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Temporal variations of potential fecundity of southern blue whiting (*Micromesistius australis australis*) in the Southeast Pacific

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ABSTRACT

Fecundity is a key aspect of fish species reproductive biology because it relates directly to total egg production. Yet, despite such importance, fecundity estimates are lacking or scarce for several fish species. The gravimetric method is the most-used one to estimate fecundity by essentially scaling up the oocyte density to the ovary weight. It is a relatively simple and precise technique, but also time consuming because it requires counting all oocytes in an ovary subsample. The auto-diametric method, on the other hand, is relatively new for estimating fecundity, representing a rapid alternative, because it requires only an estimation of mean oocyte density from mean oocyte diameter. Using the extensive database available from commercial fishery and design surveys for southern blue whiting *Micromesistius australis australis* in the Southeast Pacific, we compared estimates of fecundity using both gravimetric and auto-diametric methods. Temporal variations in potential fecundity from the auto-diametric method were evaluated using generalised linear models considering predictors from maternal characteristics such as female size, condition factor, oocyte size, and gonadosomatic index. A global and time-invariant auto-diametric equation was evaluated using a simulation procedure based on non-parametric bootstrap. Results indicated there were not significant differences regarding fecundity estimates between the gravimetric and auto-diametric method ($p > 0.05$). Simulation showed the application of a global equation is unbiased and sufficiently precise to estimate time-invariant fecundity of this species. Temporal variations on fecundity were explained by maternal characteristic, revealing signals of fecundity down-regulation. We discuss how oocyte size and nutritional condition (measured as condition factor) are one of the important factors determining fecundity. We highlighted also the relevance of choosing the appropriate sampling period to conduct maturity studies and ensure precise estimates of fecundity of this species.

1. Introduction

Fecundity is the number of eggs produced by a female during a given season, and thus it is one of the key population attributes determining population renewal. When fecundity is combined with female abundance, the total egg production can be estimated. Egg production is a proxy for stock reproductive potential, and is used to predict recruitment (Marshall et al., 1998; Trippel, 1999). However, implementation of reproductive potential is difficult in species with sparse estimates of fecundity and populations composed by multiple stocks, as is the case with southern blue whiting *Micromesistius australis australis* (Norman, 1937). This species supports fishery activities, in terms of landings and economic importance, off the coasts of Chile and Argentina (Contreras et al., 2014; Macchi et al., 2005). An understanding of spatio-temporal dynamics of fecundity requires extensive data about reproductive season, spawning areas and a range of appropriately-sized females that likely contribute to reproductive activity. Additionally, other factors such as skipped spawning and down-regulation are relevant for evaluating fecundity dynamics in fish populations. Skipped spawning refers to mature females that interrupt their normal reproductive cycle in a given year, but without interfering with the spawning in subsequent year, while fecundity down-regulation is the presence of atresia in vitellogenic oocytes, which adjusts egg production prior to spawning (Kurita et al., 2003; Rideout et al., 2005; Rideout and Tomkiewicz, 2011). Such mechanisms are associated with adverse environmental conditions, lack of males, or decreased nutritional condition affecting the channeling of energy into reproduction (McBride et al., 2015).

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Several procedures to estimate fecundity in fish species (for details see Murua et al. (2003) and references therein) exist, but the most widely applied is the gravimetric method with which fecundity is calculated as the product of ovary weight and oocyte density, referring to oocyte number per gram of ovarian tissue (Murua et al., 2003). The method is relatively simple, cheap and accurate, but time consuming, because its application relies on counting and measuring all oocytes in a sample of gonadal tissue. Thorsen and Kjesbu (2001) proposed as alternative the auto-diametric method to estimate fecundity in Atlantic cod, *Gadus morhua*. This approach consists of estimating oocyte density from mean yolked oocyte diameter. Moreover, their method significantly reduces the time involved in measuring oocyte size by using image analysis (Thorsen and Kjesbu, 2001). Although, the relationship between average oocyte size and density is fairly new, the use of oocyte size to estimate fecundity was established by Kjesbu et al. (1998) based on first principles underpinning oocyte growth through maturation cycle (Kjesbu et al., 1996).

The auto-diametric method has been applied to different fish species with determinate fecundity, such as *Alosa sapidissima* (Friedland et al., 2005), *Gadus morhua* (Klibansky and Juanes, 2008; Witthames et al., 2009), *Melanogrammus aeglefinus* (Alonso-Fernández et al., 2009; Witthames et al., 2009), *Clupea harengus* (Kurita and Kjesbu, 2009; Witthames et al., 2009), and *Pseudopleuronectes americanus* (McElroy et al., 2013). It has also been applied in fish species with indeterminate fecundity, such as *Paralichthys olivaceus* (Kurita and Kjesbu, 2009), *Scomber scombrus* (Witthames et al., 2009), *Merluccius merluccius* (Korta et al., 2010; Witthames et al., 2009), and *Engraulis encrasicolus* (Schismenou et al., 2012). Friedland et al. (2005) showed that the application of the auto-diametric method can be extended to other fish species, using a flatbed scanner instead of a microscope and camera setup plus a rather expensive software image analysis. Klibansky and Juanes (2008) extended the auto-diametric method to *G. morhua*, using a flatbed scanner with free image analysis software. Last, Kurita and Kjesbu (2009) proposed employing the auto-diametric method combined with the stereologic method, reporting that volume-based mean oocyte diameter (ODV) is a better metric of oocyte packing density than arithmetic mean oocyte diameter (ODN). The auto-diametric method has not yet been applied in *M. a. australis*, therefore a species-specific calibration of this method is needed prior to its application to estimate fecundity (Witthames et al., 2009).

