



Short communication

A stock–recruitment model for highly fecund species based on temporal and spatial extent of spawning

Mark N. Maunder^{a,b,*}, Richard B. Deriso^a^a Inter-American Tropical Tuna Commission, 8604 La Jolla Shores Drive, La Jolla, CA 92037-1508, USA^b Center for the Advancement of Population Assessment Methodology, Scripps Institution of Oceanography, La Jolla, USA

ARTICLE INFO

Article history:

Received 11 January 2013

Received in revised form 27 March 2013

Accepted 28 March 2013

Keywords:

Density dependence
 Fisheries management
 Recruitment
 Stock assessment
 Stock–recruitment

ABSTRACT

A stock–recruitment model is described for highly fecund species based on the contraction of the spatial and temporal extent of spawning when a population is reduced in size: $R = \alpha K(1 - \exp[-S/(mK)])$, where S is the number of spawners, K is the carrying capacity in units of the number of habitat patches that can produce recruits, α is the average number of recruits per unit of habitat, and m is the number of spawners that group together to spawn. The model is based on three simplifying assumptions: (1) the environment is divided into K units; (2) the presence of one spawner provides sufficient eggs to fill the capacity of that unit, any additional spawners in that unit will not increase recruitment; and (3) groups of fish are randomly distributed over the environment. The model allows for a flat top curve, which is consistent with highly fecund species that are continuous spawners and do not aggregate to spawn. It also allows for a strong relationship between spawners and recruits, which is more consistent with species that aggregate in time and space to spawn. This stock–recruitment model can be approximated in terms of parameters commonly used in contemporary stock assessment models (virgin recruitment, R_0 , and steepness of the stock–recruitment relationship, h , virgin spawning biomass, S_0): $R = R_0(1 - \exp(5\ln(1 - h)S/S_0))$. The functional form is compared with the Beverton–Holt stock–recruitment model.

© 2013 Elsevier B.V. All rights reserved.

1. Introduction

Recruitment is one of the fundamental processes that drive population dynamics, and it has been the focus of intense study. In particular, research on the relationship between stock size and recruitment and its role in determining sustainable yields has had a long history, and has been controversial (Hjort, 1914; Skud, 1975; Walters and Parma, 1996; Platt et al., 2007). Debate still remains about the relative importance of the environment versus spawning biomass in determining recruitment. For example, Myers et al. (1999) conducted a meta-analysis of the steepness of the stock–recruitment model for a wide range of species, identifying that spawning biomass determined recruitment for many species, at least at low spawner abundance. Gilbert (1997), however, showed that regime-shifts, presumably related to environmental conditions, could explain recruitment just as well as the stock–recruitment model for a similar data set, and Vert-pre et al. (2013) showed that regime-shifts explained recruitment more often than abundance, based on data for 230 fish stocks.

The Beverton and Holt (1957) and Ricker (1954) stock–recruitment models are well known and widely used.

These models are based on linear density dependence related to the spawner or cohort abundance for the Ricker and Beverton–Holt models, respectively. However, neither of these linear relationships may be appropriate. For example, density dependence may be stronger as the population approaches carrying capacity, particularly for low-fecundity species. This led to the development of the Maunder–Taylor–Methot stock–recruitment model, which has been used in stock assessments of sharks (Taylor et al., 2013). There is little evidence of a stock–recruitment relationship for many highly fecund species, and estimation can consequently be problematic (Magnusson and Hilborn, 2007; Conn et al., 2010; Lee et al., 2012). Therefore, an alternative approach is needed to model the relationship between stock and recruitment for highly fecund species.

Highly fecund species such as tunas produce orders of magnitude more eggs than the environment can support (the bottleneck between eggs and recruits may occur at a variety of life-stages, depending on the species), even if the population is at a low level. Consequently, many of these eggs eventually die. This suggests that the amount of spawning biomass may not be important in determining recruitment for highly fecund species, even at low spawning biomass. However, contraction of the spatial or temporal extent of the spawning biomass may leave viable areas of habitat without eggs, and therefore a relationship between recruitment and stock size may occur for species that tend to aggregate in

* Corresponding author. Tel.: +1 858 546 7027; fax: +1 858 546 7133.
 E-mail address: [mmaunder@iattc.org](mailto:mmmaunder@iattc.org) (M.N. Maunder).

time and space to spawn. We develop a stock–recruitment model for highly fecund species based on this premise. The concept and resulting stock–recruitment model is similar to that used for modeling salmon redd superimposition (McNeil, 1964; Chapman, 1973; Maunder, 1997; Quinn and Deriso, 1999).

