The utility of length, age, liver condition, and body condition for predicting maturity and fecundity of female sablefish

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ABSTRACT: The objectives of this study were to determine if relative body condition and relative liver size (hepatosomatic index, HSI) could be utilized to predict maturity 6–8 months prior to spawning, when samples are readily available, and if these condition measures were related to fecundity. Female sablefish were sampled on four survey legs during a summer longline survey in July and August 2015 and during a winter survey in December 2015, which is 1 to 3 months prior to the spawning season in the Gulf of Alaska. The relative body condition and relative liver weight (hepatosomatic index, HSI) of fish increased throughout the summer survey, reaching measurements similar to those observed during the winter. There were significant differences between immature and mature fish HSI and relative body condition and these differences increased throughout the summer, making these factors useful for predicting maturity on the last legs of the survey. On these later legs, models that utilized relative body condition and HSI, as well as length and age, to predict whether a fish was immature or would spawn produced maturity curves that best matched models based on histological maturity classifications. However, models without HSI may be the best choice for future work because liver weight is not regularly collected on annual surveys and on the last leg of the survey they provided maturity curves that were very similar to those models that included HSI. Utilizing the winter data set when fecundity could be enumerated, fecundity was significantly related to relative condition and HSI. Increasing or decreasing these measures of condition by one standard deviation in a model of fecundity, which also included length, resulted in an estimated decrease in fecundity of 32% or an increase of 47% for an average size fish (78 cm). These results show the importance of incorporating fish condition into measures of population productivity.

Keywords: maturation, age at maturity, skip spawning, *Anoplopoma fimbria*, hepatosomatic index, egg production

1. Introduction

A decrease in fish condition, often measured as relative liver weight, Fulton’s condition factor (Fulton 1904), or relative condition, have been linked to reduced fecundity and delayed maturation (e.g., Lambert and Dutil 2000; Rideout and Rose 2006; Skjaeraasen et al. 2012; Skjaeraasen et al. 2015). Because of these relationships, condition has been used successfully to predict spawning (Morgan 2004; Morgan and Lilly 2005; Rideout et al. 2006) and fecundity (Skjaeraasen et al. 2013). For populations that experience a fluctuating environment and accompanying variable condition, it is important to evaluate how condition indices relate to aspects of reproduction and population productivity. For example, condition indices have been used in place of spawning biomass in the stock-recruitment relationship for Atlantic cod because they served as an accurate measure of population productivity (Marshall and Frank 1999; Marshall et al. 1999; Marshall et al. 2000; Marshall et al. 2003).

Relative liver weight and body condition are commonly used as measures of energy storage, both because liver weight, body weight, and length are relatively easy to collect and because they are related to fecundity and maturation (Morgan and Lilly 2005; Rideout et al. 2006; Skjaeraasen et al. 2013). The utility of liver weight and body condition are dependent on when measurements are collected within the reproductive cycle. For example, if a fish is depleted from spawning and is sampled prior to restoring energy reserves, measurements of condition may not indicate future spawning (e.g., Atlantic cod, Skjaeraasen et al. 2009). In addition, for many species, oocyte development leading to a future spawning event is only evident during a portion of the reproductive cycle. Finding the appropriate period for both 1) collecting liver samples and condition measurements and 2) accurately determining if a fish will spawn in the future spawning season is essential when using these data as indicators of future spawning and fecundity.

Sablefish *Anoplopoma fimbria* inhabit the northeastern Pacific Ocean from northern Mexico to the Gulf of Alaska, westward to the Aleutian Islands, and into the Bering Sea (Wolotira et al. 1993). In Alaska, fish age-3 and older (maximum age is 94) (Kimura et al. 1998) reside in waters approximately 150–1,000 m deep along the continental slope, in cross-shelf gullies, and in nearshore deep channels (Rutecki et al. 2016). They spawn in the late winter or early spring throughout Alaska (Sigler et al. 2001; Rodgveller et al. 2016) and are batch spawners with group synchronous oocyte development and determinate fecundity (Hunter et al. 1989). They are a commercially importance species off Alaska, the U.S. west coast, and British Columbia, Canada. The sablefish *Anoplopoma fimbria* fishery in Alaska was valued at $97.6 million in 2016 (Fissel et al. 2017).

In Alaska, the National Oceanic and Atmospheric Administration’s (NOAA) Alaska Fisheries Science Center (AFSC) conducts an annual longline survey from June–August throughout Alaska to estimate the abundance of select groundfish species. Although this is not close to the time of year when fish are spawning, it is the only time period when samples are regularly available for maturity classification. Maturity is assessed annually on these summer surveys macroscopically (with the naked eye) while at-sea. Histology is not regularly used for classification because of time constraints at-sea and the high costs associated with slide preparation and interpretation. At-sea observations have not been used for assessment because macroscopic classifications can be biased if collections are early in development. Possible reasons for this error are: 1) some fish that will spawn have not initiated oocyte maturation yet; 2) ovaries with maturing oocytes are not easily distinguishable from fish that will not spawn because the ovary is still small and the oocytes are not yet visible macroscopically; or 3) an effect of staff changes (observer effect).

The objectives of this study were to: 1) examine the progression of liver size and body condition throughout the survey to determine at what point there is a separation between immature fish and those that will spawn; 2) determine if future spawning can be predicted during any portion of the survey using condition, length, and age, but no maturity information; and 3) determine if condition is related to measurements of fecundity, in collections in winter just prior to spawning. This information could be used to provide a time series of maturity at age and fecundity based on measurements that can easily be collected at-sea.

2. Methods

2.1 Annual summer survey

The annual Alaska Fisheries Science Center longline survey extends throughout the Gulf of Alaska (GOA) and into the eastern Bering Sea in odd years and the Aleutian Islands in even years (Rutecki et al. 2016). For this study, sampling occurred in 2015 in the Gulf of Alaska only, including the East Yakutat (EYAK), West Yakutat (WYAK), and Central GOA management areas (CGOA) (Legs 3–7 of the survey, Figure 1). As part of the regular survey design, stations were placed systematically 37–56 km apart along the continental shelf and in cross-shelf gullies. Gear was set at depths from approximately 150–1,000 m. At this depth range the great majority of sablefish are >2 years old (Rutecki et al. 2016). Sablefish were collected for biological samples using a random, systematic sampling design so that samples were taken from all depths at 100–200 m intervals, as they are in all years. Leg 3 began on 5 July, 2015 at the southern-most station in EYAK and then sampling progressed westward (Table 1, Figure 1). The last day of sampling was on 26 August 2015. Dates of sampling for each leg are presented in Table 1. Leg 4 overlaps the area sampled on Leg 5 and Leg 4 is only two days long; therefore, in analyses legs 4 and 5 were combined (termed Legs 4/5). Different scientists are deployed on each leg of the survey and the personnel vary each year, but training is provided for scientists and photographs are provided as a reference. The station positions and sampling dates remain the same each year.

2.2 Winter survey

A special project was conducted nearby Kodiak Island in the CGOA (Figure 1), which is the approximate center of the Alaska sablefish population and overlaps parts of Legs 6 and 7 (Hanselman et al. 2016). A trawl vessel was chartered to conduct fishing operations from 3–10 December 2015. Measurements and tissues were collected from all females. To locate specimens from the full range of ages and lengths of mature and immature females, trawling operations were planned to sample the continental slope and cross-shelf gullies. Locations were chosen based on commercial fisheries catch rates, AFSC bottom trawl survey catches, catches during a sablefish maturity study in December 2011, and their proximity to Kodiak, Alaska (Rodgveller et al. 2016).

2.3 Fish sampling

Sablefish selected for biological sampling were measured (fork length in mm) and weighed (g) on a motion-compensating scale. Sagittal otoliths were extracted and stored dry in vials. Otoliths were aged by personnel of the AFSC Age and Growth Program using standard, validated methods (Kimura and Anderl 2005; Kimura et al. 2007). Ovaries were placed into individual cloth bags with labels and submerged in a 5-gallon bucket containing ExCell Plus^{TM}

tissue fixative. Livers were frozen at-sea, transported to the laboratory frozen, and then thawed and weighed. Fish lengths, weights, and otoliths are collected annually and livers and ovaries were collected in 2015 for this study.

2.4 Maturity classification

Histological slides were prepared from sections taken from the middle of the ovary. Each sample included a portion of the ovarian wall. The thickness of the ovarian wall has been used to determine if a fish has previously spawned in several fish taxa (Rideout and Tomkiewicz 2011) including sablefish (Rodgveller et al. 2016). Previously, Rodgveller et al. (2016) found that oocyte development did not vary within both ovaries and so one sample was analyzed per fish.

Ovarian tissues were embedded in paraffin, sectioned at 5–6 µm, stained with hematoxylin, and counterstained with eosin. Histological slides were examined microscopically and the stages of oocyte development were recorded using methods used in Rodgveller et al. (2016) for sablefish (Table 2), which utilized samples from the winter, approximately 2 months prior to spawning. The maturity classification was based on the most advanced oocyte stage present in the ovary and other structures (Table 2). Skip spawning fish were arrested in development in either the multiple nucleoli, perinucleolar, or early cortical alveoli stages. Unlike immature fish, they also had evidence of past spawning, such as a thick ovarian wall and other characteristics (Table 2) (Rodgveller et al. 2016). Because skip spawning fish in Rodgveller et al. (2016) and Rodgveller et al. (2018) did not have advanced cortical alveoli stages present, ovaries with oocytes in this stage in the summer were staged as developing toward spawning.

Fish were also classified macroscopically at-sea by scientists, who varied among legs. Fish were classified as immature, maturing, and resting. No attempt was made to identify skip spawning macroscopically because it was first identified in sablefish in 2011 (Rodgveller et al. 2016) and is difficult to identify without histology. Immature fish were defined as having thin, tubular ovaries where oocytes were indistinct through the ovarian wall. Mature ovaries were defined as distended with opaque, white, and discernable oocytes. Ovaries were classified as resting if they were large, but not flaccid, and oocytes were not discernable. Fish in the resting and mature stages were classified as mature in logistic models of age at maturity, as described in section 2.7.

