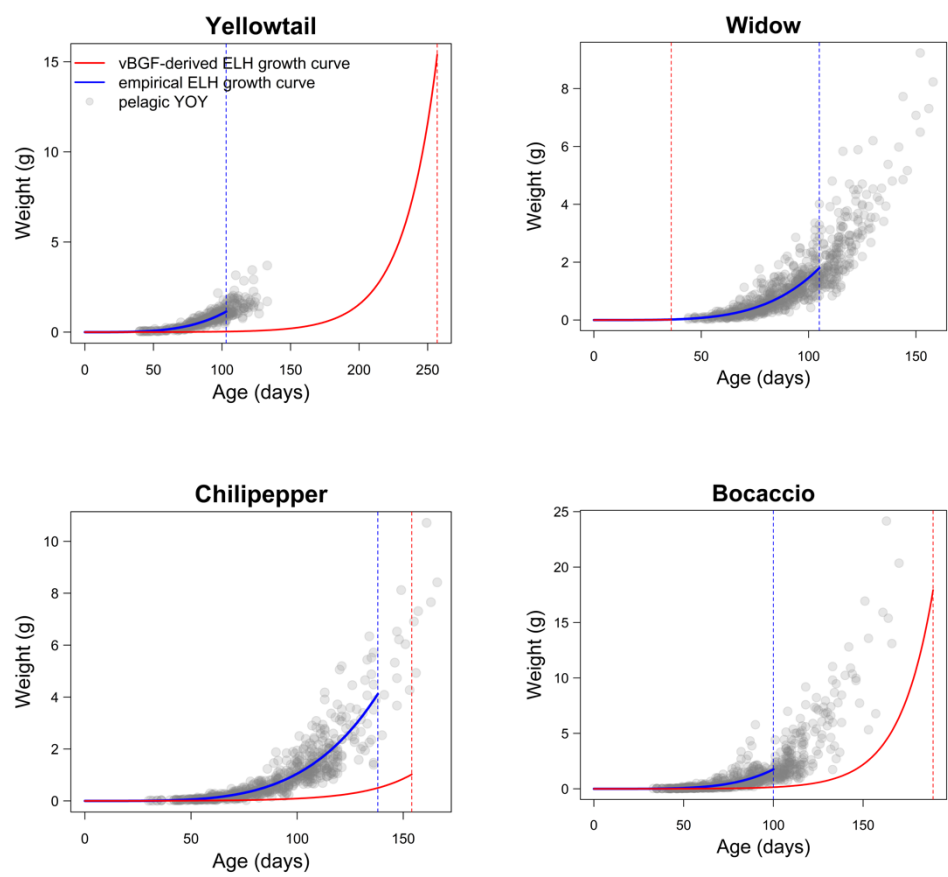
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45 Having the converted ELH weight-at-age data in hand, we assumed exponential growth
 46 in mass during the ELH prior to the onset of von Bertalanffy growth after settlement. We fitted
 47 the ELH weight-at-age growth curves (simple linear regression on log-log transformed data) to

the converted weight-at-age data for each species. To prevent biologically implausible values, which lead to unrealistically high daily natural mortality rates, we replaced any values that were less than the weight-at-birth in the very early days of growth by weight-at-birth (Figure SM2-3). Using the results in Figure SM2-3, we calculated dry weight-at-age as 20% of the wet weight (McGurk, 1986) and then estimated survival during the ELH using the allometries relating instantaneous mortality and size (Equations 24-26).

In Figure SM2-4 we compare ELH growth based on vBGF parameters to the empirical growth model. It is clear that the vBGF poorly captures the growth early in the life history by underestimating size, which thus leads to an underestimate of survival during the pelagic larval phase if holding the duration of the ELH period constant between methods.

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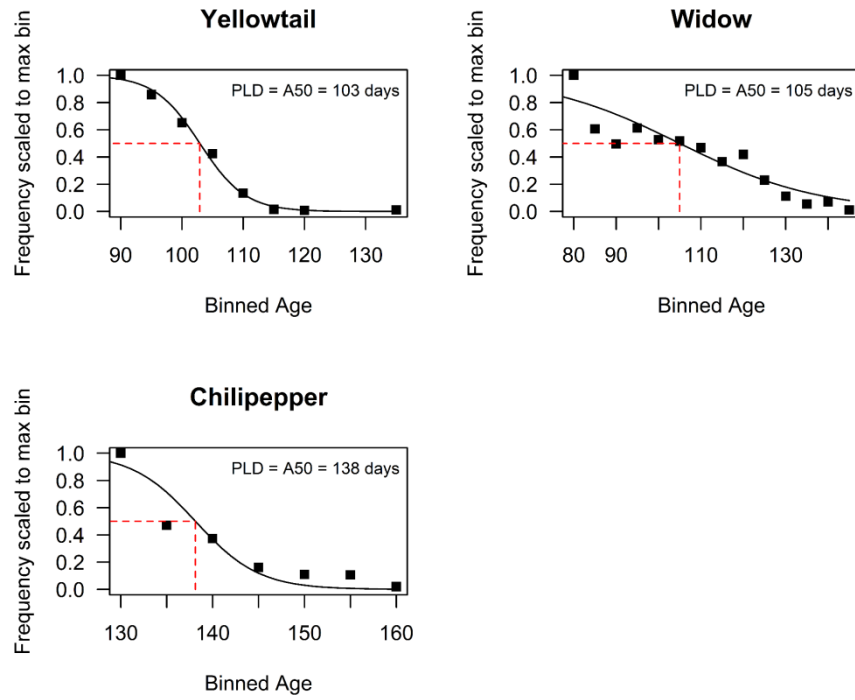
Figure SM2-4. Comparison of growth estimated from the empirical data (gray circles, solid blue line) and the vBGF (solid red line) during the early life history phase. The vertical dashed lines show our estimates of the empirical Pelagic Laval Duration (PLD, dashed blue line) and the estimate of *ELH* duration based on the vBGF method (dashed red line).

65

Pelagic Larval Duration as an estimate of *ELH*

As described in the main text, computing $\alpha_{empirical}$ requires the empirical estimate of the duration of the ELH, that is, the Pelagic Larval Duration (PLD). For Yellowtail, Widow and Chilipepper, we defined PLD as the age at which 50% of larvae have settled out of the pelagic habitat (Figure SM2-5). For Bocaccio, we adopted the value of D'Souza (1998) and set PLD = 100 days.

To determine the empirical PLD for Yellowtail, Widow and Chilipepper, we began with the binned age distributions in the RREAS dataset (Ralston et al., 2013; Woodbury & Ralston, 1991). The subsampled ages were expanded and standardized to a 100-day interval as described in Ralston et al. (2013). Ages were binned in 5-day increments. Since we were interested in when juveniles began settling, we analyzed the right tail of the distribution, when juveniles are assumed to be settling out of the pelagic mid-water area sampled by the survey to benthic habitat. For the analysis, only age bins including the peak frequency and older were included. We used the frequency information for only these ages to fit a logistic regression, weighted by the counts in each length bin. From the logistic regression, we calculated the age at 50% decline from the peak and used this as our estimate of the PLD for Yellowtail, Widow and Chilipepper.



84

85 **Figure SM2-5.** Empirical Pelagic Larval Duration (PLD) for Yellowtail, Widow and

86 Chilipepper based on data from YOY rockfish in the RREAS survey.

87

For Bocaccio, we extracted from D’Souza (1998) data on length-at-age of pelagic juveniles, newly settled and fully settled Bocaccio in central California. We used the data for newly settled juveniles to determine the empirical PLD for Bocaccio (Figure SM2-6).

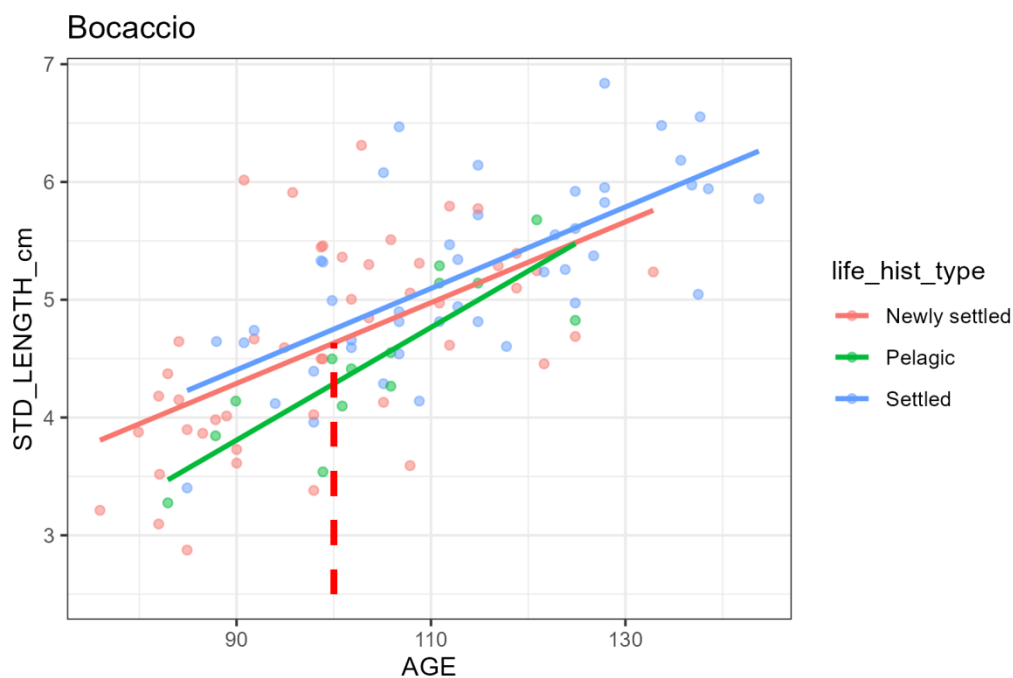


Figure SM2-6. Data extracted from D’Souza (1998) on length-at-age of pelagic juveniles, newly settled and fully settled Bocaccio in central California. We used the mean age of newly settled juveniles (vertical red dashed line) as the empirical PLD for Bocaccio.

In summary, we used two methods to estimate the empirical PLDs (Table SM2.1). In the first method (“Logistic regression”), based on a logistic regression of pelagic juvenile rockfish

survey data, we determined the age at which 50% of the individuals settled from pelagic to benthic habitat. The second method (“Direct observation”), applicable only to Bocaccio because we lacked the data for the other three species, was based on the mean ages of newly settled Bocaccio juveniles in central California (D’Souza, 1998). Our estimates of pelagic larval duration are consistent with those made by Laidig et al. (2010) for blue rockfish, a species with similar ELH dynamics, based on an evaluation of age at which settlement rings are observed in the otoliths of recently settled juveniles with an average of 119 to 124 days, depending on the region.

Table SM2.1. Estimates of Pelagic Larval Duration (in days) for the focal species.

Method	Yellowtail	Widow	Chilipepper	Bocaccio
Logistic regression	103	105	138	NA
Direct observation	NA	NA	NA	100

114 Literature cited in this Supplementary Material

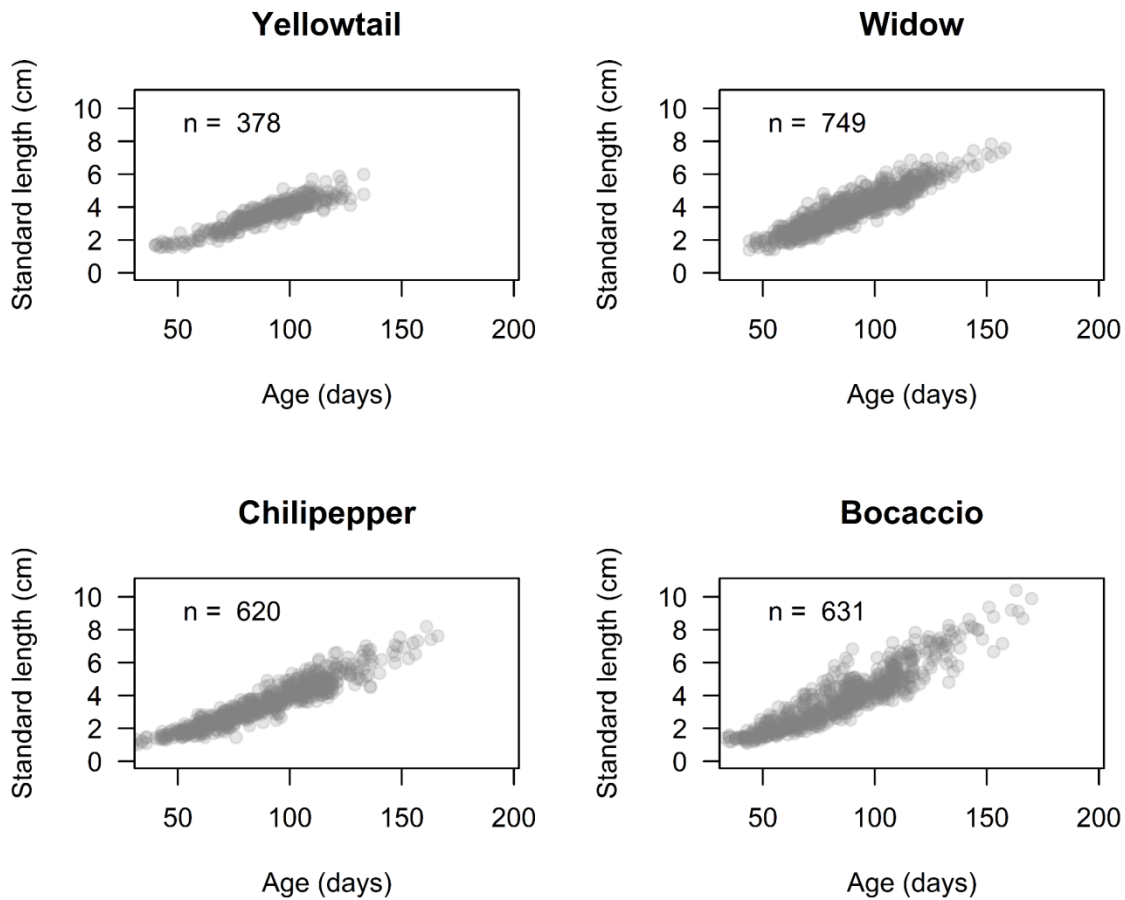
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Supplementary Materials 2: Early Life History (ELH) growth and Pelagic Larval Duration (PLD)

These methods are novel in the context of the computation of steepness so we carefully show the intermediate steps. ELH growth parameters are necessary to calculate the stage- and weight-based rates of daily natural mortality (McGurk, 1986) during the pre-recruit, ELH period.

Early Life History (ELH) growth

To determine the ELH growth curves, we first separated length-at-age data by focal species from the NOAA SWFSC Rockfish Recruitment and Ecosystem Assessment Survey (RREAS) (Fig. SM2-1). The RREAS samples Young-of-Year (YOY) rockfish in a mid-water trawl, and for a subset of fish, measures standard length (cm) and collects otoliths to interpret daily growth increments, reporting age in days (Ralston et al., 2013; Woodbury & Ralston, 1991).



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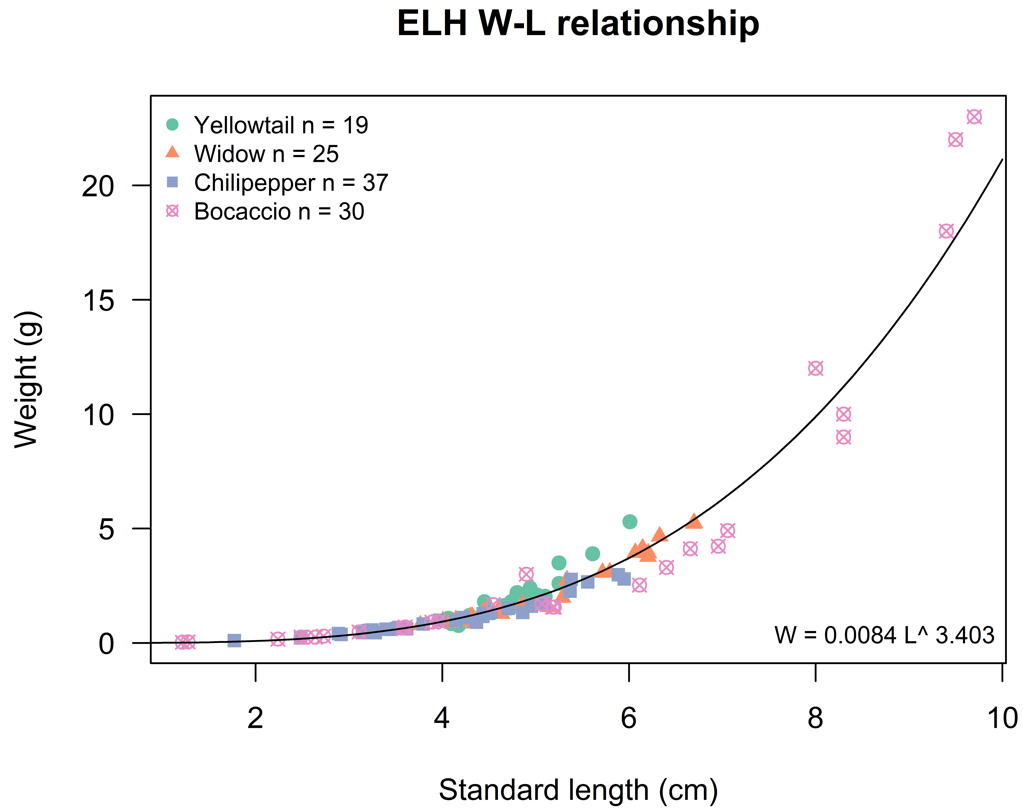
15 **Figure SM2-1.** Early life history length-at-age relationships for the four focal species based on
 16 data from the NOAA SWFSC Rockfish Recruitment and Ecosystem Assessment Survey
 17 (RREAS), a mid-water pelagic trawl survey that targets pelagic Young-of Year (YOY) rockfish
 18 in the months prior to settlement. Data are gray circles with sample size shown for each species.

19

Because our method for computing ELH survival requires weight, and paired length and weight data for larval rockfish is very limited, we pooled length (standard length, cm) and wet weight (g) data for the four focal species to develop a general weight-length key to convert length-at-age observations to weight-at-age needed to apply the weight- and stage- based daily natural mortality rates to estimate ELH survival.

Length and weight data to develop the weight-length key came from three data sources. The first was the RREAS, which included Yellowtail ($n=10$), Widow ($n=25$), Chilipepper ($n=37$) and Bocaccio ($n=21$). The second came from newly settled juvenile rockfish in nearshore kelp forests in central California that sampled Yellowtail ($n=9$) but none of the other study species, as part of unpublished data from Laidig (2010). The third data source came from juveniles of the study species that became trapped in the San Onofre, California nuclear power plant seawater intake and cooling system (Field et al., 2010) that sampled Bocaccio ($n=9$). Data from these three sources were used to develop a single ELH weight-at-length relationship (Fig. SM2-2) since there were not enough data for the range in larval and pelagic juvenile fish length over the ELH period to develop independent, species-specific ELH weight-length relationships for each of the focal species.

We assumed wet weight W_{ELH} increases exponentially with standard length L_{ELH} of the form $W_{ELH} = a_{wELH} L_{ELH}^{b_{wELH}}$ (equation 13 of main text) (Kaji et al., 1996). We fit a generalized linear mixed effects model (GLMM) to the natural log transformed ELH weight and length data (Gelman & Hill, 2007) to estimate the ‘population-level’ scaling factor (a_{wELH}) and exponent (b_{wELH}) parameters for the fixed effect of length, with individual species modeled as a random effect. The intercept parameter was back-transformed from log-space using the bias-correction term $\exp(\sigma^2/2)$.



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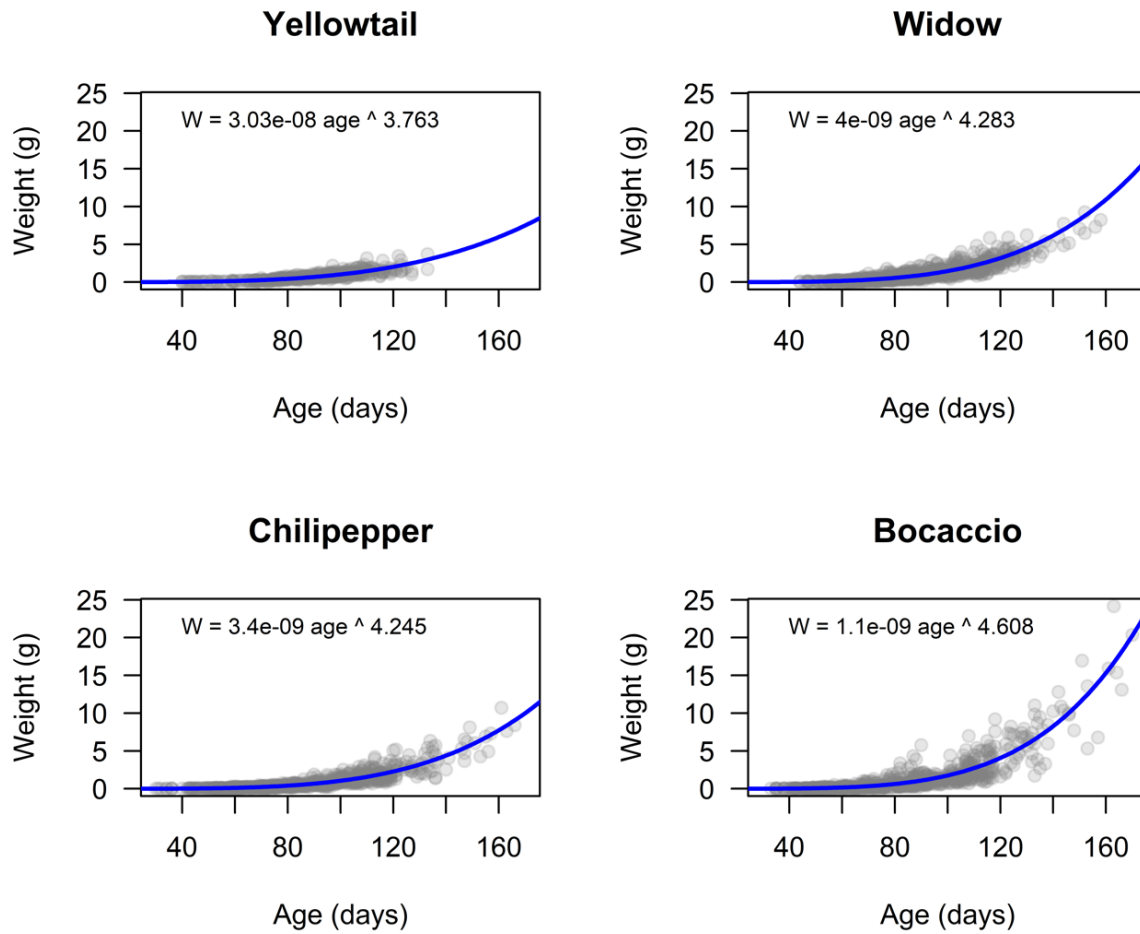
44 **Figure SM2-2.** The ELH weight-length relationship from the generalized linear mixed effects
 45 model, with species identity modeled as a random effect. The data come from pooled study
 46 species information for pelagic juveniles collected by RREAS, newly settled juveniles collected
 47 from kelp forests in central California and nearshore small juveniles sampled at the San Onofre,
 48 California power plant for Yellowtail (green circles), Widow (orange triangles), Chilipepper
 49 (blue squares) and Bocaccio (purple open circle with x).

50

Table SM2-1. Early life history weight-length parameters estimated from the generalized linear mixed effects model (Equation 13 in the main text). The model estimates ‘population-level’, fixed effect parameters to predict weight-at-length for a ‘general’ rockfish in our study.

Description	$a_{w_{ELH}}$	$b_{w_{ELH}}$
Fixed effect parameters for a ‘general’ rockfish in our study (Eq. 13)	$8.36 \cdot 10^{-3}$	3.403

We used the general ELH weight-at-length relationship (Table SM2-1, Fig. SM2-2) to convert the species-specific length-at-age data in figure SM2-1 to species-specific weight-at-age for each of the four focal species (SM2-3).



60

61 **Figure SM2-3.** Species-specific weight-at-age growth curves, determined by combining the data
 62 shown in figures SM2-1 and SM2-2. The gray circles are ELH length-at-age observations
 63 converted to weight-at-age through the general ELH weight-length relationship. The curves
 64 correspond to exponential daily growth in mass.

65

Next we assumed exponential growth in mass by day (d) during the ELH period (Buckley et al., 2006; Kaji et al., 1996; Shoji et al., 2005). We fit the ELH weight-at-age growth curves of the form $W_{ELH}(d) = a_{empirical}d^{b_{empirical}}$ (equation 14 in the main text) to the converted weight-at-age data for each species using a simple linear regression of the natural log-transformed data with the back-transformation bias-correction of the intercept parameter as above.

To prevent biologically implausible values, which lead to unrealistically high daily natural mortality rates, we replaced any values that were less than the weight-at-birth in the very early days of growth by weight-at-birth. For each species, the number of days replaced with the weight-at-birth was 14 days for Yellowtail, 17 days for Widow, 20 days for Chilipepper and 19 days for Bocaccio.

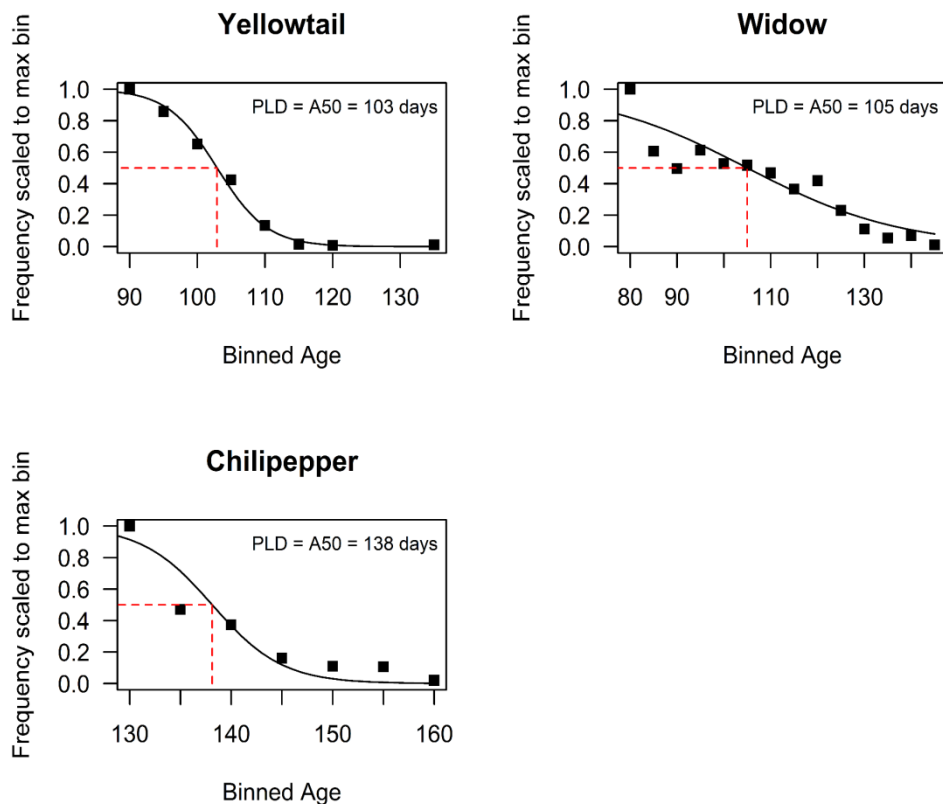
Using the results in Figure SM2-3, we calculated dry weight-at-age as 20% of the wet weight (McGurk, 1986) and then estimated survival during the ELH using the allometries relating instantaneous mortality and size (Equations 9-11 in the main text).

