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Maternal reproductive exhaustion in a broadcast spawning marine finfish cultured for conservation

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ABSTRACT

Reproductive exhaustion can be defined as a decline in reproductive potential or output over time. We studied seasonal maternal reproductive exhaustion in a large, freely mating captive population of white seabass (*Atractoscion nobilis*), a marine finfish cultured in southern California for conservation. Using genetic parentage data, we identified 34 single-maternity spawns produced during the 2008 spawning season and quantified four physical egg characteristics for each spawn, including egg volume (EV), oil volume (OV), percent oil volume (POV), and the number of oil globules (NOG). The mean batch egg measures decreased between the beginning and end of the spawning season by 19%, 45%, 33%, and 12%, respectively. OV and POV declined linearly, whereas the trend in NOG was parabolic and negatively correlated to water temperature and light duration, which reach apices mid-season. EV displayed a similar, though not significant, trend. We also evaluated the egg measures within and among six dames that solo-spawned two or more times. The seasonal trends were similar to those observed at the population-level, but the relative measures varied significantly among dames, indicating factors other than the common broodstock diet and holding conditions may influence egg production in individual *A. nobilis* females. In terms of species conservation, assessing these egg characteristics, some of which may be associated with larval quality in *A. nobilis*, in conjunction with estimating genetic diversity for each spawn is important when choosing spawns to rear for stock supplementation, but more research into their relationship with subsequent offspring quality is warranted.

1. Introduction

Reproductive exhaustion can be defined as a decline in reproductive potential or output over time. Aspects of the phenomenon, such as physiological and biochemical changes, sex-specificity, and timescale, have been broadly noted across taxa, from plants (Ehrlén, 1997) to invertebrates (Brokordt et al., 2000; Müller et al., 2001; Palacios et al., 1998), fish, birds, and mammals, including humans (Edwards et al., 1998; Jordan and Brooks, 2010; Neal-Perry et al., 2010; Ribeiro et al., 1996; Wise, 1994; Wise et al., 1997). In iteroparous species, the decline in reproductive output can manifest as fewer or smaller spawns or clutches produced by adults, decreasing hatch rates and survival of progeny, or increasing genetic and morphological mutation rates in progeny (e.g. Jordan and Brooks, 2010; Ribeiro et al., 1996). Hence, reproductive exhaustion impacts not only the reproductive success of breeding adults in a population but also offspring fitness.

Although often assessed in terms of aging over a lifetime (e.g. Fisher, 1930; Kirkwood, 1977), reproductive exhaustion can occur on much shorter timescales. It has been reported during the course of a single spawning season or just a few spawns in shrimp (*Penaeus* spp.; Palacios et al., 1999), anchovy (*Engraulis* spp.; Ribeiro et al., 1996), and striped trumpeter (*Latris lineata*; Bransden et al., 2007). At an extreme, sockeye salmon (*Onchorynchus nerka*) spawn, senesce, and die over a period of 11–23 days (e.g. *O. nerka*; Healey et al., 2003; McPhee and Quinn, 1998; Shrimpton et al., 2005).

Here, we focused on reproductive exhaustion in a broadcast spawning marine finfish called the white seabass (*Atractoscion nobilis* Ayres 1860). *A. nobilis* is a typical member of the family Sciaenidae native to rocky bottom and kelp bed habitat along the west coast of North America (CDFG, 2002). During the latter half of the last century, *A. nobilis* experienced severe declines in abundance off southern California due to an unfortunate blend of regulatory and environmental circumstances (Allen et al., 2007). Because the species supported (and continues to support) a regionally-important commercial and recreational fishery, it was chosen in 1983 for a pilot experimental stock replenishment program still in operation today (CDFG, 2002), where juvenile fish are produced in a hatchery and released to supplement the wild population.

The *A. nobilis* breeding program is well-suited for studying intrinsic reproductive behaviors and characteristics. Relatively large groups

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of up to 50 wild-caught fish are allowed free mate choice within mesocosm-like breeding pools. *A. nobilis* is iteroparous and a batch spawner, releasing gametes multiple times over a spawning season for multiple years (Gruenthal and Drawbridge, 2012; Moser et al., 1983), and broadcast spawning in captivity is induced by photothermal control that mimics seasonal changes in water temperature and light duration (Bartley et al., 1995).

We used genetic parentage analysis and quantified changes in basic physical egg characteristics, some of which may be associated with egg and larval quality (hatch rates and larval survival and viability; Brooks et al., 1997; Gauger, 2010; Kjørsvik et al., 2003), both non-invasively and within and among female brood fish to assess the presence of seasonal maternal reproductive exhaustion in *A. nobilis*. Because egg and larval quality is an important limiting factor in developing culture techniques for many species (Bromage, 1995; Kjørsvik et al., 1990), we discuss the knowledge gained about reproductive exhaustion in *A. nobilis* in terms of developing juvenile propagation protocols, particularly for species cultured for conservation.