2.5 Liver size and body condition

For both summer and winter samples, the relative liver weight was calculated as an index of liver size, termed the hepatosomatic index, where $LW_{i2}$is the liver weight and $W_{i2}$was the total fish weight (HSI; equation 1). The HSI can be correlated with maturation and fecundity because the liver serves as energy storage and is where vitellogenin is synthesized (Petersen 1979, Emmersen and Emmersen 1976).

(1) $HSI_{i2} = 1002—$

Relative body condition (RC) in g was calculated as the deviation in measured weight from the length-weight curve of all fish sampled in the 2015 summer samples, where $L_{i2}$was the fish length and $W_{i2}$was the total fish weight (equation 2).

(2) *RC* is the residual of $W_i = 2\ {L_i}^{b2}$

The HSI or RC for each leg were compared to one another, for mature and immature fish separately, using an ANOVA. Within each ANOVA, pair-wise comparisons between legs were analyzed using Tukey-Kramer HSD tests (Zar 2010). Within each leg, t-tests were used to test for significant differences between immature and mature HSI or RC. Shifts in these indices throughout the year may indicate when immature and mature fish begin to show different energy storage strategies. HSI and RC were also used in models to predict fecundity and maturity, as described in section 2.6 and 2.7.

2.6 Fecundity

Ovaries from the winter were chosen for fecundity estimation if they had vitellogenic oocytes and no post-ovulatory follicles in histological ovary cross sections, which would indicate that partial spawning had occurred. The advanced (mature) cohort of oocytes was clearly separable from the early developing (immature) cohort based on oocyte size and appearance, as described for sablefish by Mason et al. (1983) and Hunter et al. (1989). This indicates that sablefish have determinate fecundity, where only one cohort of oocytes develop within a spawning season. Fish of a wide range of lengths were chosen for fecundity measurements.

Fecundity was measured using the gravimetric method (Murua et al. 2003), where a subsample of mature oocytes from an ovary is weighed, the number of oocytes counted, and the number of eggs per g multiplied by the total ovary weight. Samples were taken from the anterior, middle, and posterior sections of one ovary. The three measures of eggs per g were averaged and then multiplied by the total ovary weight.

A multiple linear regression of fecundity and measurements of maternal size and condition were fit using the full model (equation 3). In equation 3, $\log(F)$2was the natural logarithm of fecundity, $I2$was the intercept, $HSI_{i2}$was the hepatosomatic index (equation 1), L_{i2} was the fish length, $W_{i2}$was the total fish weight, $RC_{i2}$was the relative condition (equation 2), and $e_{i2}$was the normal, random error.

(3) $$\log(F_i) = I + HSI_{i2} + L_{i2} + W_{i2} + RC_{i2} + e_{i2}$$

In equation 3, fecundity was log transformed so that q-q plots of the residuals from linear regressions with the explanatory variable were linear, indicating normally distributed residuals (Thode 2002). Akaike Information Criterion (AIC_c) values for the full and reduced models were compared and the model with the smallest AIC_c was chosen as the best model (Akaike 1974). For the fecundity analysis fish were sampled in winter; therefore, the RC values for this analysis were calculated using fish sampled for maturity and fecundity in the winter (equation 2). All fish sampled in winter were included, not just those sampled for fecundity. The adjusted R^2 (equation 4) was calculated for models of fecundity, where *DF* is the degrees of freedom and *CT* is the corrected total (equation 4):

(4) $$Adjusted\ R2 = 1 - 2\frac{Mean\ Square\ (error)2}{Sum\ of\ squares\ (CT) / DF(CT)2}\ .$$

2.7 Predicting maturity using fish condition, size, and age

A logistic model was used to predict whether an individual fish was functionally mature (would spawn in the coming winter) or immature for samples collected on all legs (3–7) of the summer survey (equation 5). The response was either mature (1) or not mature (0). There were too few fish that were skip spawning, as evident in the histology slides, to include them as a response variable in the model. There were 11 skip spawning fish in the summer data set and there were only 0 to 6 skip spawning fish on each leg.

In equation 5, the survey leg (3–7), Leg_i, is represented as 4 categories or pooled into 2 categories. Three pooling options were explored: 1) Leg 3 as one category and and Legs 4/5, 6, 7 as another; 2) Legs 3, 4/5, 6 as one category and Leg 7 as the other; 3) or Legs 3 and 4/5 as one category and Legs 6 and 7 as other. $L_{j2}$is the fish length, $A_{j2}$is the age, $HSI_{j2}$is the hepatosomatic index (equation 1), $RC_{i2}$was the relative condition (equation 2), and the interactions between HSI and RC with leg were included to account for differences that may occur due to geography or sampling timing:

(5) $$M2turity_{ij2} = Leg_i + L_j + A_j + HSI_j + RC_i + Leg_i * HSI_j + Leg_i * RC_{j2}.$$

Fish from Leg 4 were not included in models where age was included because there are no ages available for these fish. The full model (M0) and several other nested models were chosen for a comparison of prediction accuracy (Table 3). In these models either age, HSI, RC, or the interaction terms were excluded (M1–M4) because these measurements are the most time consuming to collect or expensive to obtain or they may not always be available on annual surveys (particularly HSI). A model with age and length only (M5) was included as the most basic model for comparison because it excludes all condition indices and pools data for all legs.

These models were used to predict if each individual fish was mature or immature and the prediction was compared to the maturity designation from histology slides. Summaries of each model's prediction success were measured as the percent classification success for immature and mature fish by survey leg.

2.8 Age at maturity

Age at maturity curves, using 1) the predicted maturity from each model as well as 2) maturity designations from histology, were examined using the two-parameter logistic function is given by,

(6) $$\hat{p}_{a2}=2 1/\left(1+e^{-\delta(a-a_{50\%})}\right),2$$

where $\hat{p}_{a2}$is the estimate of the proportion mature at age, δ is the parameter that describes the slope of the logistic curve (the speed at which maturity approaches 100%), and $a_{50\%}$ is the parameter that describes the age at which 50% of the fish are mature. The observed proportion at age was calculated as,

(7) $$p_{a2}=2\frac{m_a}{n_{a2}},$$

where m_a was the number of mature fish observed at age-a and n_a was the total number of fish at age-a. We used the binomial likelihood to fit the observed proportion mature at age with the logistic model given in equation 6. Because no sablefish are known to be mature at age-0, we penalized the likelihood when maturity at length or maturity at age-0 was greater than 0%. The penalty function was a weighted least-square between the estimated maturity at age-0 and 0%, given by:

(8) $$P2 = \lambda(p_0 - 0)2,$$

where *P* is the penalty term added to the binomial likelihood, $p_{02}$is the estimated proportion mature at age-0 and λ is the weighting term, which was selected to be 100 in order to balance fit at age-0 and fit to older ages where maturity is greater than 0%.

3. Results

3.1 Body condition and hepatosomatic index: summer and winter

The RC was highest for mature fish (those fish that would spawn) on each leg (Figure 2A); using t-tests, there were significant differences between mature and immature fish on all legs and in the winter (Figure 2A). Skip spawning fish were documented on Legs 3 (N = 6), 4/5 (N = 3), and 7 (N = 2). In Figure 2B, much of the same data are presented as in Figure 2A, except that each maturity category is presented together and skip spawning fish are included for each season (winter and summer). An ANOVA was used to test for significant differences between each leg for each maturity category and a Tukey-Kramer HSD test was used to conduct pair-wise comparisons within each maturity category. Significant differences based on these tests are noted in Figure 2. There was a progressive increase in RC for mature fish from Leg 3 to Leg 7 (Figure 2B); mature fish on Leg 3 had significantly lower RC than fish on Legs 6 and 7 and the RC on Legs 4/5 was significantly lower than Leg 7.

On Leg 7, the RC was at its peak and was similar to the RC in the winter (Figure 2B). Winter sampling sites were in the same area as those collected at the tail end of Leg 6 and on Leg 7. It is possible that either, 1) the winter indices were closer to the Leg 7 than other areas because of a geographic effect, or 2) samples in the eastern GOA would have been more similar to Leg 7 and the winter if sampled later in the summer, a time effect. There were no significant differences between immature fish on any legs or between skip spawning fish in the summer and winter (Figure 2B). Trawl gear, which was used in the winter, catches a wider length range than longline gear; however, the condiiton indices are likley comparable if the length at maturity does not differ among those caught in trawl and longline gear.

The same analytical tools were used for HSI as for RC. The trends in HSI values were similar to those for RC. The HSI for fish that would spawn was higher than immature fish on each leg (Figure 3A). Like RC, in the winter the HSI of skip spawning fish was similar to immature fish (Figure 3A). Unlike RC, the HSI for immature fish was significantly larger on Leg 7 than on any other time period (Figure 3B). Despite this increase, there was still a significant difference between immature and mature HSI on leg 7, because the HSI of mature fish was also higher than on other legs. There was a gradual, significant increase in HSI from Legs 4/5 to 7 for immature and mature fish (Figure 3B). The mean RC and HSI for skip spawning fish increased from summer to winter, but in both cases the increase was not significant, possibly a result of small sample sizes (Figures 2B, 3B; Table 4). Overall, RC and HSI later in the survey, particularly on Leg 7, were higher (Figures 2 and 3).

