



A stock–recruitment relationship based on pre-recruit survival, illustrated with application to spiny dogfish shark

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ABSTRACT

Understanding the relationship between abundance of spawners and subsequent recruitment is one of the central issues in fisheries stock assessment. We developed a new, pre-recruit survival based stock–recruitment model that enables explicit modeling of survival between embryos and age 0 recruits, and allows the description of a wide range of pre-recruit survival curves. The model is especially useful for low fecundity species that produce relatively few offspring per litter and exhibit a more direct connection between spawning output and recruitment than species generating millions of eggs. The proposed model provides additional flexibility in the stock–recruitment options that may be explored in any fishery stock assessment, and it is now available within the Stock Synthesis assessment platform. In this paper, we describe the mathematical formulation of the new stock–recruitment model, explain how this model can be specified within Stock Synthesis, and use it to model the stock–recruitment relationship of the spiny dogfish shark in the Northeast Pacific Ocean. We compare the results of the application of our new stock–recruitment model, with those from traditional Beverton–Holt relationship, and illustrate why the new approach is more appropriate for this species.

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1. Introduction

Understanding the relationship between parental stock abundance and subsequent recruitment is one of the central issues in fisheries stock assessment, as it forms the basis for estimation of population parameters needed to effectively manage fisheries populations (Hilborn and Walters, 2001; Quinn and Deriso, 1999; Walters and Martell, 2004). Various mathematical formulations have been proposed to describe the stock–recruitment relationship. The most common forms are the models developed by Beverton and Holt (1957) and Ricker (1954). The Beverton–Holt model, the most commonly used model in fisheries, can be derived from the assumption that juvenile competition (for food or space) results in a mortality rate that is linearly dependent on the number of fish in the cohort, so that when the cohort is larger, the individuals die faster (Hilborn and Walters, 2001; Walters and Martell, 2004). The model, therefore, implies a constraint on the recruitment when the stock gets larger, which translates into a near constant recruitment level at high stock abundance (Quinn and

Deriso, 1999). The Ricker model, which is more commonly used for modeling salmon population dynamics, can be derived from the assumption that the spawning stock size inhibits the abundance of young fish (through a mechanism such as cannibalism), and therefore, juvenile mortality is proportional to the number of spawners, with recruitment decreasing at large spawner abundance (Hilborn and Walters, 2001; Quinn and Deriso, 1999; Walters and Martell, 2004).

Most stock assessments for groundfish species inhabiting waters off the west coast of the United States rely on the Beverton–Holt model to describe the stock–recruitment relationship (PFMC, 2011). For some species, particularly those with low fecundity, a more appropriate stock–recruitment relationship may be one that is expressed in terms of offspring survival rather than recruitment. Unlike fish producing millions of eggs, species with low fecundity (e.g. sharks), produce few offspring per litter and exhibit relatively little variability in litter size among spawners. This suggests both low productivity in general and a more direct connection between spawning output (which is commonly expressed in numbers of eggs or embryos) and recruitment than for many species. The commonly used Beverton–Holt and Ricker models can be stated in terms of pre-recruit survival, with two parameters controlling the shape of the function. Both models,

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however, would result in survival decreasing fastest at low stock size (concave decreasing survival) even though it is reasonable to expect that for low fecundity species, offspring survival would instead decrease faster due to competition when the population approaches carrying capacity (convex decreasing survival).

Models that directly relate the maternal fecundity to numbers of recruits have been used to model marine mammal populations. For example, Punt (1999) and Breen et al. (2003) applied a density-dependent fecundity relationship for whales and sea lions, respectively. Taylor (2008) used a special case of this model that assumes a linear decline in survival as a function of population density, to describe the survival of spiny dogfish (*Squalus suckleyi*) in a manner similar to that used by Wood et al. (1979). All of these models, however, were rather case-specific, and were not incorporated into a generalized stock assessment framework. They also had functional forms for survival or fecundity that would go negative at population densities above some level and thus were truncated at 0. To ensure that the model was differentiable, as required by the AD Model Builder software (Fournier et al., 2012), Breen et al. (2003) used a smoothing function to make this truncation smooth at a value slightly above 0.