Pelagic Larval Duration (PLD) as an estimate of ELH

As described in the main text, computing $\alpha_{empirical}$ also requires the estimate of the duration of the ELH, that is, the Pelagic Larval Duration (PLD). For Yellowtail, Widow and Chilipepper, we defined PLD as the age at which 50% of larvae have settled out of the pelagic habitat from the RREAS (Figure SM2-4). For Bocaccio, we followed D'Souza (1998) and set PLD = 100 days.

To determine the PLD for Yellowtail, Widow and Chilipepper, we began with the binned age distributions in the RREAS dataset (Ralston et al., 2013; Woodbury & Ralston, 1991). The

subsampled ages were expanded and standardized to a 100-day interval as described in Ralston et al. (2013). Ages were binned in 5-day increments. Since we were interested in when juveniles began settling, we analyzed the right tail of the distribution, when juveniles are assumed to be settling out of the pelagic mid-water area sampled by the survey to benthic habitat. For the analysis, only age bins including the peak frequency and older were included. We used the frequency information for only these ages to fit a logistic regression, weighted by the counts in each length bin. From the logistic regression, we calculated the age at 50% decline from the peak and used this as our estimate of the PLD for Yellowtail, Widow and Chilipepper.



98 **Figure SM2-4.** Pelagic Larval Duration (PLD) for Yellowtail, Widow and Chilipepper based on
99 data from pelagic YOY rockfish in the RREAS.

For Bocaccio, we extracted data from D’Souza (1998) on the length-at-age of pelagic juveniles, newly settled, and fully settled Bocaccio in central California. We used the data for newly settled juveniles to determine the PLD for Bocaccio (Figure SM2-5).

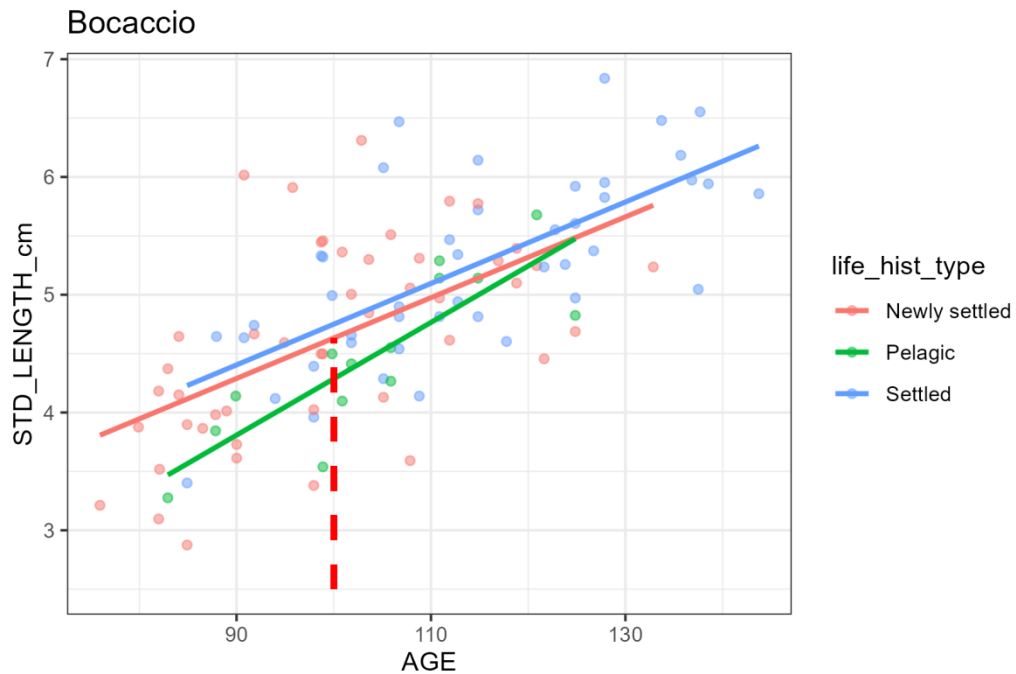


Figure SM2-5. Data extracted from D’Souza (1998) on length-at-age, in days, of pelagic juveniles, newly settled, and fully settled Bocaccio in central California. We used the mean age of newly settled juveniles (vertical red dashed line) as the PLD for Bocaccio.

In summary, we used two approaches to estimate the PLDs (Table SM2.1). In the first approach (“Logistic regression”), based on a logistic regression of pelagic juvenile rockfish survey data, we determined the age at which 50% of the individuals settled from pelagic to benthic habitat. The second approach (“Direct observation”), applicable only to Bocaccio because we lacked the data for the other three species, was based on the mean age of newly settled Bocaccio juveniles in central California (D’Souza, 1998). Our estimates of pelagic larval duration are consistent with those made by Laidig et al. (2010) for blue rockfish, a species with similar ELH dynamics, which was based on an evaluation of age at which settlement rings are observed in the otoliths of recently settled juveniles with an average of 119 to 124 days, depending on the region.

Table SM2.1. Estimates of Pelagic Larval Duration (PLD, in days) for the focal species.

Approach	Yellowtail	Widow	Chilipepper	Bocaccio
Logistic regression	103	105	138	NA
Direct observation	NA	NA	NA	100

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- 146 Shoji, J., Maehara, T., & Tanaka, M. (2005). Larval growth and mortality of Japanese Spanish
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148 *the Marine Biological Association of the United Kingdom*, 85(5), 1255–1261.
149 <https://doi.org/10.1017/S0025315405012403>
- 150 Woodbury, D., & Ralston, S. (1991). Interannual variation in growth rates and back-calculated
151 birthdate distributions of pelagic juvenile rockfishes (*Sebastes* spp.) off the central
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153

Supplementary Materials 3: Deterministic sensitivities

In the main text, we demonstrated the sensitivity of the point estimate of steepness (h) to a range in early life survival (α , Figure 2), to our empirical estimate of pre-settlement duration (PLD, Figure 5) and to a range in natural mortality (M) when using the empirical method for α (Figure 6). We also included an elasticity analysis showing how a 20% change in a parameter influences the point estimate of h (Figure 3). In this supplemental, we expand on some of the single parameter deterministic sensitivity analyses to include a sensitivity of h to a range in lifetime egg production (LEP_0), the sex ratio at birth, r and the full natural mortality M sensitivity. These variables are important because α , LEP_0 and r are required to compute h in Equation 13. Also, natural mortality is often highly uncertain for fish stocks and is used to calculate the probability of survival to age in the post-recruit stages and thus influences the calculation of LEP_0 .

We also include a sensitivity to multiple brooding capabilities (spawning frequency) for Chilipepper and Bocaccio to better understand the effect of multiple brooding on productivity. For the multiple brooding sensitivity, we changed the probability of producing up to two broods per year for Chilipepper and Bocaccio to zero for all ages, meaning all females are limited to a single brood, such as occurs in Yellowtail and Widow. We end with showing the elasticity analysis for h , as calculated using the vBGF to estimate early life survival, α .

Figures SM3-1, SM3-2 and SM3-3 complement Figures 2 and 5 of the main text. Figure SM3-4 complements Figure 3 of the main text.

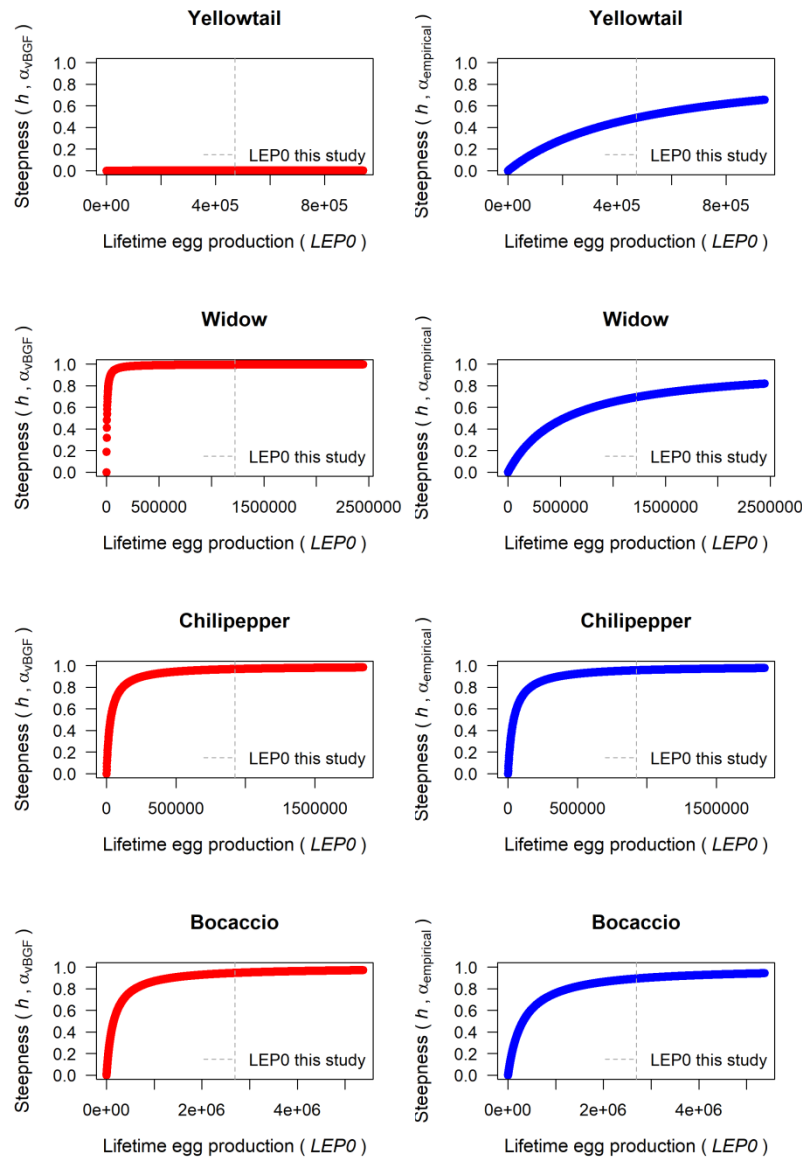
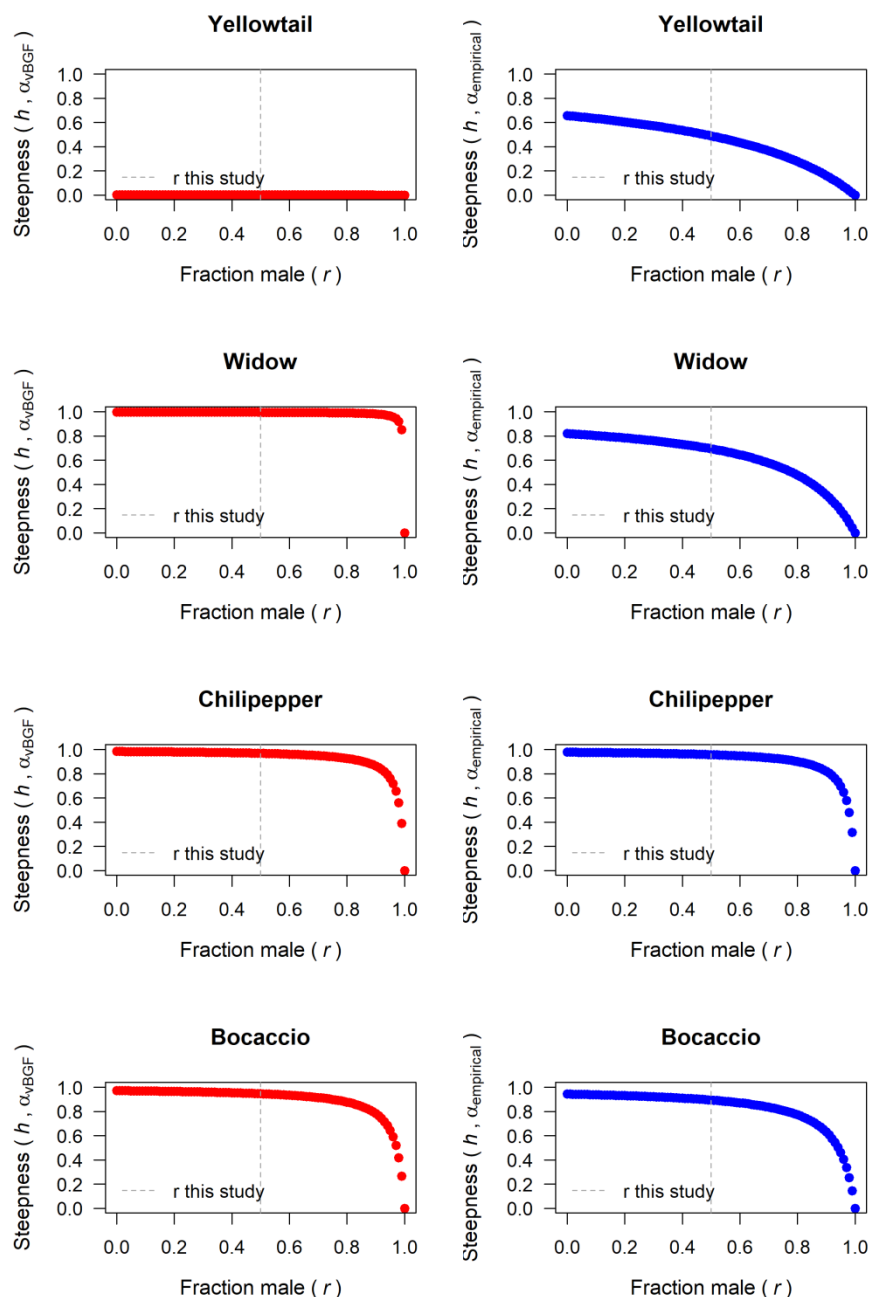


Figure SM3-1. Sensitivity of steepness (h) to expected lifetime egg production in the steady state (LEP_0). The left column corresponds with computation of alpha using the vBGF and size dependent mortality, and the right column using empirical growth and Pelagic Larval Duration with size dependent mortality. The vertical dashed line is the point estimate from the main text with a sensitivity to 100% less and more of the calculated LEP .



27

28 **Figure SM3-2.** Sensitivity of steepness (h) to the sex ratio at birth (fraction male, r). The left

29 column corresponds with computation of alpha using the vBGF and size dependent mortality,

30 and the right column using empirical growth and Pelagic Larval Duration with size dependent

31 mortality. The vertical dashed line at $r = 0.5$ is the value we use in the main text.

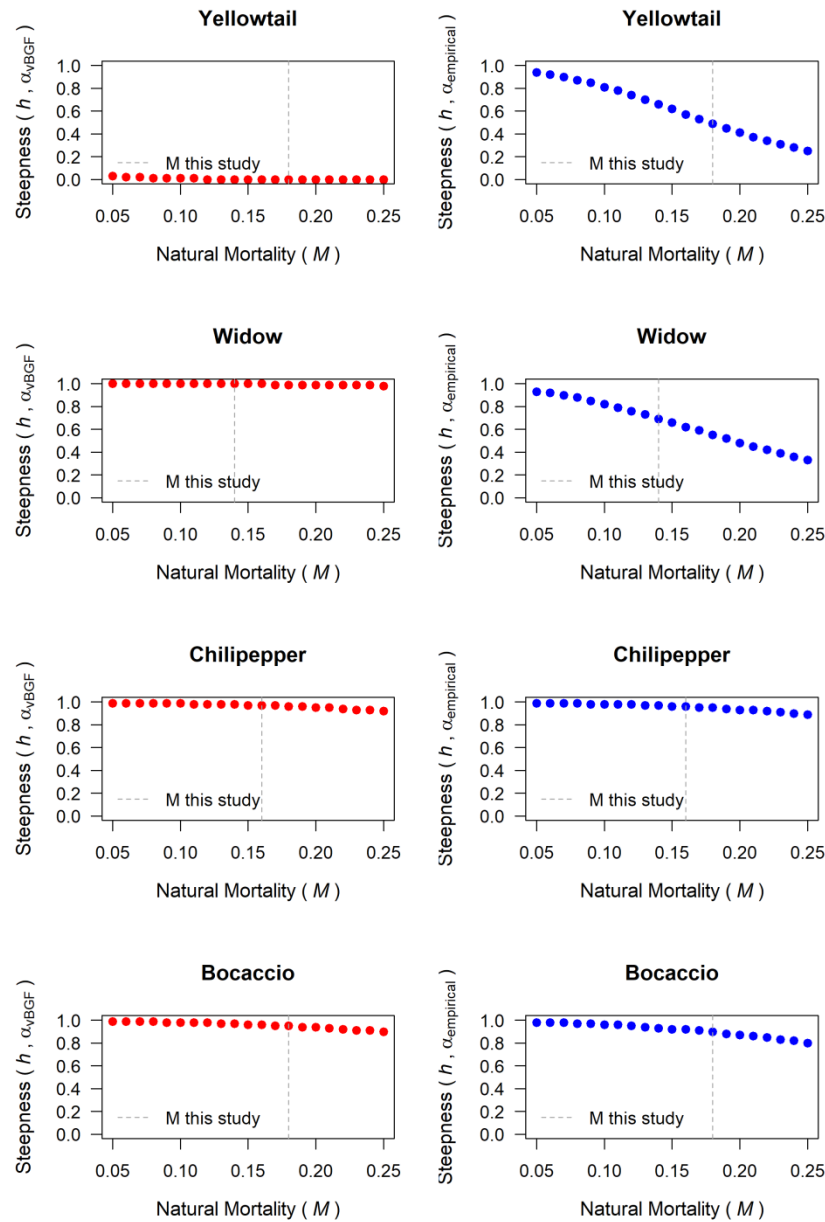


Figure SM3-3. Sensitivity of steepness (h) to the post-recruitment annual natural mortality rate (M). The left column corresponds with computation of alpha using the vBGF and size dependent mortality, and the right column using empirical growth and Pelagic Larval Duration with size dependent mortality. The vertical dashed line is the point estimate from the main text with a sensitivity to other possible values of M .

Steepness was not very sensitive to the spawning frequency within a year for Chilipepper and Bocaccio (Table SM3-1). Restricting Chilipepper and Bocaccio females to only produce a single brood a year rather than multiple broods decreased expected lifetime egg production, as expected, and slightly decreased the point estimates of steepness (h) for both the vBGF derived and empirical methods to estimate early life survival (α).

Table SM3-1. Sensitivity of steepness (h) to spawning frequency (multiple brooding) for two methods to estimate ELH survival (α).

Species	Two broods a year possible	Expected Lifetime Egg Production (LEP)	Steepness (h) (α_{vBGF})	Steepness (h) ($\alpha_{empirical}$)
Chilipepper	Yes (base model)	923,455	0.97	0.96
	No (sensitivity)	544,160	0.95	0.93
Bocaccio	Yes (base model)	2,688,207	0.95	0.90
	No (sensitivity)	2,020,356	0.93	0.87

50 In the main text we show an elasticity analysis for a 20% change in each parameter using
51 the empirical method to estimate α (Figure 3 of the main text). Here we show the corresponding
52 elasticity analysis using vBGF assumptions to estimate α . The elasticity analysis failed for
53 Yellowtail because steepness was calculated at 0 using the vBGF assumptions to estimate α .
54

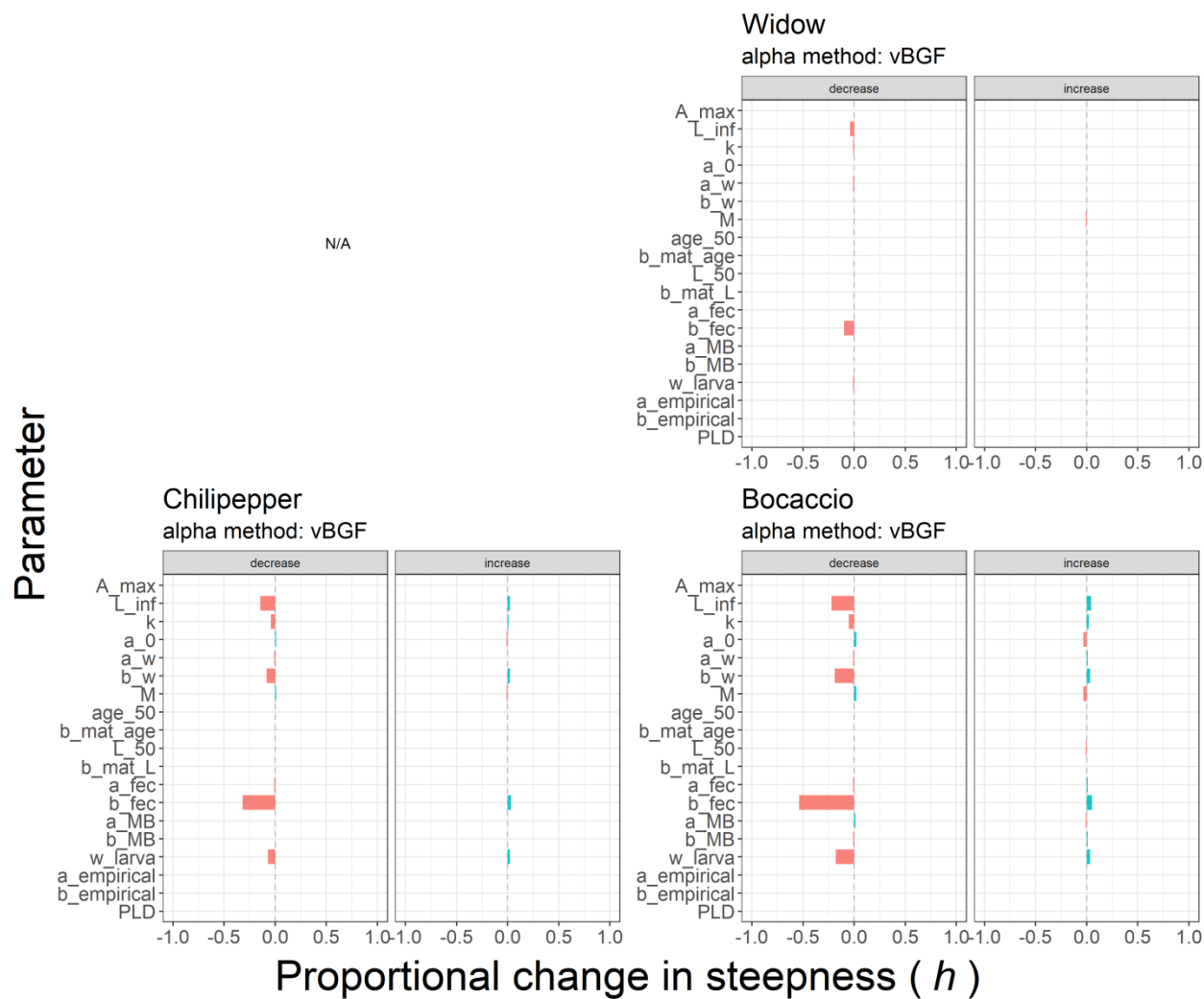


Figure SM3-4. Proportional change in steepness, using α_{vBGF} , when all but one parameter is held constant and the focal parameter is decreased by 20% and increased by 20%. Note that the elasticity analysis fails for Yellowtail because h is calculated as 0.

Supplementary Materials 3: Deterministic sensitivities

Background and Methods

In the main text, we showed the sensitivity of the point estimate of steepness h to variation in early life survival (α , Figs. 2, 4), pelagic larval duration (PLD, Fig. 5) and natural mortality (M , Fig. 6). Here, we expand some of the single parameter deterministic sensitivity analyses (**sub-section 1**), focus on a sensitivity to multiple brooding (**sub-section 2**), and consider an alternative size- and age- based method for post-recruit natural mortality (**sub-section 3**). The sensitivities in this Supplemental use the empirical ELH growth method to estimate α .

Sub-section 1 includes a sensitivity of h to a range in values for 1) lifetime egg production $\overline{LEP}_0$, and 2) the sex ratio at birth, r . These variables are important because α , $\overline{LEP}_0$ and r are required to compute h in Equation 1. The sensitivity to a range in α is shown in the main text (Figs. 2, 4).

In **sub-section 2** we include a sensitivity to multiple brooding capabilities (spawning frequency) for Chilipepper and Bocaccio to better understand the effect of multiple brooding on h . For the multiple brooding sensitivity, we changed the probability of producing up to two broods per year for Chilipepper and Bocaccio to zero for all ages, meaning all females were limited to a single brood, as with Yellowtail and Widow. At the extreme, this is equivalent to assuming a survival rate of zero for all larvae produced in a second brood.

In **sub-section 3**, we show a sensitivity of h to an alternative, post-recruit size- and age-based annual natural mortality rate, M . This sensitivity assumes a higher M for post-recruit juveniles prior to maturation and a constant M for adults post-maturation (following Brodziak et al., 2011)

24

25

$$M(a) = \begin{cases} M_c \frac{L_{50}}{L(a)} & \text{for } a < a_{50} \\ M_c & \text{for } a \geq a_{50} \end{cases} \quad (\text{SM3.1})$$

26

27 where $M(a)$ is the annual natural mortality rate at age a , M_c is the constant natural mortality rate

28 from the base model (Table 2 in the main text), L_{50} is the length at which 50% of females in the

29 population are mature from the base model (Table 2 in the main text), $L(a)$ is the length at age a

30 and a_{50} is the age at which 50% of the females in the population are mature from the base model

31 (Table 2 in the main text).