3.2 Fecundity

The range in lengths of fish used in analyses of fecundity ranged from 530 to 1010 mm and from 4 to 38 years old (sample size = 39). The best-fit model included *RC*, *HSI*, and *L* (or *W*), with very similar results when either lengths or weight were included (Table 5). The linear model (equation 3) used to estimate relative condition was $\mathrm{W} = 2.598 * 10^{-5}(L2^{862})$. The model that included *RC*, *HSI*, and *L* was used to predict fecundity when *HSI* and *RC* were average *(RC* = 0) and when *HSI* and the *RC* were one standard deviation from average. For a fish that was 782 mm (average length), the predicted fecundity with an average *HSI* and *RC* was 497 thousand eggs (Figure 4). When *HSI* was one standard deviation from average, the number of eggs was either 91 thousand eggs below (18%) or 111 thousand eggs above average (22%) (Figure 4). When *RC* was one standard deviation from average, the number of eggs was either 82 thousand eggs below (17%) or 99 thousand eggs above average (20%). When both were one standard deviation from average, the number of eggs was either 158 thousand eggs below (32%) or 232 thousand eggs above average (47%).

3.3 Predicting maturity

The model with leg as 2 categories (Legs 3 and 4/5 combined and Legs 6 and 7 combined) performed better than the model with leg as 4 categories (one category per leg) or other pooling options. The $\mathrm{AIC_c}$ for the full model with leg as 2 categories (MO) was 259 (Table 6) and the $\mathrm{AIC_c}$ for the full model when leg was 4 categories was 267. For this reason, the full and nested models in Table 6 (M0–M4) have leg as two categories. M0, the full model, and M1, the full model minus the interaction terms, had the best model fits, as indicated by $\mathrm{AIC_c}$ and R^2 (Table 6). The next best fit was achieved by M2 (excludes HSI) (Table 6). The model with only age and length, M5 (no leg, RC, or HSI), had the worst fit.

Classification was defined as a success when the prediction by the model was the same maturity classification as histology. There was lower classification success for immature fish than functionally mature fish (those that will spawn; termed “mature” for simplicity) (Table 7). The lowest success for immature fish was on Leg 3 (59%–68%), whereas on other legs the success rate was 73%–91%, when models with Leg and condition indices were used. The success rate for classification of mature fish was higher (83%–98%) than for immature fish and was highest for Legs 3 and 4/5 (90%–98%). For the combined data (mature and immature fish) the highest success rates were also on Legs 3 and 4/5, likely because more older, mature fish were sampled on these legs than on Legs 6 and 7 and there was a higher success rate for mature fish.

The predicted maturities of individual fish using each model were used to fit logistic models to the proportion of fish mature at age (see Table 8 for parameter values; Figures 5 and 6 for logistic curves; Figures 7 and 8 for parameters with confidence intervals). The model currently used in the Alaska stock assessment, which utilizes data collected from 1978–1983, is also included in each figure for comparison. In the stock assessment a single model is used for all areas and so the same curve is all panels in figures (Hanselman et al. 2016). In addition, age-at-maturity curves that utilized macroscopic classifications made at-sea in 2015 are included.

For Legs 3 and 4/5, all curves produced younger maturity-at-age estimates than what is used in the stock assessment model currently (Figures 5, 7, Table 8). The maturity curves from Models 0–4 produced younger maturity-at-age estimates than the curve fit to data from histology slides, particularly on Leg 3, which is the earliest leg and the leg furthest to the east (Figures 5, 7). On both legs the macroscopic curve and the Model 5 curve, which includes only length and age, were the most similar to the histology curve (Figure 5). In other words, adding condition indices did not produce curves most similar to histology on these legs. For Legs 3 and 4/5 the prediction success for Model 5 for immature fish was high, but low for mature fish (Table 7). These results indicate that prediction success does not always result in the maturity curve most similar to histology. This was because the effect of each incorrect prediction affected the proportion mature at age differently in each case. For example, in one model a 5-year old fish could have been incorrectly predicted to be mature and in another model a 3-year old fish could have been incorrectly predicted to be mature, which could affect the maturity-at-age curve in different ways.

For Leg 6 the maturity curves were more variable than for Legs 3 and 4/5, because condition indices were more influential on later legs than on earlier legs. The models that were closest to the histology curve were Models 0 and 1 (Figure 6, Table 8), which included leg, length, age, RC, and HSI (Table 3). The macroscopic curve had much younger estimates of ages at maturity than all other curves; the age-at-50% maturity and the slope parameter confidence intervals did not overlap those from any other model (Figures 7 and 8, Table 8). Model 5, which included only age and length, had younger estimates of age-at-maturity than other models and the histology curve. The models with age, length, and some measure of condition were the most similar to histology (Figure 6). The curve currently used in the stock assessment was closer to histology on Leg 6 than on Legs 3 and 4/5 (Figures 5 and 6).

For Leg 7, Models 0, 1, and 2, which excluded HSI, were close to the histology curve (Figure 6). Like Leg 6, 1) the macroscopic curve for Leg 7 had the youngest estimates of ages-at-maturity and the steepest slope parameter, and 2) Model 5, the model with age and length only, had estimates of maturity that were younger than other predictive models and was the most dissimilar to histology (Figures 6, 7). Unlike leg 6, the stock assessment model had older ages at maturity than other all models. For all legs the prediction success did not always translate into a maturity-at-age curve that was the most similar to histology.

When the maturity of skip spawning fish was predicted, where the only classification options were mature (will spawn) and immature, 2/11 fish (82%) were predicted to be mature and the rest as immature. Those categorized as immature were 1) 550 mm long, age 6, HSI = 1.35, RC = -54 on Leg 5 and 2) 620 mm long, 7 years old, HSI = 1.52, RC = -132, on Leg 7. When the model included age and length only a third fish was identified as immature (length = 640, age = 5, HSI = 1.83, RC = -94).

In summary, the models that were most similar to histology included measures of condition on Legs 6 and 7. On Legs 3 and 4/5 the model without measures of condition had the curve closest to histology. The macroscopic curves differed from other curves on Legs 6 and 7, but were similar to other curves on Legs 3 and 4/5. The curve currently used in the stock assessment was more similar to the models and histology on Legs 6 and 7 than on Legs 3 and 4/5.

4. Discussion

We found that maturity predicted using some combination of the survey leg, age, length, RC, and HSI produced maturity curves that were similar to the histology curve, but the closest model varied by leg. On earlier legs of the survey in the eastern portion of the GOA, Legs 3 and 4/5, the maturity-at-age model that was closest to histology included only age and length (Model 5). Later in the survey, on Legs 6 and 7, the models that produced curves most similar to histology included length, age, and measures of condition. The sampling timing relative to the reproductive cycle are likely the reason for this discrepancy. A higher portion of fish on earlier legs had oocytes in early stages of vitellogenesis whereas more fish were in later stages of vitellogenesis on Leg 7. (The progression of development on the summer survey, utilizing the samples in this study, was reported in Rodgveller 2018.) A trend of increasing condition with development has been observed in other studies. For example, developing Atlantic cod have a higher HSI as spawning approaches (Skjaeraasen et al. 2009). This increase in energy storage occurs in the liver because this is where the precursor to vitellogenin is synthesized (Korsgaard and Petersen 1979; Emmersen and Emmersen 1976). Because on Legs 3 and 4/5 there were smaller differences in condition between immature and developing fish (functionally mature), condition indices were not useful for predicting maturity. The condition of immature fish were more stable than developing fish throughout the survey, likely because these fish are still devoting energy to growth over reproduction (Roff 1983).

To determine if differences in condition may have been affected by geography and if the reproductive cycle follows the same schedule throughout the GOA, all areas would need to be sampled at the same time in at least two time periods (such as July and August) to compare oocyte development and RC and HSI geographically. For a direct comparison of condition by area, fish should be sampled when they are at a similar point in the reproductive cycle. In this study the potential effects of geography and sampling timing were confounded because each area was sampled at a different time.

The earlier development stages on Legs 3 and 4/5 also indicated a potential issue with maturity classification accuracy. A large portion of developing fish on Legs 3 and 4/5 had oocytes in the early stages of vitellogenesis (Rodgveller 2018). This creates a challenge for classifying maturity correctly, even with histology, because this early in the cycle some fish that appear to be immature or skip spawning may move into a developing stage later in the summer and spawn in the winter. If some of the fish classified as not functionally mature were in fact going to develop and spawn, the histology maturity curve would have been further to the left, possibly closer to the model-predicted maturity curves (Figure 5). This could be tested if samples were collected later in development in these areas. Because of this uncertainty, on the AFSC longline survey models should be used to predict maturity for Legs 6 and 7 only. Leg 7 is the most reliable because 1) more developing fish are in the later stages of vitellogenesis and it is unlikely that immature fish will initiate development after the survey (Rodgveller 2018) and 2) the largest differences in the condition of developing and immature fish was on Leg 7, increasing their utility in predictive models.

Models 0 and 1 contained all factors and produced the maturity curves closest to histology for Legs 6 and 7, and so these models are preferred. However, HSI is not collected regularly on the annual longline surveys. Models 2 and 4 are more practical because liver weight is not required. On both legs these curves were relatively close to the histology curves and the models had similar AIC_c values. Model 2 curve was closer to the histology maturity curve and therefore Model 2, which includes the interaction of Leg and RC, is preferred over Model 4, which excludes this interaction. A caveat to using these models to predict maturity is that the effect of the predictor variable on maturity is assumed to be static. If there is an interaction between the year and the effect of these predictors, the maturity designations may be less accurate in other years. More years of histology and condition data are needed to ensure the relationships hold.

In some cases the confidence intervals for the age-at-maturity curve parameters were not significantly different. However, a vector of maturity-at-age values from the maturity curve are used in the sablefish stock assessment to estimate spawning stock biomass and variability is not incorporated. It will be important to evaluate the effect of different age-at-maturity curves resulting from candidate models to see if there are meaningful differences in estimates of spawning stock biomass and resulting fishing reference points.