2. Methods and results

The underlying concept of the proposed stock–recruitment model is that highly fecund fish species (e.g. tunas) will always produce more eggs than there will be recruits, and recruitment is not necessarily related to total egg production. Rather, recruitment is controlled by spawning taking place at the right time and in the right location, following the optimal environmental window hypothesis (Cury and Roy, 1989). The apparent relationship between stock and recruitment is therefore related to how aggregated in space and time the population becomes as abundance declines. Based on these principles, a stock–recruitment model is developed under the assumptions that:

- (1) the environment is divided into K units, which could be space, time, or both – space will be used here, as it is easier to conceptualize;
- (2) the presence of one female spawner (or group of spawners, see below) in a unit provides sufficient eggs to fill the recruit capacity of that unit, and any additional females (or groups) in that unit will not increase recruitment; and
- (3) fish (or groups of fish) are randomly distributed over the environment.

These assumptions can be used to calculate the expected number of recruits (R) resulting from a given number of spawners (S). Following Maunder (1997), who used a similar rationale for modeling salmon redd superimposition, the number of units with successful spawning can be calculated as the probability of each additional spawner (or spawner group) choosing a unit that is unoccupied. If there is only one spawner, the expected number of units with successful spawning is one. If there are two spawners, the first spawner will spawn in an unoccupied unit, but the second spawner will have $1/K$ chance of spawning in a unit that is already occupied, thus not contributing to recruitment, making the expected number of units with successful spawning equal to $1 + (K - 1)/K$. The series of units successfully spawned as a function of the number of spawners is given in Table 1. This series can be well approximated, particularly when K is large, by the following simple function:

$$R^* = K \left(1 - \exp \left[-\frac{S}{K} \right] \right) \tag{1}$$

where R^* is the expected number of units with successful spawning. This stock–recruitment model is completed by letting m represent the number of individuals that spawn in the same unit at the same time (i.e. group or school size) and α represent the average number of recruits from a unit:

$$R = \alpha K \left(1 - \exp \left[-\frac{S}{mK} \right] \right) \tag{2}$$

Table 1
Equations giving the successfully spawned units for a given number of spawners (from Maunder, 1997).

Spawners	Successfully spawned units	Simplified
1	1	1
2	$1 + (K - 1)/K$	$2 - 1/K$
3	$2 - 1/K + (K - 2 - 1/K)/K$	$3 - 3/K + 1/K^2$
4	$3 - 3/K + 1/K^2 + (K - (3 - 3/K + 1/K^2))/K$	$4 - 6/K + 4/K^2 - 1/K^3$
.	.	.

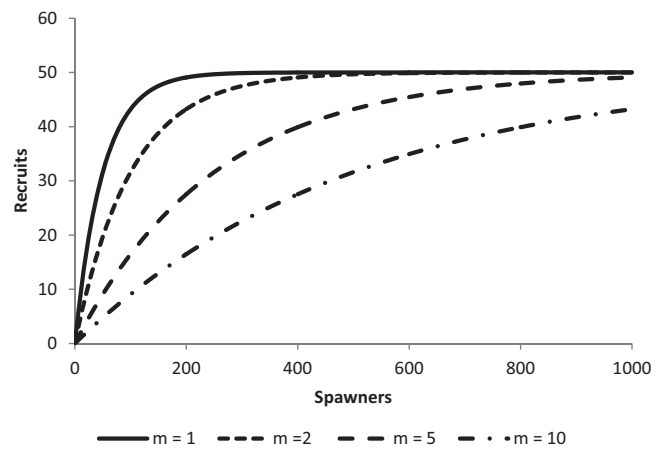


Fig. 1. The spatial extent stock–recruitment model for different values of the grouping parameter, m . $K = 50$ and $\alpha = 1$.

Fig. 1 shows this stock–recruitment model for different values of the grouping parameter, m , illustrating the possible forms that the stock–recruitment relationship can take. A stronger relationship between spawners and recruits occurs as the spawning group size increases. This stock–recruitment model is an alternative parameterization of that suggested by Equation 3.23 of Quinn and Deriso (1999). The model can be reparameterized to eliminate parameter confounding and redundancy and to use parameters which are more common when formulating stock–recruitment models in fisheries stock assessment (R_0 , the average recruitment from an unexploited population, and h is the steepness of the stock–recruitment model [the fraction of R_0 obtained when the spawning biomass is 20% of the virgin spawning biomass, S_0])