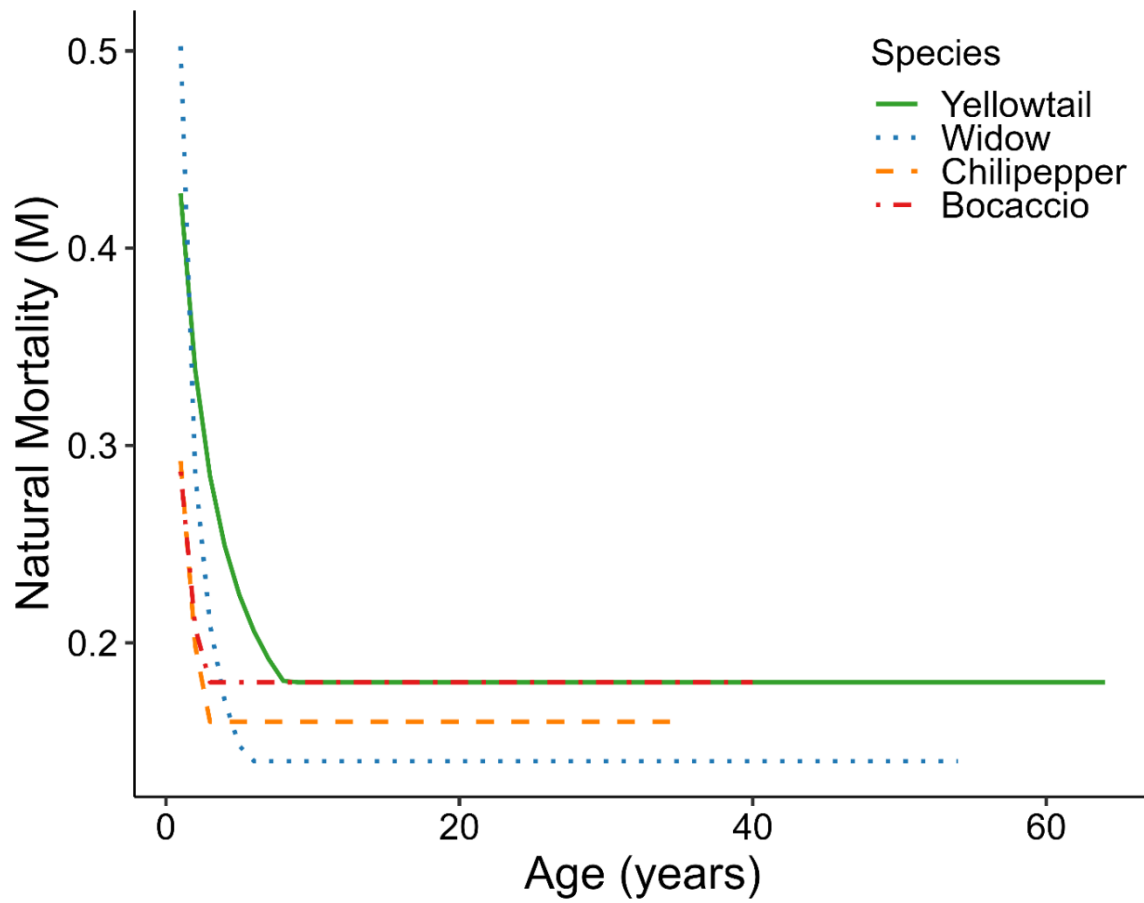
32 The resulting post-recruit size- and age- based natural mortality rates at age used in the

33 sensitivity analysis are show in Figure SM3-1 with a constant M applied for adults post-

34 maturation.

35

36



37

38 **Figure SM3-1.** The size- and age- based annual natural mortality rates from Equation SM3.1

39 used in the sensitivity analysis of steepness to an alternative, post-recruit size- and age- based

40 rate of natural mortality prior to maturation. A constant M is assumed for mature adults. Natural

41 mortality rates are plotted to the maximum age for each species.

42

Results

1: Sensitivity to $\overline{LEP}_0$ and r

Figures SM3-2 and SM3-3 complement figures 2, 5 and 6 of the main text.

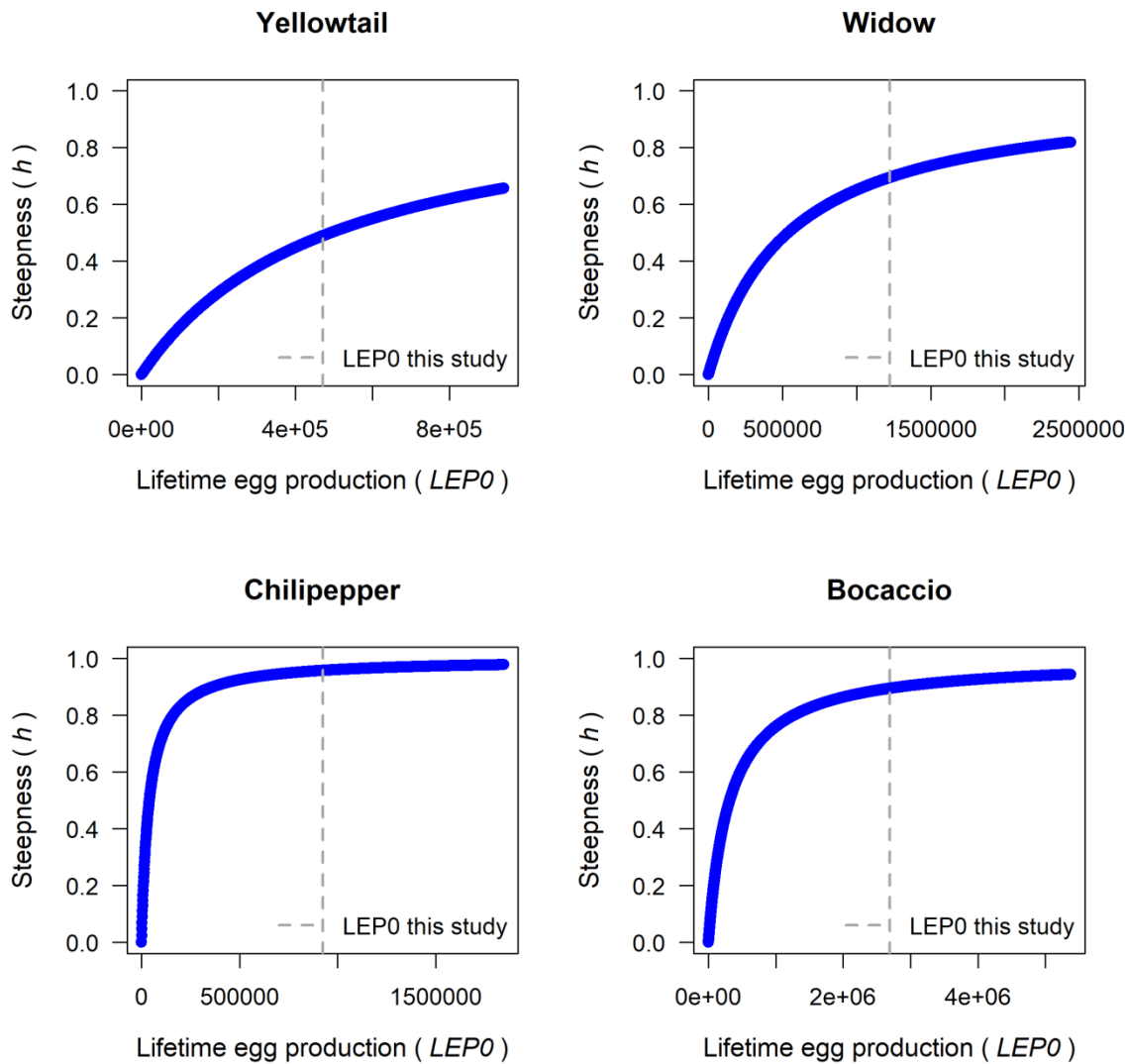


Figure SM3-2. Sensitivity of steepness (h) to expected lifetime egg production in the steady state $\overline{LEP}_0$. The vertical dashed line is the point estimate from the main text with a sensitivity to 100% less and more of the calculated $\overline{LEP}_0$.

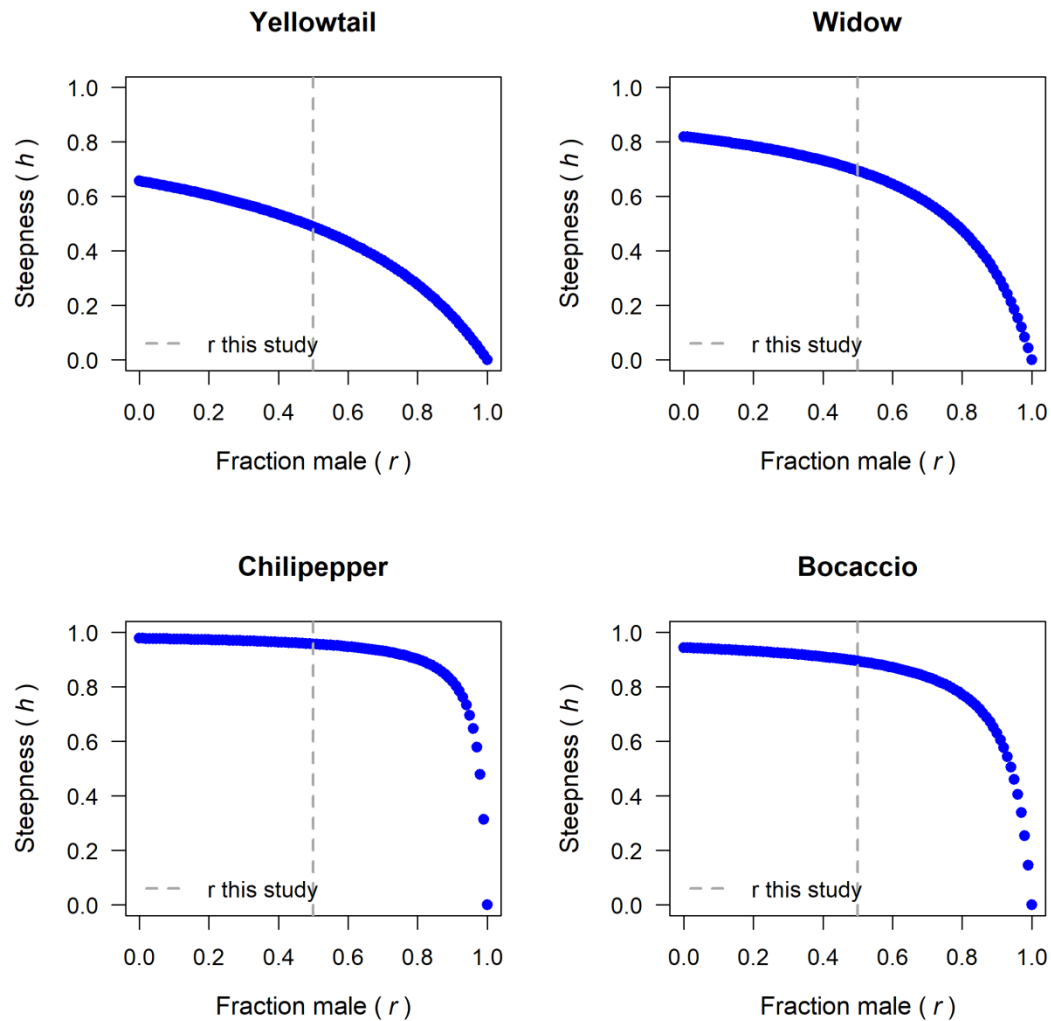


Figure SM3-3. Sensitivity of steepness (h) to the sex ratio at birth (fraction male, r). The vertical dashed line at $r = 0.5$ is the value we use in the main text.

2: Sensitivity to multiple broods

Steepness was not highly sensitive to the spawning frequency within a year for Chilipepper and Bocaccio (Table SM3-1). Restricting Chilipepper and Bocaccio females to produce only a single brood per year, rather than up to two broods, decreased expected lifetime egg production $\overline{LEP}_0$, as expected, and slightly decreased the point estimate of steepness h .

Table SM3-1. Sensitivity of steepness (h) to restricting spawning frequency to a single brood per year for the multiple brooding capable Chilipepper and Bocaccio.

Species	Two broods a year possible?	Expected Lifetime Egg Production ($\overline{LEP}_0$)	Steepness ($h_{empirical}$)
Chilipepper	Yes (base model)	923,455	0.96
	No (sensitivity)	544,160	0.93
Bocaccio	Yes (base model)	2,688,207	0.90
	No (sensitivity)	2,020,356	0.87

3: Sensitivity to an alternative, post-recruit size- and age- based M

Steepness was lower for all four study species when applying a post-recruit, size- and age- based natural mortality rate (M) prior to maturation (Table SM3-2). The reduction in steepness h was less for Chilipepper and Bocaccio because of their earlier age at maturation, and thus fewer years with higher M prior to maturation, relative to Yellowtail and Widow that mature at older ages.

Table SM3-2. Sensitivity of steepness (h) to assuming a post-recruit, size- and age- based natural mortality (M) prior to maturation and a constant M in the adult stage post-maturation. The base model in the main text assumes a constant M for all post-recruit ages.

Species	Post-recruit rate of natural mortality (M)	Expected Lifetime Egg Production ($\overline{LEP}_0$)	Steepness ($h_{empirical}$)
Yellowtail	Constant M (base model)	470,871	0.49
	Size- and age- based M prior to maturation (Equation SM3.1)	242,896	0.33
Widow	Constant M (base model)	1,222,789	0.69
	Size- and age- based M prior to maturation (Equation SM3.1)	660,803	0.55
Chilipepper	Constant M (base model)	923,455	0.96
	Size- and age- based M prior to maturation (Equation SM3.1)	778,902	0.95
Bocaccio	Constant M (base model)	2,688,207	0.90

	Size- and age- based M prior to maturation (sensitivity)	2,350,623	0.88
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76

77 Literature cited in this Supplementary Material

78

79 Brodziak, J., Ianelli, J., Lorenzen, K., & Methot Jr, R. D. (2011). *Estimating Natural Mortality in*80 *Stock Assessment Applications* (NMFS-F/SPO-119; NOAA Technical Memorandum, p.81 38). U.S. Department of Commerce. <http://www.st.nmfs.noaa.gov/>

82

Supplementary Materials 4: Simulation to Generate Priors

In the main text we treated the life history parameters as perfectly known as proof of concept for using reproductive biology and early life history information to inform steepness. In practice, each of these parameters will have associated variability and measurement error. The knowledge of this variability can be used in simulation methods to generate biologically meaningful prior distributions for steepness.

Here we describe a general simulation method to develop prior distributions for steepness for the four focal study species. We also discuss current limitations, which should be fully explored before using these prior distributions to inform population modeling.

Simulation procedure:

1. *Covariance among parameters:* To demonstrate the method, we treat each life history parameter as an independent random variable even though this is overly simplistic. Future investigations should consider covariance among parameters estimated from model fitting and from knowledge of biology. For example, when estimating parameters for the vBGF $L(a) = L_{\infty}(1 - e^{-k(a-a_0)})$ it is well known that estimates of asymptotic size L_{∞} and growth rate k are inversely correlated. Furthermore, since the size at age 0 is $L(0) = L_{\infty}(1 - e^{-k a_0})$ there is an additional correlation between size at birth, growth rate and theoretical age of zero size. These correlations are both a result of the form of the vBGF and biology (Mangel 2006, pg 23-29). In addition to covariance of growth parameters, covariance should also be explored for other size- and age- dependent traits, such as the allometric length-weight relationship, size-dependent maturity, fecundity, etc.

- 24
- 25 2. *Parameter distributions:* Accepting the limitation of omitting parameter covariance, we
- 26 assign a mean, μ , and standard deviation, σ , to each parameter assuming a normal
- 27 distribution. This is another simplification because some parameters must be positive and
- 28 the normal distribution allows for negative values. We show this assumption is adequate
- 29 for most parameters. As a check, we reject any negative values for a parameter that must
- 30 be positive. For parameters that must be positive, future investigations should consider
- 31 other distributions with only positive support, such as the log-normal or gamma densities.
- 32 For the standard deviation, we used literature values, if reported, or assumed reasonable
- 33 values when not reported (Table SM4-1).
- 34
- 35 3. *Simulation and bootstrapping:* We ran 1000 simulations to develop a distribution for
- 36 steepness which incorporates the variability in life history parameters. For each
- 37 simulation we randomly draw from the relevant life history parameter distributions to
- 38 simulate trait-at-length and trait-at-age relationships needed to calculate lifetime egg
- 39 production. The full simulation produces 1000 trait-at-length and trait-at-age vectors for
- 40 which we calculate the 0.025, 0.50 and 0.975 quantiles to plot median values with 95%
- 41 confidence intervals from bootstrapping. We visually check that both the individual
- 42 parameter draws and resulting trait-at-length and trait-at-age relationships are reasonable
- 43 and consistent with the species biology, including knowledge of the variability typically
- 44 associated with these traits.
- 45
- 46 4. *Distribution for steepness:* For each species, we run the simulation for both the empirical
- 47 and vBGF methods of estimating early life survival. We simulate only these two methods

48 since our method of estimating ELH survival at population persistence will always lead
49 to $h = 0.2$. Here, we show the empirical distribution of h using both methods of α , for
50 which other statistical distributions could be fitted to.

51
52 The simulation produces a distribution for values of steepness, which can then be used in
53 population modeling to inform fisheries productivity. It is important to consider variability of the
54 life history parameters, which are likely to reflect spatial and temporal variability, and other
55 measurement error. The simulation could also be used for forward projections of steepness when
56 life history parameters are known to co-vary with environmental conditions (see methods of Hsu
57 et al., 2024). In summary, we provide the framework for developing prior distributions for
58 steepness but there is further research needed to operationalize the method.

Table SM4-1. Life history parameter distributions used in the simulation. We assume a normal distribution with mean, μ and standard deviation, σ for all parameters. Equations and definitions of parameters presented in the main text. Source references indicated by superscript.

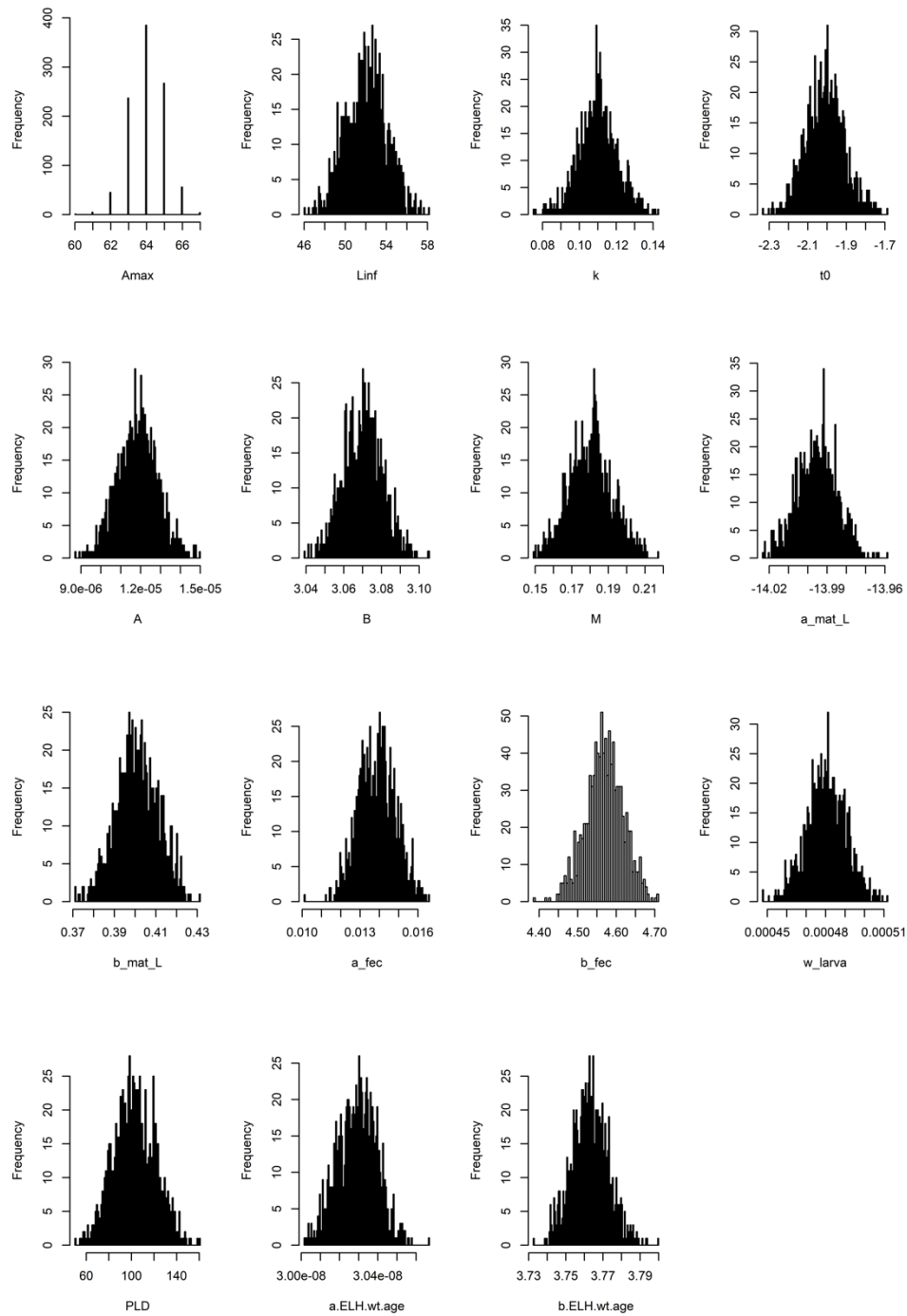
Category	Parameter	Yellowtail $\mu(\sigma)$	Widow $\mu(\sigma)$	Chilipepper $\mu(\sigma)$	Bocaccio $\mu(\sigma)$
Age	Max_age	64 ^b (1 ^a)	54 ^b (1 ^a)	35 ^d (1 ^a)	40 ^d (1 ^a)
Growth (Eqn. 14)	L_{∞}	52.1 ^e (2 ^a)	50.4 ^b (2 ^a)	48.3 ^f (2 ^a)	37.7 ^g (2 ^a)
	k	0.11 ^e (0.01 ^a)	0.17 ^b (0.01 ^a)	0.20 ^f (0.01 ^a)	0.23 ^g (0.01 ^a)
	a_0	-2.01 ^e (0.1 ^a)	-0.10 ^b (0.1 ^a)	-0.62 ^f (0.1 ^a)	-0.87 ^g (0.1 ^a)
Length- Weight (Eqn. 15)	A	0.000011843 ^e (0.000001 ^a)	0.000017355 ^b (0.000001 ^a)	0.00000405 ^f (0.000001 ^a)	0.000007355 ^h (0.000001 ^a)
	B	3.07 ^e (0.01 ^a)	2.96 ^b (0.01 ^a)	3.20 ^f (0.01 ^a)	3.11 ^h (0.01 ^a)
Natural Mortality	M	0.18 ^e (0.012 ^e)	0.14 ^b (0.010 ^b)	0.16 ^f (0.013 ^g)	0.18 ^g (0.013 ^g)
Maturity (Eqn. 17)	a_mat	-13.995 ^e (0.01 ^a) (at-length)	-4.23925 ^b (0.01 ^a) (at-age)	-6.588 ^f (0.01 ^a) (at-length)	-12.5918 ^h (0.01 ^a) (at-length)
	b_mat	0.401 ^e (0.01 ^a) (at-length)	0.775 ^b (0.01 ^a) (at-age)	0.270 ^f (0.01 ^a) (at-length)	0.334 ^h (0.01 ^a) (at-length)
Brood fecundity (Eqn. 18)	a_fec	0.0139 ⁱ (0.001 ^a)	0.0104 ⁱ (0.001 ^a)	0.1383 ⁱ (0.001 ^a)	0.1210 ⁱ (0.001 ^a)
	b_fec	4.57 ⁱ (0.05 ^a)	4.63 ⁱ (0.05 ^a)	3.77 ⁱ (0.05 ^a)	3.82 ⁱ (0.05 ^a)

Spawning frequency (Eqn. 19)	a_MB	NA	NA	-3.900 ⁱ (0.43 ^j)	-7.983 ^j (1.75 ^j)
	b_MB	NA	NA	0.114 ⁱ (0.01 ^j)	0.12 ^j (0.03 ^j)
Weight -at-birth (g)	w_larva	0.00048 ^k (0.00001 ^a)	0.00057 ^k (0.00001 ^a)	0.00104 ^k (0.00001 ^a)	0.00068 ^k (0.00001 ^a)
Empirical Pelagic Larval Duration (days)	PLD	103 ^l (18 ⁿ)	105 ^l (18 ⁿ)	138 ^l (18 ⁿ)	100 ^m (18 ⁿ)
ELH growth (d) (Eqn. 28)	a_ELH.wt.age	3.03 * 10 ⁻⁸ ^l (1.0 * 10 ⁻¹⁰ ^a)	3.96 * 10 ⁻⁹ ^l (1.0 * 10 ⁻¹⁰ ^a)	3.40 * 10 ⁻⁹ ^l (1.0 * 10 ⁻¹⁰ ^a)	1.07 * 10 ⁻⁹ ^l (1.0 * 10 ⁻¹⁰ ^a)
	b_ELH.wt.age	3.763 ^l (0.01 ^a)	4.283 ^l (0.01 ^a)	4.245 ^l (0.01 ^a)	4.608 ^l (0.01 ^a)

References: ^a assumed for simulation; ^b Shaw and Archibald 1981; ^c Adams et al 2019; ^dLove et al 2002; ^eStephens and Taylor 2018; ^fField et al 2015; ^gHe and Field 2017; ^hHe et al 2015; ⁱDick et al. 2017 (total lengths converted to fork lengths); ^jRe-fit of data in Beyer et al. 2015, Lefebvre et al. 2018, Beyer et al. 2024; ^kCalculated from data in Beyer et al. 2015 and Beyer et al. 2024; ^lCurrent study; ^mD'Souza; ⁿLaidig 2010

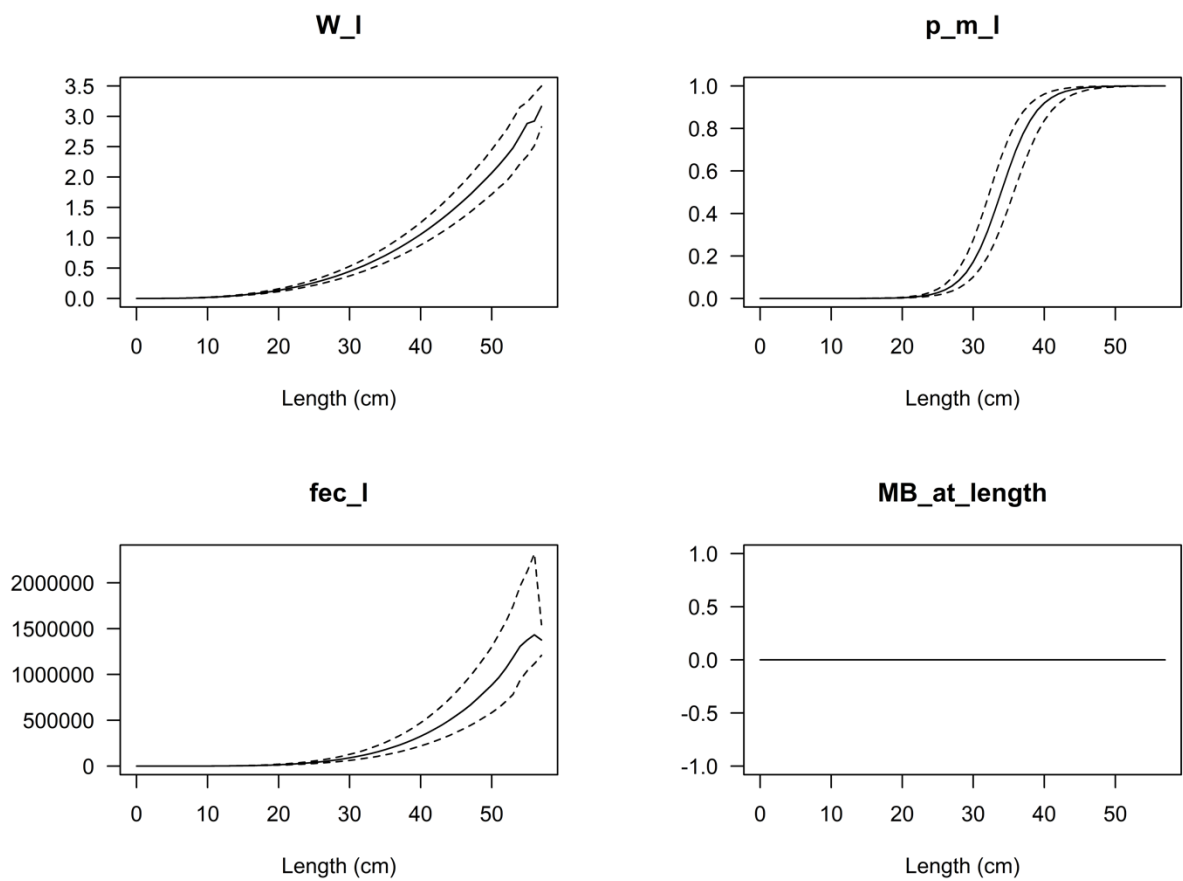
The following sets of plots are the distributions of parameter draws from the simulations, the resulting median trait-at-length and trait-at-age relationships with 95% confidence intervals from bootstrapping, and the empirical distributions of steepness for both the vBGF and empirical ELH growth methods to estimate early life survival, α . Plots are presented by species.

