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Spatial and annual variation in fecundity and oocyte atresia of yellowtail flounder, *Limanda ferruginea*, in U.S. waters

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ABSTRACT

Potential annual fecundity (PAF) was estimated over three years (2010–2012) for yellowtail flounder with individuals from the three stocks off the northeast U.S. coast. Down-regulation of PAF, the resorption of oocytes during development, was evident as the vitellogenic cohort advanced, so we directly measured atresia of vitellogenic oocytes using stereological techniques. PAF models including relative fish condition, stock area, year, and oocyte diameter of the leading cohort explained more variation than models with just size alone based on Akaike information criteria. In a given year, Gulf of Maine females had lower PAF at size than southern New England females. Interannual differences were evident: PAF of both stocks was higher in 2010 and lower in 2012, with 2011 showing less synchronization between these stocks. Differences in size at age and relative condition suggested that energy available for somatic and reproductive growth was lower in some years in the Gulf of Maine and Georges Bank, especially in 2011. Georges Bank PAF and condition were intermediate to the other stocks or more similar to the Gulf of Maine, varying annually. A latitudinal gradient in PAF is evident based on our results and relative to earlier studies that included Canadian stocks. The magnitude of down-regulation was variable across stocks and typically 3–25% of PAF. This can be accounted for in fecundity estimates, by the seasonal schedule of sampling and use of an oocyte diameter term in the fecundity model. Theoretical models of atresia patterns suggested variable rates over the later portion of clutch development. The timing of down-regulation varied among years, and its intensity was influenced by female relative condition. Fecundity was related to fish size, but was also affected by fish condition and oocyte diameter (a proxy for time until spawning), and spatial and temporal effects. A longer time series of PAF may identify environmental drivers that modulate annual stock reproductive potential.

1. Introduction

Spawning stock biomass (SSB) is commonly used in fisheries assessments as a proxy for reproductive potential (Saborido-Rey and Trippel, 2013). SSB is generally favored as a proxy because it is relatively easy to calculate from estimates of abundance at age and maturity at age. Given the inherent difficulties in predicting recruitment from SSB, alternative measures of reproductive potential have been proposed (Fitzhugh et al., 2012; Marshall et al., 2003; Morgan, 2008). Direct measures of egg production may be more representative of a stock's reproductive potential because egg production is highly variable; as it is dependent upon dynamic life-history parameters such as maturity, growth, sex ratio, and fecundity, which are all influenced by a fluctuating environment (Lambert, 2013; Rideout and Morgan, 2007; Stares et al., 2007). Alternative measures of reproductive potential can be more responsive to changes in stock demographics and environmental conditions, thereby providing more information to annual stock reproductive potential and subsequent year class strength than biomass metrics alone (Lambert, 2013; Marteinsdottir and Thorarinsson, 1998; Rideout and Morgan, 2010).

Incorporating fecundity and other proxies of reproductive potential into stock assessment models can affect reference points and may improve predictions of year class strength (Brooks, 2013; Morgan et al., 2009, 2011). Attempts to investigate reproductive potential in an assessment context continue to be constrained by the lack of available data, particularly in the western North Atlantic Ocean where limited stock-specific fecundity data is available (Tomkiewicz et al., 2003; Trippel, 1999). Yellowtail flounder, *Limanda ferruginea*, exemplifies this paucity of data, with few published annual fecundity estimates that are limited in time, geographic scale, or both (Howell and Kesler, 1977; Pitt, 1971; Rideout and Morgan, 2007). Furthermore, of the three stocks in United States waters, annual fecundity has only been estimated for the southern New England stock (Howell and Kesler, 1977).

Oocyte development in yellowtail flounder is group synchronous (Howell, 1983; Howell and Kesler, 1977) with a distinct cohort of

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maturing (secondary growth) oocytes leading up to spawning, hence fecundity is determinate. The estimation of the number of oocytes in this maturing cohort – referred to here as the potential annual fecundity (PAF) – can be partially automated by image analysis systems, using the autodiametric method (Ganias et al., 2014; Thorsen and Kjesbu, 2001; Witthames et al., 2009). The autodiametric method estimates oocyte density (number of oocytes/g ovary, NG) from the mean diameter of secondary growth oocytes (i.e. the developing cohort), facilitating measurement of fecundity, but has not yet been applied to yellowtail flounder.

Many fish 'fine-tune' their annual fecundity as the clutch develops. Therefore, estimates of PAF should be measured as close as possible, but prior, to spawning so that PAF estimates are considered the best approximation of realized annual fecundity (RAF; Ganias et al., 2014; Murua et al., 2003), defined as the actual number of eggs released. Differences between PAF and RAF can arise when atresia of developing oocytes reduces the standing crop of secondary-growth oocytes (termed down-regulation) or when the entire clutch, or portions of, is not released, evidenced by residual eggs in the spent ovary (Kurita et al., 2003; Murua et al., 2003). Both atresia and residual eggs have been noted in yellowtail flounder (Howell, 1983; Zamarro, 1991); hence, we sought to quantify annual rates of atresia using a Weibel grid stereological procedure (Sterio, 1984; Weibel, 1979; Weibel et al., 1966), as applied to fecundity analysis (Andersen, 2003; Emerson et al., 1990).