$$R = R_{\max} \left(1 - \exp \left[-\frac{S}{m'R_{\max}} \right] \right) \tag{3}$$

$$R_0 = R_{\max} \left(1 - \exp \left[-\frac{S_0}{m'R_{\max}} \right] \right) \tag{4}$$

$$h = \frac{1 - \exp[-0.2S_0/(m'R_{\max})]}{1 - \exp[-S_0/(m'R_{\max})]} \tag{5}$$

where R_{\max} is maximum recruitment, and $m' = m/\alpha$. See Appendix A for an alternative parameterization. A closed-form solution is not available for Eq. (3) parameterized in terms of R_0 and h , but a good approximation is:

$$R \approx R_0 \left(1 - \exp \left[\frac{5 \ln(1 - h)S}{S_0} \right] \right) \tag{6}$$

The reliability of this approximation is evaluated in Appendix B and the process for calculating maximum sustainable yield (MSY) quantities outlined in Appendix C. The stock–recruitment model is compared with the Beverton and Holt (1957) stock–recruitment model for the same values of h and R_0 and when the values of h and R_0 in the Beverton–Holt stock–recruitment model are set so that the two stock–recruitment models are as similar as possible. Selection of h and R_0 is based on minimizing an objective function based on log-transformed least squares, with spawning biomass levels in increments of 1 up until the virgin spawning biomass where $S_0 = 200$, $R_0 = 100$ and $h = (0.65, 0.75, 0.85, 0.95)$. There is a discrepancy between the proposed stock–recruitment model and the Beverton–Holt stock–recruitment model, and this discrepancy cannot be eliminated by adjusting the parameter values (Fig. 2). MSY and the exploitation rate corresponding to MSY are similar for Eq. (6) and the Beverton–Holt model (Fig. 3). There is a larger difference for the biomass corresponding to MSY and the difference