74 Yellowtail Rockfish



75

76 **Figure SM4-1.** Life history parameter distributions from 1000 simulations.

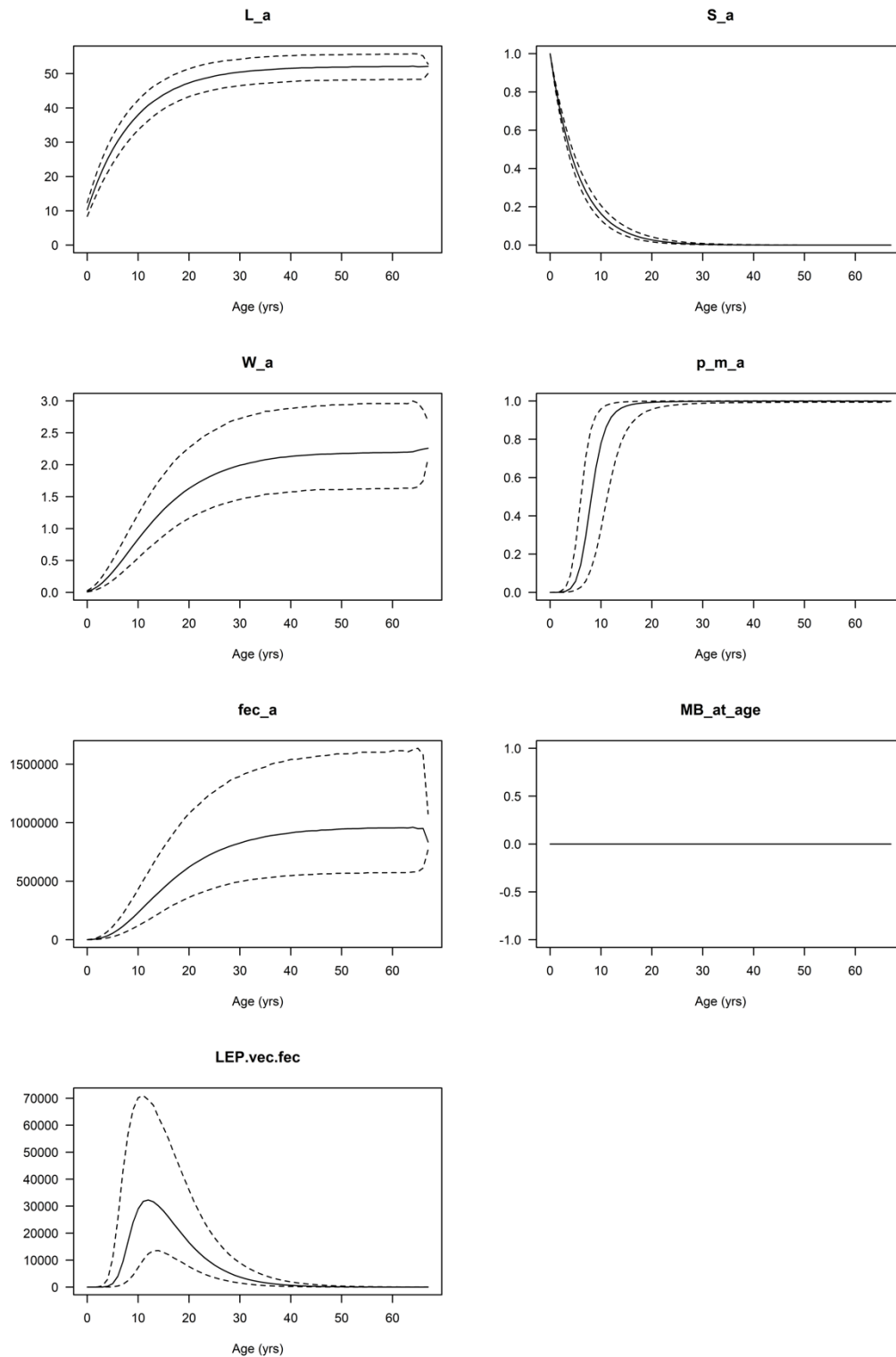


77

78 **Figure SM4-2** Trait-at-length relationships showing the median (solid line) and 95% confidence

79 intervals from bootstrapping (dashed lines).

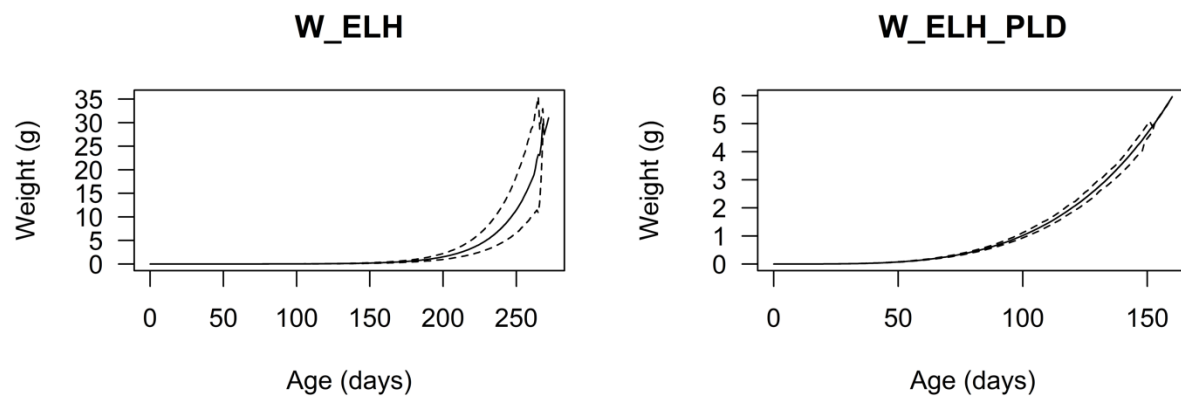
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81

82 **Figure SM4-3.** Trait-at-age relationships showing the median (solid line) and 95% confidence

83 intervals from bootstrapping (dashed lines).



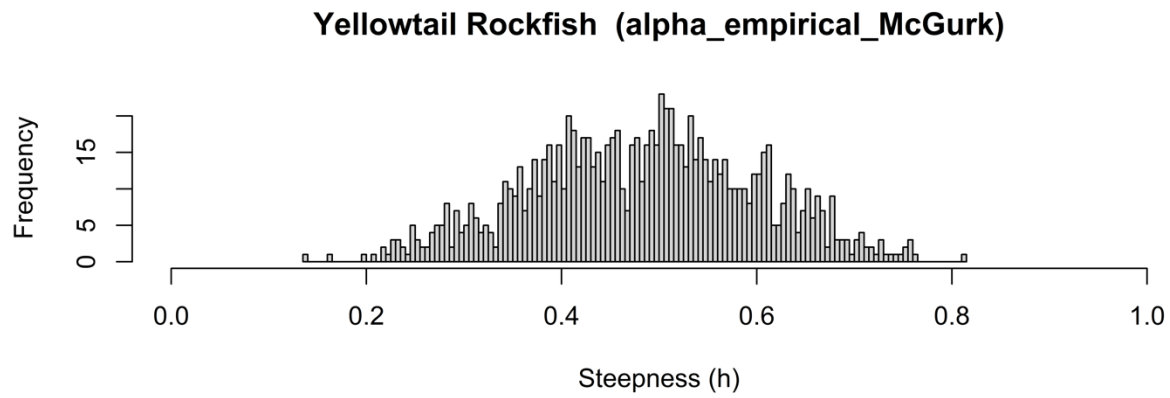
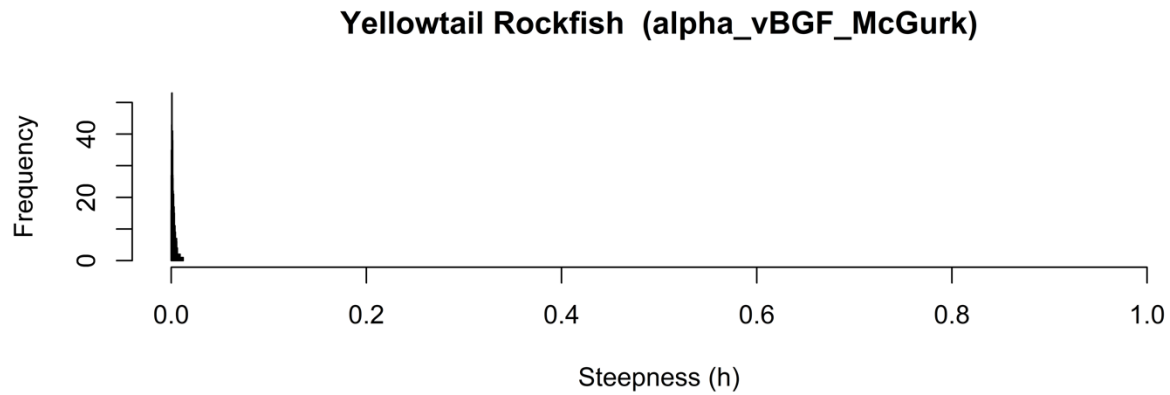
84

85 **Figure SM4-4.** Early life history growth using either vBGF assumptions (left) or empirical

86 growth and estimates of pelagic larval duration (right).

87

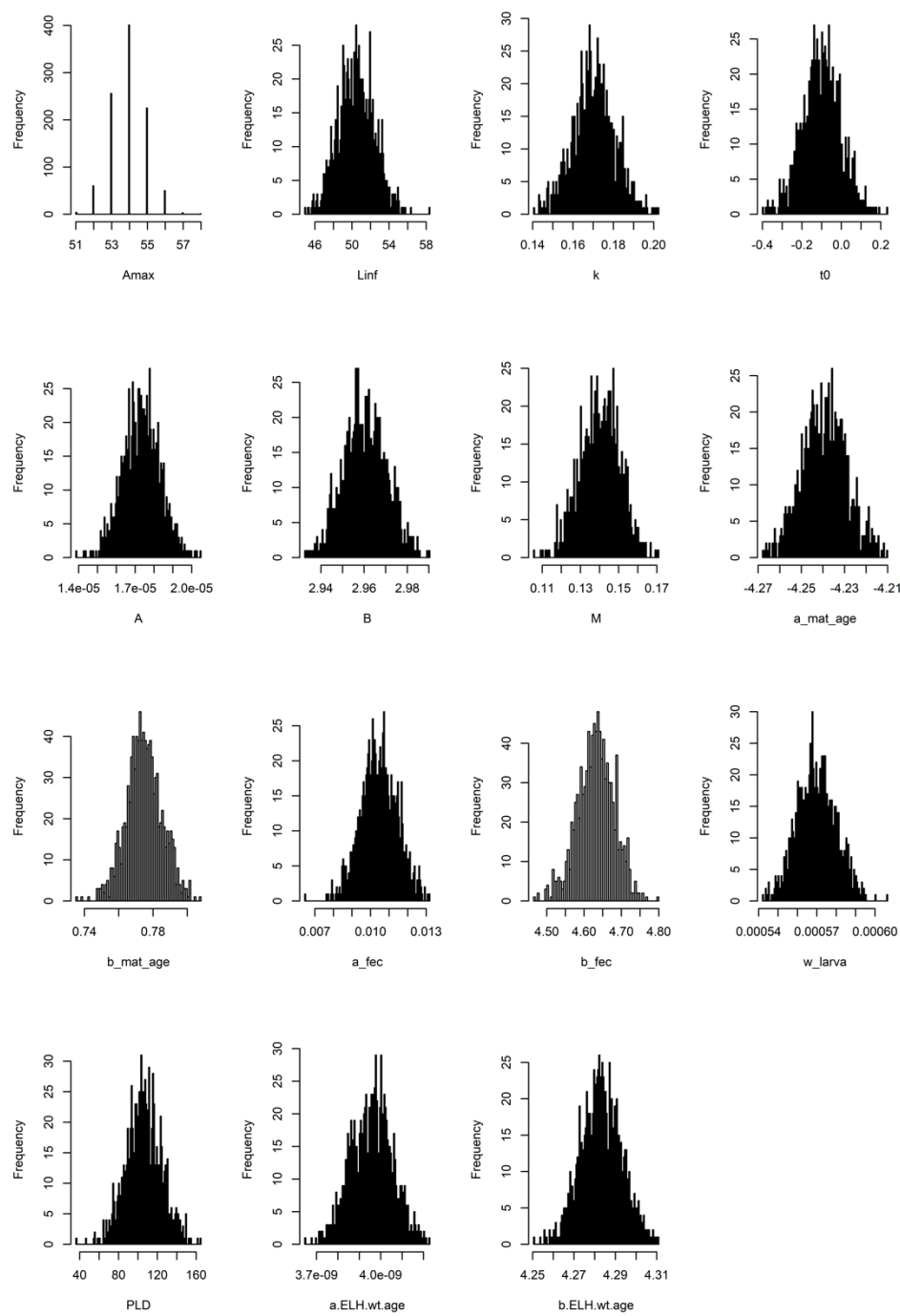
88



89

90 **Figure SM4-5.** The distribution of steepness using either vBGF assumptions (top) or empirical
 91 data (bottom) to calculate early life history growth and survival.

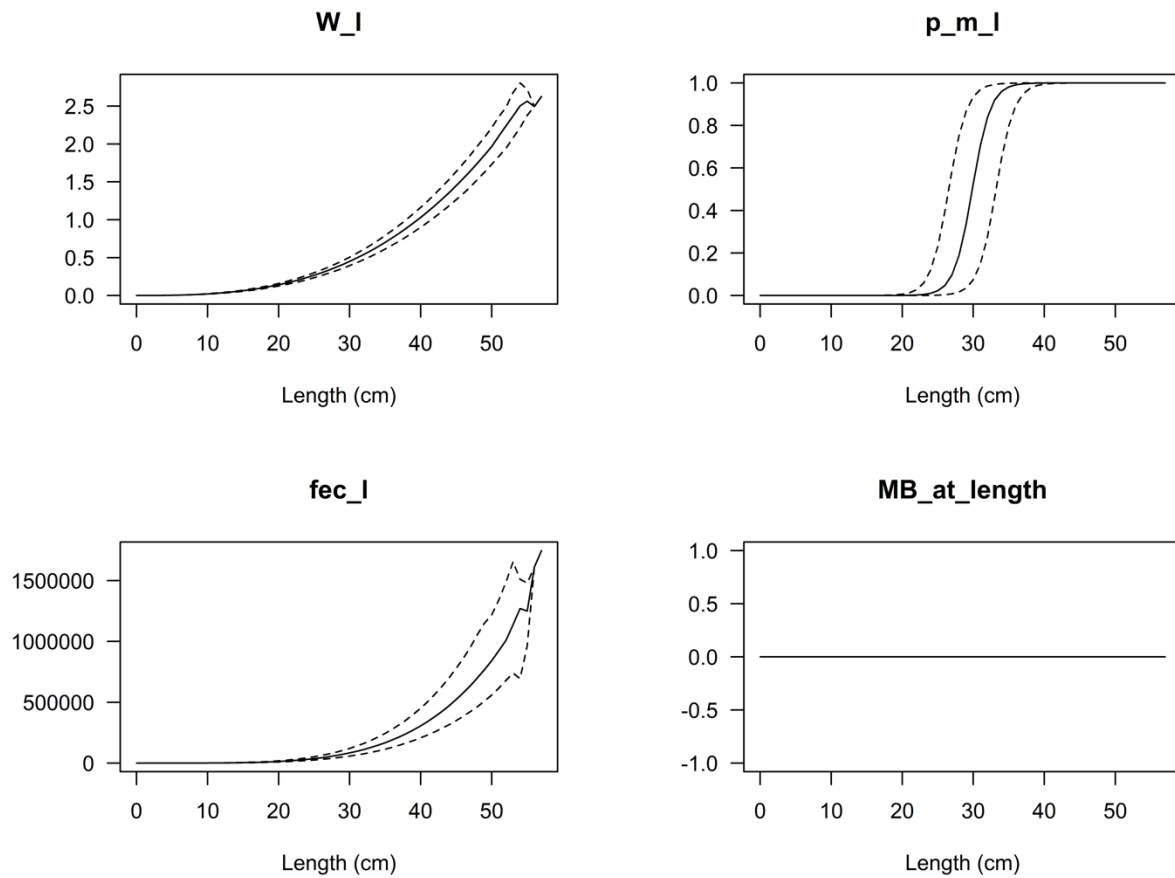
92 Widow Rockfish



93

94 **Figure SM4-6.** Life history parameter distributions from 1000 simulations.

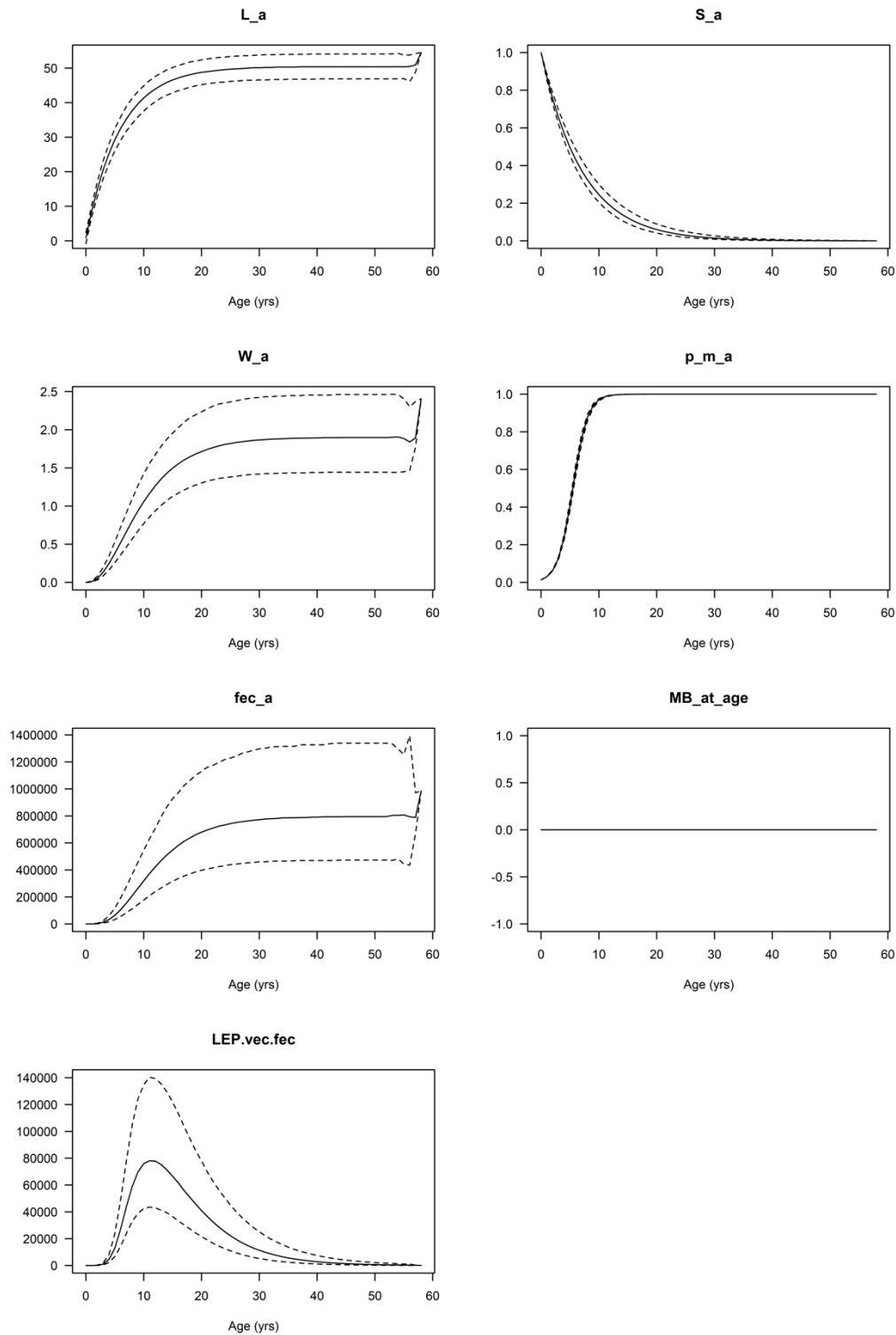
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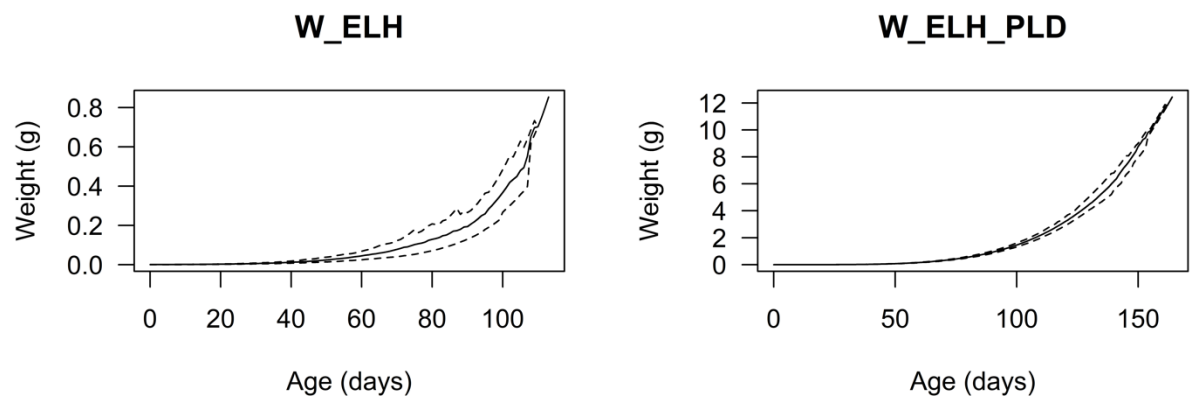
98 **Figure SM4-7.** Trait-at-length relationships showing the median (solid line) and 95% confidence
 99 intervals from bootstrapping (dashed lines).



100

101 **Figure SM4-8.** Trait-at-age relationships showing the median (solid line) and 95% confidence
 102 intervals from bootstrapping (dashed lines).