Skip spawning was documented in this study and has been documented in sablefish previously (Rodgveller et al. 2016, Rodgveller et al. 2018). Because there were so few skip spawners observed in this study, skip spawning could not be included in predictive models as a category. This could be added in the future if more skip spawning fish are collected in the summer and identified with histology. The majority of skip spawning fish were identified as mature (82%). This will produce a maturity curve that reflects the number of fish that are mature and not just those that are functionally mature (will spawn this season). More data on skip spawners is needed before it can be added as a third maturity category in predicative models.

Skip spawning was documented in this study as well as during the winters of 2011 and 2015 in the Gulf of Alaska (Rodgveller et al. 2016, Rodgveller et al. 2018). For all data combined (N = 48) the average age was 11.6 years old (median = 11, mode = 7). Because skip spawning sablefish are generally young (maximum age is 94 years, Kimura et al. 1998) and the rate of skip spawning decreases with age (Rodgveller et al. 2018), the standard logistic curve, where maturity asymptotes at 1, should be adequate for describing the maturity-at-age. If skip spawning was more prevalent at older ages or if there was senescence, a curve that reaches a maximum of less than 1 or a curve with an alternate shape, such as dome-shaped, may be more appropriate (Secor 2008; Brooks 2013).

Samples were collected in 2015 when the North Pacific Ocean was in a warm, positive Pacific Decadal Oscillation phase, resulting in the formation of the warm water “blob” in the Gulf of Alaska, which continued through 2016 (Zador 2015, North Pacific Marine Science Organization 2016). However, the deep-water on the continental slope where the sablefish fishery and surveys occur is thermally stable and cold; the annual deviation from average on the AFSC longline surveys from 2009–2018 was 0–5% in each area and the direction did not coincide with warm phases (unpublished, Rodgveller, AFSC). The changes in surface water productivity may have affected the food chain in deeper-water, but this has not been studied. It is not likely that development timing was affected dramatically by the surface water warming event in 2015 because no fish were found in spent condition or in near spawning condition in July or August and the appearance of fresh ovaries was consistent with past years.

Fecundity was significantly related to liver and body condition. Fecundity has been shown to be negatively affected by poor condition in other species as well. For example, in haddock (*Melanogrammus aeglefinus)* condition indices were significant predictors of fecundity and neither factor was correlated with length (Skjaeraasen et al. 2013). The same trend was observed in captive Atlantic cod, where the realized fecundity was only 20% to 80% of the potential fecundity, depending on the nutritional status (Kjesbu et al. 1991). The effects of fluctuating sablefish HSI and RC by +/- 1 SD were substantial, 31–47% for a fish of average length. Similar to our study, a model used to predict fecundity of haddock was improved by including measures of condition (Blanchard et al. 2003); a 25% increase in relative condition resulted in a 1.9-fold increase in fecundity-at-length and when relative liver size doubled there was a 2.0-fold increase in fecundity (Blanchard et al 2003). These studies demonstrate that fluctuations in condition have the potential to make large, population-wide differences in total egg production. There are other maternal effects that may also affect the fecundity of sablefish. The relative fecundity of sablefish in Alaska (fecundity/body weight) decreased with age, indicating that the productivity of fish may decrease as they get older (Rodgveller et al. 2018). Our results and these studies demonstrate that there are factors that affect fecundity and reproductive output that are poorly understood and not accounted for in population models, including sablefish.

Besides using condition to predict maturity, these indices have been used directly as an index of egg production in place of spawning biomass. Spawning stock biomass is a proxy for total egg production. It incorporates population structure, maturation rates, and weight, but does not include the effects of fish condition or other maternal effects. For Atlantic cod a condition index has proven to be related to egg production and recruitment (Marshall and Frank 1999, Marshall et al. 1999), even in a 50-year time series (Atlantic cod, Marshall et al. 2000). At the same time spawning stock biomass was shown to be a poor index for total egg production (Marshall et al. 1998; Marshall et al. 1999). Because condition can be related to fecundity, spawning, and recruitment, it is important to evaluate how these indices be used to predict annual reproductive potential.

The maturity-at-age curve currently used in the stock assessment has fish maturating at older ages than all models for Leg 7 but at younger ages than many models on Leg 6, including histology (difference in $a_{50\%}$ between the stock assessment and histology was 0.3 years on Leg 6 and 0.5 years on Leg 7), but the differences were much smaller on these legs than on Legs 3 and 4/5. Although these differences on Legs 6 and 7 may not produce meaningful changes to management in 2015, annual differences in other years may be more significant if fish condition fluctuates. Predictive models from this study could be used to produce a time varying maturity curve for the assessment, which could lead to more accurate estimates of biological reference points and stock status.

In summary, we found that female sablefish maturity can most accurately be predicted on the latest legs of the survey, which were in the central GOA. Despite being 6–7 months away from the spawning season, the predictive models used in the last month of the survey were able to utilize measures of condition to improve the prediction of maturity. For sablefish, the model that was best in terms of accuracy and practicality of obtaining data at-sea was the model that included length, age, and relative body condition. If liver weight is collected, this should also be included in models, but it is not currently part of the regular survey operations.

In other species these same methods may be used for predicting maturity if the sampling timing is appropriate. The proportion of females with oocytes in later stages of vitellogenesis should be high, which indicates that the spawning population has initiated oocyte maturation and histological classifications of maturity are reflective of future spawning. To utilize condition indices, there should be a measurable difference in condition between mature and immature fish. The models used to predict maturity should be tested over time, utilizing histology, to ensure that there are not meaningful differences in the predictive model coefficients from year to year. Fecundity was also sensitive to changes in condition and so fluctuations in condition may affect productivity both by affecting total egg production and maturation. When condition affects reproduction (the fecundity-length or fecundity-weight relationship and the age at maturity curve), its effects on estimates of population productivity should be evaluated. Management may be adjusted for changes in productivity by either lowering fishing rates to avoid overfishing when condition is low, or allowing for higher fishing rates when productivity is high.

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Table 1

Start and end dates of each Alaska Fisheries Science Center longline survey leg. Dates remain the same each year.

Leg	Start date	End date
3	July 5	July 19
4	July 21	July 22
5	July 24	August 2
6	August 5	August 15
7	August 17	August 26

Table 2

Sablefish (*Anoplopoma fimbria*) ovarian maturity classification and accompanying oocyte development stages identified histologically during July and August (on survey Legs 3 through 7) in the Gulf of Alaska.

Structures defining maturity	Maturity
Oocytes with multiple nucleoli and/or perinucleolar; thin ovarian wall.	Immature
Oocytes with multiple nucleoli and/or perinucleolar oocytes; may also contain oocytes in early cortical alveoli stage; thick ovarian wall; thick stroma; blood vessels present.	Skip spawning
Early cortical alveoli stage.	Immature
Late cortical alveoli stage.	Maturing, will spawn
Yolk accumulated within eosinophylic spheres (vitellogenesis).	Maturing, will spawn

Table 3

Parameters included in each logistic regression model of maturity where the response was either mature (will spawn) or immature.

Model	Parameters							Descritption
	Leg	Length	Age	HSI	RC	Leg*RC	Leg*HSI	
M0	X	X	X	X	X	X	X	Full model
M1	X	X	X	X	X	-	-	No interactions
M2	X	X	X	-	X	X	-	No HSI
M3	X	X	-	X	X	X	X	No age
M4	X	X	X	-	X	-	-	No HSI; no interactions
M5	-	X	X	-	-	-	-	Length/age only

Table 4

Number of mature, immature, and skip spawning fish used for comparisons of relative condition and relative liver size of female sablefish (*Anoplopoma fimbria*).

Leg	Immature	Mature	Skip spawn	Total
3	37	170	6	213
4/5	41	134	3	178
6	48	65	0	113
7	38	55	2	95
Winter	177	270	13	460

Table 5

Best-fit models for maternal parameters that helped explain the variability in fecundity, where *RC* is the relative condition, *HSI* is the hepatosomatic index, R^2 Adj is the adjusted R^2 for the model, and SE is the standard error. When either length or weight were included, the R^2 values were very similar. The sample size was 39 fish.

Dependent	Explanatory	Estimate	SE	t-ratio	p	R^2 Adj
Ln(F)	*intercept*	11.75	0.19	61.24	<0.00	0.73
	RC	0.77	0.25	3.07	0.00	
	HSI	0.15	$6.95{*}\,10^{-}$	2.10	0.04	
	Weight	$1.69 * 10^{-4}$	$1.95{*}\,10^{-5}$	8.69	<0.00	
Ln(F)	*intercept*	9.62	0.33	29.13	<0.00	0.74
	RC	*1.69*	0.28	5.96	0.00	
	HSI	*0.16*	0.07	2.29	0.03	
	Length	$3.88 * 10^{-3}$	$4.40{*}\,10^{-4}$	8.81	<0.00	

Table 6. Logistic regression parameter estimates for each logistic regression model used to predict whether a fish would spawn or was immature. “Inter.” is the intercept, “Len.” is the fish length, “HSI” is the hepatosomatic index, “RC” is the relative condition, and “Leg” is the survey leg. “Leg*RC” and “Leg*HSI” were interaction terms. Leg is equal to -1 when Legs 3 and 5 are pooled into one category and equal to 1 when Legs 6 and 7 are pooled. Model 3 also includes samples where there were lengths and no ages because it does not include an age term (see N for sample size). The corrected Akaike Information Criterion (AIC_c), the correlation coefficient (R^2), and model degrees of freedom (df) are also listed for each model.