In this study we estimated female yellowtail flounder fecundity during three spawning seasons, 2010–2012, among the three stocks in U.S. waters: Gulf of Maine (GOM), Georges Bank (GB), and Southern New England-Middle Atlantic (referred herein simply as SNE, the only sub-region we obtained samples from). The Georges Bank stock is a shared stock with Canada, and only the U.S. portion of the stock was sampled. Determination of both fecundity and atresia allowed us to assess the scale, timing, and spatiotemporal variation in down-regulation during the development of the annual clutch. Data on the reproductive output of yellowtail flounder are especially relevant in light of the current low levels of biomass and recruitment in the SNE and GB stocks (Legault et al., 2013; NEFSC, 2012a, 2012b).

2. Methods

Yellowtail flounder were sampled monthly from January 2010 through June 2011, and in 2012 sampling was narrowed to just the three months prior to peak spawning for each stock. Fish were collected primarily by commercial fishing vessels participating in the Northeast Fisheries Science Center, Northeast Cooperative Research Program's (NEFSC-NCRP) Study Fleet ($n = 310$ females) and from other NEFSC-NCRP research studies ($n = 56$). Fishermen were paid to provide a subset of 30–40 random fish distributed over the size range captured, and depending on the catch volume this was typically from one or two hauls. The fishermen tracked which haul the fish were from, along with the location and time of the haul, using electronic fisheries logbook software used for catch reporting. To ensure a high quality of the tissues, fish were requested from the last day (or tows) of a fishing trip, iced during transport, and processed upon arrival at the laboratory. Supplemental samples were acquired from the Massachusetts Division of Marine Fisheries trawl survey ($n = 21$) and NEFSC bottom trawl survey ($n = 23$). Two fish per 1 cm bin were randomly selected on the NEFSC survey, and all developing fish observed on a tow were selected for the MADMF survey. Both surveys have a random stratified survey design. Fish were obtained from core areas of abundance, and the sizes were representative for all three stock areas in United States' waters (Fig. 1; Table 1). Fish total length (TL, mm), body mass (M_b, ± 0.1 g), and ovarian mass (M_o, ± 0.001 g) were measured, and an approximately 1 cm^3 piece of tissue from the middle of the right ovarian lobe was fixed in 10% neutral-buffered formalin. A few fish were sampled while at sea (TL $\pm$ 0.5 cm, M_b and M_o $\pm$ 0.001 kg, $n = 44$).

Age was determined for each fish by counting annuli on scale impressions following methods developed at the NEFSC, which are used in the three stock assessments (Legault et al., 2013; NEFSC, 2012a, 2012b). Specifically, about 5 or 6 scales from the eyed side along the lateral line were impressed on a laminated plastic slide using a roller press and viewed on a microprojector at a magnification of 52× with transmitted light (Penttila and Dery, 1988). Details on aging methods and quality control/quality assurance procedures and results are available at http://www.nefsc.noaa.gov/fbp/.

2.1. Relative condition

Relative condition (K_n) was calculated as the ratio of the observed mass over the predicted body mass (Le Cren, 1951) using an overall length-mass equation determined from all females sampled for fecundity. This was calculated using a log-transformed least squares regression: $\ln(M_{ofb}) = -11.364 + 2.934 \ln(TL)$, ($n = 410$, SE $a = 0.271$, SE $b = 0.046$, $r^2 = 0.91$). Ovary-free body mass M_{ofb} was used to examine changes in condition independent of ovarian development. Differences in K_n among stocks and years were tested by ANOVA with a Tukey HSD post-hoc test if overall significant differences were found. This

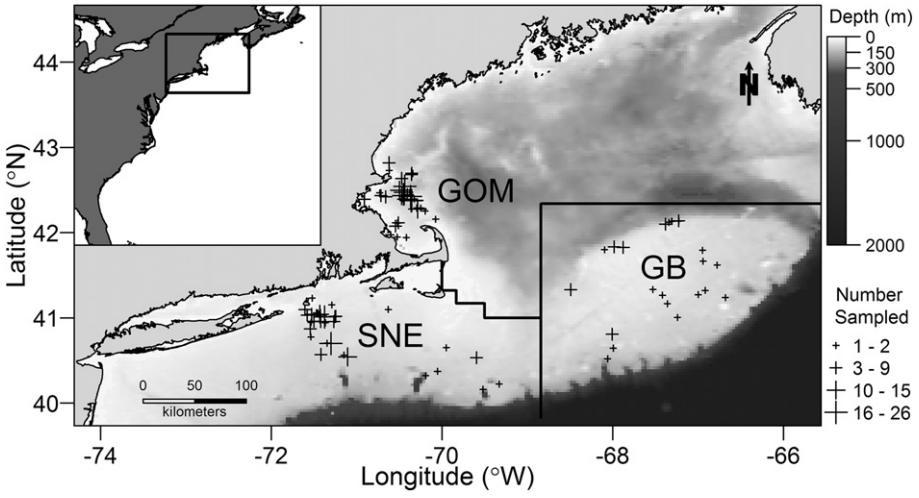

Fig. 1. Capture locations of yellowtail flounder sampled for fecundity during 2010–2012 ($n = 410$). Solid lines indicate boundaries for the three stocks: Gulf of Maine (GOM), Georges Bank (GB), and Southern New England (SNE). Box on inset map indicates the location of the study region off the U.S. Atlantic coast.