In order to generalize and improve the methods used in previous efforts, we developed a new, flexible three-parameter stock–recruitment model (Maunder–Taylor–Methot stock recruitment model), based on pre-recruit survival. This new model enables the description of a wider range of pre-recruit survival curves than either Beverton–Holt or Ricker, including those that correspond to shapes ranging from convex to concave. Thus it could be applied to a variety of species, including those with low productivity. To make this new model available for exploration within the context of fishery stock assessment, it was incorporated into the Stock Synthesis modeling framework (Methot and Wetzel, 2013). We also illustrate the application of the new survival based model for the spiny dogfish shark population in the Northeast Pacific Ocean. For spiny dogfish, we compare results from a survival based relationship, with those from the Beverton–Holt stock–recruitment model and illustrate why the new approach is more appropriate for low productivity species.

2. Description of the new pre-recruit survival based stock–recruitment model

2.1. Mathematical formulation

The survival of pre-recruit individuals at unfished equilibrium can be calculated from any stock–recruitment model as:

$$S_0 = \frac{R_0}{B_0} \quad (1)$$

where R_0 is the recruitment at unfished equilibrium, and B_0 is the corresponding equilibrium spawning output (in units of number of eggs or embryos). B_0 is calculated by projecting the numbers at age forward under natural mortality, starting with R_0 at age 0, then converting to numbers at length using the growth curve and variability in length at age, and finally applying the maturity and fecundity relationships (which may be functions of weight, length, or age in Stock Synthesis) to get total spawning output (Methot and Wetzel, 2013).

Recruitment at age 0 for each year in the time series is then calculated as:

$$R_y = S_y B_y \quad (2)$$

where B_y is the spawning output in year y , and S_y is the pre-recruit survival.

The relationship between survival and spawning output is based on parameters which are on a log scale. These are,

$$z_0 = -\log(S_0) \quad (3)$$

which is the negative of the log of the equilibrium survival, and can be thought of as pre-recruit instantaneous mortality rate at equilibrium, and

$$z_{\min} = -\log(S_{\max}) = z_0(1 - z_{\text{frac}}) \quad (4)$$

which is the negative of the log of the maximum pre-recruit survival rate (S_{\max} , the limit as spawning output approaches 0), and is parameterized as a function of z_{frac} (which represents the reduction in mortality as a fraction of z_0) so the expression is well defined over the parameter range $0 < z_{\text{frac}} < 1$.

Finally, the pre-recruit survival in year y is given by the equation:

$$S_y = \exp \left(-z_0 + (z_0 - z_{\min}) \left(1 - \left(\frac{B_y}{B_0} \right)^\beta \right) \right) \quad (5)$$

where β is a parameter controlling the shape of the density-dependent relationship between spawning depletion B_y/B_0 and pre-recruit survival (with limit $\beta > 0$).

The choice to parameterize the function in terms of the log-scale parameters z_0 and z_{frac} , instead of S_0 and S_{\max} , as in the similar, but simpler, approach used by Taylor (2008), was made to limit the resulting S_y values to the range between 0 and 1. The function is therefore differentiable as required by AD Model Builder (Fournier et al., 2012) without requiring a smoothing function such as that used by Breen et al. (2003).

2.2. Parameters of the new stock–recruitment model as implemented in Stock Synthesis

As implemented in Stock Synthesis, the parameters needed to apply the stock–recruitment relationship based on the pre-recruit survival are $\log(R_0)$, z_{frac} , and β . The value of $\log(R_0)$ defines the equilibrium quantities of B_0 , S_0 , and z_0 for a given set of biological inputs (either estimated or fixed), regardless of the values of z_{frac} , and β .

The interpretation of the quantity $z_0 = -\log(S_0)$ as pre-recruit instantaneous mortality rate at unfished equilibrium is imperfect because the recruitment in a given year is calculated as a product of the survival fraction S_y and the spawning output B_y for that same time period so that there is not a 1-year lag between quantification of eggs or pups and recruitment at age 0, which is when recruits are calculated in Stock Synthesis. However, if age 0 or some set of youngest ages is not selected by any fishery or survey, then density dependent survival may be assumed to occur anywhere before the first appearance of any cohort in the data or model expectations. In such cases, the upper limit on survival up to age a is given by $S_{\max} e^{-aM}$.

