Techniques for improving estimates of maturity ogives in groundfish using double-reads and measurement error models

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Abstract

The reproductive output of a population depends upon physiological factors, including maturation rates and fecundity –at-size and –at-age, as well as the rate at which post-maturation females fail to spawn (i.e. skipped spawning). These rates are increasingly included in stock assessment models, and are thought to change over time due to harvest and environmental factors. Thus, it is important to accurately estimate maturation and skipped spawning rates while also including information on imprecision. For this task, we developed a new double-read and measurement-error modeling protocol for estimating maturity that is based on the use of multiple histological reads of ovaries to account for reader error caused by poorly prepared slides, nuclear smear, and early yolk development. Application to three U.S. West Coast groundfishes (Pacific hake *Merluccius productus*, darkblotched rockfish *Sebastes crameri*, and canary rockfish *Sebastes pinniger*) indicates that reader uncertainty is strongly predictive of reader error rates. Results also show differences in rates of skipped spawning among species, which should be further investigated. We recommend that future maturity studies record reader certainty, use models that incorporate covariates into the analysis, and conduct an initial double reader analysis. If readers exhibit little variation, then double reads may not be necessary. In addition, slide quality should also be recorded, so that future studies do not confuse this with reader imprecision. This improved protocol will assist in estimating life history, as well as environmental, and anthropogenic effects on maturity.

Keywords: maturity ogive; skipped spawning; histological error; reader certainty; groundfish; measurement error model

1. Introduction

Reproduction is a basic demographic process in population dynamics, and density-independent and -dependent changes in reproductive success contribute to a large portion of variability in marine populations. Timing of sexual maturity will vary among individuals according to individual size, age, season, location, and other factors (Jørgensen and Fiksen, 2006). Maturity is a function of length and age, and fast growing fish generally mature at much younger ages. Growth rates slow during reproduction, with immature fish growing faster than mature fish, and increase following skipped spawning events (Folkvord et al., 2014). These factors, paired with errors in correctly identifying maturity stages, influence our ability to accurately estimate the probability of sexual maturity as a function of length and/or age (termed the "maturity ogive"). In addition, since many individuals do not spawn annually following initial maturation, the average skipped spawning rate may be poorly estimated. Skipped spawning and reader error remain understudied and often go unaccounted for in fisheries models (Rideout et al., 2000; Kennedy et al., 2011). Understanding how shifting marine environments and anthropogenic impacts affect these life history processes and our ability to accurately quantify them is vital to the accuracy of stock recruitment models used in fisheries management (Burton, 1999; Kennedy et al., 2011).

In recent years, improvements in survey design and statistical methods have revolutionized how other demographic processes are estimated. For example, estimation of growth curves now uses methods that explicitly account for misreading of individual ages (e.g., Cope and Punt, 2007), while estimates of natural mortality involve state-space modeling of individual tagged fishes (e.g., Schaub and Royle, 2013). Estimating reader error variability for aging fish is routinely based on double reads of a single otolith by different individuals, along with validation methods that confirm the accuracy of the results or indicate the degree of bias (Campana, 2001; Hamel, 2008; Punt et al., 2008). Hierarchical models are used to process the results of double-reads, allowing error to propagate and be accurately reported (Royle and Dorazio, 2008) when estimating emergent biological process such as shifts in size- or age-at-maturity and skipped spawning. Research has revealed maturity ogives shift over time, e.g. Atlantic cod (Olsen et al., 2004). Skipped spawning and incidence of high intensity atresia (breakdown and reabsorption of vitellogenic oocytes) are correlated with nutrient availability and temperature, factors that are highly variable over space and time (Rideout et al., 2006). Including spatial and temporal variables in hierarchical maturity models allows differences in sampling to be 'controlled' when estimating decadal changes in maturity. Recent research has proposed using mixed-effects models or covariates to smooth time-variation in the maturity ogive given sparse annual sampling of fish maturity (Cadigan et al., 2014; Wright et al., 2011; Xu et al., 2015).

Reader variability is often calculated for age reading, but to the authors' knowledge it has not been incorporated into maturity models. In studies on age, re-aging or double reading otoliths is considered important for data reliability (Hare, 2007). Maturity studies based on macroscopic examination of ovaries found high variability in the determination of mature and immature fish (Costa, 2009). Histological analysis allows for greater accuracy and insight into skipped spawning events, but the effect of reader error on variability of microscopic determination of maturity states is unclear. Accounting for variability in measurements of maturity (either using histological or macroscopic methods) also allows analysts to more accurately characterize uncertainty regarding estimates of the maturity ogive. Uncertainty in these maturity analyses can then be incorporated in stock assessment models and resulting management advice (Stewart et al., 2013).