103

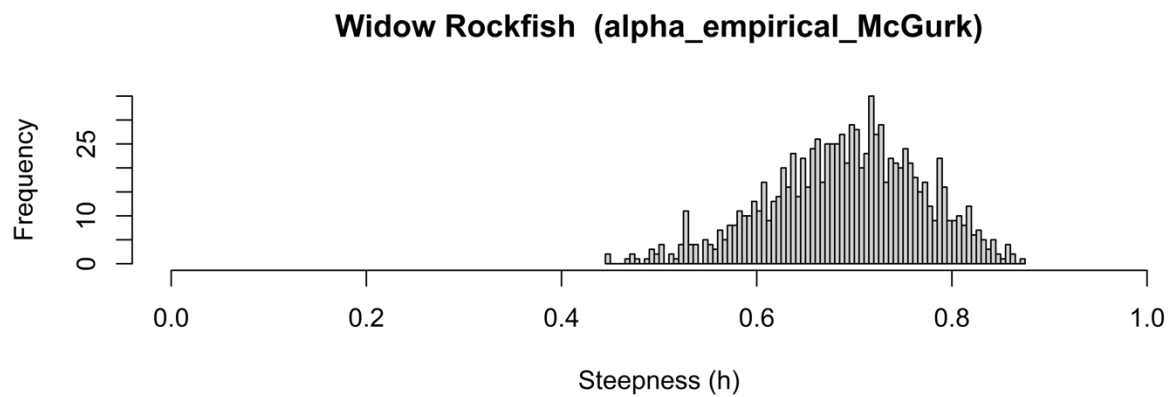
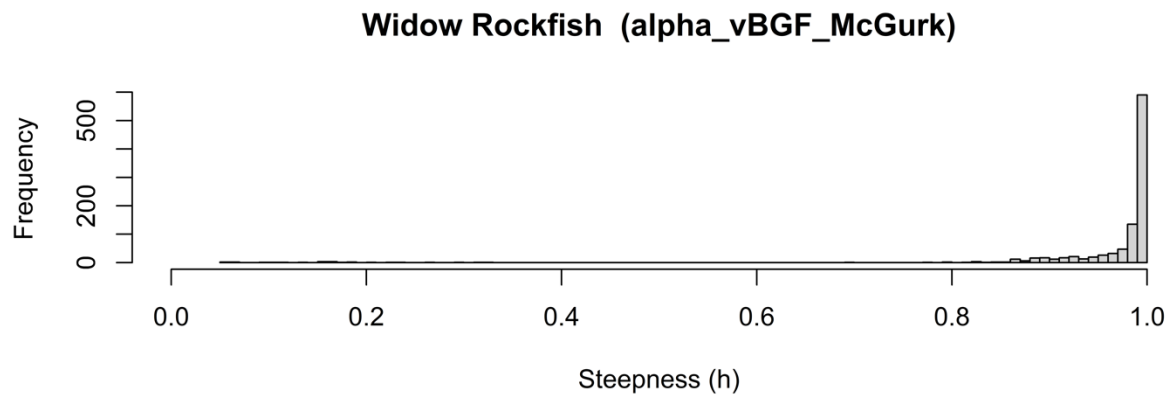


104

105 **Figure SM4-9.** Early life history growth using either vBGF assumptions (left) or empirical
106 growth and estimates of pelagic larval duration (right).

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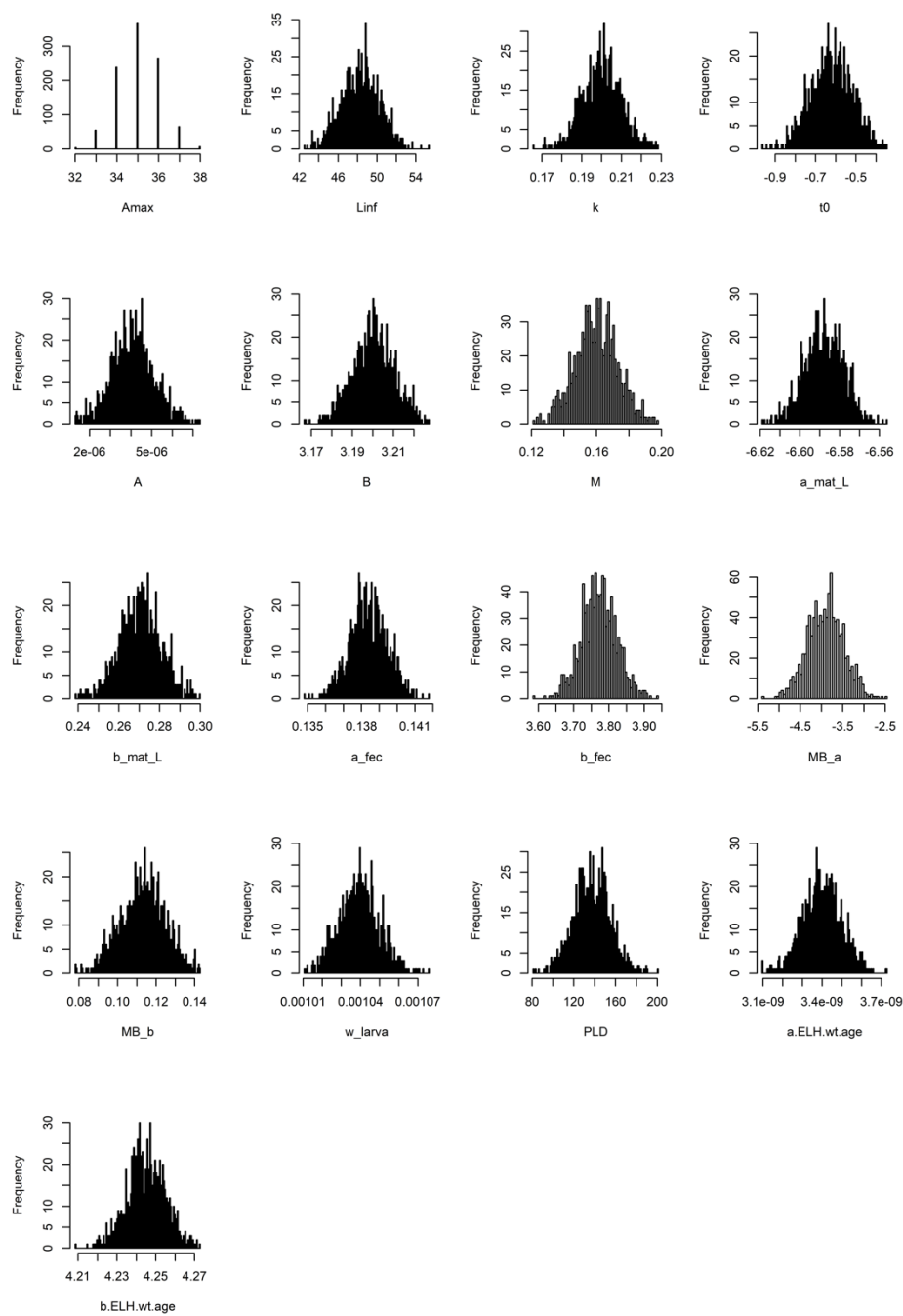
108



109

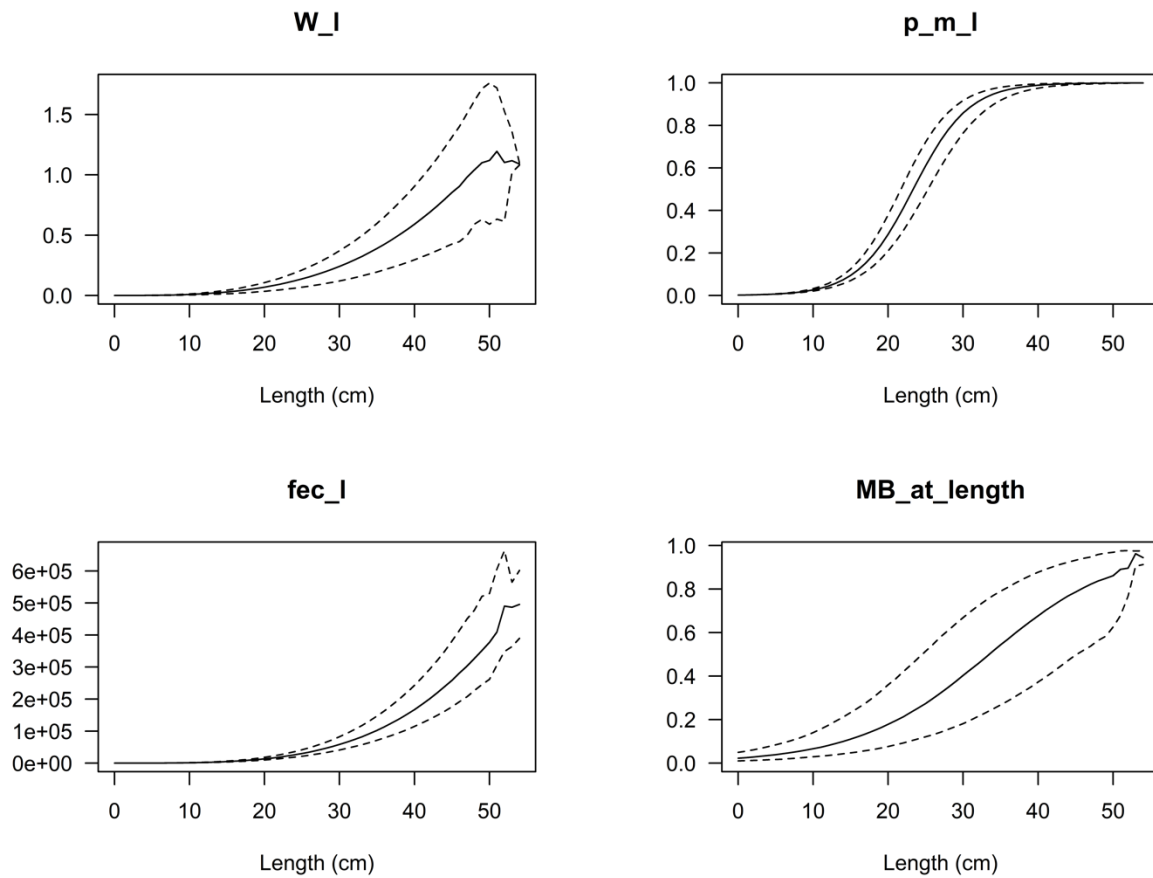
110 **Figure SM4-10.** Distributions of steepness using either vBGF assumptions (top) or empirical
 111 data (bottom) to calculate early life history growth and survival.

112 Chilipepper



113

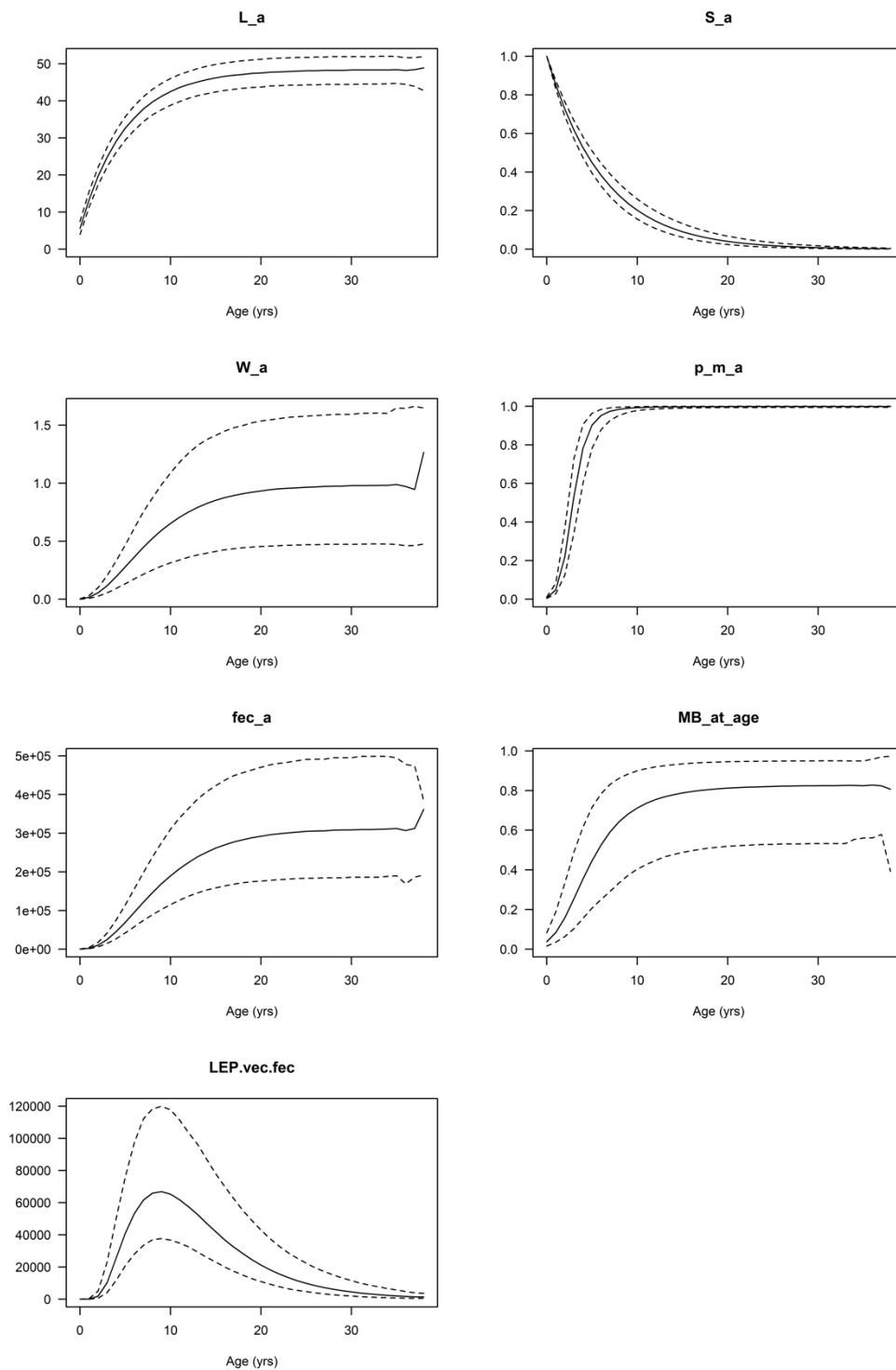
114 **Figure SM4-11.** Life history parameter distributions from 1000 simulations.



115

116 **Figure SM4-12.** Trait-at-length relationships showing the median (solid line) and 95%

117 confidence intervals from bootstrapping (dashed lines).

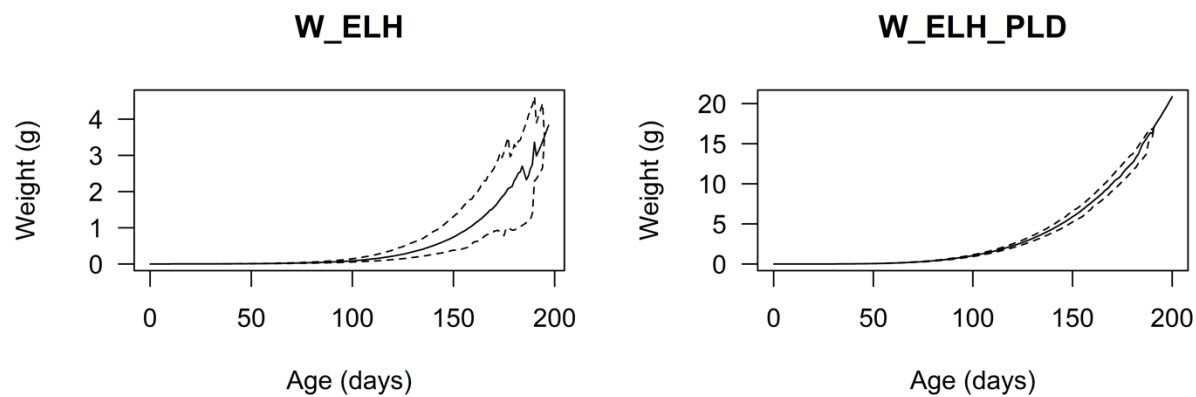


118

119 **Figure SM4-13.** Trait-at-age relationships showing the median (solid line) and 95% confidence

120 intervals from bootstrapping (dashed lines).

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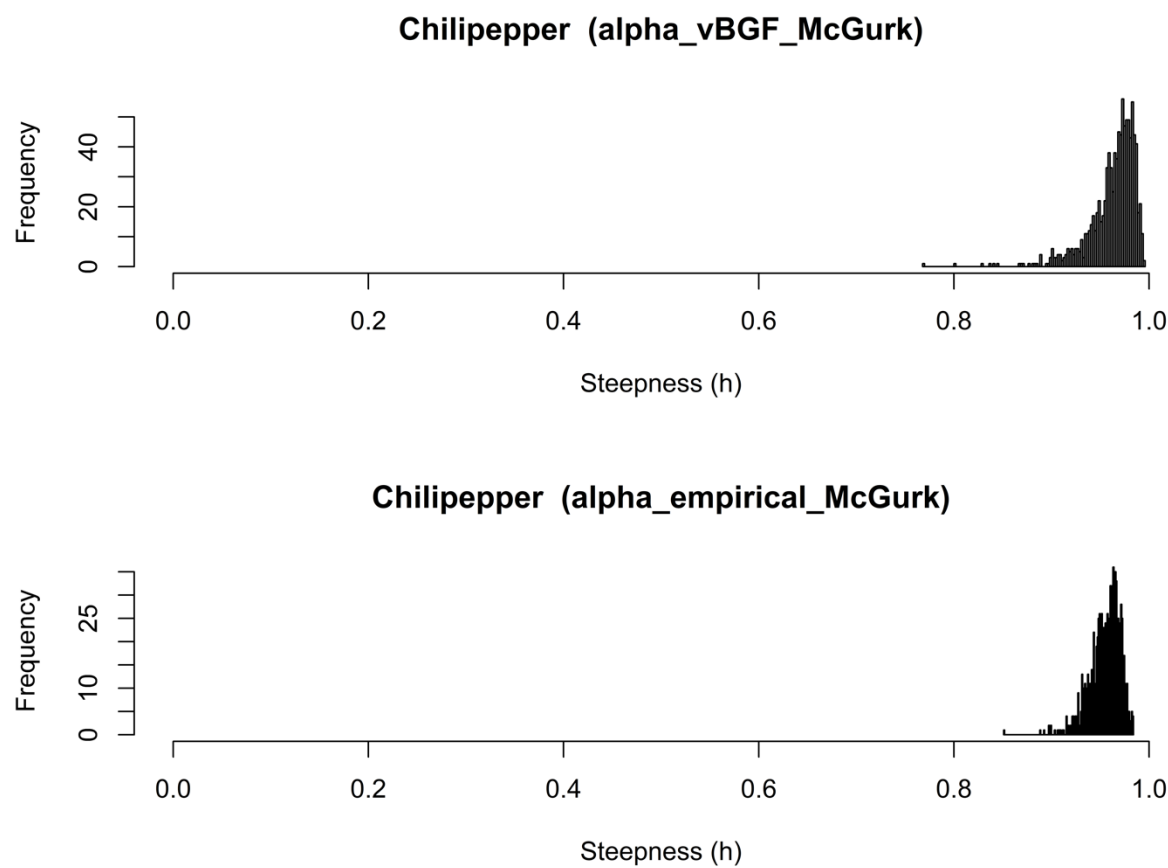
Figure SM4-14. Early life history growth using either vBGF assumptions (left) or empirical

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growth and estimates of pelagic larval duration (right).

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Figure SM4-15. Distributions of steepness using either vBGF assumptions (top) or empirical

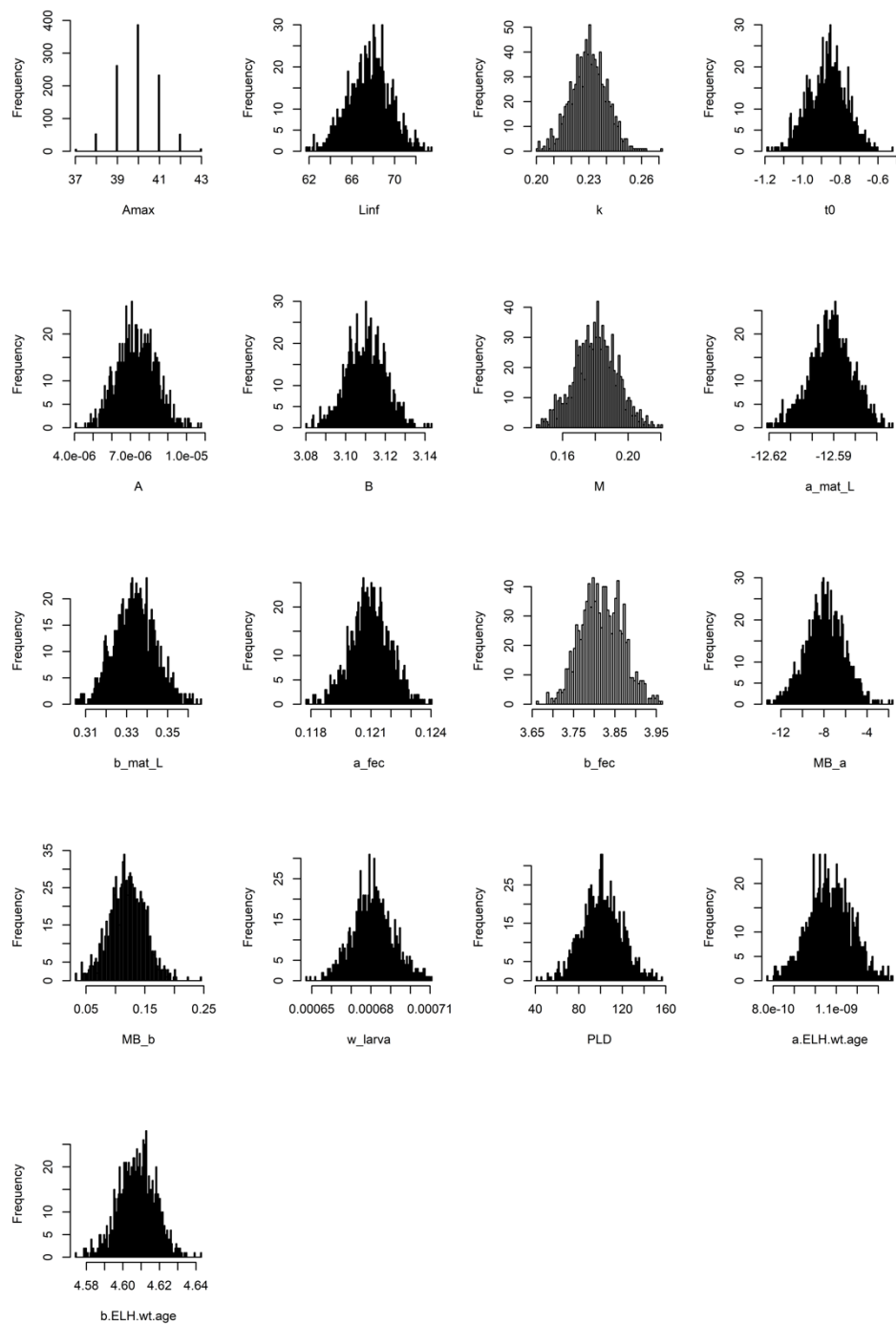
129

data (bottom) to calculate early life history growth and survival.

130

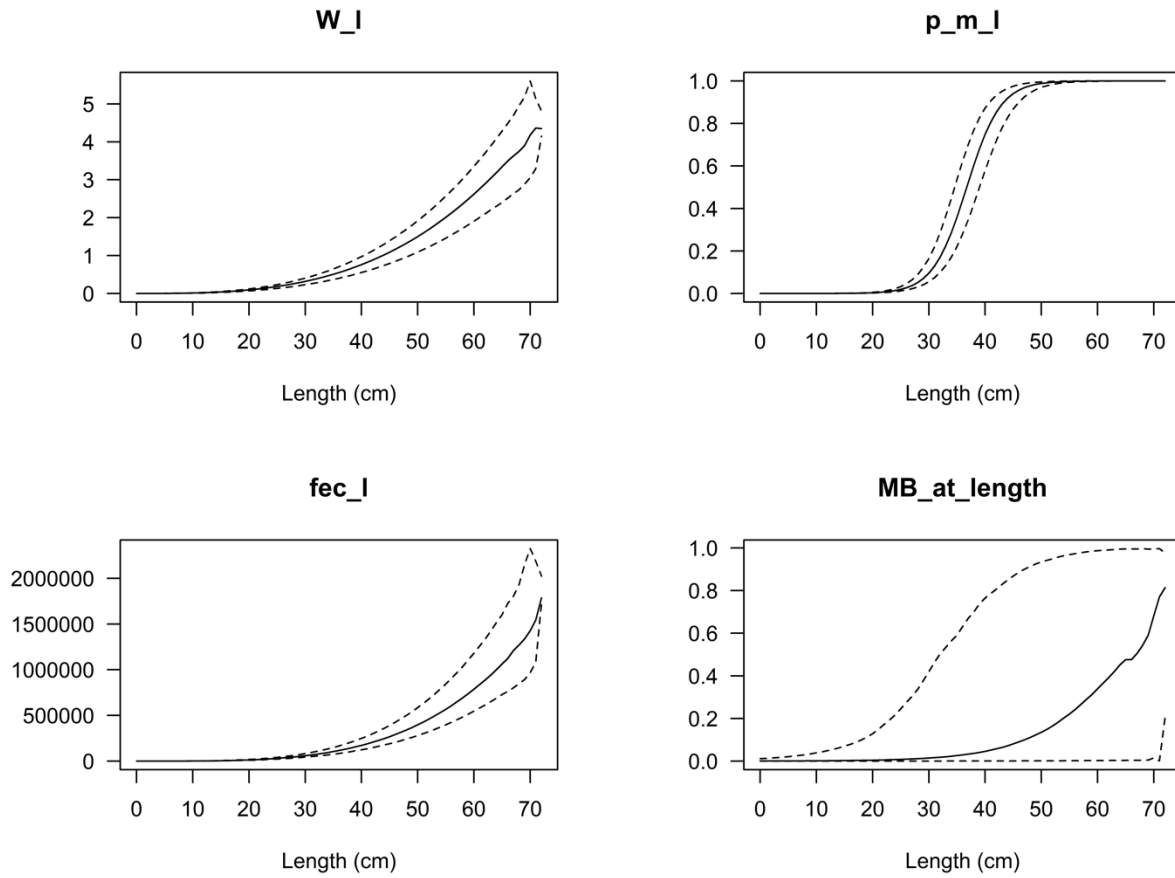
131 Bocaccio

132



133

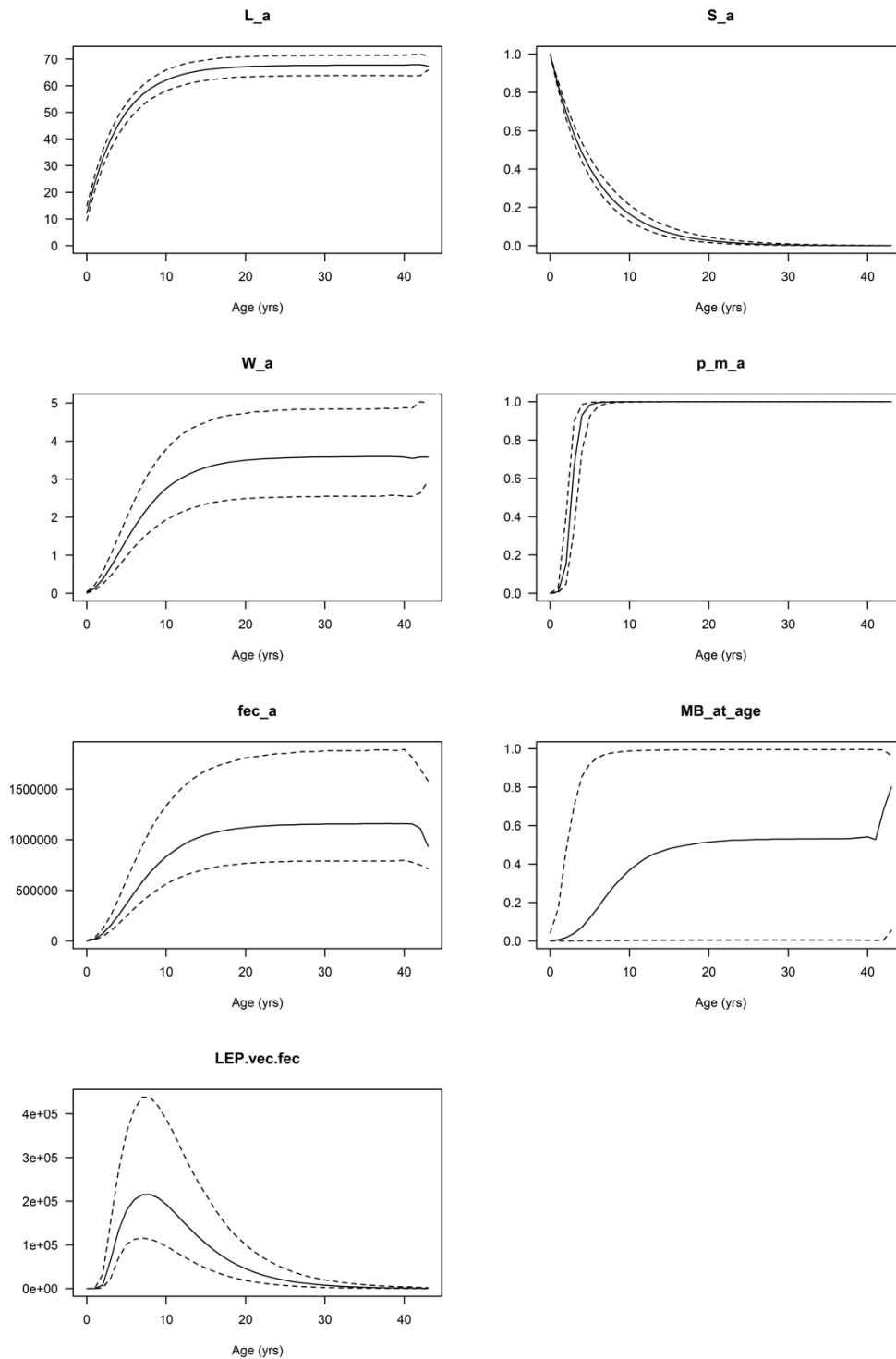
134 **Figure SM4-16.** Life history parameter distributions from 1000 simulations.