Nevertheless, interpreting z_0 as an instantaneous mortality helps with the understanding of z_{frac} . This parameter controls the magnitude of the density-dependent increase in survival associated with a reduction in spawning output. It represents the fraction by which this mortality-like rate is reduced as spawning output is reduced from B_0 to 0. This is approximately equal to the increase in survival as a fraction of the maximum possible increase in survival. That is,

$$z_{\text{frac}} = \frac{\log(S_{\max}) - \log(S_0)}{-\log(S_0)} \approx \frac{S_{\max} - S_0}{1 - S_0} \quad (6)$$

For example, if $S_0 = 0.4$, $z_{\text{frac}} = 0.8$, then the resulting fractional increase in survival is $(S_{\max} - S_0)/(1 - S_0) = 0.72$.

The parameter β controls the point where survival changes fastest as a function of spawning depletion. A value of $\beta = 1$ corresponds to a linear change in log survival and an approximately

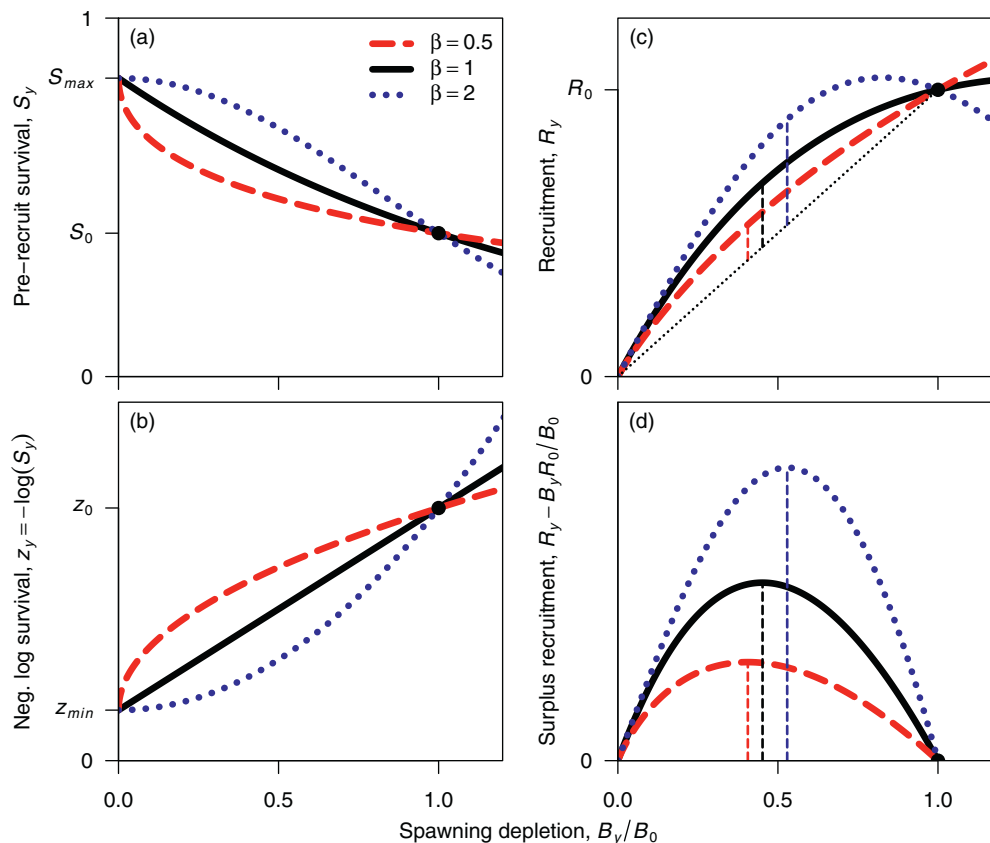


Fig. 1. Patterns and parameters for three stock–recruitment relationships which differ only in the β parameter ($z_{\text{frac}} = 0.8$ and $S_0 = 0.4$): (a) pre-recruit survival, (b) negative log survival, (c) recruitment, and (d) surplus recruitment, defined as the difference $R_y - (B_y R_0 / B_0)$ between recruitment and the replacement line (dotted line in c). Vertical lines in (c) and (d) indicate the positions of maximum surplus recruitment.

linear relationship between survival and spawning depletion. Values of $\beta < 1$ have survival increasing fastest at low spawning output (concave decreasing survival) whereas $\beta > 1$ has the increase in survival occurring fastest closer to the unfished equilibrium (convex decreasing survival). Fig. 1 shows pre-recruit survival, negative log survival, recruitment and surplus recruitment, defined as the difference between the predicted and replacement levels of recruitment as a function of spawning depletion for three stock–recruitment relationships which differ only in the β parameter, while z_{frac} and S_0 are fixed at 0.8 and 0.4 respectively. One effect of the change in shape of this curve is that with increasing β , the spawning output associated with the peak surplus recruitment is increased relative to B_0 . The task of choosing β is thus similar to the task of choosing the shape parameter in the Pella–Tomlinson, a problem which [Maunder \(2003\)](#) suggested should not be avoided by blindly choosing a less flexible model.