Here, we use a measurement error model to estimate maturity ogives for three species inhabiting the California Current system: Pacific hake (*Merluccius productus)*, darkblotched rockfish (*Sebastes crameri*), and canary rockfish *(Sebastes pinniger)*, and also incorporate a double read analysis. These species were selected based upon the availability of samples, variations in life history, and importance along the U.S. West Coast. The objectives of this study are to: (1) to identify and reduce the main sources of reader error in estimating maturity of fish, (2) to add uncertainty in maturity reads and reader precision to model analysis and (3) to select the best fit maturity ogive model for each species. We noted that reader uncertainty was a strong predictor of reader error rates, implying that reader certainty should be documented during histological analysis.

2. Methods

2.1 Study species

The life history strategies for the three species studied varied greatly, but all are commercially important either economically or as catch-limiting species along the West Coast. Pacific hake occur from 25°N to 55°N on the West Coast of North America, and are typically found from southern California waters to the Queen Charlotte Sound. The coastal Pacific hake stock is the most abundant groundfish species in the California Current system. A study conducted from 1990-92 visually assessed maturity for female Pacific hake, with length-at-50%-maturity estimated as 37.8 cm (Dorn and Saunders, 1997). Spawning reportedly takes place off the coast of California from January to March, but more recent studies suggest spawning may occur in multiple batches throughout the year (Taylor et al., 2015). It is uncertain whether batches spawned outside of the winter spawning season are viable. Pacific hake are estimated to live up to 20 years of age (Hesler and Alade, 2012).

Canary rockfish (*Sebastes pinniger)* are distributed from Baja California to the Gulf of Alaska with the highest concentrations between British Columbia, Canada and central California to

Bodega Bay (Love et al., 2002; Miller and Lee, 1972). This species has an estimated lifespan of 75 - 95 years and a maximum female size of 61 cm; though, females are rarely observed over 30 years of age. Recent histological analysis of ovaries collected by the Oregon Department of Fish and Wildlife (ODFW) and the West Coast groundfish bottom trawl survey (WCGBTS) estimated the length-at-50%-maturity to be approximately 42 cm (Thorson and Wetzel, 2015). Canary rockfish, like all *Sebastes* are viviparous, live bearing fish, and spawn in the winter months (Love, 1996; Thorson and Wetzel, 2015).

Darkblotched rockfish (*Sebastes crameri)* are found in the southeast Bering Sea and Aleutian Islands to Santa Catalina Island, California, and are commercially important from Northern California to the Canadian border. Darkblotched rockfish have an estimated maximum lifespan of 105 years and size of 58 cm (Gertseva and Thorson, 2014; Love, 1996). Length-at-50%-maturity was recently assessed for darkblotched rockfish using ovaries collected during the 2011 – 2012 WCGBT survey, and found to be 30 cm (Frey et al., 2015). Similar to canary rockfish, they are viviparous and spawning occurs during the winter months (Nichol and Pikitch, 1994; Frey et al., 2015).

2.2 Data collection and Histological Analysis

Pacific hake, canary rockfish, and darkblotched rockfish were sampled during the Northwest Fisheries Science Center's (NWFSC) annual fishery-independent bottom trawl survey off the U.S. West Coast from May – October (see Bradburn et al., 2011 for sampling methods). A random subsample of each species was selected from the catch at each site to determine sex, fork length (cm), weight (kg), and age (yr). Age was subsequently determined from extracted otoliths using the break-and-burn method (Beamish and Chilton, 1982). From 2009 - 2011, ovaries were collected opportunistically from females with associated age samples. Since 2012, collections were based on length bins to ensure a broad size range of fish for inclusion in maturity analysis. Ovaries were stored in cloth sampling bags and stored in 10% neutral buffered formalin (sodium bicarbonate). Pacific hake (n = 329), darkblotched rockfish (n = 307), and canary rockfish (n = 131) ovaries were histologically examined by two independent readers (R1 and R2). Four hake samples were excluded from the model analysis due to missing ages.

Tissue samples from individual ovaries were embedded in paraffin, thin-sectioned to 4-µm, mounted on slides, and stained with hematoxylin and eosin (H&E) stain (Sheehan and Hrapchak, 1980). To determine maturity, each prepared ovary section was examined using a Leica DM1000 binocular microscope at 40x – 400x magnification, equipped with a Leica DFC295 camera and imaging software (Leica Microsystems LAS EZ 4.0).