M. australis is differentiated into two subspecies, *M. a. australis* in South America and *M. a. pallidus* in New Zealand (Inada and Nakamura, 1975; Ryan et al., 2002). *M. a. australis* shows migratory habits, feeding in the Atlantic during the austral summer and concentrating for reproduction during the austral winter in the Southeast Pacific (Lillo et al., 1999) and Southwest Atlantic (Pájaro and Macchi, 2001). The reproductive strategy of this species is characterised by a group-synchronous ovary development with determinate fecundity (Lillo et al., 1999). In Chile, *M. a. australis* is targeted by industrial trawling fishery which operates mainly on the continental shelf and slope off the austral zone between 42°00′S and 57°00′S, and in depths of 30 to 800 m (Aguayo et al., 2010). Landings of this species in Chile have fluctuated between 29,000 tons in 2001 to 11,000 tons in 2014. Likewise, spawning biomass showed variations between 800,000 tons in 1997 and 350,000 tons in 2012. Currently, spawning biomass is below the maximum sustainable yield and thus classified as over-exploited, according to with Chilean fishing law (Contreras et al., 2014).

Acoustic surveys conducted yearly during spawning seasons by the Instituto de Fomento Pesquero (IFOP-Chile) reported that estimated average potential fecundity varied between 700,000 oocytes in 2003 and 300,000 oocytes in 2015 (Saavedra et al., 2016). Temporal analysis of egg production and its link with population renewal will contribute to understanding the current over-exploited status of this stock in Chile. However, time-dependent comparative analysis of fecundity of this species is particularly difficult given the high inter-annual variability of its reproductive traits (Saavedra et al., 2015). Current studies in *M. a. australis* only relate fecundity to female size although determinate spawners may exhibit other maternal characteristics, such as oocyte size, condition factor, and gonadosomatic index, which contribute to temporal variability of fecundity (Thorsen et al., 2006). For example, temporal changes on fecundity in *G. morhua* are explained by a trade-off between size and number of spawned eggs (Thorsen et al., 2006). Condition factor (as proxy for nutrition status of females) also plays an important role in determining production of oocytes into vitellogenesis and regulate fecundity by atresia (Thorsen et al., 2010).

Fecundity time series of *M. a. australis* was computed using the traditional gravimetric method in which oocytes were separated with sieves of different sizes and manually counted under a stereomicroscope. During 2011 and 2012, the gravimetric method was combined with a system of automated measuring and counting of particles. However, even with this latest improvement, this technique is still time consuming to be applied in the laboratory, due to the intensive sampling required in the fishery. Given methodological drawbacks of the current method and the lack on integrative temporal analysis to estimate fecundity in *M. a. australis*, this paper has two main objectives. First, we assess potential fecundity on this species using the auto-diametric method, and second, we evaluate the effects of maternal characteristics on temporal variations of fecundity using generalised linear models.

2. Materials and methods

2.1. Data

Two sources of data collected between 2008 and 2011–2012 were used for this study. First, we used the database available from a commercial trawl fishery targeting *M. a. australis*, which concentrated fishing efforts between 44°00′S and 56°00′S (Fig. 1). Samples were collected from the hauls using a bottom trawl with a mesh size of 130 mm. Second, we used samples collected from acoustic surveys conducted every year in the spawning area (Fig. 1). Each haul uses a midwater trawl with lined cod ends of 50 mm of mesh size especially adapted to retain small fish. Random samples of fish were collected from a selected number of hauls by onboard scientific observers as part of a fishery monitoring program and acoustic surveys conducted by the Instituto de Fomento Pesquero (IFOP-Chile). Details of the sampling design of both database sources can be found in Céspedes et al. (2014) and Saavedra et al. (2015). Data regarding month, number of hauls, and total length (TL, cm) of females sampled are summarized in Table 1. Additionally, total weight (TW, g), gutted weight (W, g) and gonad weight (GW, g) were recorded. Macroscopic maturity stages were assigned using the scale in Balbontín and Fischer (1981) which defines the following stages: virgin (stage 1), immature (stage 2), maturing (stage 3), mature (stage 4), spawning (stage 5), and regressing (stage 6). Fish of macroscopic maturity stage $\geq$ 3 and $<$ 6 were classified as active mature female (MAT).

A relative condition factor was computed (Le Cren, 1951) as:

$$K = \frac{W}{\alpha \times TL^{\beta}} \tag{1}$$

where α and β are regression coefficients of the length-weight relationship. This index was selected because K is standardized and independent of female size ($p > 0.05$).

The gonadosomatic index (GSI) was computed for each individual using the following equation:

$$GSI = \frac{GW}{W} \times 100. \tag{2}$$

2.2. Determining period for fecundity estimates

All females collected from commercial trawling were used to