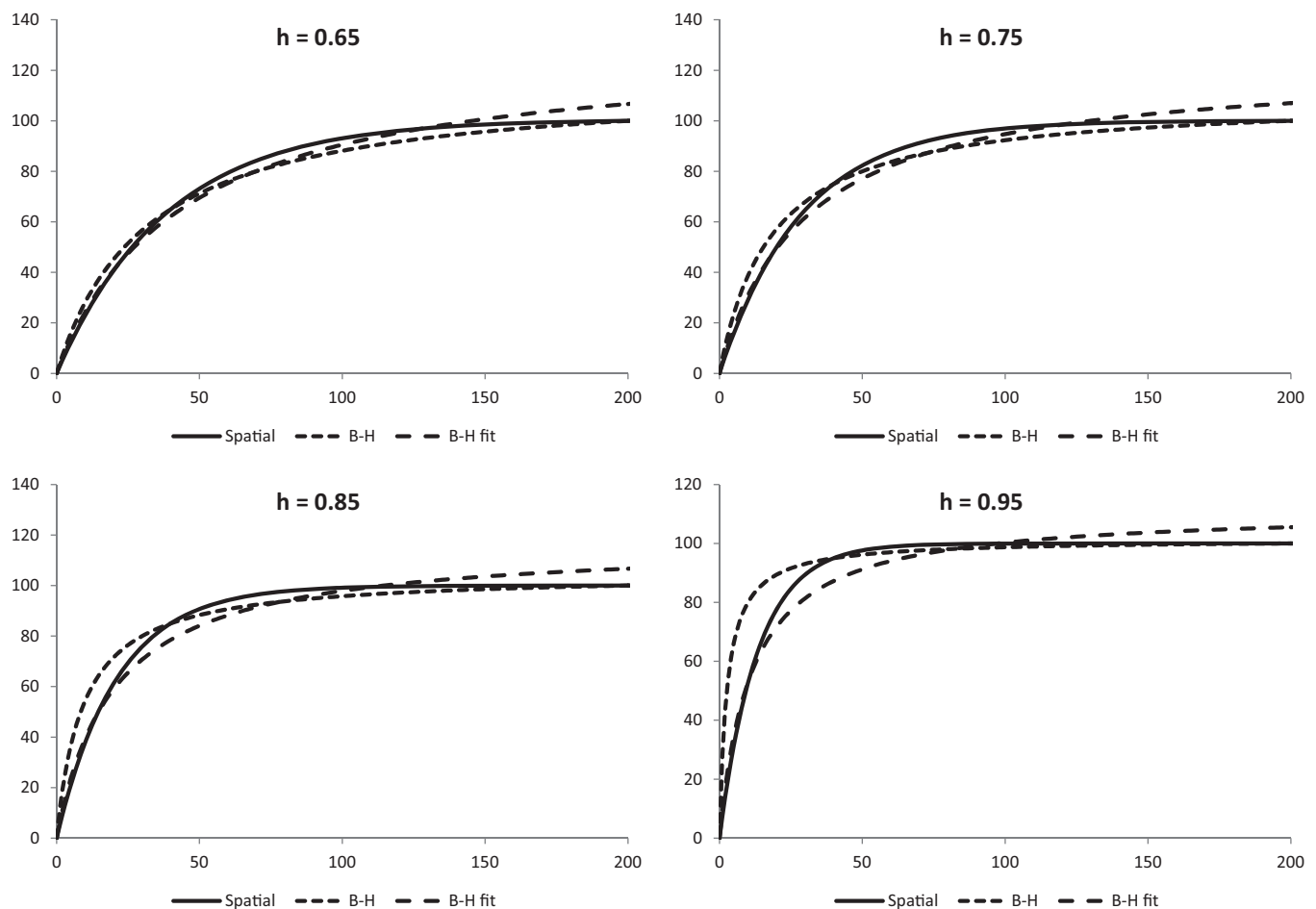


Fig. 2. Comparison of the spatial extent stock–recruitment model with the Beverton–Holt stock–recruitment model for the same values of steepness, h , and virgin recruitment, R_0 , and with the Beverton–Holt stock–recruitment model with h and R_0 that give the best correspondence with the spatial extent stock–recruitment model.

increases with steepness, except for very low levels of steepness (Fig. 3).

3. Discussion

The new stock–recruitment model (Eq. (6)) is parameterized in terms of parameters that are commonly used in fisheries stock assessment: R_0 and h . It approximates well the theoretical relationship between randomly arriving spawners and the consequent recruits when new spawners arriving at already occupied sites do not add to the number of recruits. It has been used to model salmon redd imposition (McNeil, 1964; Maunder, 1997), and it is extended here to highly fecund marine species. It is reasonable to expect that a similar relationship may occur between spawners and recruits if a highly fecund species randomly distributes itself across the ocean during spawning and habitat is limited. Few spawners may be needed to saturate a unit of habitat, and units of habitat without spawners will not produce recruits. An understanding of the mechanism is not needed – only an assumption that it exists. Timing of recruitment is just as important as the spatial aspects of recruitment so units of habitat are defined in both space and time. Of course, this is a simplification of recruitment dynamics, but it is no less of a simplification than the linear density dependence assumptions which underlie the Beverton–Holt and Ricker stock–recruitment models.

Spawning groups are assumed to randomly distribute themselves across the environment. One group (e.g. school) of spawners (rather than an individual) can saturate a unit. The larger the

groups, the less likely that all available habitat units will be occupied by spawners producing recruitment and there will be a stronger relationship between spawning stock-size and recruitment. This implies that species that migrate and aggregate to spawn, have a limited number of spawning locations (e.g. orange roughy, *Hoplostethus atlanticus*), and maintain spawning group size rather than number of spawning groups, may have a stronger relationship between spawning stock size and recruitment than those that do not migrate and spawn all year around (e.g. yellowfin tuna), despite both being highly fecund.

Rose et al. (2001) categorized species from Myers et al. (1999) into three recruitment groups based on egg size and fecundity: (i) opportunistic – small, rapidly maturing, short-lived fishes; (ii) periodic – larger, highly fecund fishes with long life spans; and (iii) equilibrium – fishes of intermediate size that often exhibit parental care and produce relatively few, large offspring. The overall average steepness value was highest for periodic species (0.70) and lower for equilibrium species (0.57) and opportunistic species (0.56). These three categorizations do not separate well into species that aggregate and those that do not, and the high-low fecundity cutoff (25,000 eggs) might imply that species in the low fecundity category are still relatively highly fecund. It would be informative to repeat the analysis of Rose et al. (2001), categorizing species based on spawning aggregation behavior in both space and time. However, the deficiencies of the Myers et al. (1999) analysis (see Gilbert, 1997; Maunder, 2012) should be taken into consideration before drawing final conclusions.