Ovaries with oocytes containing dark-stained vitellogenin yolk (eosin positive) and more advanced stages (hydration and/or embryonic development) were classified as mature. We used an oocyte development table to assess each sample following similar methods developed to stage maturity for *Sebastes aleutianus* and *S. borealis* (McDermott, 1994), *S. crameri* (Nichol and Pikitch, 1994), and *Pleurogrammus monoptergius* (McDermott and Lowe, 1997). Oocyte developmental stage 4 and maturity stage 3 were defined as mature for all three species (Tables S1 & S2). Samples estimated with over 25% oocytes in an atretic state were marked as high intensity atresia following McDermott (1994). Oocytes exhibiting atresia were not used for maturity determination; therefore, only non-atretic oocytes were used in maturity analysis. Ovary samples were identified as mature solely by the presence of yolk and characteristics associated with more advanced maturity stages, for the purposes of identifying fish that would be contributing to the overall spawning biomass in any one year (Fig. S1 & S2). Determination of maturity was independent of size and age. Post spawning samples (termed “spent”) were characterized by the presence of a large number of post ovulatory follicles (POFs) and did not necessarily contain yolked oocytes, but were also classified as mature. Resting fish, if encountered would be recorded as mature, but the sample period (late May – October) does not overlap with the normal resting periods for the species examined here.

2.3 Double Reads and Certainty

Two readers determined the maturity for each species examined. Reader 1 (R1) had three years of experience conducting maturity analysis on multiple groundfish species, and recorded the maturity status, oocyte stages present, the proportion of atretic oocytes, presence of (POFs), oocyte diameters, and certainty of the maturity determination for each sample. Certainty of the determination was recorded as a 1 (certain) or 0 (uncertain). Reader 2 (R2) had no experience determining histological maturity, and was trained by R1 for two weeks previous to conducting this research project. R2 recorded maturity and certainty level for each ovary sample. Both readers examined each sample twice to confirm their results and level of certainty, but recorded only the final reads. Results were not discussed prior to completion of data collection to ensure that any disagreements in maturity assignment were statistically independent between the two readers.

2.4 Model development

We developed a model that synthesizes information from two readers while flexibly estimating the maturity ogive and form of reader error. Only double maturity reads with both length and age data were used in this model. Both readers followed the same protocols and are treated identically in the model. A basic assumption of the model was that fish mature as a function of age and length before reaching an asymptotic level. The asymptote is less than 1.0 if a fraction of fully mature individuals skipped spawning. This definition of maturity thus includes both the process for first reaching maturity and subsequent rates of skipped-spawning. Specifically, the probability that ovary O_i for individual i is either mature ($O_i=1$) or immature ($O_i=0$) follows a Bernoulli distribution:

$$O_i \sim Bernoulli(p_i) \tag{1}$$

where $Bernoulli\ (p_i)$ is a Bernoulli distribution with estimated probability of maturity p_i for ovary i. The probability of maturity, p_i, is defined as:

$$p_i = \Phi(\beta_0 + \beta_A A_i + \beta_L L_i + \beta_D D_i) \cdot \beta_{max} \tag{2}$$

with β_0 the intercept, β_A the effect of age on maturity, β_L the effect of length on maturity, β_{max} the estimated asymptotic maturity rate, β_D the effect of calendar date on maturity probability. Φ is the logit-function where $\Phi(X) = e^X/(1+e^X)$ which transforms the linear predictors of the model to a response variable (i.e., expected proportion mature) that is bounded between 0 and 1, such that β_{max} is the maximum for p_i.

We then specified that the j-th read of ovary i, $\tilde{O}_{i,j}$, has some probability of incorrectly defining the maturity state:

$$\tilde{O}_{i,j} \sim Bernoulli(O_i(1-q_i) + (1-O_i)q_i) \tag{3}$$

where q_i is the probability of reader error for ovary i:

$$q_i = 0.5\Phi(\eta_0 + \eta_U U_{i,j}) \tag{4}$$

where η_0 is the intercept for reader-error probability, and η_U is the effect of reader uncertainty on reader error probability. Equation 4 uses 0.5 times the logit-transformation to ensure that the probability of reader error is bounded between 0 and 0.5, i.e., that reader error is never more likely to be wrong than right. Uncertainty $U_{i,j}$ is noted by reader j for ovary i and equals 1 whenever the reader expresses uncertainty about the state of maturity for a sample, and 0 otherwise.