2.3. Parameterization in terms of stock–recruitment steepness

The Beverton–Holt stock–recruitment relationship, commonly used for groundfish stock assessments, is parameterized in Stock Synthesis in terms of $\log(R_0)$, and steepness of the stock–recruitment curve (h), which represents the recruitment as a fraction of R_0 when spawning output is at 20% of B_0 . The steepness parameter determines the response of stock productivity to changes in spawning output, and ranges between 0.2 and 1 (the higher the value, the stronger the stock’s resilience to perturbations, and vice versa).

The pre-recruit survival based function can also be parameterized in terms of steepness. The steepness (h) of the stock–recruitment curve based on pre-recruit survival can be

derived from the parameters discussed above according to the relationship and associated inequality:

$$h = 0.2 \exp(z_0 z_{\text{frac}} (1 - 0.2^\beta)) < 0.2 \exp(z_0) = \frac{1}{5S_0} = \frac{B_0}{5R_0} \quad (7)$$

Unlike the Beverton–Holt stock–recruitment relationship, recruitment can increase above R_0 for stocks that are below B_0 and thus the steepness is not fundamentally constrained below 1. However, in many cases, steepness will be limited well below 1 by the inequality (7), which implies an inverse relationship between the maximum steepness and equilibrium survival. Specifically, the inequality (7) bounds steepness below 1 for all cases where $S_0 > 0.2$, which are those with the lowest fecundity—an intuitively reasonable result. For example, with $S_0 = 0.4$, the steepness is limited below 0.5, regardless of the choice of z_{frac} or β . This natural limit on steepness may be one of the most valuable aspects of this stock–recruitment relationship.

3. Application of the pre-recruit survival based stock–recruitment model for spiny dogfish shark

The stock–recruitment model was used within a Stock Synthesis assessment for spiny dogfish shark in the Northeast Pacific Ocean ([Gertseva and Taylor, 2011](#)). Spiny dogfish is a small to medium-sized cartilaginous fish that inhabits temperate waters of the North Pacific Ocean. This is a low fecundity species with a particularly long gestation period (up to 24 months) ([Campana et al., 2009](#); [Di Giacomo et al., 2009](#); [Taylor, 2008](#)). The number of pups in each litter ranges between 5 and 15, with larger females bearing more pups ([Campana et al., 2009](#); [Di Giacomo et al., 2009](#); [Taylor, 2008](#)).

In this study, to illustrate properties of the pre-recruit survival based stock–recruitment relationship, we adopted biological parameters used in spiny dogfish assessment model (Gertseva and Taylor, 2011) to estimate $\log(R_0)$. Those biological parameters were treated in our analysis as fixed inputs. Such an approach removes the added complexity of the feedback between estimated biological parameters, the stock–recruitment relationship, which depends on them, and the estimates of selectivity and fishing pressure which are influenced by the stock–recruitment relationship while also influencing the estimated biological parameters.

3.1. Biological inputs used

Biological characteristics of spiny dogfish used as inputs in the present analysis included natural mortality, somatic growth, weight–length, maturity and fecundity relationships. These parameters were either estimated from the available data or obtained from published sources. Since the stock–recruitment relationship depends on females only, here we discuss female parameters alone. Information on both genders can be found in Gertseva and Taylor (2011).

Natural mortality was set to $M=0.064 \text{ yr}^{-1}$ based on Hoenig (1983) method. This value is within a range of those estimated for spiny dogfish by other studies. It is also consistent with natural mortality for spiny dogfish in the Northeast Pacific Ocean (0.065 yr^{-1}) estimated by Smith et al. (1998).