		Parameter estimates										
Model	Inter.	Leg	Len.	Age	HSI	RC	Leg*RC	Leg*HSI	AIC_c	R^2	df	N
M0	-20.946	0.760	0.026	0.330	1.265	$1.40*10^{-3}$	Leg*([RC+9.102]*[-1.352*10^{-3})	(Leg*-0.382)*(HSI-2.03)	259	0.63	7	543
M1	-19.745	0.773	0.024	0.299	1.231	$1.59*10^{-3}$	-	-	262	0.62	5	543
M2	-20.121	0.628	0.029	0.290	-	$2.23*10^{-3}$	Leg*([RC+9.102]*[-1.337*10^{-3})	-	273	0.60	5	543
M3	-22.610	0.911	0.032	-	1.240	$1.43*10^{-3}$	Leg*([RC+8.552]*[-7.72*10^{-4}])	(Leg*-0.300)*(HSI-2.03)	289	0.60	6	580
M4	-19.430	0.639	0.028	0.277	-	$2.34*10^{-3}$	-	-	276	0.60	4	543
M5	-19.521	-	0.028	0.299	-	-	-	-	301	0.55	2	543

Table 7

Percent of female sablefish (*Anoplopoma fimbria*) with maturity classifications that matched designations from histology slides for each model (M0 through M5). The cells highlighted have the highest prediction success for that leg (row). “Count” is the number of fish with lengths and ages. In parentheses is the number of fish with lengths only. Leg 4 did not include any fish with ages. Three fish from Leg 6 were not aged.

Histology	Leg	M0	M1	M2	M3	M4	M5	Count
Immature	3	68%	65%	68%	59%	65%	68%	37
Immature	4/5	85%	85%	83%	83%	83%	90%	40 (41)
Immature	6	91%	85%	83%	88%	83%	65%	46 (48)
Immature	7	78%	78%	86%	73%	86%	68%	37
Mature	3	98%	98%	98%	98%	98%	93%	168
Mature	4/5	98%	98%	98%	98%	98%	90%	100 (133)
Mature	6	89%	89%	90%	85%	92%	95%	61 (62)
Mature	7	93%	91%	87%	93%	83%	93%	54
Combined	3	92%	92%	92%	91%	92%	89%	205
Combined	4/5	94%	94%	94%	95%	94%	96%	140 (174)
Combined	6	90%	88%	87%	86%	88%	82%	107 (110)
Combined	7	88%	86%	87%	85%	85%	82%	91

Table 8

Age at 50% maturity ($a_{50\%}$) and slope parameters of logistic regressions fit to maturity-at-age data from maturity designations produced from each predictive model (M0-M5) and for maturity designations from histology slides (histo). Parameters for the maturity-at-age curve using maturity classifications from macroscopic classifications at-sea (Macro) are included as well as the parameters currently used in the Alaska stock assessment population model (SA). The SA model is used for all geographic areas in Alaska. All data were collected on the 2015 Alaska Fisheries Science Center annual summer longline survey, except for data used in the SA model. For each leg (row), values that share the same letter are not significantly different from one another. Those that have different letters are significantly different from one another.

	Leg	M0	M1	M2	M3	M4	M5	Histo	Macro	SA
$a_{50\%}$	3	5.25a	5.24a	5.3a	5.08a	5.19a	5.64a	5.68a	5.07a	6.60b
	4/5	5.45a	5.45a	5.36a	5.26a	5.36a	5.66a	5.72a	5.58a	6.60b
	6	7.10a	6.93a	6.66ab	7.46a	6.56ab	5.84b	6.90ac	4.78d	6.60ac
	7	5.76ac	5.85ac	6.21ac	5.65a	6.41ac	5.38a	6.07a	3.76b	6.60c
Slope	3	1.37a	1.32a	1.30a	1.30a	1.34a	1.35a	1.08a	1.31a	6.60b
	4/5	1.53a	1.53a	1.52a	1.51a	1.52a	1.50a	1.32a	1.42a	0.84b
	6	0.96abc	1.00abc	1.08abc	0.77ad	1.14bc	1.18bc	0.93abd	1.35c	0.84d
	7	1.05a	1.05a	1.05a	1.03a	1.00a	1.23a	1.04a	1.99b	0.84c

Fig. 1. Stations sampled on Legs 3 through 7, in July and August 2015, of the Alaska Fisheries Science Center annual longline survey in the Central Gulf of Alaska (CGOA), Western Yakutat (WYAK), and East Yakutat (EYAK) management areas. Circles with no fill are stations sampled in December 2015.

Fig. 2. Relative condition (RC) for sablefish collected on Legs 3 through 7 of the summer longline survey (S) or in the winter (W). Immature (I), mature (M), and skip spawning (SS) fish are labeled for the winter so that skip spawning fish can be differentiated from the other two groups. In Panel A, an * represents a significant difference between maturity categories during that sampling period. Panel B includes much of the same data in panel A, except that each maturity category is presented together and significant differences within each maturity category between sampling periods are denoted by a different letter. In Panel B, SS samples are pooled for all of summer (N = 11) and compared to those collected in the winter (N = 16). The 95% confidence intervals (CI) are marked with whiskers and the lower portion of the CI for summer skip spawning fish is truncated to maintain the same scale as Panel A.

Fig. 3. Hepatosomatic index (HSI) for sablefish collected on Legs 3 through 7 of the summer longline survey (S) or in winter (W). Immature (I), mature (M), and skip spawning (SS) fish are labeled for the winter because skip spawning must be differentiated from the other two groups. In Panel A, on every survey leg the mean for immature fish is lower than the mean for fish that will spawn. An * represents a significant difference between maturity categories during that sampling period. Panel B includes much of the same data in panel A, except that each maturity category is presented together and significant differences within each maturity category between

sampling periods are denoted by a different letter. In Panel B, SS samples are pooled for all of summer (N = 11) and compared to those collected in the winter (N = 16).

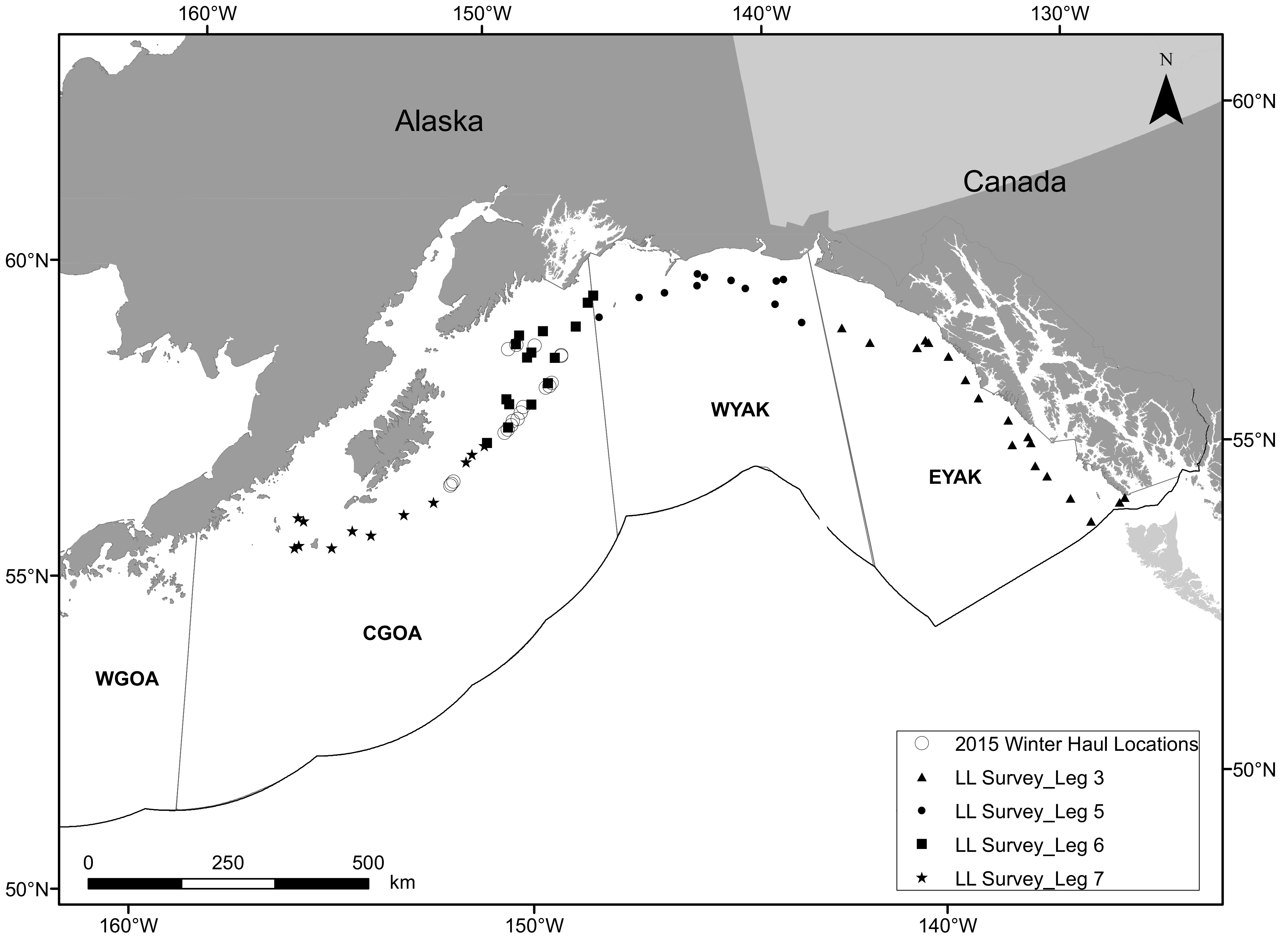
Fig. 4. Relationship between length and fecundity when the residual condition (RC) is average and the hepatosomatic index (HSI) is average (solid, black line), when HSI is average and RC is either plus or minus one standard deviation (blue lines), when RC is average and the HSI is either plus or minus one standard deviation (red lines), or when both RC and HSI are plus or minus one standard deviation (dashed, black lines).