Parameters for this model are estimated by maximum marginal likelihood:

$$\widehat{\boldsymbol{\beta}},\widehat{\boldsymbol{\eta}} = argmax_{\boldsymbol{\beta},\boldsymbol{\eta}}\left(L(\boldsymbol{\beta},\boldsymbol{\eta}|\tilde{O}_{i,j}\right) \quad (5)$$

where:

$$L\left(\boldsymbol{\beta},\boldsymbol{\eta}\middle|\widetilde{\boldsymbol{O}}\right) = \prod_{i=1}^{n_i}\sum_{O_{i=0}}^{1}\left(\Pr[O_i|\boldsymbol{\beta}]\prod_{j=1}^{n_j}\Pr[\tilde{O}_{i,j}|O_i,\boldsymbol{\eta}]\right) \quad (6)$$

The model treats the 'true' state of each ovary as unknown, and thus estimates the state as a random effect. This is done by 'integrating across' the true but unknown state for each ovary (Thorson and Minto, 2015). This integral is computationally feasible because each ovary has only two possible states (mature or immature), and hence the integral is accomplished using the summand term:

$$\sum_{O_{i=0}}^{1}\left(\Pr[O_i|\boldsymbol{\beta}]\prod_{j=1}^{n_j}\Pr[\tilde{O}_{i,j}|O_i,\boldsymbol{\eta}]\right) \quad (7)$$

where $\Pr[O_i|\boldsymbol{\beta}]$ is the prior probability of each state and $\Pr[\tilde{O}_{i,j}|O_i,\boldsymbol{\eta}]$ is the probability of each observation conditional on that unknown state. Standard errors for each parameter are derived from the maximum likelihood estimate, and for estimated parameters they were derived using the delta method. These computations were done using the R statistical platform (R Development Core Team, 2014). A Nelder-Mead nonlinear minimization algorithm (i.e., the *nlminb* function in the base package of the R statistical environment) was used to identify values of fixed effects that maximize the likelihood function.

For each species, we fit the model including or excluding all combinations of age, length, date, and an asymptotic maturity rate less than 1.0, as well as the effect of reader certainty on reader error probability. The best fit model was selected using the Akaike Information Criterion (AIC) (Burnham and Anderson, 2002).

3. Results

Estimated maturity ogives differ among species (Table 1). Most significantly, maturity asymptotes were 1.0 (i.e., no skipped spawning) for canary rockfish, 0.96 (SE = 0.144) for darkblotched, and 0.81 (SE = 0.131) for Pacific hake. No models with asymptotes equal to 1.0 were considered plausible models (i.e. ΔAIC<10) for Pacific hake. However, for darkblotched rockfish a number of models with asymptotes of 1.0 exhibited ΔAICs ranging from 3.24 to 7.18, suggesting that evidence for skipped spawning was weak for this species. Species also differ in terms of which factors contribute to the maturity ogive: maturity for hake is best predicted by age, while maturity in darkblotched and canary rockfishes is best predicted by length. Similarly, the date sampling occurred was positively and significantly related to maturity in both hake and darkblotched rockfish, but was negative for canary rockfish (Table 1).

Additionally, there are large differences in reader error probabilities when reads are recorded as “certain” or “uncertain” (Table 1). For all three species, reads marked as “certain” had <2% probability of exhibiting disagreement between readers. By contrast, the model predicts that maturity reads marked as “uncertain” had an 11% error probability for Pacific hake, 18% error probability for darkblotched rockfish, and 27% error probability for canary rockfish (Table 1). This implies that maturity readers are generally capable of identifying when their maturity determination is less likely to be correct.

The readers had varying degrees of disagreement among the three species assessed. For darkblotched rockfish, R1 and R2 disagreed on maturity assignments for 9 of 307 samples (3.2% disagreement), when both readers were certain (n = 4), when only R2 was uncertain (n = 3), and when both readers were uncertain (n = 2) (Table 2). Similarly, R1 and R2 disagreed on maturity for Pacific hake 9 out of 329 samples (2.7 %), when both readers recorded certainty (n = 6), and when R2 was uncertain (n = 3) (Table 2). For canary rockfish, the readers disagreed 11 out of 131 samples (8.4 %), when both readers were certain (n = 3), when both were uncertain (n = 2), and when R2 was uncertain (n = 6) (Table 2). R1 (experienced) recorded uncertainty for < 2% of the samples, while R2 (inexperienced) recorded uncertainty for about 11% of all maturity samples read.

Inspection of the estimated maturity ogive revealed very different results for each species. Hake rapidly matured between ages 1 and 2 (Fig. 1). This was reflected in the age at 10% maturity (A_{10} = ~1 year), 50% maturity (A_{50} = ~2 years) and 90% maturity (A_{90}= ~4 – 6 years), with standard errors increasing with age (Fig. 1). Darkblotched rockfish by contrast had a relatively smooth maturity ogive as a function of length, with 50% maturity (L_{50}) occurring at ~ 30 cm, and a range from 10% maturity (L_{10}) at 25 – 26 cm to 90% mature (L_{90}) at 34 – 35 cm. Canary rockfish had the shallowest ogive slope, with a length at 50% maturity of 43 - 44 cm, a range of size at maturity from 35 - 36 cm (L_{10}) to 51 - 53 cm (L_{90}) and greater imprecision, due to a small sample size.