The von Bertalanffy growth function, parameterized in terms of length at a reference age (Methot and Wetzel, 2013) was used to model the relationship between length and age in spiny dogfish. The length (cm) at age A for females is given by

$$L_A = L_\infty + (L_1 - L_\infty)e^{-k(A-A_1)} \quad (8)$$

where $k=0.026 \text{ yr}^{-1}$ is the growth coefficient, $L_\infty=109 \text{ cm}$ is asymptotic length, and $L_1=25$ is the size associated with a reference age $A_1=0$. The distribution of length at age (Methot and Wetzel, 2013) is assumed to be normal with a CV that increases linearly with length from 0.123 at L_1 to 0.240 at L_∞ . A complete description of the derivation of these growth parameters is provided by Gertseva and Taylor (2011).

The relationship between weight and length was described with power function

$$W = \Omega_1(L)^{\Omega_2} \quad (9)$$

where W is individual weight (kg), L is total natural length (cm) and Ω_1 and Ω_2 are coefficients used as constants. Data from a bottom trawl shelf-slope survey in the Northeast Pacific Ocean conducted by the United States National Marine Fisheries Service between 2007 and 2010 (Bradburn and Keller, 2011) were used to estimate weight–length parameters. For females, based on the length and weight observations from 1579 fish, Ω_1 was estimated as 2.3065×10^{-6} and Ω_2 as 3.1526.

The relationship between female size and maturity was taken from recently published work (Taylor and Gallucci, 2009), based on 499 fish collected in the past decade. The logistic function used was

$$M(\%) = \frac{1}{1 + e^{\Omega_3(L-\Omega_4)}} \quad (10)$$

where $M(\%)$ is the proportion of mature females in the stock by length, $\Omega_3 = -0.27 \text{ cm}^{-1}$ is a parameter controlling the rate of increase in maturity and $\Omega_4 = 88.2 \text{ cm}$ is the length at 50% maturity.

The fecundity of mature fish was also set equal to values from Taylor and Gallucci (2009), which were calculated from 106 pregnant fish from a maturity study for which counts of embryos

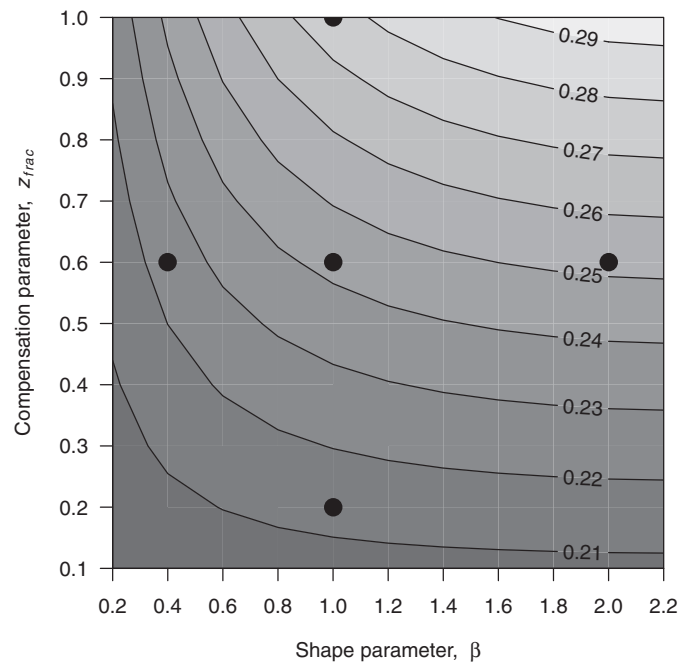


Fig. 2. Steepness values resulting from the survival based stock–recruitment relationship applied to spiny dogfish for a range of values of the parameters Z_{frac} and β . Black points indicate models for which yield curves and other derived quantities are shown in Fig. 3 (below).

were available. A linear relationship between female length (L) and fecundity (expressed in number of pups) was assumed:

$$\text{Pups} = \Omega_5 + \Omega_6 L \quad (11)$$

with estimated parameters $\Omega_5 = -14.7$ and $\Omega_6 = 0.214 \text{ cm}^{-1}$. This relationship results in an increase from 0 pups at 66 cm (when maturity is less than 0.3%) to about 7 pups per litter at 100 cm (when maturity is 97%) and about 15 pups per litter at the largest size of 136 cm. A sex ratio of 50% was assumed. However, to account for the 24 months gestation period of dogfish and associated 2-year cycle of pupping, the fecundity relationship above was divided by 2.