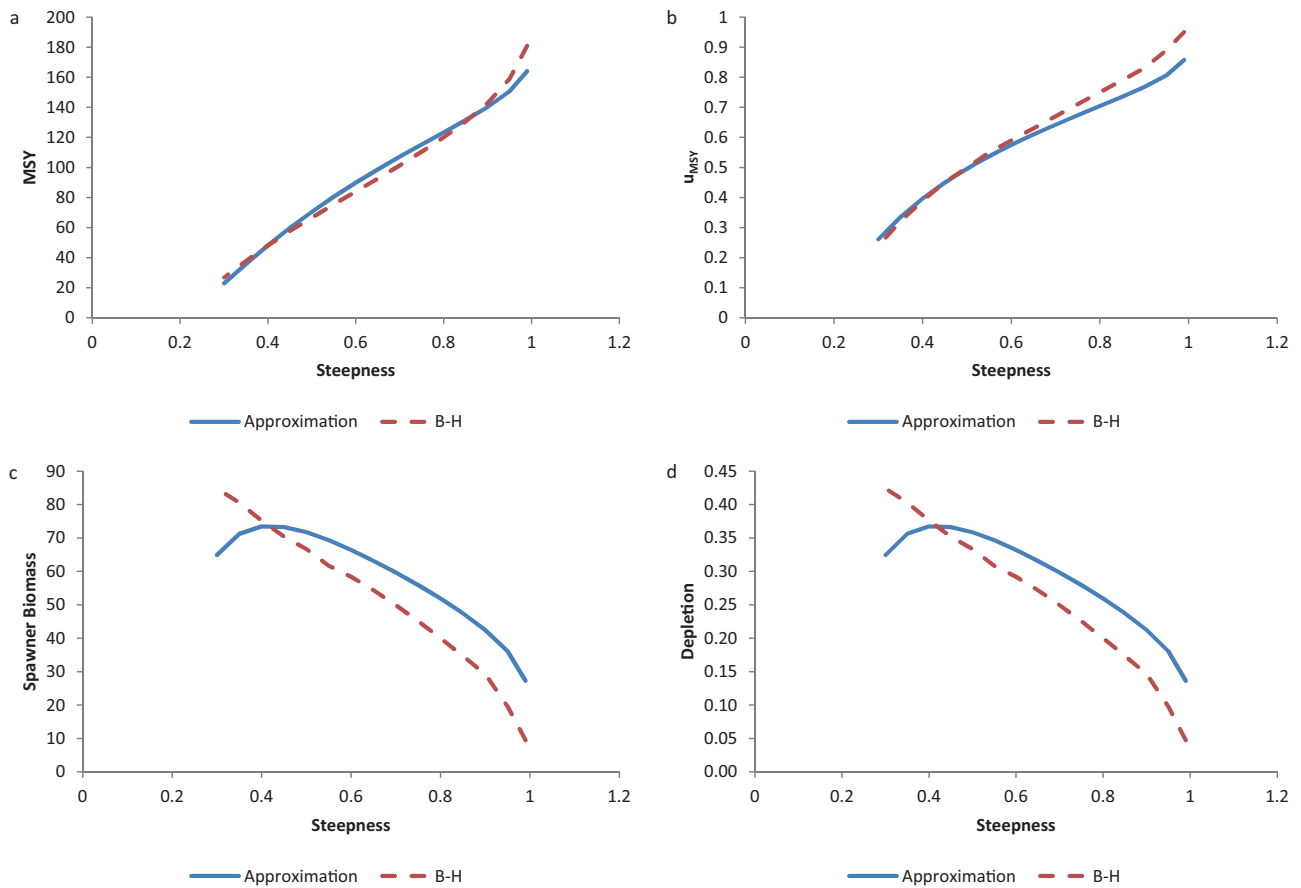


Fig. 3. Comparison of management quantities from the spatial extent stock–recruitment model with the Beverton–Holt stock–recruitment model for the same values of h and R_0 : (a) maximum sustainable yield (MSY); (b) exploitation rate corresponding to MSY; (c) spawning biomass corresponding to MSY; and (d) spawning biomass corresponding to MSY as a ratio of S_0 .

The distribution of spawners across the environment may not be random. The ideal free distribution, which is often applied when analyzing habitat selection, assumes that individuals are distributed among habitats such that their fitness is maximized (Morris, 1987). Individuals will occupy less favorable habitat to avoid competition for resources in more favorable habitat. This suggests that the spatial range of the population will decrease as individuals occupy the favorable habitat as the population decreases in size (the basin effect, MacCall, 1990). Shepherd and Litvak (2004) argue that it is unlikely that individuals would be informed beyond their immediate perceptual range, thus violating the ideal free distribution given the scale at which fish populations are distributed. Habitat selection may occur beyond an individual's perceptual range as it moves in preference to a gradient. However, the ideal and free distribution is violated if movement between habitats is limited (not ideal and free) (Shepherd and Litvak, 2004).