4. Discussion

4.1 Error in Maturity Reads

It is important to identify all sources of potential error in maturity determinations. This is especially true for fisheries managers comparing results for life history models based on historical data with estimates using current length/age at maturity information. Methods typically vary between historical and current maturity studies. Often older estimates were based on macroscopic maturity determinations. Several studies have evaluated macroscopic versus histological maturity determinations, and found variable agreement (Costa, 2009; McBride et al., 2013). Often disagreements occur in fish that are shifting from immature to mature and in partially spent fish. To the authors' knowledge, no previous studies of maturity in fish have evaluated histological reader error. Our study shows that there is variation between readers, similar to the findings of otolith reader comparison studies (e.g., Punt et al., 2008). If modeled correctly, data from multiple readers may be able to more accurately predict the maturity state of fish and provide less uncertain estimates of maturity status. We conclude that 1) level of certainty is an important component in maturity studies conducted using one or more readers, 2) reader error may be attributed to slide quality and if so should be recorded as such, 3) reader error may also by linked to samples in early stages of vitellogenesis, when yolk is beginning to form, and 4) best fit models using selected covariates with the lowest AIC value can provide more accurate estimates of length- or age-at-50%-maturity for use in fisheries management.

Three primary explanations for variation and uncertainty between readers in maturity analysis include: poor slide quality, nuclear smear, and determination of early yolk formation. Poor slides (Fig. 2a) often result when the stain is either too dark or light, if contamination from other fish samples occurs, and if ovarian tissue is folded during thin sectioning or mounting. When dull blades are used to section an ovary, the nucleus can be smeared across portions of the oocyte. We define this as nuclear smear (Fig. 2b) and note that it is problematic if cell structures critical for maturity determination are obscured. Finally, determining maturity is difficult for some fish with oocyte development stages III and IV, since very few yolk droplets may be present (Fig. 2c). When yolk is present in only one or two oocytes, a reader may miss this early stage of development. An experienced reader may be able to recognize other characteristics that are associated with maturing fish ovaries (larger oocytes, thicker ovarian wall tissue, etc.), which could explain some of the variation we observed among the two readers.

Our results show that while skill level is important when estimating uncertainty, the data are valuable even with readers of different skill, provided each reader records their level of certainty.

R1, with greater experience, marked more reads as “certain” than R2 and both readers produced consistently agreeable reads on slides marked as “certain”. By incorporating uncertainty in model results, readers with variable levels of experience produce valuable data for determining maturity ogives.

4.2 Suggested Future Research Design

Given the results of this study, we suggest that future research include: documentation of reader certainty/uncertainty and its relationship to slide quality, double reads by a single reader or two independent readers when beginning a study on a new species, or if there is high variation between two readers, notes on slide quality and other factors used in estimating maturity status, estimates of atresia, and seasonal variation in sample collections. This study highlights the importance of recording both uncertainty and why a sample was defined as uncertain. If a maturity determination is uncertain because of poor slide quality, then it should not be used in reader imprecision estimates. We recommend that double reads be conducted on either all or a subset of samples to produce requisite data for comparisons between reads. In addition, reader uncertainty could vary as improvements are made in maturity sampling. Reader uncertainty and variation among two readers’ maturity analysis should also be evaluated for samples collected in and out of the spawning season. The authors acknowledge that double reads may be time consuming, and providing up to date information from one reader is higher priority than from two readers. However, conducting double reader analysis when a new reader is used will standardize techniques for maturity determinations. Our study assumed both readers were equally able to identify if fish were mature. Alternative models could be developed where one reader is assumed correct but the other reader’s results are variable. Information and notes that indicate any difficulty in assigning maturity to a sample would be a valuable addition for analyses. Estimating the proportion of oocytes in atresia for each sample should be recorded, so that mass atresia events can be accounted for.

Our results show that calendar date was positively associated with the maturity for darkblotched rockfish and Pacific hake, but negatively related to canary rockfish. We speculate that differences in maturity within a given season are caused by both an increase in the proportion of fishes that have matured over time, and a change in the proportion of atresia. However, we conclude that the effects of sampling seasonality are species dependent, and should be investigated at the species level. When targeting the spawning season for a given species is not possible, we recommend that date be included as a covariate in future models. Our samples were collected primarily from May to October, outside of the observed spawning season for canary and darkblotched rockfishes (January to March). Identifying the presence of early yolk is essential to predicting sexual maturity outside of the spawning season, the higher level of uncertainty from the two readers for canary rockfish (8.4%) may be related to when sampling occurred, since some samples were collected within a few months following the spawning season Several of the mature ovaries collected in late May were in the early vitellogenesis stage, when it is more difficult to see early yolk development. Additionally, we have noted that the observed resting/recovering period varies greatly among the studied species. An in-depth histological analysis of ovary development throughout the year would likely enhance the accuracy of the maturity estimates predicted by the model. Previous research indicates temporal variation in fish reproduction, including onset of sexual maturity and spawning events (Lowerre-Barbieri et al., 2011). In particular, interannual changes in skipped spawning imply that spawning output varies among years, and could contribute to observed variability in recruitment. Including skipped spawning events in stock-recruitment models is critical, but identifying this may not be possible throughout the entire annual reproductive period (Jørgensen et al., 2006). Recent advances in state-space modeling of maturation schedules may be useful when accounting for interannual variability in skipped-spawning rates (Cadigan et al. 2014; Xu et al. 2015).