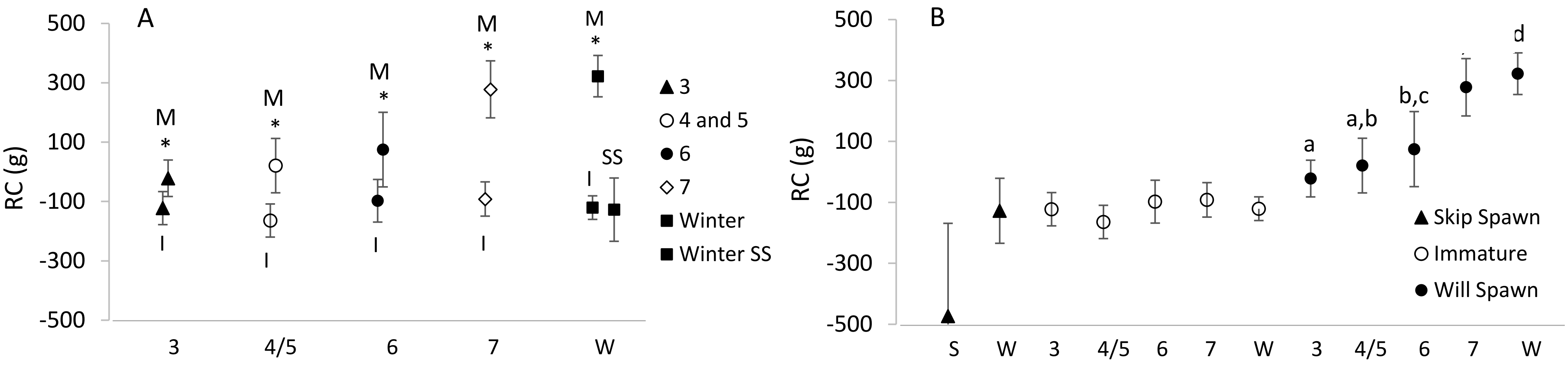
Fig. 5. Logistic curves of maturity at age when maturity was determined using histology slides (Histo), predicted using models M0 through M5, or classified macroscopically at-sea (macro) for Legs 3 and 4/5 of the summer Alaska Fisheries Science Center's longline survey. The maturity-at-age curve currently used in the Alaska sablefish stock assessment (SA) population model is also included; the same curve is used for all legs. Note that on Leg 3 M0, M1, and M4 are nearly identical and cannot be visually differentiated. In the Leg 5 panel M0 through M4 are very similar and in some cases cannot be visually differentiated. M5 is very similar to Macro.

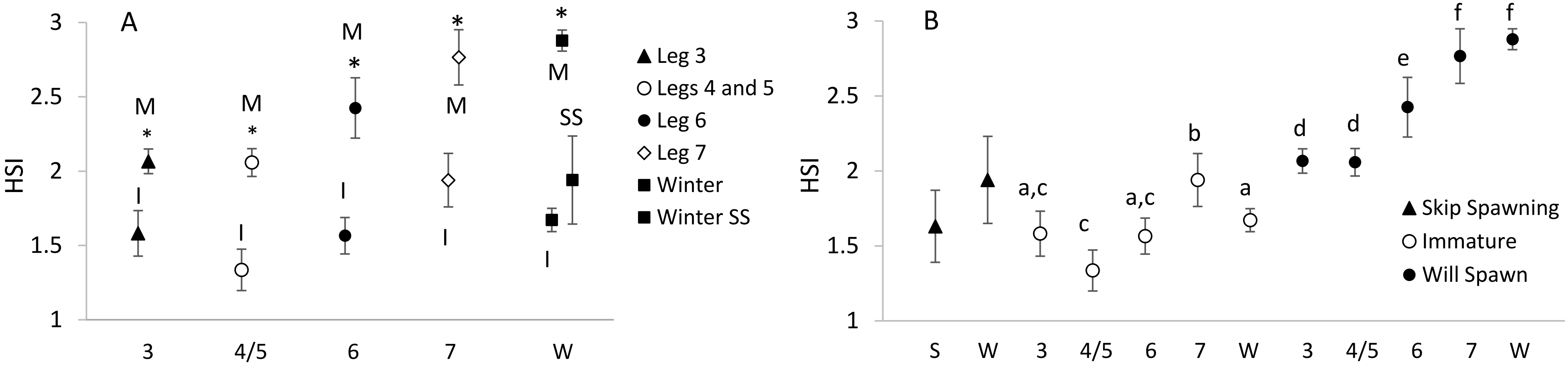
Fig. 6. Logistic curves of maturity at age when maturity was determined using histology slides (Histo), predicted using models 0–5 (M0 through M5), or classified macroscopically at-sea (macro) for Legs 6 and 7 of the Alaska Fisheries Science Center longline survey. The maturity-at-age curve currently used in the Alaska sablefish stock assessment (SA) population model is also included; the same curve is used for all legs. Note that in the Leg 6 panel M1 cannot be seen because it is matches very closely to Histo.

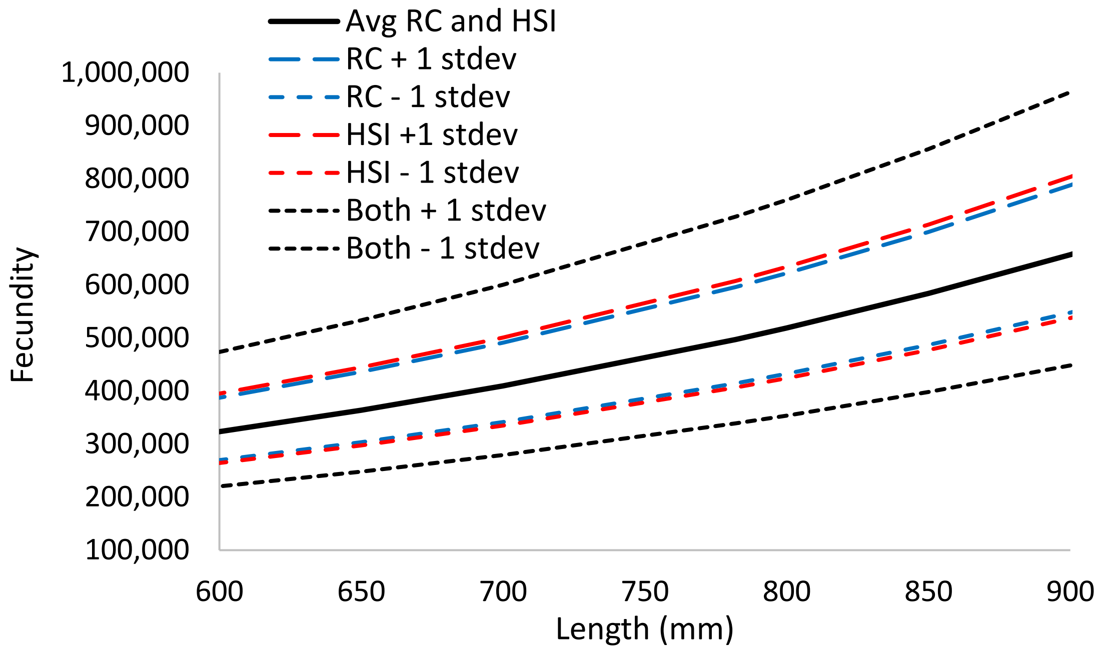
Fig. 7. Age-at-50% maturity parameters of logistic regressions fit to maturity-at-age data for each survey leg from either 1) maturity designations produced from each predictive model (M0-M5); 2) maturity designations from histology slides (histo); 3) for maturity designations made at-sea from fresh ovaries (macro); or 4) the parameter used in the stock assessment (SA). The SA model is used for all geographic areas in Alaska. All data were collected on the Alaska Fisheries Science Center annual longline survey, except for data used in the SA model. The 95% confidence intervals were obtained from running 1,000 bootstraps. There is no raw data available for the SA curve and so there are no confidence intervals. Values are presented in Table 8.

Fig. 8. Slope parameters of logistic regressions fit to maturity-at-age data for each survey leg from either 1) maturity designations produced from each predictive model (M0-M5); 2) maturity designations from histology slides (histo); 3) for maturity designations made at-sea from fresh ovaries (macro); or 4) the parameter used in the stock assessment (SA). The SA model is used for all geographic areas in Alaska. All data were collected on the Alaska Fisheries Science Center annual longline survey, except for data used in the SA model. The 95% confidence intervals were obtained from running 1,000 bootstraps. There is no raw data available for the SA curve and so there are no confidence intervals. Values are presented in Table 8.

