Fisheries Research 165 (2015) 54–62

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

Effects of size-dependent relative fecundity specifications in fishery stock assessments

Xi He[a,*], John C. Field[a], Sabrina G. Beyer[a,b], Susan M. Sogard[a]

[a] Fishery Ecology Division, Southwest Fisheries Science Center, National Marine Fisheries Service, 110 Shaffer Road, Santa Cruz, CA 95060, USA
[b] Institute for Marine Sciences, University of California Santa Cruz, Santa Cruz, CA, 95060, USA

ARTICLE INFO

Article history:
Received 3 September 2014
Received in revised form 5 December 2014
Accepted 5 December 2014
Handling Editor A.E. Punt

Keywords:
Size-specific relative fecundity
Maternal effects
Stock depletion
Steepness
Rockfish
Reference points

ABSTRACT

A comprehensive understanding of reproductive biology is fundamental to the accurate assessment of a given stock's spawning potential relative to the unfished level. Such an understanding is particularly important given the growing recognition of size, age or weight dependent relative fecundity (Φ_{rel}, eggs per kg of female weight), or other maternal effects that may demonstrate a relatively greater contribution of specific demographic components of a population toward reproduction. However, size-specific data on Φ_{rel}, or other data on maternal effects on reproductive output, are not always available for many stock assessments because intensive efforts are required to collect such data. In the absence of data, the assumption of no size-specific Φ_{rel} relationship is typically made, which can lead to bias in estimating stock status and related management parameters. We examined effects of misspecifications of size-specific Φ_{rel} functions on estimated stock assessment parameters and related management quantities using two stocks as case studies and three sets of simulation models, chosen to represent wide ranges of life and fishing histories. The results showed that misspecification effects were relatively small when stocks were less depleted (e.g. 75% of virgin spawning output), but could lead to more substantive misspecifications in more depleted stocks with slower growth and lower mortality rates. For example, we found that stock was estimated to be as much as 20% less depleted if a strong size-specific Φ_{rel} exists in a population, but no size-specific Φ_{rel} is used in the model. This represents a non-trivial shift in the perception of status for most stocks. The results also showed that overestimating the strength of the size-specific Φ_{rel} function in stock assessment models led to smaller estimation errors in assessment outputs compared to underestimating the size-specific Φ_{rel}. The results are insightful with respect to the importance of gathering data on size-dependent Φ_{rel} and other aspects of reproductive ecology, as well as with respect to the nature of assumptions that are made with regards to reproductive ecology in data limited situations.

Published by Elsevier B.V.

1. Introduction

The importance of understanding the reproductive biology of fishes has been recognized as key to the development of realistic population models since the earliest studies of marine fish population dynamics. The allometric effects of size on total fecundity have long been recognized. However, the effects of size on relative fecundity and on other aspects of reproductive success did not begin to be formally quantified until the late 1980s (e.g., Hislop, 1988; Haldorson and Love, 1991; Trippel et al., 1997). Since then, numerous studies across a broad taxonomic and geographic range of species have documented that larger, older females often have higher relative fecundity (Φ_{rel}: eggs per kg of female weight), producing more progeny per unit biomass compared to smaller, younger females (Marteinsdottir and Begg, 2002; Morgan and Brattey, 2005; Morgan, 2008; reviewed in Hixon et al., 2014). This is a particularly important factor to account for in stock assessment models when fisheries reference points are based on the assessment of a given stock's spawning potential relative to the unfished level (Murawski et al., 2001; Mangel et al., 2010, 2013; Methot and Wetzel, 2013), as exploited stocks typically have smaller and younger individuals than unexploited stocks (Murawski et al., 2001; Berkeley et al., 2004a).

Where data on size- or age-dependent Φ_{rel} are available, they are typically incorporated into stock assessment models.

* Corresponding author. Tel.: +1 831 420 3948; fax: +1 831 420 3977.
E-mail address: xi.he@noaa.gov (X. He).

http://dx.doi.org/10.1016/j.fishres.2014.12.023
0165-7836/Published by Elsevier B.V.

Table 1
The most recent age-structured assessments by species for rockfish (*Sebastes*) managed on the U.S. West Coast, and whether the assessment included explicitly modeled size-specific relative fecundity (Φ_{rel}).

Stock	Species	Most recent assessment year	Fecundity explicitly modeled
Aurora Rockfish	*S. aurora*	2013	No
Bank Rockfish	*S. rufus*	2000	Yes
Black Rockfish	*S. melanops*	2007	Yes
Blackgill Rockfish	*S. melanostomus*	2011	Yes
Blue Rockfish	*S. mystinus*	2007	Yes
Bocaccio Rockfish	*S. paucispinis*	2011	Yes
Canary Rockfish	*S. pinniger*	2009	No
Chilipepper Rockfish	*S. goodei*	2007	No
Cowcod[a]	*S. levis*	2009	No
Darkblotched Rockfish	*S. crameri*	2011	Yes
Gopher Rockfish	*S. carnatus*	2007	No
Greenspotted rockfish	*S. chlorostictus*	2011	Yes
Greenstriped Rockfish	*S. elongatus*	2009	Yes
Pacific Ocean Perch	*S. alutus*	2011	Yes
Rougheye Rockfish	*S. aleutianus*	2013	No
Shortbelly Rockfish	*S. jordani*	2007	No
Splitnose Rockfish	*S. diploproa*	2009	Yes
Vermillion[b]	*S. miniatus*	2005	No
Widow Rockfish	*S. entomelas*	2011	No
Yelloweye Rockfish	*S. ruberrimis*	2011	Yes
Yellowtail Rockfish	*S. flavidus*	2005	No

[a] The most recent (2013) assessment did not use an age structured model.
[b] Assessment not adopted for use by management.

