Batch Fecundity and an Attempt to Estimate Spawning Frequency of King Mackerel (*Scomberomorus cavalla*) in U.S. Waters

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ABSTRACT

Previous fecundity estimates for king mackerel assumed a determinate spawning pattern, but recent evidence for king mackerel and similar species indicates that they are indeterminate spawners, with the possibility of multiple spawning events over a protracted (months long) reproductive season. Our objective was to estimate the batch fecundity and the spawning frequency needed for an indeterminate fecundity approach. We found regional and temporal differences in batch fecundity. Batch fecundity was lower in east Florida (Atlantic) than NW Florida (NE Gulf of Mexico). This regional difference was largely attributed to the low oocyte density of females sampled from the early portion of a bi-modal spawning season in the Atlantic, a pattern not seen in the Gulf. Mean spawning fractions by region and year ranged from 7.1 to 11.5%. However, our finding that 88% of the histologically assessed fecundity samples contained both old and more recent post-ovulatory follicles suggests that spawning fractions are much higher, and thus spawning is occurring more frequently than estimates made by observing females with visibly hydrated ovaries. Estimates of annual fecundity could not be determined due to difficulties in spawning frequency estimation; improved estimates would require histological calibration and expanded spatio-temporal sampling. For stock assessment purposes, we ultimately had to assume that batch fecundity was an adequate metric to estimate reproductive potential for the population model. Due to limited sample sizes, the assessment advice was to apply a single batch fecundity function covering both the Gulf and Atlantic management units in southeastern U.S. waters.

KEY WORDS: King mackerel, batch fecundity, spawning frequency

Fecundidad por Desove e Intentos para Estimar Frecuencia de Desove del Carite Lucio o Peto (*Scomberomorus cavalla*) en Golfo de México y Costa Atlántica de los Estados Unidos

Previos estimados de fecundidad para el carite lucio (peto in México) asumen un patrón de desove total, pero información reciente indica que el carite lucio tienen un patrón de desove seriado, con múltiples desoves durante la temporada de reproducción. El objetivo del estudio fue determinar fecundidad por desove y frecuencia de desoves para estimar fecundidad total. Se encontraron diferencias regionales y temporales en la fecundidad por desove. La Fecundidad por desove fue menor en la costa Atlántica de Florida comparado con costa del Golfo de México. Esta diferencia regional se atribuye principalmente a una baja densidad de ovocitos en las hembras muestreadas en el Atlántico durante la primera temporada del período reproductivo, el cual muestra una distribución bi-modal. Este patrón bi-modal no se observo en el Golfo de México. Promedios de frecuencia de desove por área y año varían de 7.1 a 11.5%. Sin embargo, los resultados mostraron que el 88% de las muestras de fecundidad evaluadas histológica-mente contenían folículos post-ovulatorios recientes y tardíos; sugiriendo que la fracción de desove es mucho mayor, y que los desoves ocurren con mayor frecuencia que los estimados obtenidos por observación visual de hembras con ovarios con ovocitos hidratados. Para efectos de la evaluación del recurso, se asumió que la fecundidad por desove es un parámetro adecuado para estimar diferencias relativas en el potencial reproductivo por edad, requerido por los modelos dinámicos de población. Estimados de fecundidad por desove fueron calculados para las poblaciones del carite lucio del Atlántico y Golfo de México por separado. Estimados más robustos y precisos requieren calibración histológica y un muestreo espacio-temporal mucho más intensivo.

PALABRAS CLAVES: Carite, fecundidad por desove, frecuencia de desove

Fécondité par Ponte et Essai D'estimation de la Fréquence de Ponte du Tharard Rayé (*Scomberomorus cavalla*) aux E.U.