3.2. Selection of the stock–recruitment model parameters

As specified earlier, the parameters needed to apply the survival based stock–recruitment relationship within Stock Synthesis include equilibrium recruitment R_0 , a parameter controlling the potential decrease in pre-recruit mortality as spawning output is reduced (Z_{frac}), and a parameter controlling the shape of the mortality–depletion relationship (β). This is unlike the Beverton–Holt stock–recruitment relationship, which is parameterized in terms of $\log(R_0)$ and the steepness of the stock–recruitment curve (h).

We ran the model over a grid of Z_{frac} and β with Z_{frac} fixed from 0.2 to 1.0 in increments of 0.1 and β from 0.2 to 2.2 in increments of 0.2. The parameter $\log(R_0)$ was estimated in all models, but under the assumptions made here with fixed parameters for growth, fecundity, and mortality, the resulting equilibrium pre-recruit survival remains constant at $S_0 = 0.668$ because R_0/B_0 is independent of the estimated R_0 . Thus, the upper bound on steepness predicted by inequality (7) is 0.299. Indeed, the steepness values resulting from the grid of parameter inputs ranged from 0.202 to 0.296 (Fig. 2), with the lowest values associated with values of $Z_{\text{frac}} = 0.1$ for which the potential increase in survival is very small. Likewise, low β values are associated with low steepness, as these are the cases where

survival is strongly concave and there is little density-dependence in survival at higher stock sizes.

In the case where the z_{frac} in the survival based stock–recruitment relationship is estimated, the parameter hits the lower boundary of $z_{\text{frac}} = 0$. This value is associated with a biologically unrealistic stock with no surplus-production (and steepness = 0.2). Likewise, when β is estimated, it hits the lower boundary of $\beta = 0$. Although the information about productivity of dogfish is inadequate to estimate these parameters, the choice of this survival based stock–recruitment relationship naturally bounds the steepness to a low range that would be expected for such a late maturing low fecundity species. Furthermore, over the grid of z_{frac} and β considered, the range of estimates of 2011 spawning output depletion for spiny dogfish estimated by the assessment model (Gertseva and Taylor, 2011), indicating considerable uncertainty in stock status in spite of many parameters having been fixed in the assessment. However, these depletion values are highly correlated with the steepness resulting from the stock–recruitment parameters ($\rho = 0.92$), indicating that the natural limits on steepness that come from the stock–recruitment relationship provide information about stock status that would be unavailable in a Beverton–Holt model with broader limits on steepness.

3.3. Comparison of pre-recruit survival based model with Beverton–Holt function

Fig. 3 shows equilibrium yield curves, stock–recruitment curves, and pre-recruit survival for spiny dogfish resulting from a set of survival based stock–recruitment relationships. This set includes curves with combinations of the survival based stock–recruitment parameters, including those with various values of z_{frac} ($z_{\text{frac}} = 0.2, 0.6$, and 1.0) at $\beta = 1.0$, and with various values of β ($\beta = 0.4$ and 2.0) at $z_{\text{frac}} = 0.6$. The parameter combinations corresponded to steepness ranging from 0.21 to 0.28. The curves generated from survival based stock–recruitment relationship (Fig. 3a, c and e) were compared to a range of models which use the Beverton–Holt stock–recruitment relationship, with steepness fixed at $h = 0.21, 0.24, 0.28$ to span this same range, along with $h = 0.4$ and estimated (Fig. 3b, d and f). As in the case of the survival based model, when steepness was estimated, it hit the lower bound of ($h = 0.2$).

The pairs of survival based models and Beverton–Holt models that had similar steepness values showed similar yield functions and stock–recruitment curves (Fig. 3). However, unlike the new survival based stock–recruitment curve, which keeps the pre-recruit survival contained within a biologically reasonable range (Fig. 3e), the Beverton–Holt models with higher steepness values