4.3 Management Implications

The U.S. West Coast groundfish fishery supports an industry with more than 90 species of fish in Washington, Oregon, and California (Pacific States Marine Fisheries Commission, 2012). Current management regulations are based on stock assessments that include catch and landings data, age and length records, and recruitment estimates, among many other model parameters. Due to the complex life histories of many of these fishes, it is also important to consider the reproductive physiology and strategies of these species. Understanding the ages and/or lengths over which a stock's members transition from immature to mature status is fundamental to identifying the proportion of the stock that can be sustainably harvested in a given year. Histological maturity determinations provide an accurate estimate for use in stock recruitment relationships, as well as provide information on abortive maturation and skipped spawning rates, spawning output, and estimated fecundity. Failing to include skipped spawning events in future recruitment estimates may lead to an overestimation of the actual spawning output (Rideout et al., 2005), and may also contribute to the substantial variation seen in spawning output and reproductive success for marine species (Morgan et al., 2011; Thorson et al., 2014). Furthermore, histological data on maturation and atresia will allow scientists to detect changes in age- and length-at-50%-maturity over time and across varying environmental conditions, and allow fisheries managers to make decisions based on these changes.

Evolving life traits in response to low nutrient availability is thought to be species-specific, and each species in this study varies greatly in life history. Skipped spawning is theorized to be unlikely for species that are short lived, because the likelihood of surviving many spawning seasons is low (Rideout el al., 2005). Heavily exploited species with longer life spans and slower growth, such as canary and darkblotched rockfishes, are of particular concern to fisheries management. Studies show these long-lived species are already more vulnerable to overexploitation and less able to compensate for warming ocean temperatures; thus a shift in bioenergetics may compromise reproductive success (Perry et al., 2005). Based on model estimates, we saw skipped spawning rate of ~ 19 % for Pacific hake and ~ 4% for darkblotched rockfish. Other studies found rates ranging from 2% to 35% (Jørgensen et al., 2006). The best fit model for canary rockfish (based on AIC values), had an asymptote of 1.0, equivalent to no skipped spawning. However, plausible models for canary rockfish (AIC < 10) suggest that skipped spawning rates as high as 14% may occur. This is further apparent in the maturity ogive. The relatively small sample size for this species coupled with the low number of large individuals may have influenced these results. In addition, canary and darkblotched rockfishes reportedly spawn during the winter months. Since samples were collected from May – October this would not be the best time to estimate skipped spawning rates. Additional samples closer to the actual spawning season are needed to confirm the presence or absence of skipped spawning.

Short lived species, such as Pacific hake, are unlikely candidates for large skipped spawning events (Rideout el al., 2005). Hake are batch spawners that reportedly spawn during the winter months. However, some samples collected in this study, from May – October, were in spawning condition with hydrated oocytes and POFs present. However, the high rates of atresia observed, suggest that recent batches may have been aborted. This may be a more common event for batch spawners and should not be treated as a 'normal' skipped spawning event. The relatively high rates of mass atresia (skipped spawning ~ 19%) observed in Pacific hake should be investigated further, and modeled differently from non-batch spawners such as darkblotched and canary rockfishes.

In recent years, stock assessment scientists and fisheries managers expressed a need for up-to-date maturity data for inclusion in annual species-specific stock assessments. Since shifts in environmental conditions impact life history processes for marine fish, alterations in size and age at maturity should be monitored closely and tied with changing oceanographic conditions. Maturity information should be collected periodically for all three species studied here to accurately estimate maturity ogives and skipped spawning rates over time. If minimal training and indication of certainty level can be achieved, maturity data may be collected with enhanced spatial and temporal coverage from fishery dependent and independent collections; thus increasing the availability of current life history information and monitoring of skipped spawning for U.S. West Coast fishes.