2. Materials and methods

2.1. Broodstock population

This study focused on one breeding group composed of 25 male and 25 female reproductively-mature wild-caught fish as described by Bartley et al. (1995) and Gruenthal and Drawbridge (2012). Fish were held in a 48 m^3 tank maintained on a separate recirculating seawater system. The recirculating flow rate in the brood pool was 560 L min^{-1}, and complete turnover occurred every 82 min. Ozonated makeup water was supplied to each recirculating system at 4–8 L min^{-1}. Spawning brood fish were fed five days per week a ration of 1% tank biomass, consisting of fresh market squid and fish (sardine, capelin, or anchovy, depending on availability) injected with a vitamin–oil mixture (vitamin premix: Ziegler Bros., Inc., Gardners, PA; Stay-C, thiamine, soy lecithin, crude menhaden oil: TPi, Madera, CA). Water temperature and photoperiod were controlled to mimic natural conditions. The non-spawning "winter" season was simulated at 13 °C and 10 h (h) of light, while spawning was achieved between 14 °C and 11 h light and a maximum of 18 °C and 14 h light. Spawning conditions were offset from the calendar year such that a total of 84 spawns occurred from 15 Jan through 14 Jun 2008 (Gruenthal and Drawbridge, 2012). Spawning typically occurred in early evening and all eggs were collected passively in a 500 μm mesh bag (egg trap) placed in the sump of the recirculation loop. Eggs were removed the following morning between 0800 h and 1000 h using an 800 μm mesh dip net and placed in 1 L graduated cylinders for volumetric estimation of spawn size. The number of eggs was estimated according to a predetermined average of 585 eggs mL^{-1} (CDFG, 2010).

2.2. Laboratory methods

A random subset of fertilized (floating) eggs from all 84 spawns was collected for gross assessment at 5× magnification of cell division stage and quality (e.g. morphology, size, lipid content) using a Digital Microscope Camera Model DMC1 (Polaroid, Minnetonka, MN). Twenty to 24 eggs were then digitally photographed at 2× magnification for archival purposes. Parent–offspring relationships (sires and dames) were genetically determined by Gruenthal and Drawbridge (2012) for 71 of the 84 spawns, and a single dame was assigned as parent to ≥95% of 1–2 day post hatch larvae for 36 spawns. Data from these spawns were retained for assessing maternal reproductive exhaustion (Table 1), since inclusion of multiple maternity spawns would make it impossible to attribute the photographed eggs to any particular dame. Archived digital photographs were available for 34 of the 36 spawns; images were unavailable (file corrupted) for 15 Jan and 26 Apr. Photographs were visualized using Image-Pro Plus software (Media Cybernetics, Inc., Bethesda, MD), and specific egg characteristics, including egg volume (EV), total oil volume (OV), percent oil volume (POV), and the number of oil globules (NOG), were measured for 15–20 eggs in full view from each spawn. Egg and oil globules were assumed to be spherical, and volumes were calculated from single measurements of diameter according to the formula for the volume of a sphere (i.e. $V = \frac{4}{3}\pi r^3$). Volumes were summed across all oil globules to obtain OV.

2.3. Statistical analyses

Basic statistics for the batch (spawning event) egg characteristics, including ranges, means, and standard deviations, were calculated using Excel 2010 (Microsoft Corp., Redmond, WA). Regression coefficients of determination (R^2) were calculated based on the best fit trendlines for each distribution. Pairwise Spearman rank-order correlation coefficients (ρ) were estimated between each of the egg characteristics and dame age, body mass, and time in captivity (Table 2), as well as water temperature and light duration, using R-based statistics software developed by Wessa (2012). Additional statistics were estimated with STATISTICA v10 (StatSoft, Inc., Tulsa, OK). The Shapiro–Wilk *W* statistic was used to test for normality within spawns, and based on the results, non-parametric Kruskal–Wallis one-way analyses of variance (ANOVA) by ranks (*H*-tests) were performed to detect significant differences in the batch egg characteristics within and among spawns and dames (except 503). Data resulting in significant *H* values were further assessed with Mann–Whitney *U*-tests to identify the values responsible for the differences. Dame 503 contributed to two spawns and the data were analyzed by *U*-test only. To detect Type I errors, the results were sequential Bonferroni corrected at the table-wide $\alpha = 0.05$ level (Rice, 1989).

3. Results

3.1. Trends in batch egg characteristics

Egg characteristics were measurable (i.e. eggs were in full view) for 20 eggs from 31 spawns, 17 eggs from 12 Feb and 15 Feb, and 15 eggs from 17 Jan. Mean batch EV, OV, POV, and NOG ranged from 0.88 to 1.56 mm^3, 0.011 to 0.029 mm^3, 1.05 to 2.22%, and 1.2 to 7.2, respectively (Table 1). OV and POV exhibited simple linear declines, whereas mean NOG and, marginally, EV displayed second-order polynomial (parabolic) regressions (Fig. 1). EV declined overall but exhibited a subtle positive trend in the latter third of the season. Mean EV, OV, POV, and NOG decreased by 19%, 45%, 33%, and 12%, respectively, as measured by the overall change in the regression line. Most, but not all, of the data were normally distributed, so further analyses performed using *H*-tests rather than standard ANOVAs revealed that comparisons among spawns were significant [H (33) ≥ 283.95, $P < 0.001$; Table 3]. EV, OV, and POV were not significantly correlated with the photothermal regime [$-0.17 \leq \rho$ (32) ≤ 0.31, $P > 0.07$], but NOG was negatively correlated with both water temperature and light duration [temperature: ρ (32) $= -0.57$, $P = 0.001$; light: ρ (32) $= -0.34$, $P = 0.05$].

3.2. Trends within and among dames

Six dames (503, 522, 525, 526, 528, and 548; Table 1) contributed to two or more single-maternity spawns, accounting for 27 of the 34 spawns analyzed. The measures declined overall, despite minor increases in EV and NOG toward the end of the season, but only mean OV and POV decreased significantly by an average of 32% and 19%, respectively. The negative trend estimation was least error prone for dames 525 and 528, who were primary contributors to the largest numbers of spawns at eight and seven, respectively (Fig. 2). The changes in batch egg characteristics as the season progressed were statistically significant within dames ($P < 0.01$; Table 3), except POV and NOG for