For example, size-dependent Φ_{rel} and other maternal effects have been reported for several rockfish (*Sebastes*) species in the Eastern North Pacific Ocean, and such effects are increasingly being included in assessments. In a comprehensive review of this highly speciose (and consequently, often data-poor) genus, Dick (2009) found that size-dependent Φ_{rel} information was used in six out of 16 stock assessments of *Sebastes* species (38%) along the U.S. West Coast through 2007, but by 2011 that fraction had increased to 12 of 19 assessments (63%, Table 1). In 2013, several more assessments of west coast rockfish were conducted, including two on previously unassessed species (Aurora, *Sebastes aurora* and Rougheye rockfish, *Sebastes aleutianus*), for which no fecundity data were available, bringing the fraction of most recent rockfish assessments with Φ_{rel} information back down to 57%.

Past sensitivity analyses of stock assessment models have shown that management reference points are sensitive to the assumptions made regarding the slope of the linear female size and Φ_{rel} relationship (Leaman, 1991; Murawski et al., 2001; Brooks, 2013; Spencer and Dorn, 2013; Spencer et al., 2013). Thus, we initiated both empirical and simulation studies to better evaluate this effect. First, we evaluated the sensitivity of two published stock assessments for West Coast rockfish, representing two contrasting life history types, using recent estimates of size-dependent Φ_{rel} to evaluate how different assumptions about the slope of the size-dependent Φ_{rel} relationship mapped to reference points and stock depletion. Second, we developed a simulation study to more objectively evaluate the expected error in reference point and stock depletion results when assessment models (based on simulated operating models) intentionally misspecified the size-dependent Φ_{rel} relationship. Both of these efforts shed light on the importance of developing and including size-dependent Φ_{rel} data in age-structured assessment models, and indicated some of the potential errors associated with modeling population dynamics in the absence of such information.

2. Methods and materials

2.1. Case study: assessments of eastern pacific rockfish

We used the most recent stock assessment models for Blackgill rockfish (*Sebastes melanostomus*, Field and Pearson, 2011) and Chilipepper rockfish (*Sebastes goodei*, Field, 2007) to examine effects of size-dependent Φ_{rel} on assessment outputs. Both assessments were accepted for use in management by the Pacific Fishery Management Council (PFMC). At the time when these two assessments were conducted, the Blackgill rockfish assessment included a fairly strong size-dependent Φ_{rel} relationship, based on the data presented in Beyer et al. (2015). By contrast, the Chilipepper rockfish (*S. goodei*) assessment did not include size-dependent Φ_{rel}, as only very limited data were available, and consequently assumed that larval output was directly proportional to spawning stock biomass.

The two species represent a fairly strong contrast in life history types, thereby capturing a range of parameter values that illustrate the relative magnitude of accounting for (or not accounting for) size-dependent Φ_{rel}. Blackgill rockfish is a deeply distributed, long lived species with maximum age estimates ranging from 64 (Field and Pearson, 2011) to 90 (Stevens et al., 2004) years, with correspondingly low natural mortality rates (estimated at 0.063 yr^{-1} for females, Field and Pearson, 2011). The von-Bertalanffy growth coefficient (K) for females was estimated in the model as 0.028 yr^{-1}, among the lowest documented for a rockfish species in the Northeast Pacific, and age at 50% maturity for females was estimated to be approximately 20 yr, among the latest ages at maturity for rockfish. The species has been subjected to fisheries, primarily bottom trawl and hook and line, since the early 1950s, and in 2011 the stock was estimated to be at 30.2% of the relative (mean unfished) spawning output level. However, this level represented an increase from an estimate of 18% for the early 1990s following intensive exploitation in the 1980s. Thus, based on the current PFMC definition of "overfished" for rockfish (<25% of the unfished level; the "target" level is 40% of the unfished spawning potential), the stock would have been (retroactively) categorized as overfished for 16 years between 1989 and 2006. In contrast to the long-lived, slow growing Blackgill rockfish, Chilipepper are relatively fast growing, early maturing and short lived. The maximum observed age is approximately 30 yr, and the 2007 stock assessment estimated natural mortality rates of 0.16 yr^{-1} and 0.20 yr^{-1} for females and males, respectively (Field, 2007). Although this stock was also estimated to be at low levels (just above 25% of the unfished level) during the late 1990s, it was assessed to be healthy in 2007, at around 70% of the unfished biomass. Although the 2007 assessment assumed constant Φ_{rel}, Beyer et al. (2015) and Stafford et al. (2014) have recently reported a reasonably strong size-dependent Φ_{rel} relationship. We used the 2007 model, updated to utilize the most recent stock synthesis software (Methot and Wetzel, 2013), to evaluate the differences in assessment results with and without a size-dependent Φ_{rel}.

Beyer et al. (2015) used both length- and weight dependent Φ_{rel} functions to describe relationships between fecundity and body sizes, and found that there were slightly higher correlations between fecundity and body weight. In this paper, we defined the size-dependent Φ_{rel} function as:

$$\Phi_{rel} = a + bW \quad (1)$$

where Φ_{rel} is number of eggs per kilogram of fish, W is total weight of fish in kilograms, and a and b are estimated parameters; i.e., absolute fecundity is a quadratic function of weight. Note that if $b = 0$, weight-specific Φ_{rel} is constant across all sizes or ages. For Blackgill rockfish, $a = 159.473$ and $b = 95$, whereas for Chilipepper rockfish, $a = 132.355$ and $b = 59$, based on results of Beyer et al. (2015).