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Double or nothing: Plasticity in reproductive output in the chilipepper rockfish (*Sebastes goodei*)

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ABSTRACT

An understanding of the reproductive biology of a species is fundamental to successful management of fish stocks. Rockfish (*Sebastes* spp.) have complex reproduction, being viviparous and generally late to mature, often with extended adolescent periods characterized by abortive maturation events. Furthermore, whereas the majority of *Sebastes* species in the California Current region produce one brood of larvae annually, several are known to produce more than one, though no stock assessments have yet considered the impact multiple brooding may have on population spawning potential for these species. We documented abortive maturation and examined the prevalence and size-dependent and regional patterns of multiple brooding using macroscopic evaluation and detailed histological analysis of ovaries from a model species, chilipepper (*S. goodei*), collected off Central and Southern California. We modeled the size-related maternal effect on the probability of multiple brooding, and quantified size-dependent fecundity relationships. Our results indicate that the most robust estimation of reproductive output, as a function of the fecundity-length relationship, is improved for chilipepper when multiple brooding is incorporated, due to the greater probability of additional broods, and thus greater spawning potential, in larger females.

1. Introduction

An understanding of reproductive potential, as well as the drivers and causes of plasticity (i.e. variability) in reproductive traits, is fundamental to successful management of fish stocks. The historical assumption that total egg production is proportional to the spawning biomass of a stock has repeatedly been shown to be incorrect when species exhibit strong maternal effects, as exemplified in rockfishes (*Sebastes* spp.; Dick, 2009; Beyer et al., 2015). Maternal size- and age-dependent traits, such as increased relative fecundity (eggs per g of maternal somatic weight) or spawning frequency (number of spawning events in a season) with increasing size or age, are evident in a variety of species with varying reproductive strategies (see reviews by Fitzhugh et al., 2012; Hixon et al., 2014). In these cases, accounting for these maternal effects when estimating reproductive output in stock assessments is more appropriate than using spawning stock biomass (Spencer and Dorn, 2013; He et al., 2015).

Rockfishes—a speciose genus of great commercial and recreational importance throughout the California Current region—display strong maternal effects, with larger, older females contributing disproportionately to production in terms of both offspring quantity and quality (Sogard et al., 2008; Stafford et al., 2014; Dick et al., 2017). Rockfishes are generally long-lived, slow-growing, and late to mature, with several species showing prolonged adolescent periods during which small, young individuals may experience “false starts” to reproduction (abortive maturation; Nichol and Pikitch, 1994; Conrath and Knoth, 2013; Lefebvre and Field, 2015). All *Sebastes* species are live-bearers, with gestation periods ranging from one to two months (Love et al., 2002). Although the majority of species produce one brood of larvae annually, several have long been known to be capable of producing multiple broods in a given reproductive season (Moser, 1967a; Love et al., 1990). The extent to which abortive maturation and multiple brooding occur is not well studied, and the mechanisms driving these two phenomena are not well understood; however, both may affect reproductive reference points used in stock assessments (age- or size-at-maturity and reproductive output, respectively).

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Mass atresia events, the arresting of development and subsequent resorption of the leading cohort of vitellogenic oocytes, are known to occur in continental slope and deep dwelling rockfishes, which tend to have the slowest growth and greatest longevity within the *Sebastes* genus (Nichol and Pikitch, 1994; Conrath and Knoth, 2013; Lefebvre and Field, 2015). Most of these mass atresia events appeared to be abortive maturation (as opposed to skip spawning), as most females were below the length or age at 95% maturity (L_{95}). Abortive maturation, as defined here and by Ramsay and Whitthames (1996), is the occurrence of the resorbing type spawning omission (Rideout et al., 2005), in which mass atresia occurs in females that have not previously reproduced. Although these females are physiologically mature, they are functionally immature as they are not yet contributing to production. Alternately, mass atresia in females that have reproduced in previous years represents skip spawning (Rideout et al., 2005). Further complexity in the reproductive traits of some rockfishes is the presence of an extended adolescent period, which is characterized by abortive maturation events or by oocyte development arrested at the oil vacuole stage (first secondary growth stage oocyte) for one or more years (Hannah and Parker, 2007; Lefebvre and Field, 2015). Maturity ogives, or more appropriately spawning ogives, can better account for the consequences of abortive maturation, extended adolescence, and skip spawning by designating such individuals as functionally immature, which results in shifts of the ogive to larger, older individuals (Hannah and Parker, 2007; Lefebvre and Field, 2015).

The phenomenon of multiple brooding in rockfishes was initially noted by Moser (1967a) and MacGregor (1970) in bocaccio (*S. paucispinis*), speckled rockfish (*S. ovalis*), and starry rockfish (*S. constellatus*). Multiple broods were macroscopically identified in ovaries containing fertilized eggs (primary brood) by the presence of developing oocytes (the eventual secondary brood), as well as in ovaries with developing oocytes (the eventual secondary brood) with entrained larvae from the primary brood that had failed to be extruded from the ovary during parturition (larval release). Multiple brooding has since been documented in more than a dozen *Sebastes* species (Table 1) with primarily southerly distributions in the Southern California Bight. It was generally believed to be uncommon north of Point Conception, CA (Echeverria, 1987; Love et al., 2002). The Southern California Bight, a region extending from Point Conception, California, to Punta Eugenia, Baja California, Mexico, is characterized by warmer, more variable and less productive conditions relative to more northern waters of the California Current, where stronger, more predictable seasonal upwelling occurs (Parrish et al., 1981; Checkley and Barth, 2009). The mechanisms driving and allowing for the production of multiple broods are not fully understood, nor are the limits to the number of broods produced by a given species annually, though macroscopic evaluations have suggested as many as three broods in some individuals (Kashef, unpublished data).