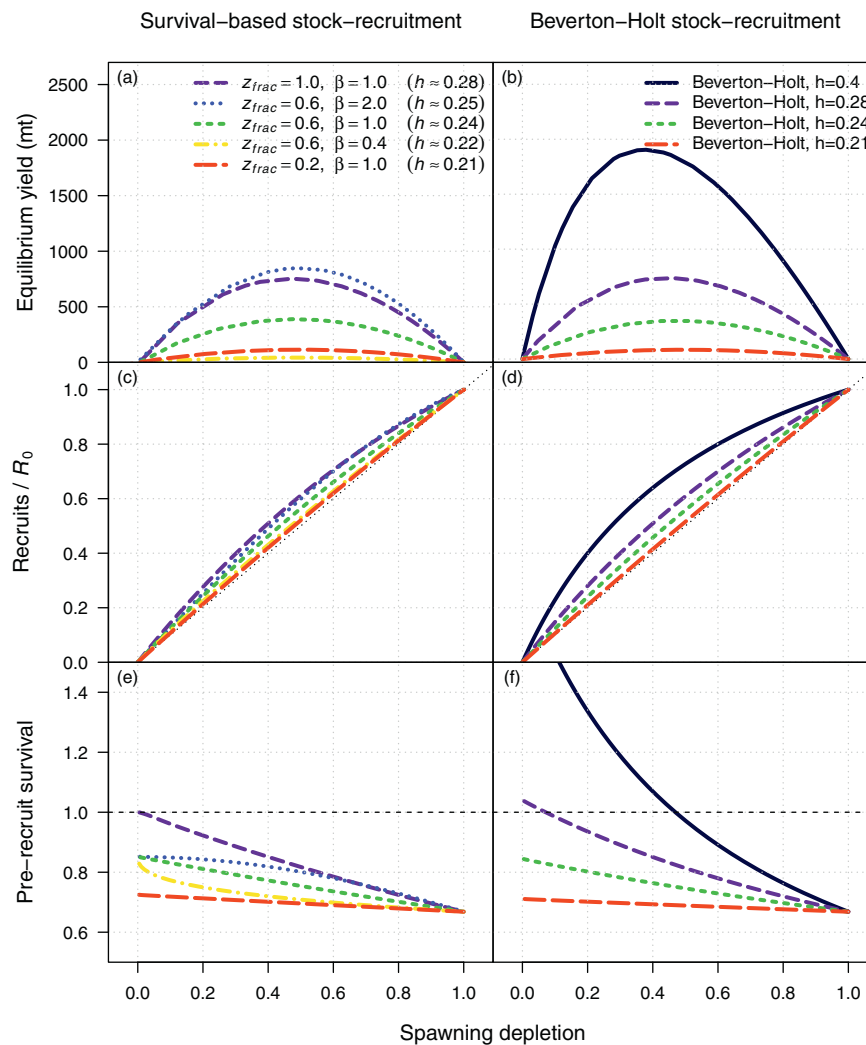


Fig. 3. Equilibrium yield curves (top row), stock–recruitment curves (middle row), and pre-recruit survival (bottom row) for spiny dogfish resulting from alternative stock–recruitment relationships, including survival based stock–recruitment relationships (left column) and Beverton–Holt relationships (right column). Note: the height of the yield curves in the top row depends on R_0 in addition to z_{frac} and β . The other panels are independent of R_0 .

($h=0.28$ and 0.4) have pre-recruit survival values that increase above 1.0 at the lowest depletion levels (Fig. 3f). Such patterns could only occur if some other process was impacting recruitment, such as large density-dependent changes in fecundity (which is unlikely for spiny dogfish which was shown to have a consistent relationship between adult size and pups per litter) or a violation of the assumption of a closed population, with a large fraction of recruitments immigrating from outside the modeled area.

4. Discussion

We presented a new stock–recruitment model, in which pre-recruit survival is expressed as a function of stock spawning output. Although the commonly used Beverton–Holt and Ricker models can also be parameterized in terms of pre-recruit survival, this new approach is based on a more flexible, three-parameter function that enables description of a wider range of pre-recruit survival curves than either Beverton–Holt or Ricker. It can be specified to reflect convex, linear or concave shapes of pre-recruit survival functions. This new approach is particularly useful for low fecundity species that produce few offspring per litter and show relatively little variability among spawners. Such biological traits generally translate into low productivity and imply a more direct connection between initial spawning output and recruitment than observed in species generating millions of eggs or larvae.