135

136 **Figure SM4-17.** Trait-at-length relationships showing the median (solid line) with 95%

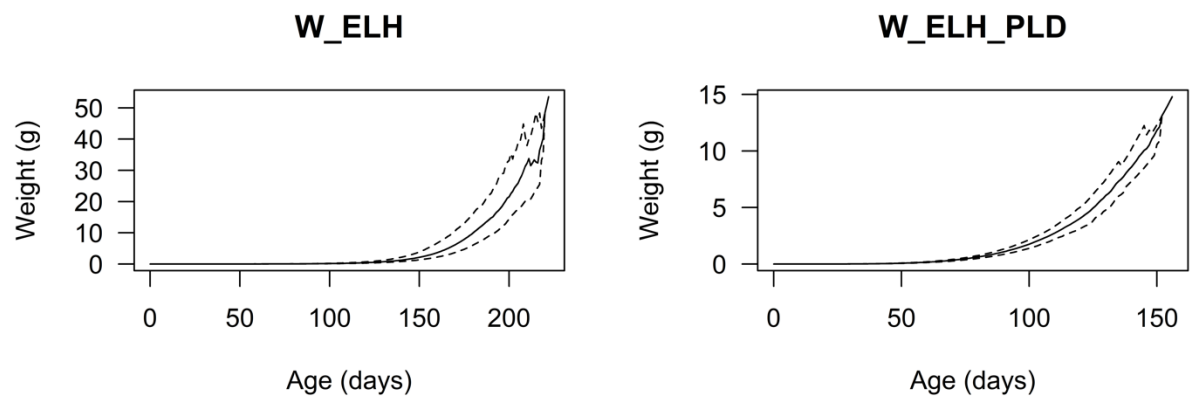
137 confidence intervals (dashed lines).



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139 **Figure SM4-18.** Trait-at-age relationships showing the median (solid line) with 95% confidence

140 intervals (dashed lines).



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142

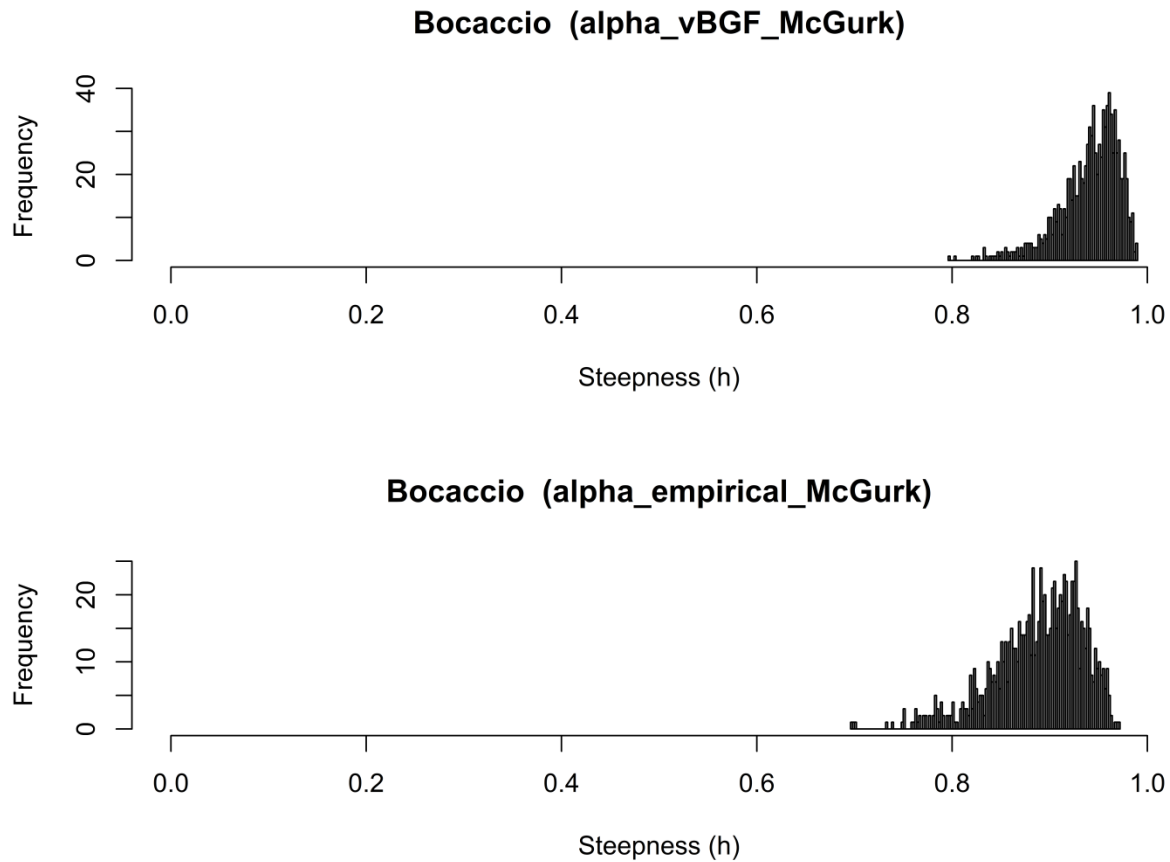
Figure SM4-19. Early life history growth using either vBGF assumptions (left) or empirical

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growth and estimates of pelagic larval duration (right).

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146

147 **Figure SM4-20.** Distributions of steepness using either vBGF assumptions (top) or empirical
 148 data (bottom) to calculate early life history growth and survival.

149

150 Literature cited in this Supplementary Material

151 Hsu, J., Chang, Y.-J., Brodziak, J., Kai, M., & Punt, A. E. (2024). On the probable
 152 distribution of stock-recruitment resilience of Pacific saury (*Cololabis saira*) in the
 153 Northwest Pacific Ocean. *ICES Journal of Marine Science*, 81(4), 748–759.
 154 <https://doi.org/10.1093/icesjms/fsae030>

Supplementary Materials 4: Simulation to Generate Priors

In the main text we treated the life history parameters as perfectly known for the proof of concept for using reproductive biology and early life history parameters to compute steepness. In practice, each of these parameters will have associated variability and measurement error. The knowledge of this variability can be used in simulation methods to generate biologically meaningful prior distributions for steepness. Here we describe a general simulation method to develop prior distributions for steepness for the four focal study species, making two simplifying assumptions. Our simulation approach involves two steps:

- 1) *Choosing distributions for the life history parameters:* To demonstrate the method, we treat each life history parameter as an independent random variable and assign a mean μ and standard deviation σ to each one assuming a normal distribution. Our two simplifying assumptions are that 1) the normal distribution is appropriate and 2) the random variables are independent. The use of normal distributions is our first simplifying assumption because some parameters must be positive and the normal distribution allows for negative values. We show this assumption is adequate for most parameters. For computations, we reject any negative values for a parameter that must be positive. Future investigations should consider other distributions with only positive support, such as the log-normal or gamma densities. For standard deviation, we used literature values, if reported, or assumed reasonable values when not reported (Table SM4-1). Future investigations should also investigate the second assumption by considering covariance among parameters estimated from model fitting and from knowledge of biology. For example, when estimating parameters for the vBGF $L(a) = L_{\infty}(1 - e^{-k(a-a_0)})$ it is

well known that estimates of asymptotic size L_∞ and growth rate k are inversely correlated. Furthermore, since the size at age 0 is $L(0) = L_\infty(1 - e^{-k a_0})$ there is an additional correlation between size at birth, growth rate and theoretical age of zero size. These correlations are both a result of the form of the vBGF and biology (Mangel, 2006, pg 23-29). Covariance should also be explored for other size- and age- dependent traits, such as the allometric length-weight relationship, size-dependent maturity, fecundity, etc.

2) *Simulation and bootstrapping*: Accepting the limitations of normal distributions with no parameter covariance, and reasonable estimates of standard deviation when not reported in the literature, we ran 1000 simulations to develop a distribution for steepness for the four focal species. For each simulation we randomly draw from the relevant life history parameter distributions to simulate trait-at-length and trait-at-age relationships needed to calculate lifetime egg production and early life survival. The full simulation produces 1000 trait-at-length and trait-at-age vectors for which we calculate the 0.025, 0.50 and 0.975 quantiles to plot median values with 95% confidence intervals from bootstrapping. We visually checked that both the individual parameter draws and resulting trait-at-length and trait-at-age relationships were reasonable and consistent with the species biology, including knowledge of the variability typically associated with these traits. In each iteration of the simulation and each species, we used the empirical ELH growth method to estimate early life history survival and combined that with the value of $\overline{LEP}_0$ for that species in the particular iteration.

The simulation thus produces a distribution for values of steepness. In summary, we provide the framework for developing prior distributions for steepness but recommend not using

the distributions shown here in stock assessments because of the key limiting assumptions described above and additional information needed on the standard deviation of individual parameters. Therefore, there is further research needed to operationalize the simulation to inform fisheries productivity and steepness. Once operational, the simulation method can also be used to forward project steepness when life history parameters co-vary with changing environmental conditions (see methods of Hsu et al., 2024), or when parameters differ regionally among different stocks of a species.

55 **Table SM4-1.** Life history parameter distributions used in the simulation. We assume a normal
 56 distribution with mean μ and standard deviation σ for all parameters. Equations and definitions
 57 of parameters are presented in the main text. Source references indicated by superscript.

Category	Parameter	Yellowtail $\mu(\sigma)$	Widow $\mu(\sigma)$	Chilipepper $\mu(\sigma)$	Bocaccio $\mu(\sigma)$
Age	Max_age	64 ^b (1 ^a)	54 ^b (1 ^a)	35 ^d (1 ^a)	40 ^d (1 ^a)
Growth (Eqn. 2)	L_{∞}	52.1 ^e (2 ^a)	50.4 ^b (2 ^a)	48.3 ^f (2 ^a)	37.7 ^g (2 ^a)
	k	0.11 ^e (0.01 ^a)	0.17 ^b (0.01 ^a)	0.20 ^f (0.01 ^a)	0.23 ^g (0.01 ^a)
	a_0	-2.01 ^e (0.1 ^a)	-0.10 ^b (0.1 ^a)	-0.62 ^f (0.1 ^a)	-0.87 ^g (0.1 ^a)
Length- Weight (Eqn. 3)	A	0.000011843 ^e (0.000001 ^a)	0.000017355 ^b (0.000001 ^a)	0.00000405 ^f (0.000001 ^a)	0.000007355 ^h (0.000001 ^a)
	B	3.07 ^e (0.01 ^a)	2.96 ^b (0.01 ^a)	3.20 ^f (0.01 ^a)	3.11 ^h (0.01 ^a)
Natural Mortality (Eqn. 4)	M	0.18 ^e (0.012 ^e)	0.14 ^b (0.010 ^b)	0.16 ^f (0.013 ^g)	0.18 ^g (0.013 ^g)
Maturity (Eqn. 5)	a_mat	-13.995 ^e (0.01 ^a) (at-length)	-4.23925 ^b (0.01 ^a) (at-age)	-6.588 ^f (0.01 ^a) (at-length)	-12.5918 ^h (0.01 ^a) (at-length)
	b_mat	0.401 ^e (0.01 ^a) (at-length)	0.775 ^b (0.01 ^a) (at-age)	0.270 ^f (0.01 ^a) (at-length)	0.334 ^h (0.01 ^a) (at-length)
Brood fecundity (Eqn. 6)	a_fec	0.0139 ⁱ (0.001 ^a)	0.0104 ⁱ (0.001 ^a)	0.1383 ⁱ (0.001 ^a)	0.1210 ⁱ (0.001 ^a)
	b_fec	4.57 ⁱ (0.05 ^a)	4.63 ⁱ (0.05 ^a)	3.77 ⁱ (0.05 ^a)	3.82 ⁱ (0.05 ^a)
Spawning frequency	a_MB	NA	NA	-3.900 ⁱ (0.43 ⁱ)	-7.983 ⁱ (1.75 ⁱ)

(Eqn. 7)					
	b_MB	NA	NA	0.114 ⁱ (0.01 ^j)	0.12 ^j (0.03 ^j)
Weight -at-birth (g)	w_larva	0.00048 ^k (0.00001 ^a)	0.00057 ^k (0.00001 ^a)	0.00104 ^k (0.00001 ^a)	0.00068 ^k (0.00001 ^a)
Empirical Pelagic Larval Duration (days)	PLD	103 ^l (18 ⁿ)	105 ^l (18 ⁿ)	138 ^l (18 ⁿ)	100 ^m (18 ⁿ)
ELH growth (d) (Eqn. 14)	a_ELH.wt.age	3.03 * 10 ^{-8 l} (1.0 * 10 ^{-10 a})	3.96 * 10 ^{-9 l} (1.0 * 10 ^{-10 a})	3.40 * 10 ^{-9 l} (1.0 * 10 ^{-10 a})	1.07 * 10 ^{-9 l} (1.0 * 10 ^{-10 a})
	b_ELH.wt.age	3.763 ^l (0.01 ^a)	4.283 ^l (0.01 ^a)	4.245 ^l (0.01 ^a)	4.608 ^l (0.01 ^a)

References: ^a assumed for simulation; ^b Shaw & Archibald (1981); ^c Adams et al. (2019); ^d Love et al. (2002);
^e Stephens & Taylor (2017); ^f Field et al. (2015); ^g He & Field (2017); ^h He et al. (2015); ⁱ Dick et al. (2017, total
lengths converted to fork lengths); ^j Re-fit of data in Beyer et al. (2015, 2024); Lefebvre et al. (2018); ^k Calculated
from data in Beyer et al. (2015, 2024); ^l Current study; ^m D'Souza (1998); ⁿ Laidig (2010)

In Figure SM4.1, we show the resulting distributions for steepness.

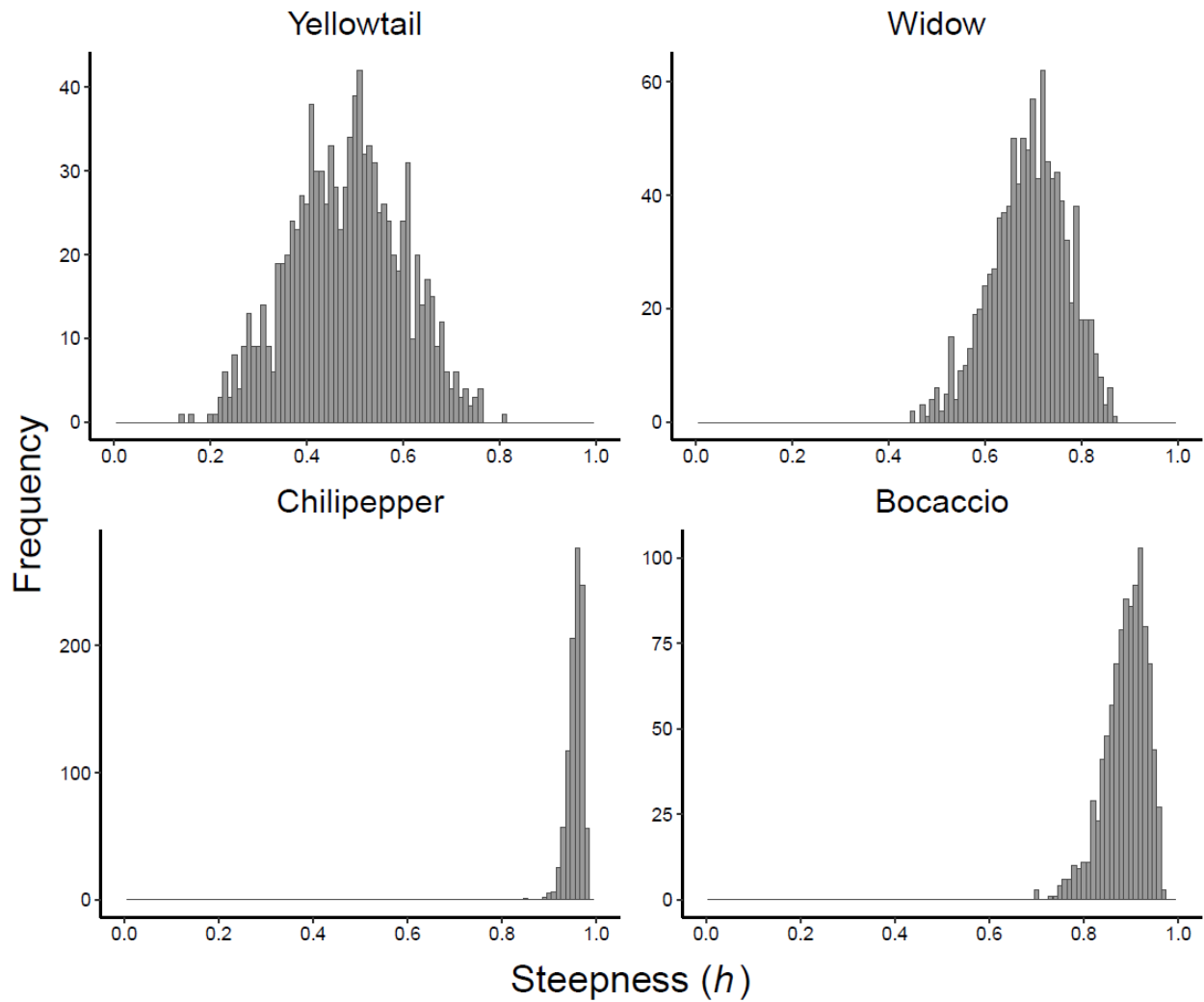
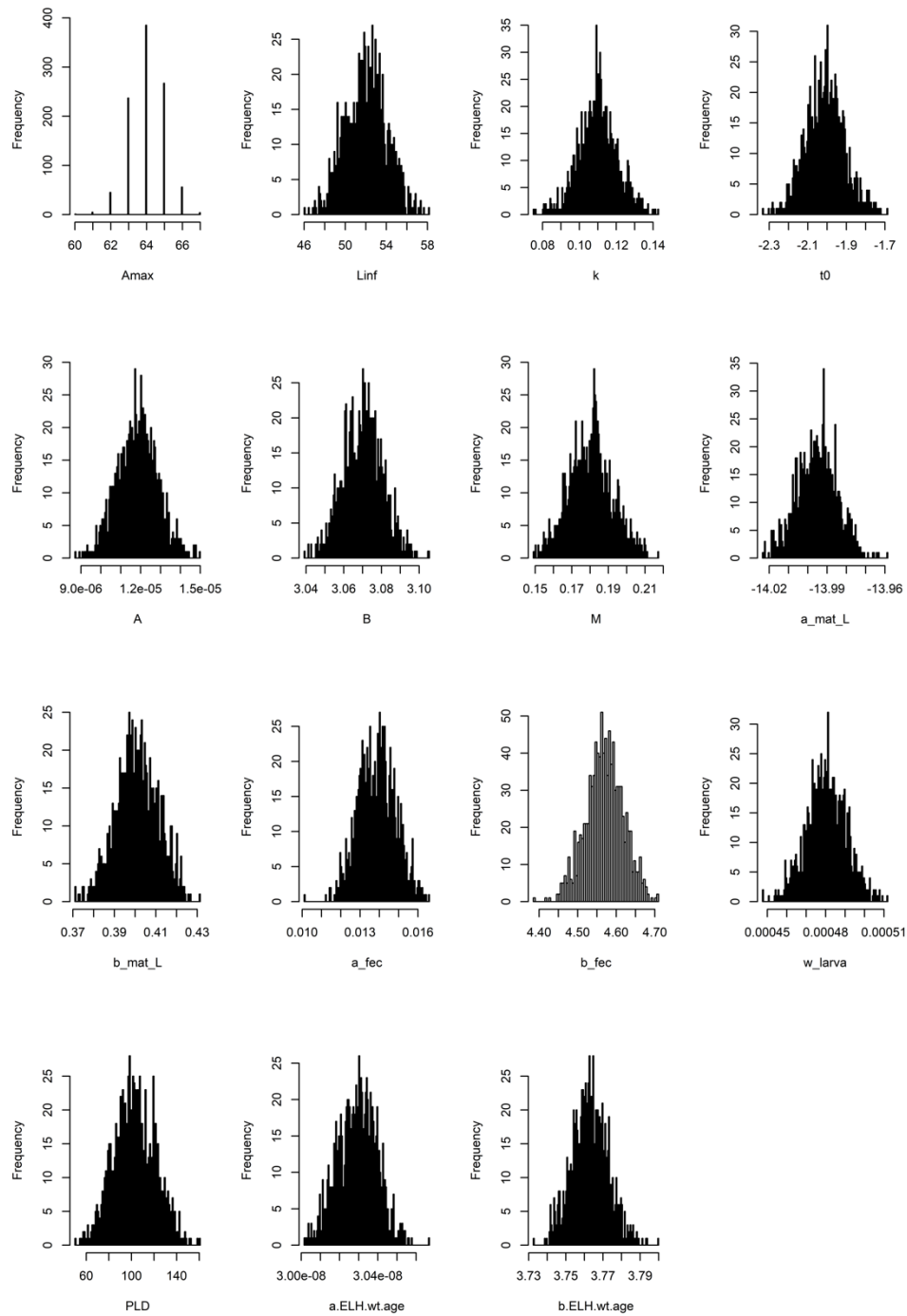


Figure SM4.1. The distribution of steepness (h) from the simulation for the four focal species using empirical data to calculate early life history growth and survival.

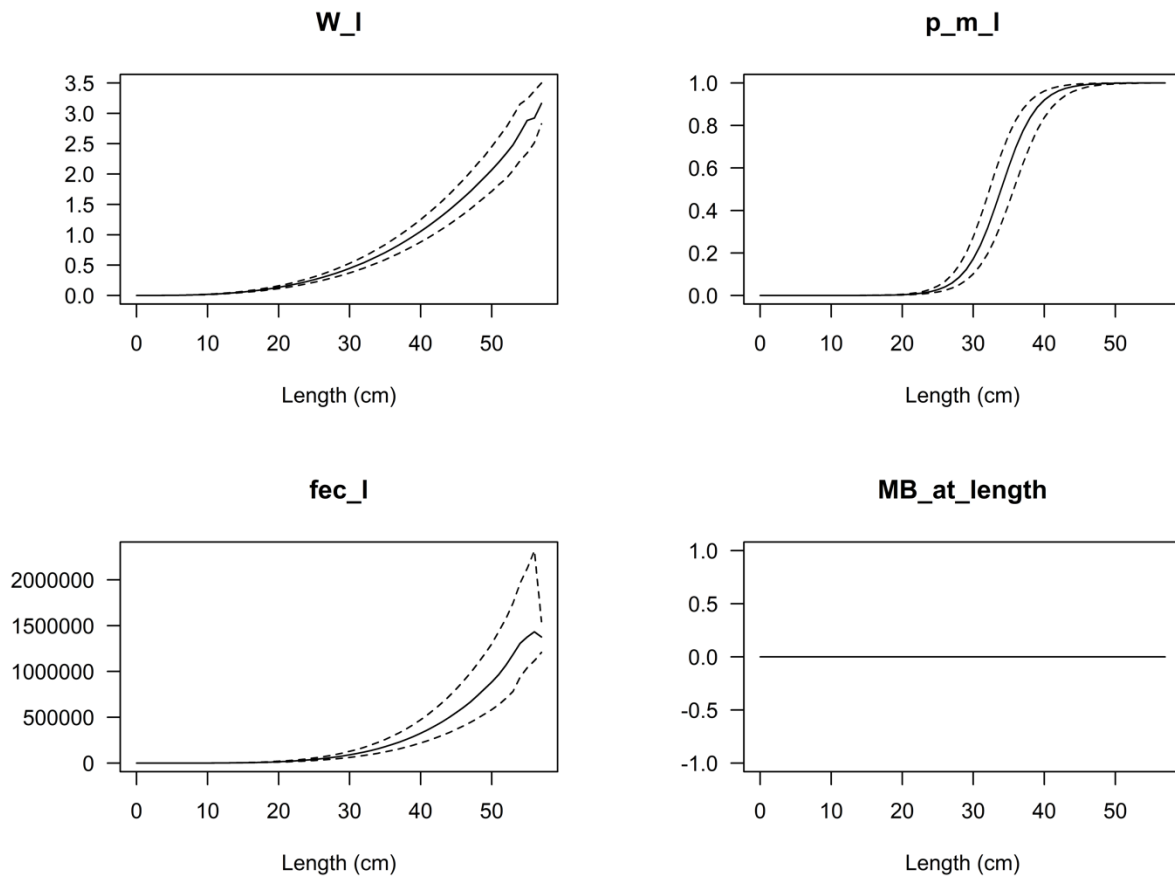
69 The following plots, separated by species, are 1) the distributions of parameter draws from the
70 simulations and 2) the resulting median trait-at-length and trait-at-age relationships with 95%
71 confidence intervals from bootstrapping.