Acknowledgements

We would like to thank Jim Hastie, Beth Horness and the entire Fishery Resource Analysis and Monitoring team at the Northwest Fisheries Science Center for their input, ideas, and guidance. A special thanks Patrick McDonald and the Northwest Fisheries Science Center Aging Laboratory for their quick analysis of the canary rockfish age data set. We also thank the West Coast Groundfish Bottom Trawl survey volunteers and research scientists involved in sample collection and processing. We express our gratitude to the National Oceanographic and Atmospheric Administration (NOAA) Ernest. F Hollings Scholarship and the Thomas L. Quay Wildlife and Natural Resources Undergraduate Experiential Learning Award at North Carolina State University for financial support. We would also like to thank Owen Hamel and Michelle McClure for their thoughtful comments.

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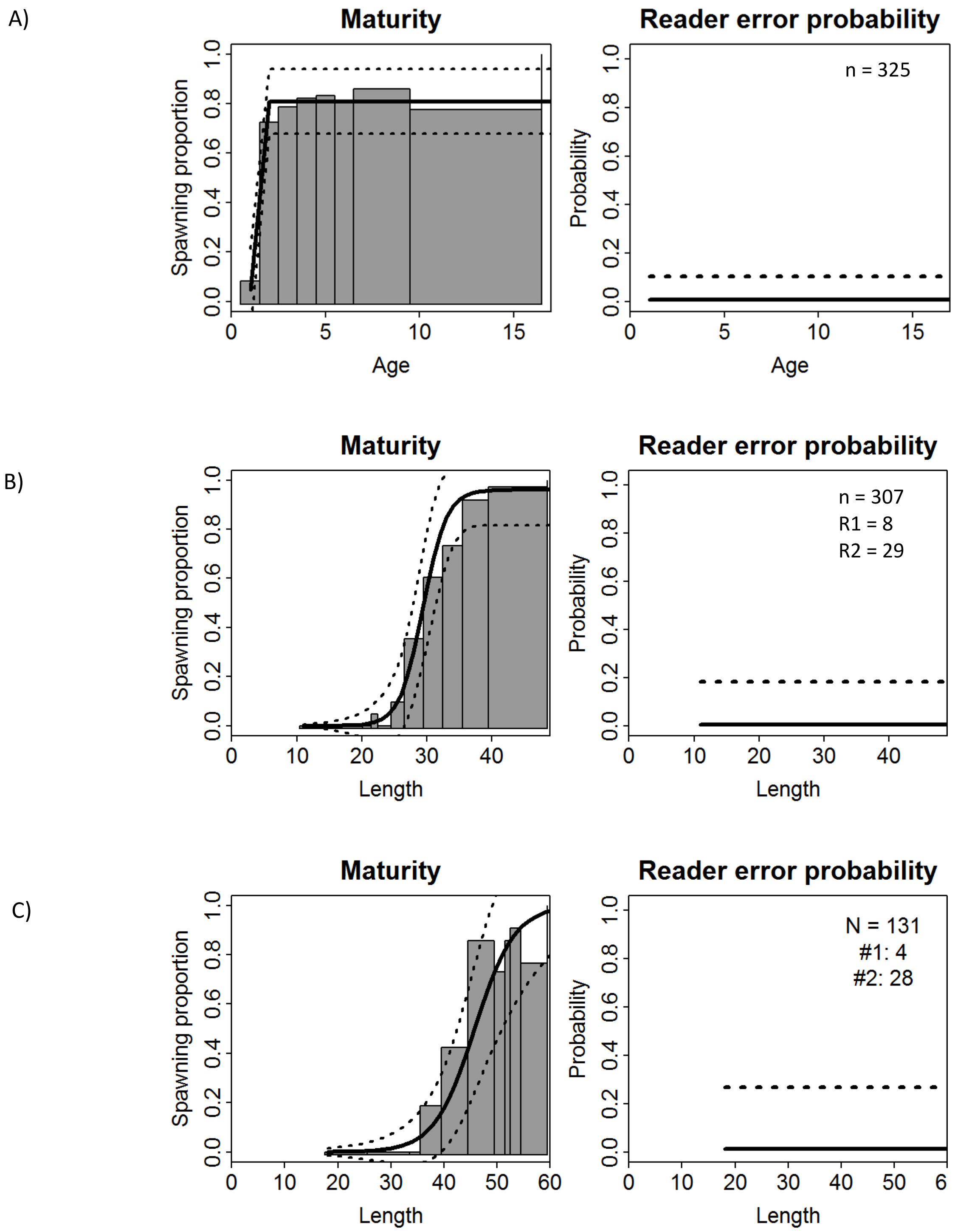

Fig. 1 – Estimated maturity ogive as a function of age (yr) or length (cm) with +/- 1 standard error (dashed line) (left panel), and reader error probability (right panel) for A) Pacific hake, B) darkblotched rockfish and C) canary rockfish. Grey bars in the left panel represent the proportion mature for each 10th percentile bin of observed ages/lengths. Total sample size is in the right panel along with the number of “uncertain” maturity reads for readers R1 and R2, and the reader error probability for “uncertain” (dashed line) and “certain” samples (solid line).