The new model, like other stock–recruit formulations, assumes that density-dependence occurs after determination of spawning output and before recruits appear in any observed or expected data source in the model. Density-dependent processes may also occur at other life stages. Indeed, the reformulation of stock–recruitment relationships in terms of pre-recruit survival could be extended to density-dependent survival in any range of ages, but such extensions are not considered here. We also assumed that biological parameters, such as growth and natural mortality, are not density-dependent. The approach assumes a closed population so that all recruits come from spawning individuals. These assumptions are consistent with those used in other stock–recruitment models.

Our application of the new model to describe stock–recruitment relationship of the spiny dogfish shark in the Northeast Pacific Ocean illustrates that, when parameterized in terms of stock–recruitment steepness, the new approach imposes a natural limit on steepness, and constrains it within bounds that are reasonable for such a long-lived, late-maturing species (in this case, below 0.3). Stock–recruitment steepness is a key biological parameter that mediates the response of stock productivity to changes in parental stock size and is often highly correlated with stock status. Thus, the natural limit on steepness is one of the most valuable aspects of this new stock–recruitment model since the Beverton–Holt stock–recruitment relationship provides no such limits on productivity. However, the inequality (7) indicates that steepness will only be limited at a value less than 1.0 for stocks with an equilibrium pre-recruit survival above 0.2 (fewer than 5 eggs or embryos produced in equilibrium for each age 0 recruit). Species with large numbers of eggs and low pre-recruit survival will not have steepness limited by the new stock–recruit relationship. For these stocks, the new approach will still provide additional flexibility in the shape of the stock–recruitment relationship. Indeed, for some combinations of parameters, the stock–recruitment relationship can be dome-shaped with steepness values greater than 1. Also, the location of the peak in surplus production (B_{MSY}/B_0) can be varied as a function of the stock–recruitment parameters in contrast to the constraints imposed by the Beverton–Holt and Ricker functions, in which peak production is pre-determined by the life-history parameters

We demonstrated (Fig. 3) that projections made using the Beverton–Holt function (when parameterized in terms of pre-recruit survival) allow pre-recruit survival of spiny dogfish to exceed 1.0, as spawning depletion approaches 0. For example, with $h=0.4$, the limit of pre-recruit survival is 1.78, a value associated with recruitment of almost 2 age-0 recruits for every estimated embryo in the spawning output (Fig. 3f). Such patterns could only occur if recruitment was dependent on some process other than the stock–recruitment relationship such as immigration. Such processes, if influential, could be modeled explicitly in the stock assessment rather than subsumed into the stock–recruitment relationship. These results suggest that the new stock–recruitment option is particularly valuable for low fecundity species.

As implemented in Stock Synthesis, the new stock–recruitment model based on pre-recruit survival is controlled by three parameters: $\log(R_0)$, z_{frac} , and β . We showed that interpretation of $\log(R_0)$ is similar to that in Beverton–Holt and Ricker models. We described both z_{frac} , a parameter controlling the potential decrease in pre-recruit mortality as spawning output is reduced, as well as β , a parameter controlling the shape of the relationship between pre-recruit mortality and stock depletion. When a stock assessor chooses to explore this new stock–recruitment relationship in Stock Synthesis, we recommend using the description of the parameters provided here to help conduct thorough sensitivity testing of z_{frac} and β , to evaluate whether the assessment model has sufficient information to estimate either of these parameters; if not, derived quantities and model outputs from the range of sensitivity runs should be analyzed to select appropriate values for each of the parameters. The range of β values considered in this analysis led to a range of values for B_{MSY}/B_0 (the peak of the yield curve in Fig. 3a), relatively close to 0.5. However, the flexibility to explore alternative values of this ratio by varying β across a wider range could be valuable for any stock (Maunder, 2003).

It should be noted that our example of application of the pre-recruit survival based model did not include deviations in recruitment. The data on spiny dogfish were too sparse to resolve year-class strength or estimate the annual signal of recruitment variability. Consideration of recruitment deviations in this new stock–recruitment relationship is a worthy topic for future research. Specifically, limiting pre-recruit survival between 0 and 1 leads to interactions between the spawning depletion and the variability in recruitment that are not present when deviations are modeled as a lognormal multiplier on expected recruitment (Methot and Taylor, 2011). Understanding the statistical properties of a more complex pattern of recruitment deviations is necessary to guide users of this relationship and ensure that including variability within this stock–recruitment relationship does not change the long-term average population dynamics away from the equilibrium reference points associated with deterministic recruitment.

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