Chapman (1973) generalized Eq. (1) to include a probability distribution for habitat quality, and showed that Eq. (1) still arises if habitat quality follows an exponential curve. He also showed that the Beverton and Holt (1957) model results from a specific habitat quality distribution. Maunder (1997) also derived an equation for the inclusion of habitat quality, which led to a relationship similar to Eq. (1), but an analytical formula was unavailable. Habitat selection suggests that favorable habitats would concentrate individuals, and the redundancy of eggs may be greater in areas of preferable habitat. Investigation of these more complicated types of dynamics may need the type of simulation methods used by Maunder (1997).

The most important contribution of this research may not be the new stock–recruitment model, but rather the concept that the

temporal and spatial extent of spawning might drive the stock recruitment relationship, and that species that widely disperse themselves and spawn relatively continuously (e.g. yellowfin tuna) will have a weak relationship between stock size and recruitment. This may explain the lack of evidence of a stock–recruitment relationship for many species. Other species may experience expansion and contraction of their spatial extent as the abundance increases and decreases as has been observed for several pelagic (MacCall, 1990; Barange et al., 2009) and demersal (Swain and Sinclair, 1994) species. The hypothesis also has some severe implications for management of species that aggregate for spawning. Aggregation generally makes species vulnerable to exploitation even when stock size is low and it may not be possible to detect declines in abundance from fisheries-derived indices of abundance. Furthermore, recruitment will be more dependent on stock size if the spatial extent recruitment hypothesis is correct. Managers must therefore consider the historical spatial extent of a population, particularly when evaluating recovery as it rebuilds. Recruitment may increase only if the population extends its spatial–temporal spawning range, and the area depleted may only slowly be repopulated by spill-over of adult fish from adjacent areas, which generate new migratory patterns (Cardinale et al., 2011).

The new spatial extent stock–recruitment model has a similar shape to the Beverton–Holt stock–recruitment model (i.e. it is asymptotic). However, it differs to some degree from the Beverton–Holt model (Fig. 2). The approximation (Eq. (6)) is nearly identical to the original model for $h > 0.6$, which is the range of steepness values that are probably reasonable for the types of dynamics represented by the model. Therefore, the use of the

approximation for highly fecund species is reasonable. Eq. (6) could also be used as a stock–recruitment model in its own right (i.e. not an approximation, simply another functional form). Other stock–recruitment models that have density dependence occurring when the abundance is closer to the carrying capacity (e.g. the Maunder–Taylor–Methot stock recruitment model; Taylor et al., 2013) should be used for species with low fecundity that have lower values for steepness. Temporal variation could be added to the stock–recruitment model following the standard approach of including a multiplicative log-normal error.

Acknowledgements

This research addresses the recruitment component of the good practices guide to stock assessment program of the Center for the Advancement of Population Assessment Methodology (CAPAM) and is contribution number 1. The research benefited from discussions with Jeanne Wexler of the Inter-American Tropical Tuna Commission. Grant Thompson, an anonymous reviewer, and the Associate Editor Andre Punt provided suggestions that improved the manuscript.

Appendix A. Alternative parameterization

Grant Thompson (AFSC, pers. comm.) suggested an alternative parameterization that is not an approximation, but changes the definition of steepness to the ratio of recruitment at $S_0/5$ and R_{max} .

$$R = R_{max}(1 - \exp(5 \ln(1 - h)S/S_0))$$

where

$$h = 1 - \exp(-S_0/(5mK))$$

Appendix B. Reliability of the approximation

The reliability of the approximation can be evaluated by comparing the recruitment calculated from S_0 with R_0 :

$$R(S = S_0) = R_0 \left(1 - \exp \left[\frac{5 \ln(1 - h)S_0}{S_0} \right] \right) \tag{B.1}$$

such that

$$\frac{R(S = S_0)}{R_0} = 1 - \exp[5 \ln(1 - h)] \tag{B.2}$$

R_0 is well approximated for $h > 0.6$ (Fig. B.1a). The reliability can also be evaluated by comparing the recruitment calculated from 20% of virgin spawning biomass with hR_0 :

$$\frac{R(S = 0.2S_0)}{hR_0} = \frac{1 - \exp[0.8 \ln(1 - h)]}{h} \tag{B.3}$$

showing that there is no bias in recruitment at $0.2S_0$, which is the definition of h . To evaluate the bias for other levels of spawning biomass, m' from Eq. (4) can be calculated as:

$$m' = \frac{-S_0}{R_{max} \ln[1 - R_0/R_{max}]} \tag{B.4}$$

However, R_{max} has to be selected iteratively to satisfy $R(S = 0.2S_0)/R_0 = h$. Comparison for $S_0 = 200, R_0 = 100$ and $h = (0.4, 0.5, 0.6, 0.7)$ show that the error decreases from spawning biomass levels equal to S_0 to zero at $0.2S_0$, then increases at lower spawning biomass levels (Fig. B.1b).