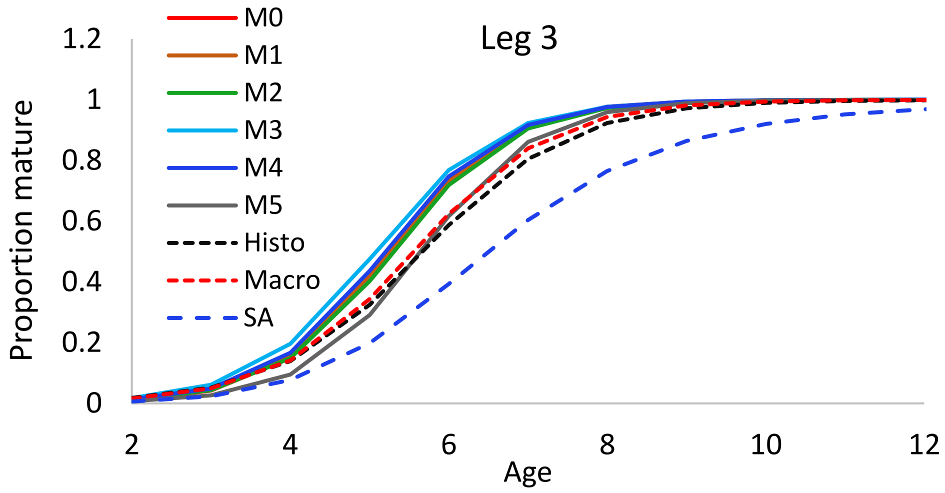

160°W
150°W
140°W
130°W
60°N
55°N
50°N
160°W
150°W
140°W
N
Alaska
Canada
WYAK
EYAK
CGOA
WGOA
○ 2015 Winter Haul Locations
▲ LL Survey_Leg 3
● LL Survey_Leg 5
■ LL Survey_Leg 6
★ LL Survey_Leg 7
0
250
500
km

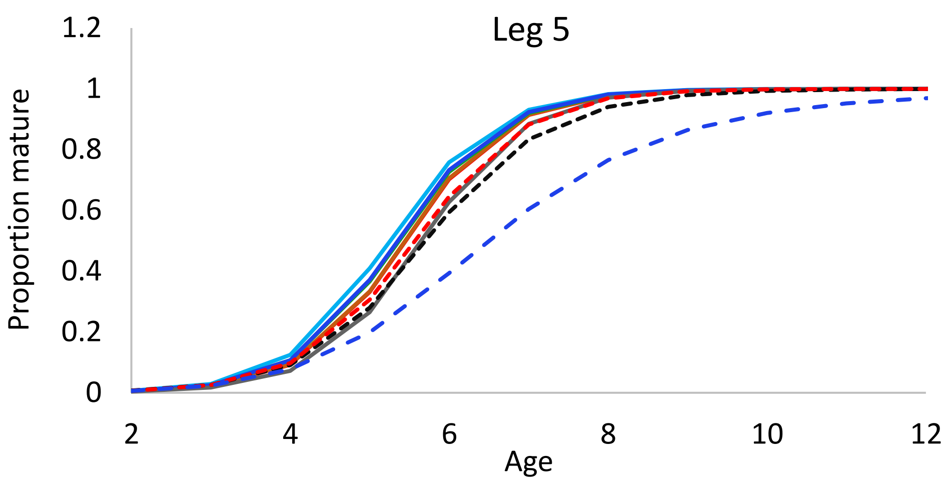

A
RC (g)
500
300
100
-100
-300
-500
M
*
I
3
4/5
6
7
W
SS
▲ 3
○ 4 and 5
● 6
◇ 7
■ Winter
■ Winter SS
B
d
a
a,b
b,c
S
W
3
4/5
6
7
W
3
4/5
6
7
W
▲ Skip Spawn
○ Immature
● Will Spawn

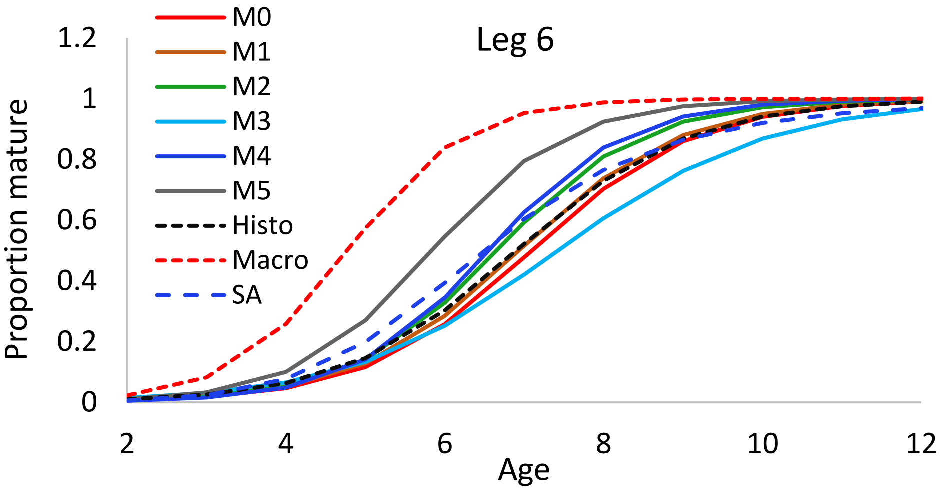

A
HSI
3
2.5
2
1.5
1
3
4/5
6
7
W
M
*
I
M
*
I
M
*
I
*
M
I
*
M
SS
I
▲ Leg 3
○ Legs 4 and 5
● Leg 6
◇ Leg 7
■ Winter
■ Winter SS
B
HSI
3
2.5
2
1.5
1
S
W
3
4/5
6
7
W
3
4/5
6
7
W
a,c
c
a,c
b
a
d
d
e
f
f
▲ Skip Spawning
○ Immature
● Will Spawn

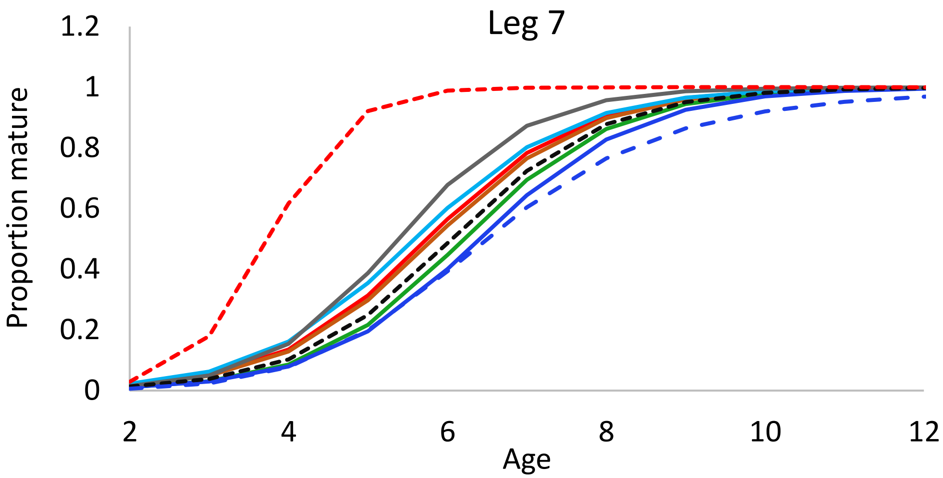


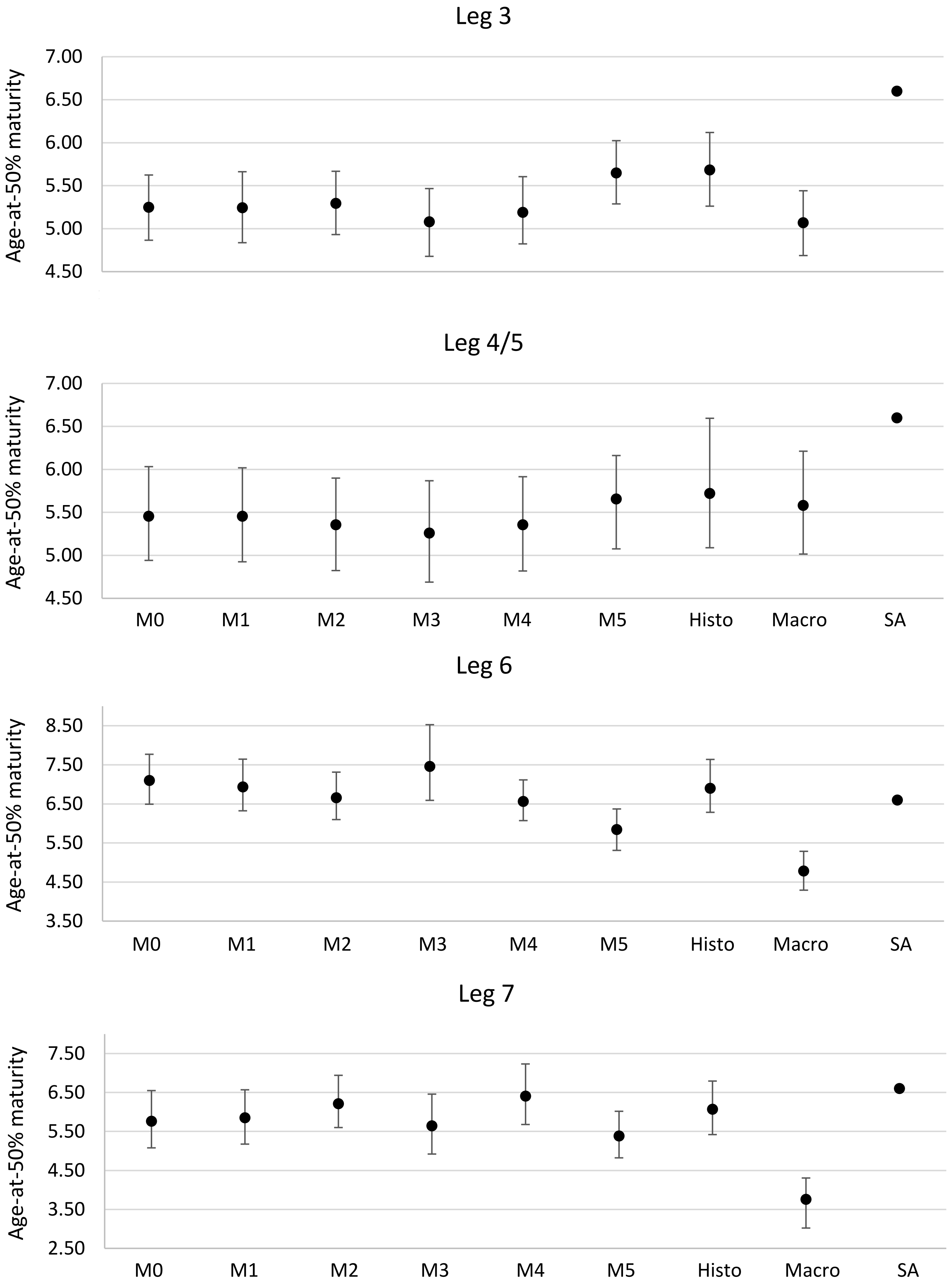
Avg RC and HSI
RC + 1 stdev
RC - 1 stdev
HSI +1 stdev
HSI - 1 stdev
Both + 1 stdev
Both - 1 stdev
Fecundity
1,000,000
900,000
800,000
700,000
600,000
500,000
400,000
300,000
200,000
100,000
600
650
700
750
800
850
900
Length (mm)