Table 1. Parameter estimates representing the intercept, the effect of age (yr), length (cm), and calendar date (Julian day) on the probability of maturity (in logit-space), as well as the asymptotic probability of maturity (i.e. the skipped spawning rate for mature individuals). Also shown are the probability of reader error for reads marked as ‘certain’ or ‘uncertain’, and finally the difference in the Akaike Information Criterion (AIC) among models (the best model has ΔAIC=0, and we only show models for which ΔAIC<10) for Pacific hake, darkblotched rockfish, and canary rockfish. Standard errors are shown in parenthesis. NA indicates that a parameter was fixed in a given model: age, length, and date effect would be fixed at 0 and asymptote fixed at 1.0.

		Maturity ogive			**Error Probability**		
Intercept	Age effect	Length effect	Date effect	Asymptote	‘Certain’	‘Uncertain’	ΔAIC
Hake							
-27.922 (97.961)	20.566 (9.895)	NA	1.447 (0.112)	0.809 (0.131)	0.007 (0.049)	0.105 (0.018)	0
-29.733 (100.706)	20.146 (10.026)	0.092 (0.479)	1.446 (0.112)	0.809 (0.131)	0.007 (0.049)	0.105 (0.018)	1.91
-27.870 (109.993)	20.513 (10.485)	NA	1.451 (0.112)	0.810 (0.131)	0.011 (0.054)	NA	4.43
-29.879 (101.546)	20.292 (10.068)	0.092 (0.479)	1.451 (0.112)	0.810 (0.131)	0.011 (0.054)	NA	6.34
Darkblotched							
-17.517 (1.904)	NA	0.555 (0.245)	3.191 (0.546)	0.961 (0.144)	0.006 (0.050)	0.182 (0.011)	0
-17.174 (2.367)	0.048 (0.448)	0.534 (0.329)	3.193 (0.542)	0.961 (0.143)	0.006 (0.050)	0.184 (0.011)	1.98
-14.992 (1.448)	NA	0.470 (0.211)	-0.755 (0.095)	NA	0.007 (0.052)	0.203 (0.012)	3.24
-14.955 (1.549)	0.001 (0.130)	0.498 (0.234)	NA	0.958 (0.155)	0.006 (0.049)	0.193 (0.011)	4.65
-13.173 (1.183)	NA	0.431 (0.200)	NA	NA	0.007 (0.052)	0.217 (0.011)	5.14
-15.009 (1.453)	0.001 (0.071)	0.470 (0.212)	-0.755 (0.095)	NA	0.007 (0.052)	0.204 (0.012)	5.28
-13.186 (1.186)	0.001 (0.071)	0.432 (0.200)	NA	NA	0.007 (0.052)	0.218 (0.011)	7.18
Canary							
-13.319 (1.698)	NA	0.265 (0.183)	-1.330 (0.126)	NA	0.015 (0.077)	0.267 (0.019)	0
-12.777 (1.942)	0.043 (0.283)	0.241 (0.234)	-1.425 (0.228)	NA	0.015 (0.077)	0.267 (0.019)	1.85
-12.808 (2.013)	0.043 (0.284)	0.241 (0.237)	6.90 (15.516)	0.999 (0.125)	0.015 (0.077)	0.267 (0.019)	3.85
-20.463 (5.043)	NA	0.495 (0.356)	NA	0.858 (0.191)	0.015 (0.079)	0.258 (0.022)	6.30
-20.458 (5.045)	0.001 (0.133)	0.495 (0.357)	NA	0.858 (0.191)	0.015 (0.079)	0.258 (0.022)	8.30
-10.617 (1.309)	NA	0.240 (0.170)	NA	NA	0.016 (0.080)	0.270 (0.021)	9.93

Table 2. Disagreements in assessment of maturity state between readers R1 and R2 for canary rockfish, darkblotched rockfish, and Pacific hake, all samples included in analysis. Disagreements are expressed based on the level of uncertainty recorded by each reader for each sample with **a** the overall number of samples with disagreements relative to **b** the total number of samples for each level of certainty (e.g. when both readers were certain for canary rockfish, they disagreed on 2.9% of the samples, and when both readers were uncertain they disagreed 100% of the time[1]).

	Proportion (a/b) : Percent Disagreement		
Certainty between readers	Canary n = 131	Darkblotched n = 307	Hake n = 329
Both certain	3/103 : 2.9%[1]	4/276 : 1.4%	6/303 : 2%
R1 certain, R2 uncertain	6/25 : 24%	3/23 : 13%	3/23 : 13%
Both uncertain	2/2 : 100%	2/5 : 40%	0/2 : 0%