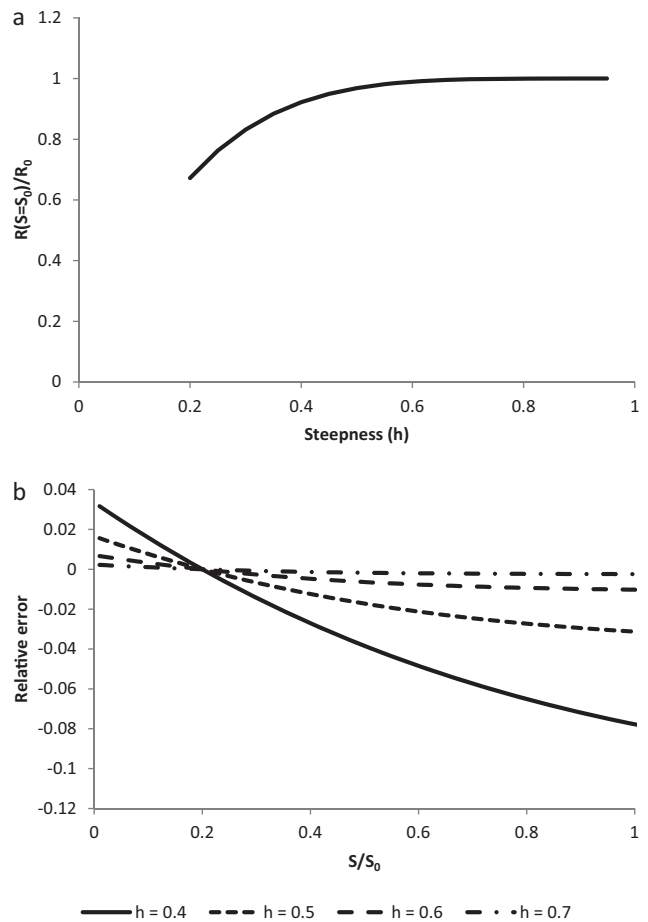


Fig. A1. (a) Error in the value for virgin recruitment (R_0) using the approximation to the spatial extent stock–recruitment model for different levels of steepness (h). (b) Relative error in the values for recruitment using the approximation to the spatial extent stock–recruitment model for different levels of spawning biomass relative to the virgin spawning biomass (S_0) for four levels of steepness.

Appendix C. Estimating maximum sustainable yield

Given that harvest occurs just before spawning, and natural mortality and growth are independent of abundance, and that individuals die after spawning (e.g. a salmon type life history) so that $C = R(S_0/R_0)u$ and $S = R(S_0/R_0)(1 - u)$, where S_0/R_0 is a measure of natural mortality and growth, and u is the exploitation rate. In equilibrium:

spatial extent stock – recruitment model

$$R = R_0(1 - \exp[5 \ln(1 - h)R(1 - u)/R_0])$$

Beverton – Holt stock – recruitment model

$$R = \frac{R(1 - u)}{aR_0/S_0 + bR(1 - u)}$$

For a given exploitation rate, recruitment can be selected so that these equations are satisfied (it is analytical for the Beverton–Holt stock–recruitment model) and yield calculated. This can be repeated for different exploitation rates to determine the exploitation rate that maximizes yield. An analytical formulation is available for the approximation to the spatial extent stock–recruitment model. Letting $C = R(S_0/R_0) - S$ and solving $dC/dS = 0$ to find S_{MSY} gives $S_{MSY} = \frac{S_0 \ln(-1/(5 \ln(1-h)))}{5 \ln(1-h)}$, which can be used to calculate the MSY based quantities.