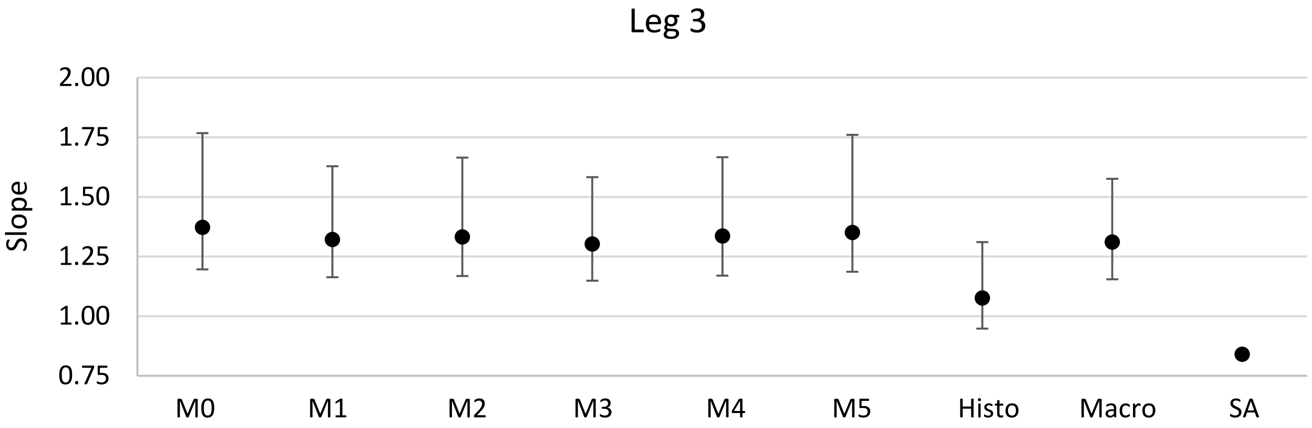

M0
M1
M2
M3
M4
M5
Histo
Macro
SA
Leg 3
Proportion mature
1.2
1
0.8
0.6
0.4
0.2
0
2
4
6
8
10
12
Age

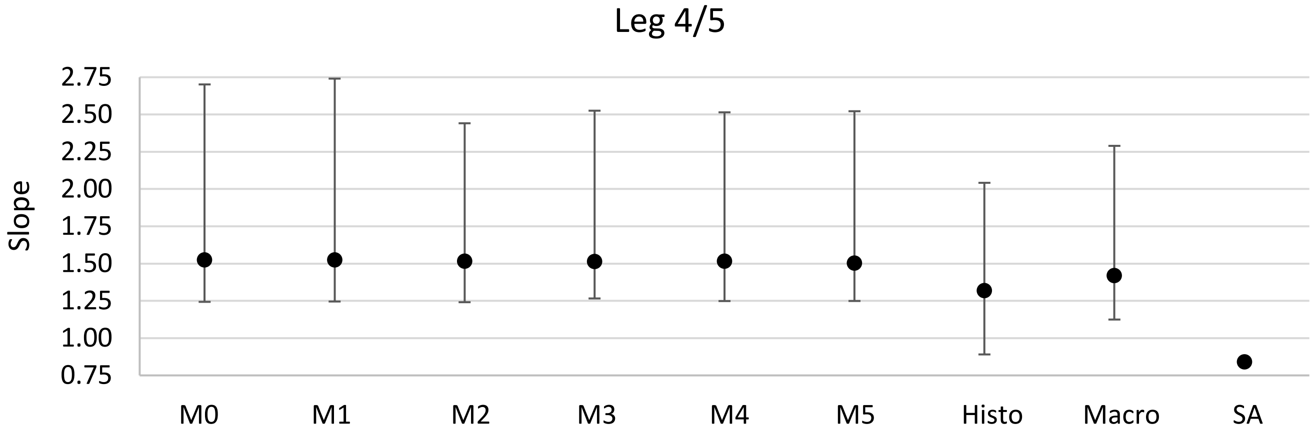

Leg 5
Proportion mature
1.2
1
0.8
0.6
0.4
0.2
0
2
4
6
8
10
12
Age

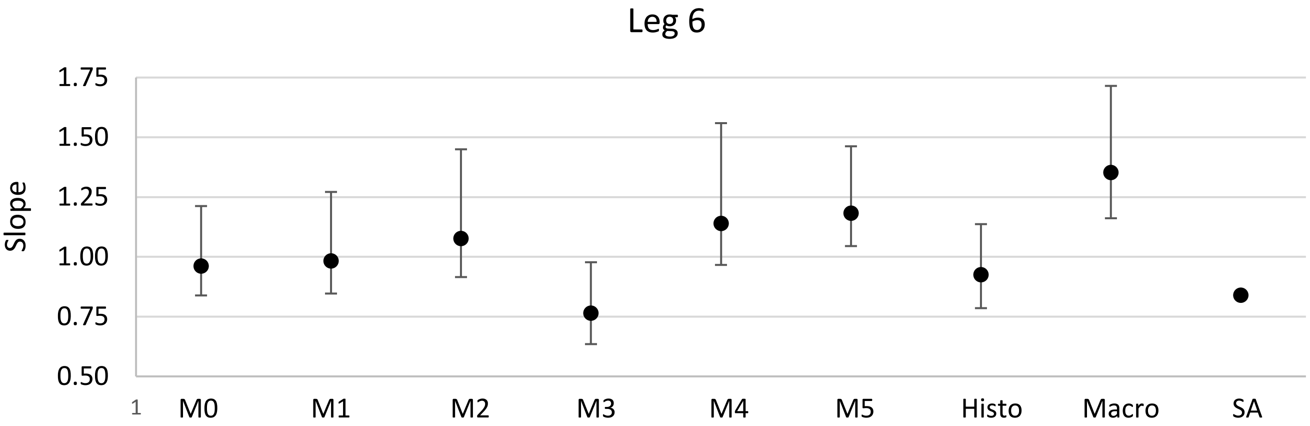

Leg 6
M0
M1
M2
M3
M4
M5
Histo
Macro
SA
Proportion mature
1.2
1
0.8
0.6
0.4
0.2
0
2
4
6
8
10
12
Age

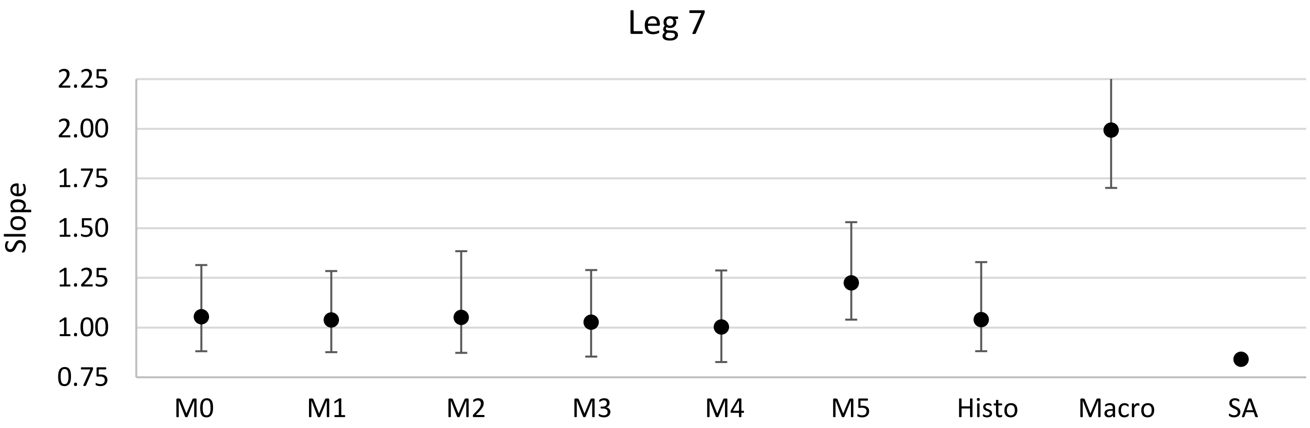

Leg 7
Proportion mature
1.2
1
0.8
0.6
0.4
0.2
0
2
4
6
8
10
12
Age


Leg 3
Age-at-50% maturity
7.00
6.50
6.00
5.50
5.00
4.50
SA
Leg 4/5
Age-at-50% maturity
7.00
6.50
6.00
5.50
5.00
4.50
M0
M1
M2
M3
M4
M5
Histo
Macro
SA
Leg 6
Age-at-50% maturity
8.50
7.50
6.50
5.50
4.50
3.50
M0
M1
M2
M3
M4
M5
Histo
Macro
SA
Leg 7
Age-at-50% maturity
7.50
6.50
5.50
4.50
3.50
2.50
M0
M1
M2
M3
M4
M5
Histo
Macro
SA


Leg 3
Slope
2.00
1.75
1.50
1.25
1.00
0.75
M0
M1
M2
M3
M4
M5
Histo
Macro
SA


Leg 4/5
Slope
2.75
2.50
2.25
2.00
1.75
1.50
1.25
1.00
0.75
M0
M1
M2
M3
M4
M5
Histo
Macro
SA


Leg 6
Slope
1.75
1.50
1.25
1.00
0.75
0.50
1
M0
M1
M2
M3
M4
M5
Histo
Macro
SA


Leg 7
Slope
2.25
2.00
1.75
1.50
1.25
1.00
0.75
M0
M1
M2
M3
M4
M5
Histo
Macro
SA