Table 1
Sebastes species in which multiple brooding has been macroscopically observed. All central California (CCA) observations are from unpublished data.

Scientific name	Common name	Region	Source(s)
S. auriculatus	Brown rockfish	CCA	E, H
S. chlorostictus	Greenspotted rockfish	SCB	D, E, I
S. constellatus	Starry rockfish	SCB, CCA	B, D, E, I
S. elongatus	Greenstriped rockfish	SCB	D, E
S. ensifer	Swordspine	SCB	D, E, I
S. goodei	Chilipepper rockfish	SCB	D, E, G, I
S. hopkinsi	Squarespot rockfish	SCB	D, E, I
S. jordani	Shortbelly rockfish	SCB	E, I
S. levis	Cowcod	SCB	D, E, I
S. ovalis	Speckled rockfish	SCB, CCA	B, D, E, G, I
S. paucispinus	Bocaccio	SCB, CCA	A, B, C, D, E, F, I
S. rosaceus	Rosy rockfish	SCB, CCA	D, E, I
S. rosenblatti	Greenblotched rockfish	SCB	D, E
S. rufus	Bank rockfish	SCB	D, E

SCB = Southern California Bight. Sources: A = Moser (1967a); B = MacGregor (1970); C = Echeverria (1987); D = Love et al. (1990); E = Love et al. (2002); F = Ralston and MacFarlane (2010); G = Beyer et al. (2015); H = Stafford and Kashef, unpublished data; I = Beyer, unpublished data.

Moser (1967a) and all other authors to more recently document multiple brooding have noted the need to account for the phenomenon in any accurate assessment of fecundity in rockfishes. Both Moser (1967b) and MacGregor (1970) noted that secondary broods were recruited from reserve oocytes after the eggs of primary broods had been fertilized, suggesting an indeterminate fecundity pattern rather than the determinate fecundity pattern typical of *Sebastes* (Love et al., 2002). In fish with determinate fecundity, annual fecundity is fixed prior to any spawning activity, whereas in fish with an indeterminate fecundity pattern, fecundity is not set prior to spawning and is the product of the number of reproductive events throughout the season and the fecundity of each batch (Murua and Saborido-Rey, 2003). In a comparison between brood fecundity estimates in chilipepper and speckled rockfish, Beyer et al. (2015) found that secondary broods were nearly as fecund as primary broods. If fecundity in chilipepper is indeterminate, then multiple brooding females could be doubling (or more, if more than two broods are produced) their annual reproductive output compared to single brooding females. It is particularly important to account for multiple brooding if the likelihood of producing two (or more) broods is size-dependent. Ralston and MacFarlane (2010) observed a higher frequency of multiple brooding in larger versus smaller female bocaccio; however, they also recognized that the challenges associated with false negatives precluded an effective accounting of the phenomenon in defining a fecundity function. If multiple brooding is size-dependent, the strength of the fecundity-size relationship would increase, resulting in a further departure from the assumption of egg production being proportional to spawning stock biomass (Dick et al., 2017). Fecundity-size relationships, which account for the disproportional reproductive contribution of larger females, have been incorporated in over half (12 of 21) of recent rockfish stock assessments on the U.S. West Coast (He et al., 2015). Additionally, a recent meta-analysis provided the basis to account for size-dependent fecundity for all species, regardless of the available data (Dick et al., 2017). The effect of multiple brooding females, however, has not yet been considered in any rockfish stock assessment, and could substantially alter the relationship between fecundity and size or age.

Chilipepper was chosen as a model species to explore the effect of multiple brooding on fecundity estimates due to the relatively high abundance and healthy status of the stock, and the relative ease of capture. Chilipepper is a continental shelf dwelling species distributed along the west coast of North America and is most common from Cape Mendocino, California, to northern Baja California, Mexico. Multiple brooding has been documented in this species off Southern and, less frequently, Central California (Beyer et al., 2015).

The objectives of this study were to 1) document the occurrence of what might be considered atypical ovarian development, such as abortive maturation, prolonged adolescence, and skip spawning; 2) determine the prevalence of and regional and size-related patterns related to multiple brooding; and 3) model how fecundity estimates and fecundity-length relationships change when accounting for multiple brooding. Furthermore, the implications of the plasticity in reproductive strategy in chilipepper and other multiple brooding rockfish species are considered in terms of potential changes in environmental conditions.

2. Materials and methods

2.1. Sample collection and processing

Female chilipepper were collected via rod-and-reel onboard chartered recreational and commercial fishing vessels in Central (near