References

- Barange, M., Coetzee, J., Takasuka, A., Hill, K., Gutierrez, M., Oozeki, Y., van der Lingen, C., Agostini, V., 2009. Habitat expansion and contraction in anchovy and sardine populations. *Prog. Oceanogr.* 83 (1–4), 251–260.
- Beverton, R.J.H., Holt, S.J., 1957. On the dynamics of exploited fish populations. *Fish. Invest.*, II. Sea Fish 19, 533.
- Cardinale, M., Bartolino, V., Llope, M., Maiorano, L., Skold, M., Hagberg, J., 2011. Historical spatial baselines in conservation and management of marine resources. *Fish. Fish.* 12, 289–298.
- Chapman, D.G., 1973. Spawner-recruit models and the estimation of the level of maximum sustainable catch. In: Parrish, B.B. (Ed.), *Fish Stocks and Recruitment*. Rapp. P.-v. Réun. Cons. Int. Explor. Mer. 164, 325–332.
- Conn, P.B., Williams, E.H., Shertzer, K.W., 2010. When can we reliably estimate the productivity of fish stocks? *Can. J. Fish. Aquat. Sci.* 67, 511–523.
- Cury, P., Roy, C., 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Can. J. Fish. Aquat. Sci.* 46, 670–680.
- Gilbert, D.J., 1997. Towards a new recruitment paradigm for fish stocks. *Can. J. Fish. Aquat. Sci.* 54, 969–977.
- Hjort, J., 1914. Fluctuations in the great fisheries of northern Europe reviewed in the light of biological research. *Rapports, Cons. Perm. Int. Explor. Mer.* 20, 1–228.
- Lee, H.-H., Maunder, M.N., Piner, K.R., Methot, R.D., 2012. Can steepness of the stock–recruitment relationship be estimated in fishery stock assessment models? *Fish. Res.* 125–126, 254–261.
- MacCall, A.D., 1990. *Dynamic Geography of Marine Fish Populations*. University of Washington Press, Seattle.
- Magnusson, A., Hilborn, R., 2007. What makes fisheries data informative? *Fish. Fish.* 8, 337–358.
- Maunder, M.N., 1997. Investigation of density dependence in salmon spawner–egg relationships using queueing theory. *Ecol. Model.* 104, 189–197.
- Maunder, M.N., 2012. Evaluating the stock–recruitment relationship and management reference points: application to summer flounder (*Paralichthys dentatus*) in the U.S. mid-Atlantic. *Fish. Res.* 125–126, 20–26.
- McNeil, W.J., 1964. Redd superimposition and egg capacity of pink salmon spawning beds. *J. Fish. Res. Board Can.* 21, 1385–1396.
- Morris, D.W., 1987. Tests of density-dependent habitat selection in a patchy environment. *Ecol. Monogr.* 57, 269–281.
- Myers, R.A., Bowen, K.G., Barrowman, N.J., 1999. Maximum reproductive rate of fish at low population sizes. *Can. J. Fish. Aquat. Sci.* 56, 2404–2419.
- Platt, T., Sathyendranath, S., Fuentes-Yaco, C., 2007. Biological oceanography and fisheries management: perspective after 10 years. *ICES J. Mar. Sci.* 64, 863–869.
- Quinn, T.J., Deriso, R.B., 1999. *Quantitative Fish Dynamics*. Oxford University Press, Oxford.
- Ricker, W.E., 1954. Stock and recruitment. *J. Fish. Res. Board Can.* 11, 559–623.
- Rose, K.A., Cowan Jr., J.H., Winemiller, K.O., Myers, R.A., Hilborn, R., 2001. Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. *Fish. Fish.* 2, 293–327.
- Shepherd, T.D., Litvak, M.K., 2004. Density-dependent habitat selection and the ideal free distribution in marine fish spatial dynamics: considerations and cautions. *Fish. Fish.* 5, 141–152.
- Skud, B.E., 1975. Revised estimates of halibut abundance and the Thompson–Burkenroad debate. IPHC scientific report No. 56. International Pacific Halibut Commission, Seattle.
- Swain, D.P., Sinclair, A.F., 1994. Fish distribution and catchability: what is the appropriate measure of distribution? *Can. J. Fish. Aquat. Sci.* 51, 1046–1054.
- Taylor, I.G., Gertseva, V., Methot Jr., R.D., Maunder, M.N., 2013. A stock–recruitment relationship based on pre-recruit survival, illustrated with application to spiny dogfish shark. *Fish. Res.* 142, 15–21.
- Vert-pre, K.A., Amoroso, R.O., Jensen, O.P., Hilborn, R., 2013. Frequency and intensity of productivity regime shifts in marine fish stocks. *PNAS* 110, 1779–1784.
- Walters, C.J., Parma, A.M., 1996. Fixed exploitation rate strategies for coping with effects of climate change. *Can. J. Fish. Aquat. Sci.* 53, 148–158.