72 Yellowtail Rockfish



73

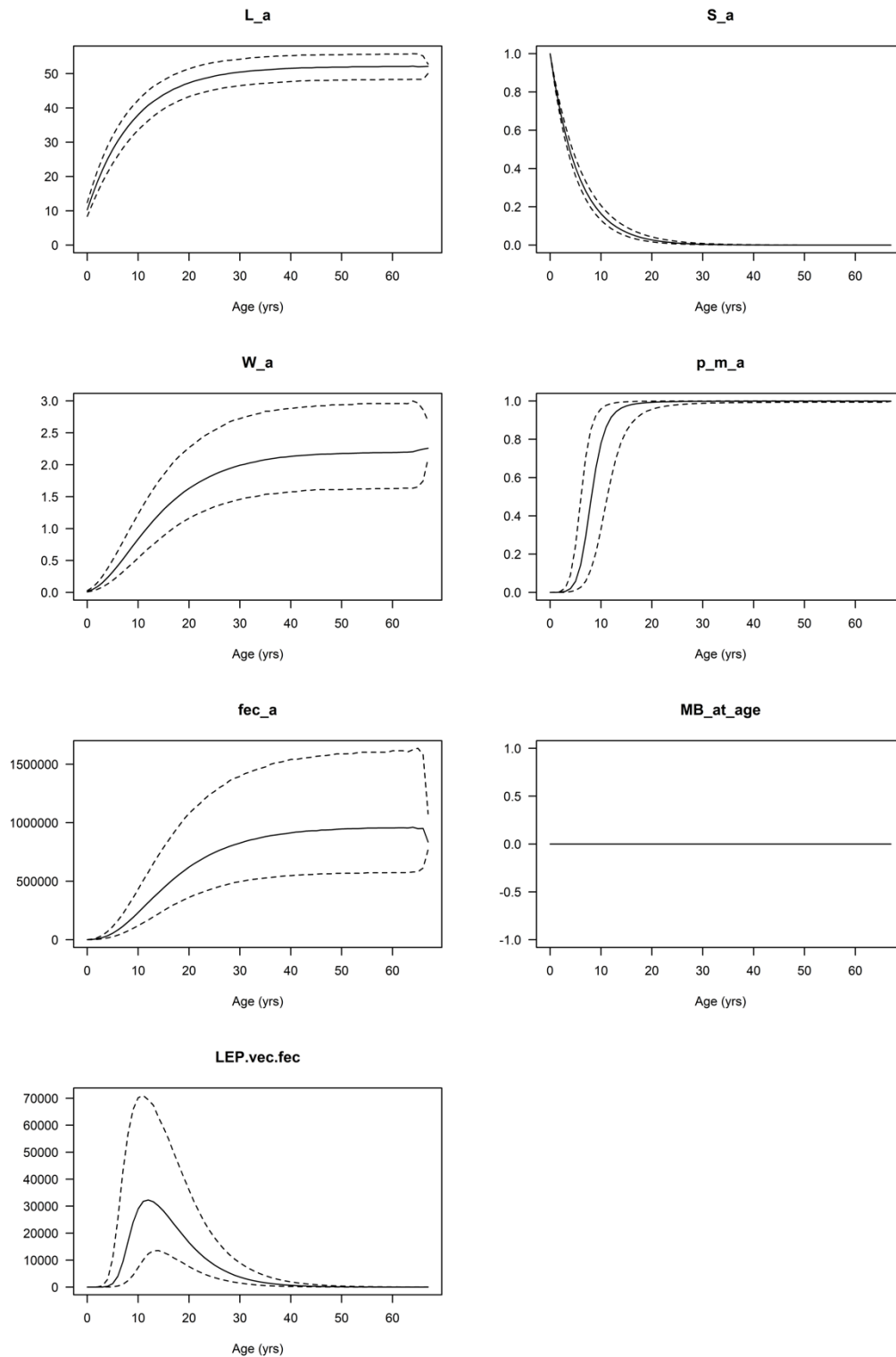
74 **Figure SM4-2.** Life history parameter distributions from 1000 simulations.



75

76 **Figure SM4-3.** Trait-at-length relationships showing the median (solid line) and 95% confidence
 77 intervals from bootstrapping (dashed lines).

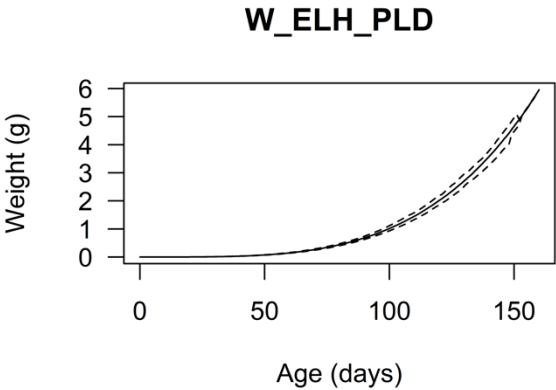
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79

80 **Figure SM4-4.** Trait-at-age relationships showing the median (solid line) and 95% confidence

81 intervals from bootstrapping (dashed lines).

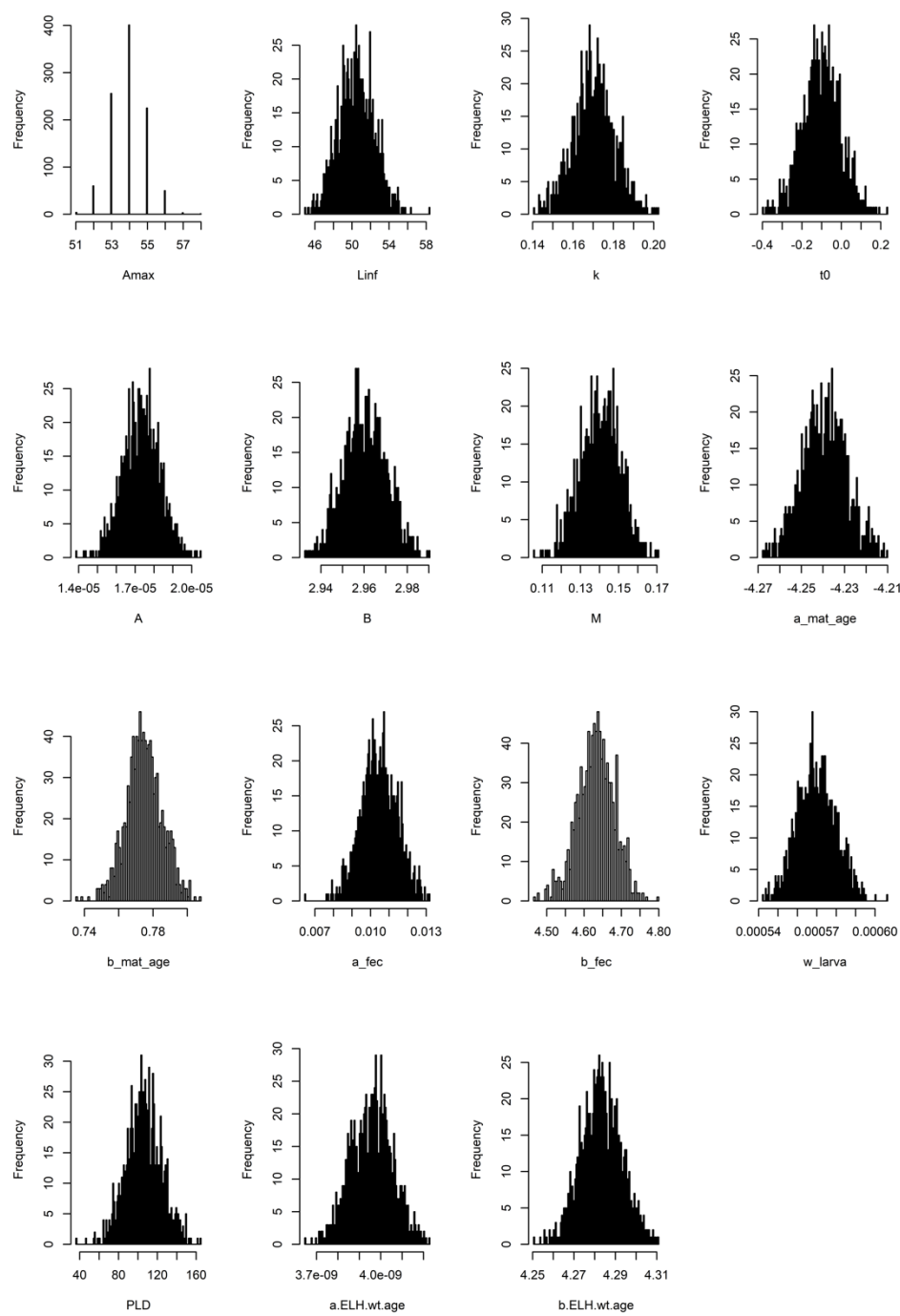


82

83 **Figure SM4-5.** Early life history growth using empirical growth and estimates of pelagic larval

84 duration.

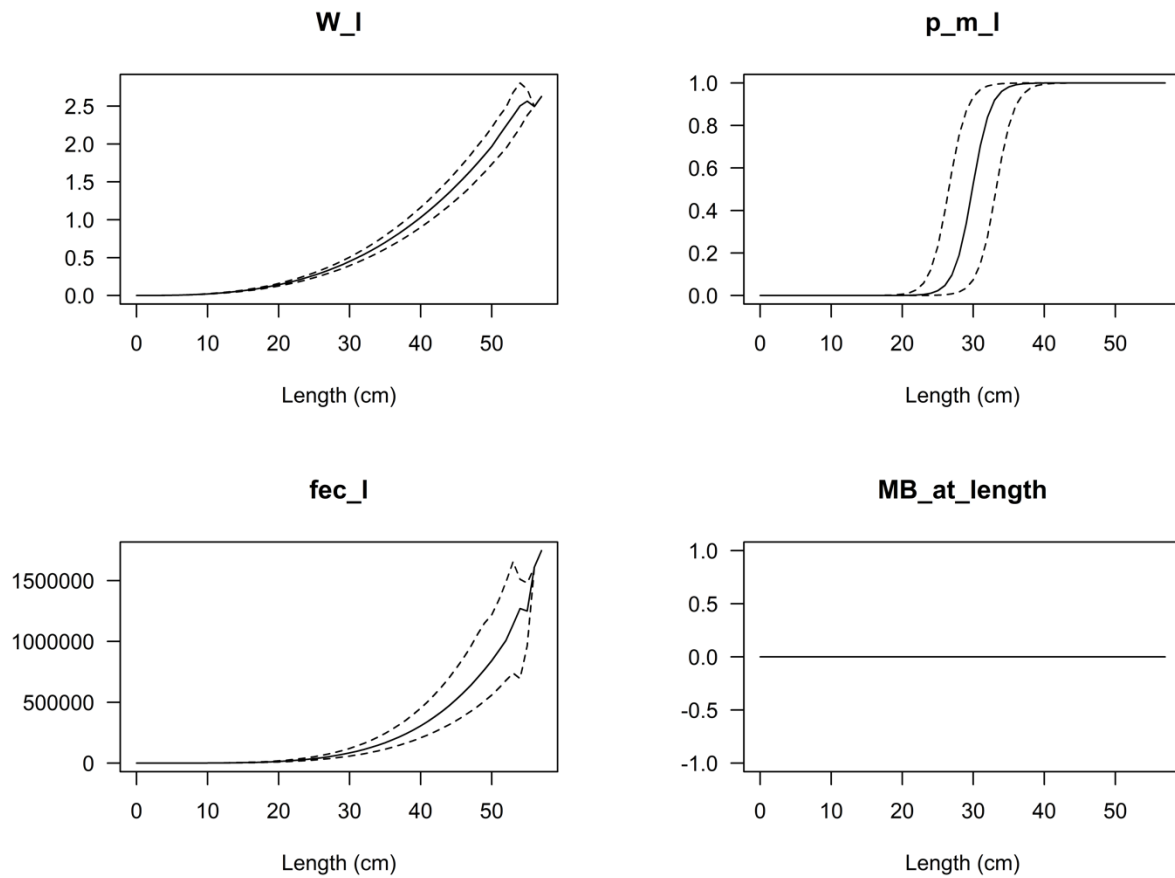
85 Widow Rockfish



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87 **Figure SM4-6.** Life history parameter distributions from 1000 simulations.

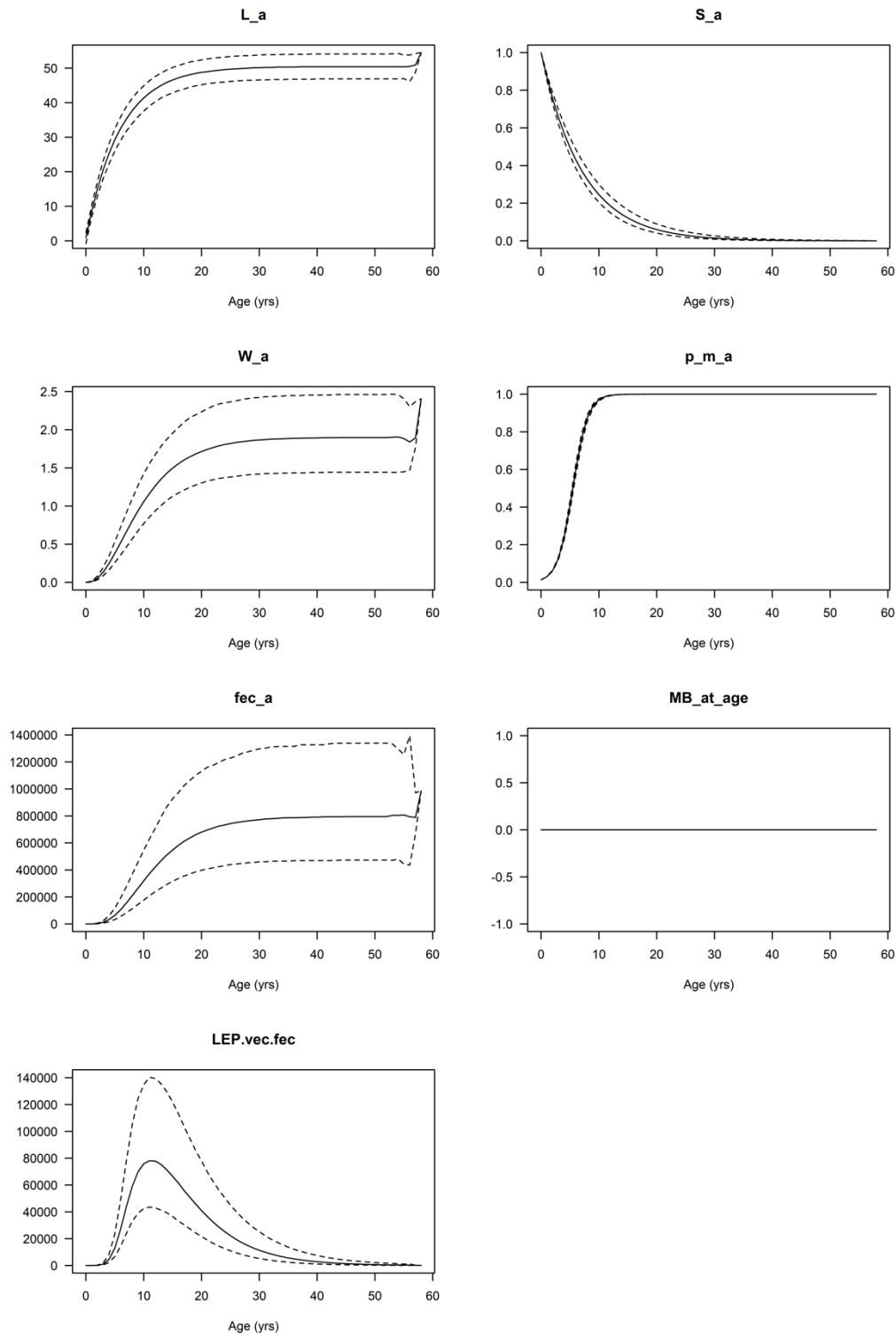
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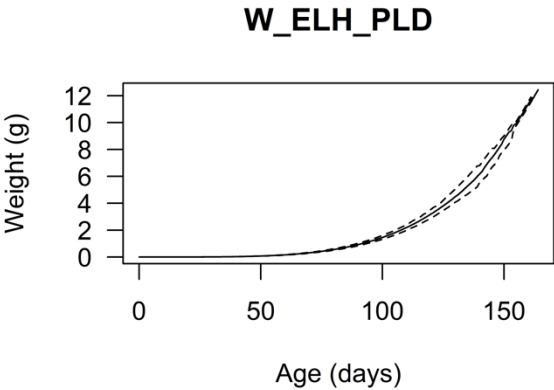
90

91 **Figure SM4-7.** Trait-at-length relationships showing the median (solid line) and 95% confidence
 92 intervals from bootstrapping (dashed lines).



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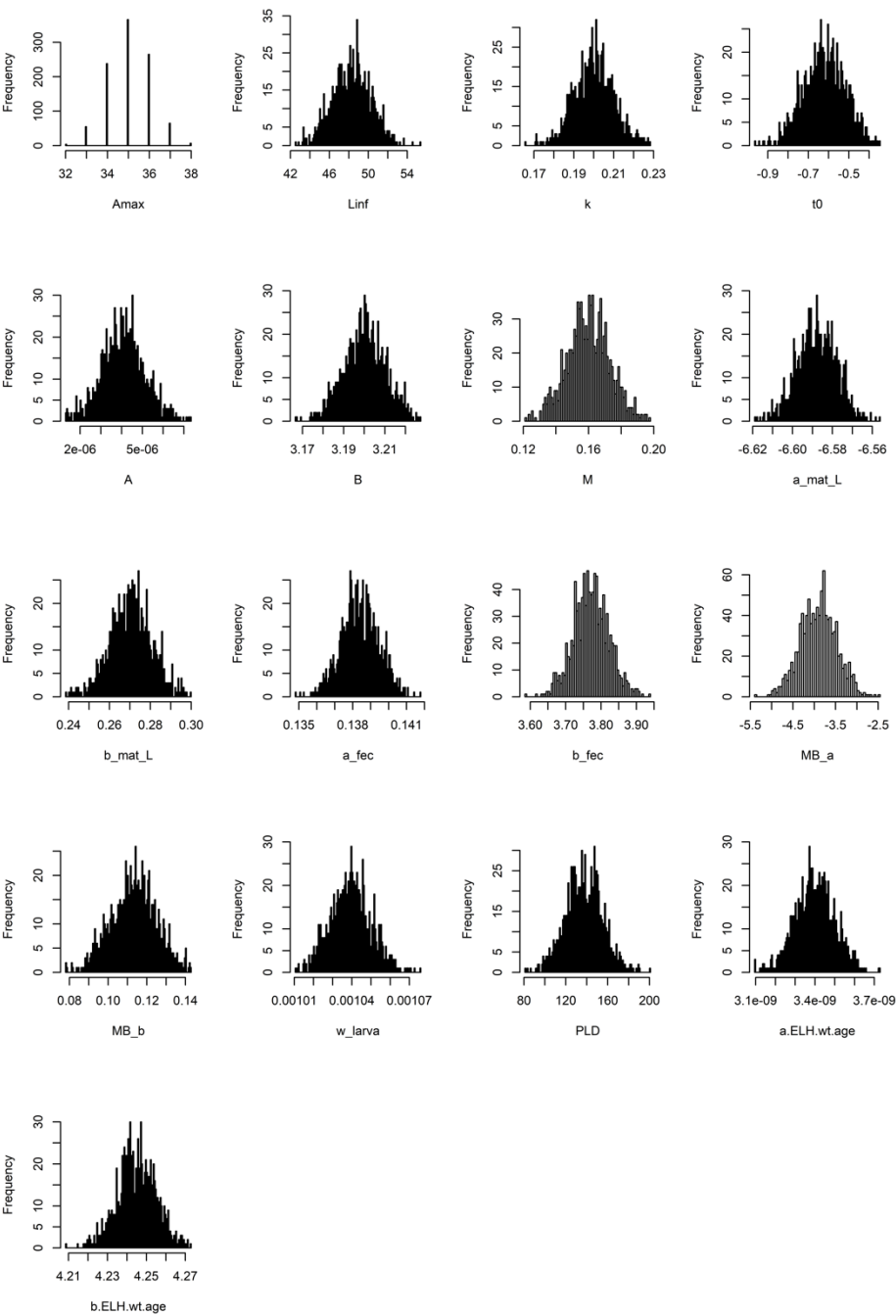
94 **Figure SM4-8.** Trait-at-age relationships showing the median (solid line) and 95% confidence
 95 intervals from bootstrapping (dashed lines).



96

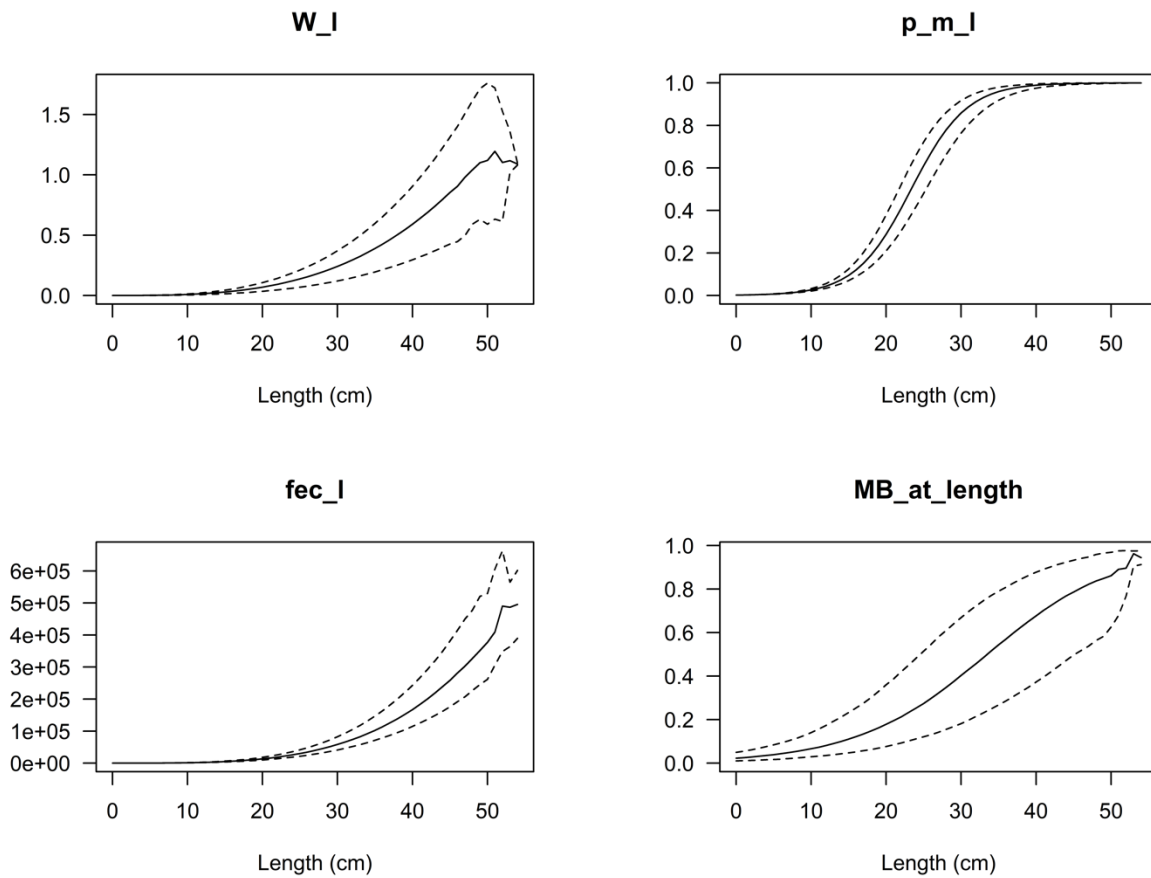
97 **Figure SM4-9.** Early life history growth using empirical growth and estimates of pelagic larval

98 duration.



100

101 **Figure SM4-10.** Life history parameter distributions from 1000 simulations.



102

103 **Figure SM4-11.** Trait-at-length relationships showing the median (solid line) and 95%

104 confidence intervals from bootstrapping (dashed lines).

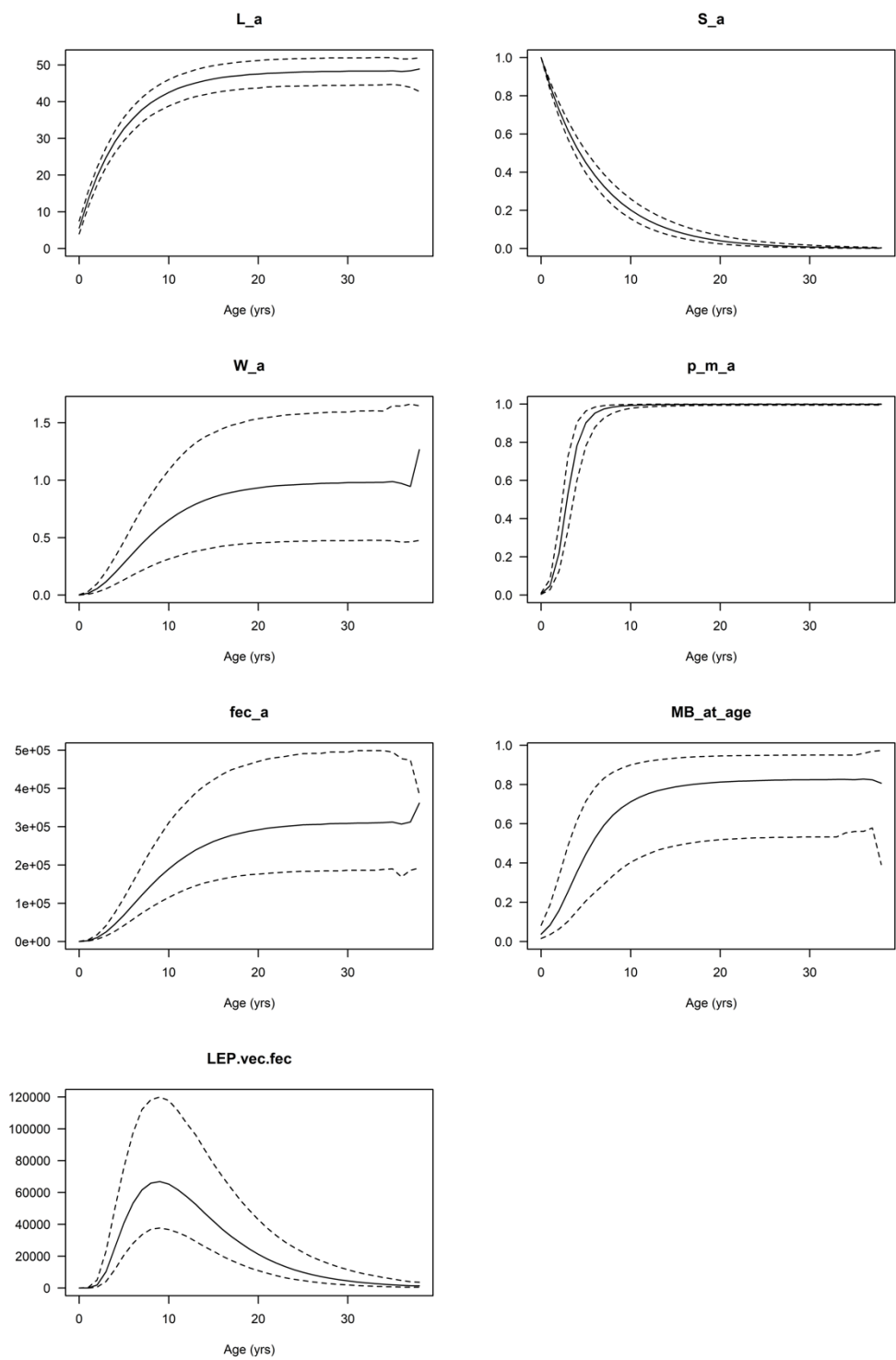
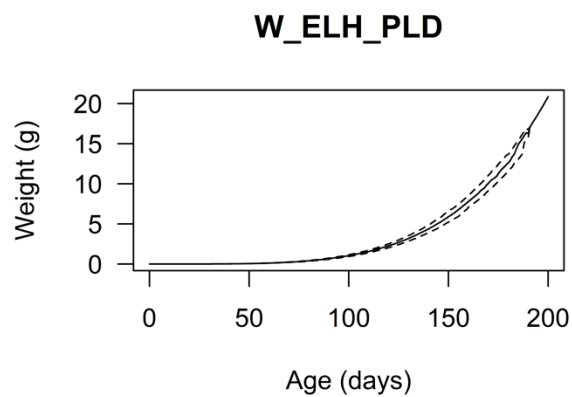


Figure SM4-12. Trait-at-age relationships showing the median (solid line) and 95% confidence intervals from bootstrapping (dashed lines).



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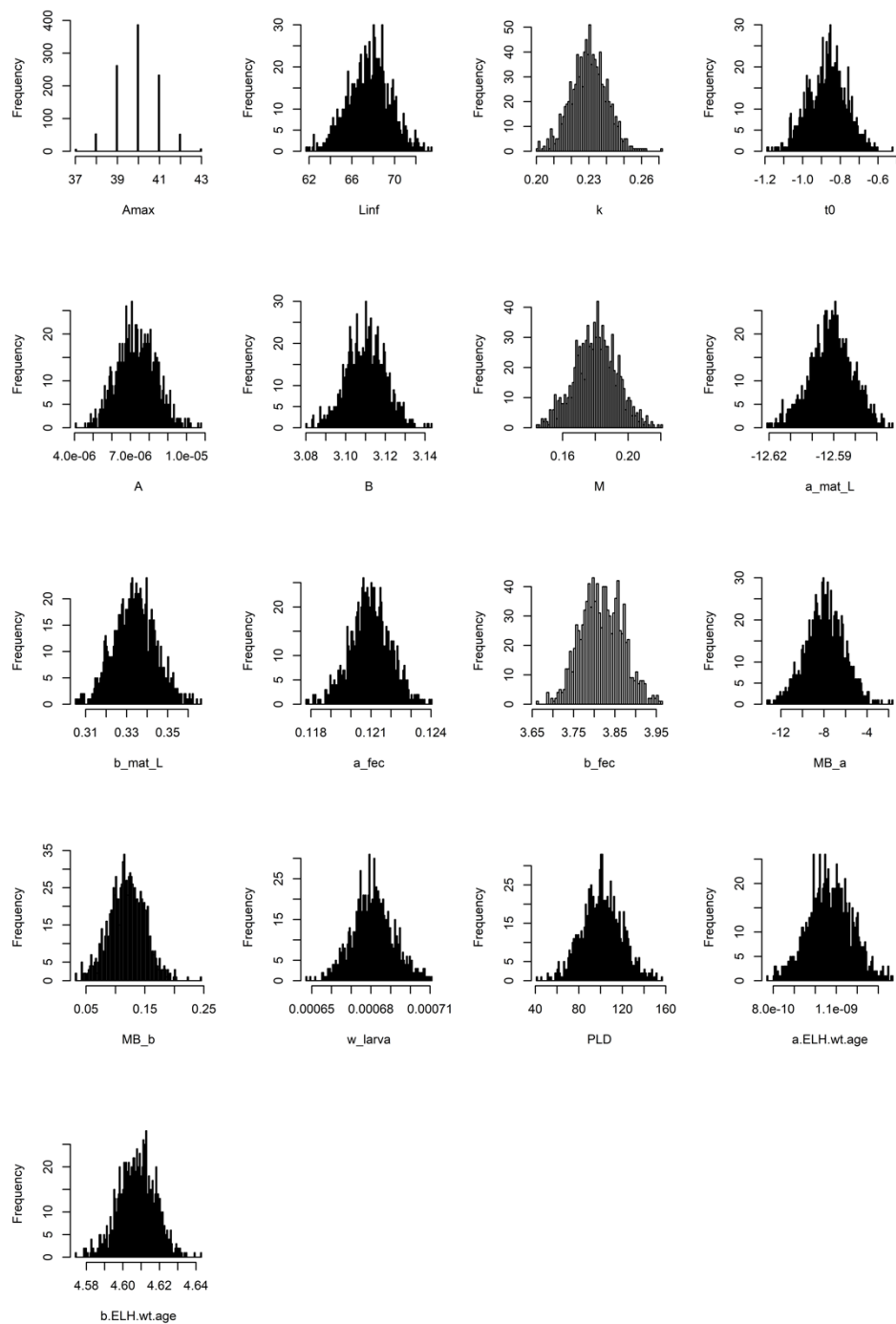
Figure SM4-13. Early life history growth using empirical growth and estimates of pelagic larval duration.

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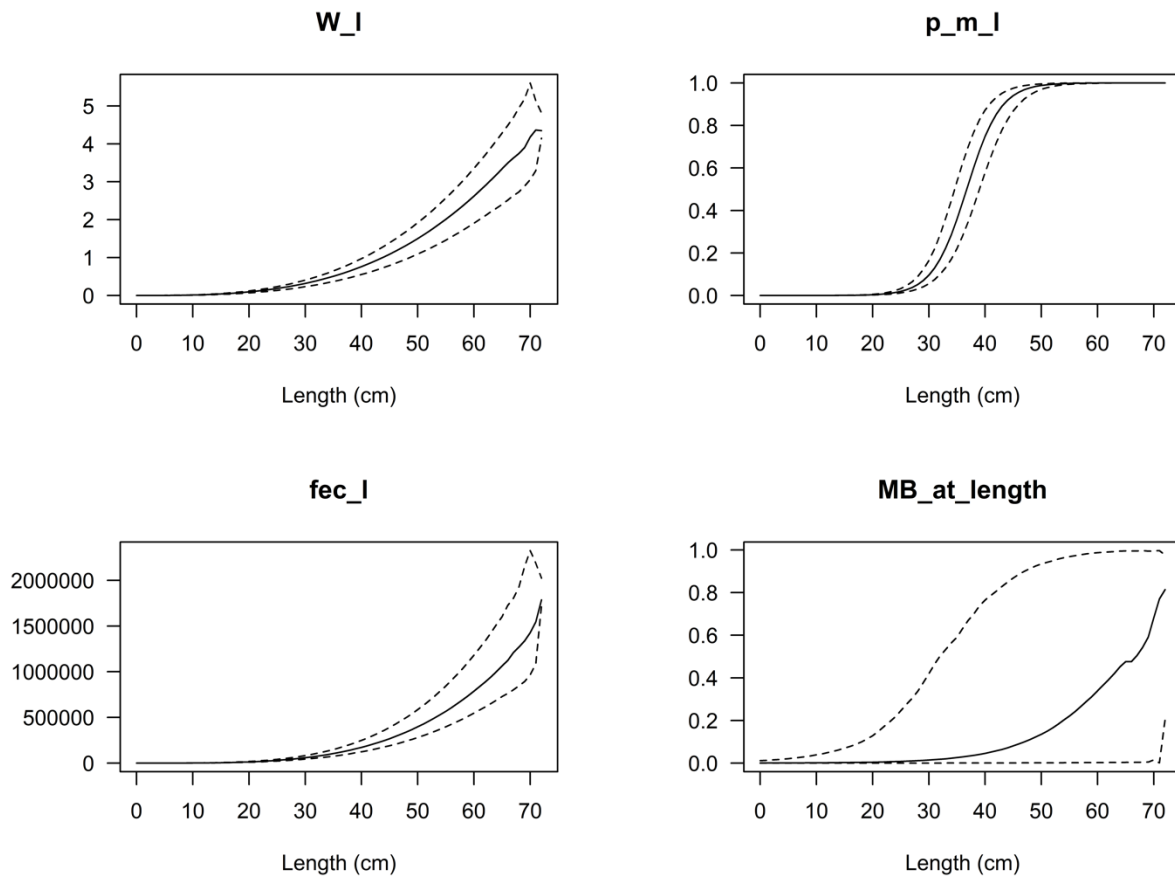
113 Bocaccio

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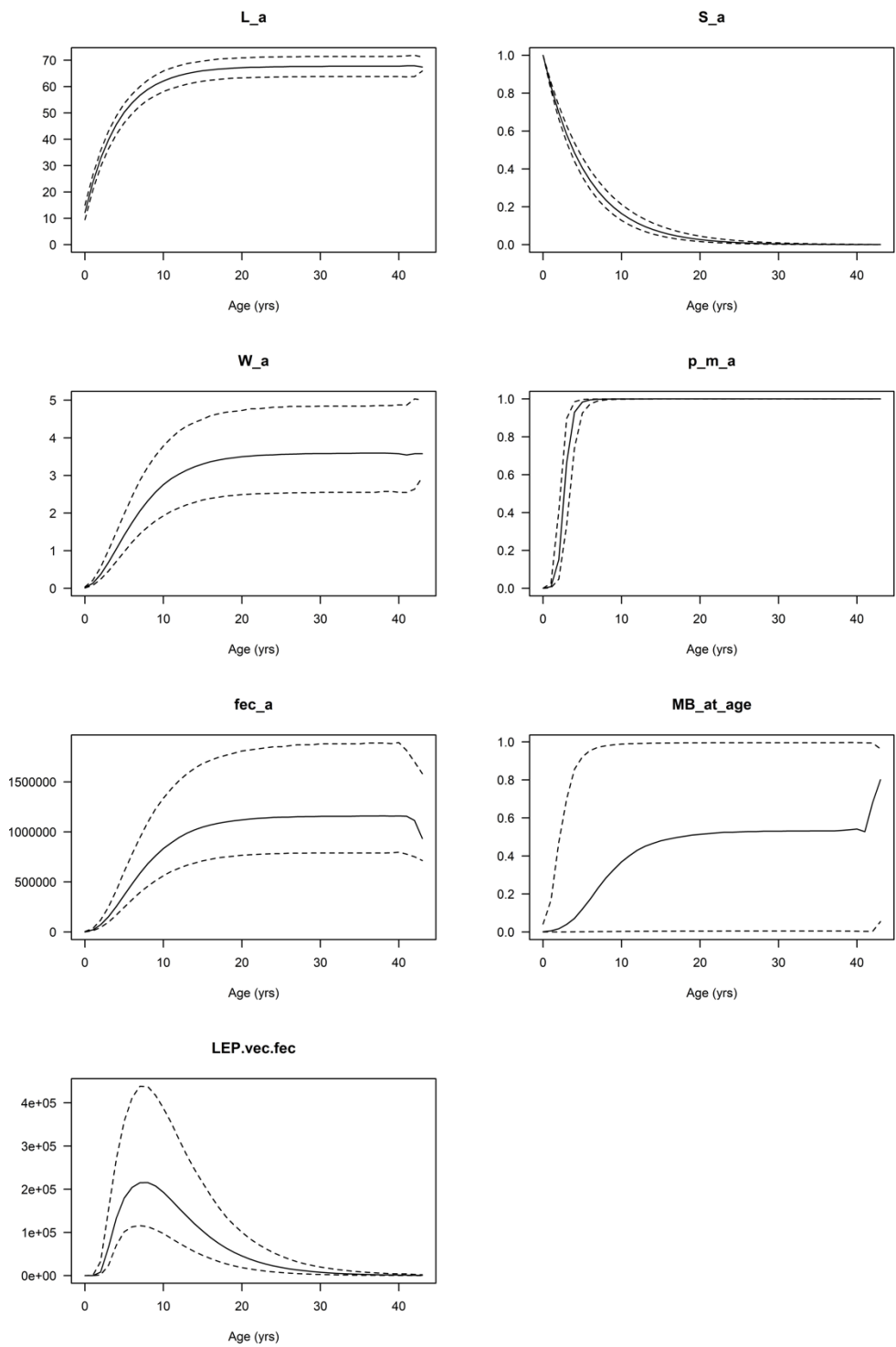
116 **Figure SM4-14.** Life history parameter distributions from 1000 simulations.



117

118 **Figure SM4-15.** Trait-at-length relationships showing the median (solid line) with 95%

119 confidence intervals (dashed lines).



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121 **Figure SM4-16.** Trait-at-age relationships showing the median (solid line) with 95% confidence

122 intervals (dashed lines).

123

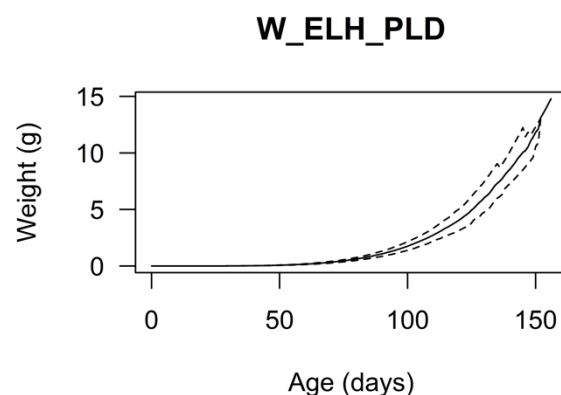


Figure SM4-17. Early life history growth using empirical growth and estimates of pelagic larval duration.

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Supplementary Materials 5: Sensitivity of steepness to using species-specific ELH weight-at-length curves

Our calculations of early life growth and survival used a ‘general’ rockfish ELH weight-length relationship to convert species-specific ELH length-at-age data to the required species-specific weight-at-age data to apply the McGurk (1986) pre-recruit, stage- and age- based daily natural mortality rates to calculate ELH survival and steepness. The ‘general’ ELH weight-length relationship pooled data from our four species due to a paucity of ELH weight data for individual species. Here we justify the approach of using a pooled-species ELH weight-length relationship by showing a sensitivity to the lack of species-specific weight data, which resulted in poor estimation of species-specific weight-length parameters, early life survival and steepness.

In **Supplementary Material 2**, we showed the steps to convert the species-specific ELH length-at-age data to the needed weight-at-age information using a ‘general’ ELH weight-length relationship. The parameters for the ‘general’ ELH weight-length relationship came from fitting a generalized linear mixed effects model (GLMM, Gelman & Hill (2007)) to the pooled, paired length and weight data for our four focal species, with species identity as a random effect. The GLMM fits fixed effect parameters for a ‘general’ rockfish in our study and also estimates species-specific parameters as random effects (Table SM2-1). Here, we show how using the species-specific length-weight parameters from the GLMM, rather than the fixed effect parameters used in the base model (SM5-1), failed in the estimation of steepness, at least for one species.

For the sensitivity analysis we used the species-specific curves in Figure SM5-1 to convert RREAS length-at-age data to weight-at-age, rather than the ‘population-level’, fixed effect parameters.

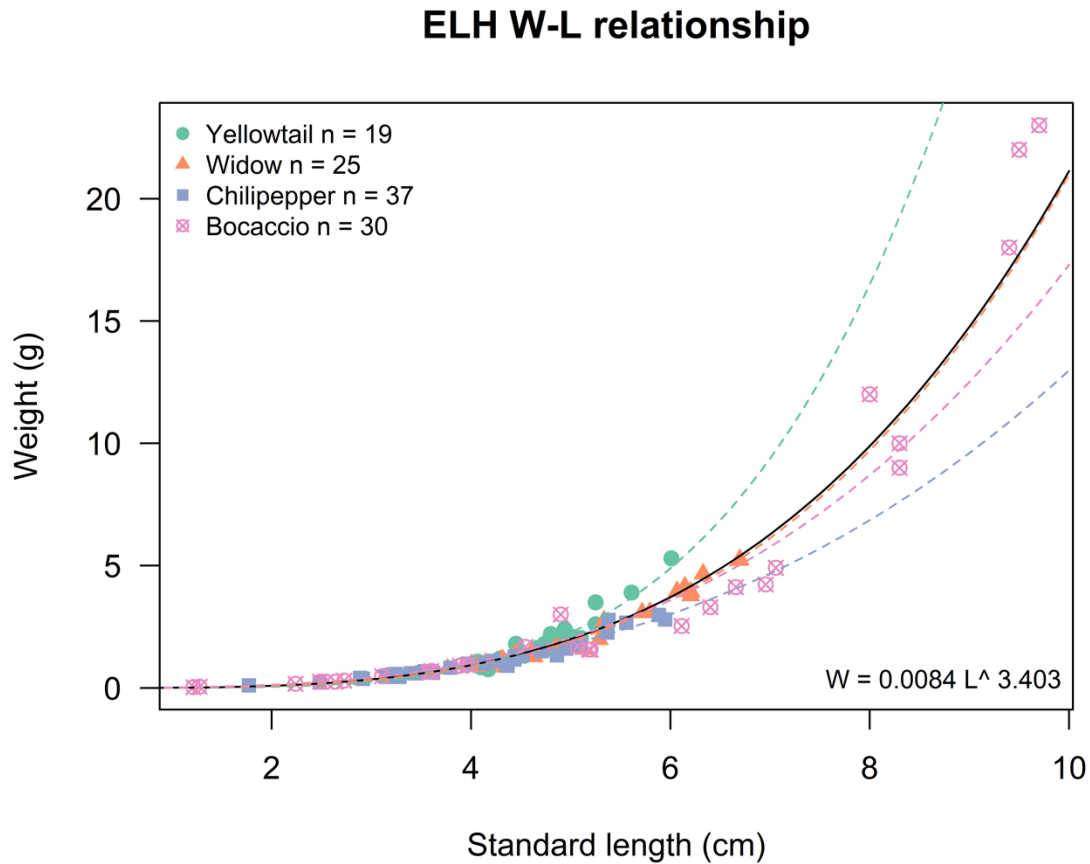


Figure SM5-1. The ELH weight-at-length relationship estimated by a generalized linear mixed effects model, with species identity modeled as a random effect. The solid black line shows the ‘population-level’ fixed effect parameters for a ‘general’ rockfish of our study species. The colored dashed lines show the offsets estimated for each species as random effects.

Table SM5-1. Early life history weight-length parameters estimated from the generalized linear mixed effects model (Equation 13 in the main text). The model estimates fixed effect, ‘population-level’ parameters to predict weight-at-length for a ‘general’ rockfish within our study (used in the base model), and species-specific random effects for the four study species (used in the sensitivity analysis) to estimate the weight-length relationship.

Description	a_{wELH}	b_{wELH}
<i>Fixed effects</i> ; Parameters for a ‘general’ rockfish in our study	$8.36 \cdot 10^{-3}$	3.403
<i>Random effects</i> ; Species-specific parameters		
Yellowtail	$2.53 \cdot 10^{-3}$	4.223
Widow	$7.42 \cdot 10^{-3}$	3.452
Chilipepper	$1.80 \cdot 10^{-2}$	2.859
Bocaccio	$1.44 \cdot 10^{-2}$	3.079

After converting the ELH length-at-age data to weight-at-age through the species-specific ELH weight-length relationship, we fit an exponential curve to the converted ELH weight-at-age information to estimate the species-specific ELH growth parameters and calculate daily weight and survival, as in the base model. In all cases (and similar to the base model), the estimated ELH weights very early in life fell below the mean birth weight so we replaced those values with the birth weight (Figure SM5-2).

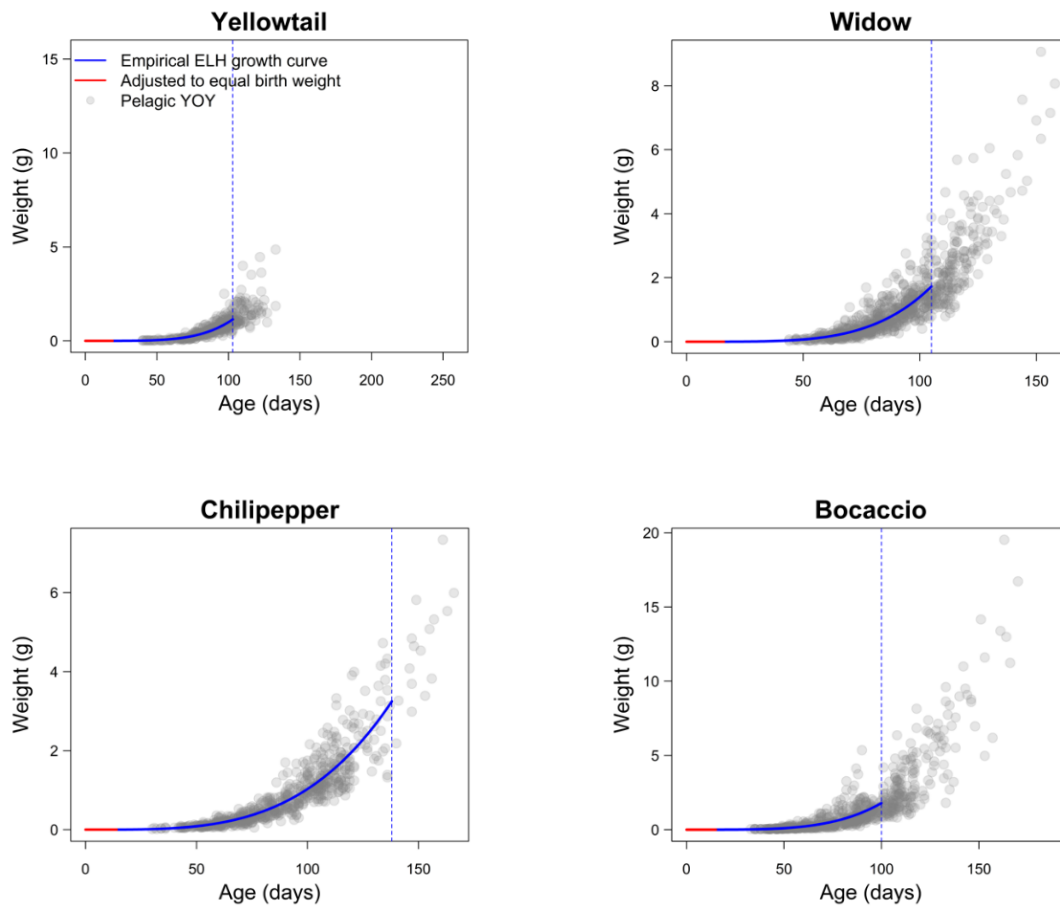


Figure SM5-2. Plots showing the converted weight-at-age information (gray circles) and the fitted ELH weight-at-age relationship (blue curves) through the extent of the Pelagic Larval Duration (PLD, vertical dashed line) for each species. The red overlay shows where the predicted weight fell below the birth weight and was replaced with the birth weight for the very early days of life.

As in the base model, we used the weight-at-age relationship to calculate a daily natural mortality rate and survival through the PLD. The early life survival, expected lifetime egg production, and sex ratio at birth is then used to calculate steepness from Equation 1 in the main text. Table SM5-2 shows the resulting estimates of early life survival α and steepness h for the

sensitivity to using species-specific ELH weight-length relationships instead of the ‘general’ ELH weight-length relationship used in the base model.

Table SM5-2. The estimates of early life survival $\alpha_{empirical}$ and steepness $h_{empirical}$, and the number of days where the modeled ELH weight-at-age fell below the weight-at-birth and was replaced with the weight-at-birth.

Species	ELH weight-length relationship	Days replaced with birth weight	Early life survival ($\alpha_{empirical}$)	Steepness ($h_{empirical}$)
Yellowtail	‘general’ (base model)	14	$1.63 \cdot 10^{-5}$	0.48
	species-specific (sensitivity)	20	$3.08 \cdot 10^{-7}$	0.02
Widow	‘general’ (base model)	17	$1.49 \cdot 10^{-5}$	0.69
	species-specific (sensitivity)	17	$1.08 \cdot 10^{-5}$	0.62
Chilipepper	‘general’ (base model)	20	$1.99 \cdot 10^{-4}$	0.96
	species-specific (sensitivity)	15	$9.85 \cdot 10^{-4}$	0.99
Bocaccio	‘general’ (base model)	19	$2.54 \cdot 10^{-5}$	0.90
	species-specific (sensitivity)	16	$1.03 \cdot 10^{-4}$	0.97

The results of the sensitivity show that using the species-specific ELH weight-at-length relationships dramatically decreases ELH survival and steepness for Yellowtail, below what is required for population persistence. Yellowtail had the least amount of weight data supporting the ELH weight-at-length model and a greater number of early days needing replacement with the birth weight relative to the base model. The daily natural mortality rates are higher when larvae are small and decrease as larvae grow. Widow was not very sensitive since the Widow ELH weight-length relationship was similar to the ‘general’ relationship. Early life survival was estimated higher for Chilipepper and Bocaccio leading to higher estimates of steepness, near the limit for Chilipepper. The sensitivity shows the need for additional ELH weight data in order to estimate species-specific weight-length and weight-at-age relationships.

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