Les données antérieures sur la fécondité du thazard rayé sont basées sur un modèle de frai déterminé, mais des données récentes pour cette espèce et les espèces similaires indiquent qu'ils ont une saison de frai indéterminée, avec la possibilité de frai multiple sur une saison de reproduction prolongée (sur des mois). Notre objectif était d'estimer la fécondité par ponte et la fréquence du frai nécessaire pour établir un modèle basé sur une fécondité indéterminée. Nous avons trouvé des différences régionales et temporelles pour ce paramètre. La fécondité est plus faible dans l'est de la Floride (Atlantique) que dans le nord ouest de la Floride (NE golfe du Mexique). Cette différence régionale a été largement attribuée à la faible densité d'ovocytes des femelles échantillon-nées au début de la saison bi-modale de ponte dans l'Atlantique, un modèle non observé dans le Golfe. La moyenne des fréquences de ponte par région et par an variait entre 7,1 et 11,5 %. Cependant, l'examen histologique a révélé que 88 % des échantillons contenait des follicules post-ovulaires à la fois récentes et anciennes. Cela suggère que les fréquences de ponte sont plus élevées et que la ponte se produit plus fréquemment qu'avec les estimations faites sur les femelles ayant des ovocytes hydratées visibles. Pour l'évaluation des stocks, nous devions supposer que la fécondité par ponte était une mesure adéquate pour estimer les différences relatives dans les potentialités de reproduction à un age nécessaire au modèle de dynamique des populations. L'estimation de la fécondité a été calculée séparément pour le Golfe et l'Atlantique, pour les deux unités de gestion du sud-est des E.U. L'amélioration

des estimations nécessiterait une calibration histologique et un échantillonnage spatio-temporel étendu.

MOTS CLÉS: Thazard rayé, Fécondation par ponte, fréquence de ponte

INTRODUCTION

Fish assessment models require data on reproductive potential, which is most appropriately measured as fecundity at age (or fecundity at size converted to age). But a common problem in fisheries has been a mis-specified fecundity approach. Previous fecundity estimates for king mackerel (Finucane *et al.* 1986) assumed a determinate spawning pattern. This approach is known to underestimate fecundity in fishes that actually exhibit indeterminate oocyte development reflected in multiple spawning events over a protracted months-long season (Murua *et al.* 2003). Thus, our objective in this study was to estimate batch fecundity based upon directed sampling during 2005 - 2007. We also sought to estimate spawning frequency using macroscopic observations of mature and hydrated females obtained during port sampling.

METHODS

Efforts were made to obtain lengths (mm), weights (kg), gonads and otoliths from king mackerel caught by commercial and recreational fisheries, from the Gulf of Mexico and U.S. South Atlantic. However, reproductive samples were only commonly available from the east coast of Florida (hereafter Atlantic) and northeastern Gulf of Mexico (northwest Florida and Alabama; hereafter Gulf). All reproductive sampling was from gear categorized as handline, whether from commercial or recreational boats (charterboats and headboats). Beginning in 2005, a cooperative research program (CRP) directed at age and growth and stock delineation (William Patterson, PI, University of West Florida) expanded sampling efforts to provide reproductive samples throughout the spawning season. Based upon a call for batch fecundity estimates for king mackerel (from advisory panels for the South Atlantic and Gulf of Mexico Fisheries Management Councils) efforts to identify and collect ovaries from hydrated females was deemed important and thus samples were taken as opportunities allowed during routine age-structure sampling and the previously mentioned CRP project. Spawning duration was estimated by looking at the temporal distribution of hydrated females. Differences in duration between the Atlantic and Gulf and between years were examined.

While most of the king mackerel females sampled for fecundity were haphazardly selected based upon whether the ovaries appeared to be hydrated, estimation of spawn-ing frequency requires random sampling and distinguishing mature non-spawning females from those in active spawning condition. There were periods in which three port samplers made this distinction; two samplers working

in the northeastern Gulf in 2006 and 2007, and one working in east Florida in 2007.

Batch Fecundity

Batch fecundity was determined using the hydrated oocyte method. Ovarian tissue samples were cross-sectioned, weighed to the nearest 0.001 g and placed in a vial along with 33% glycerol to separate oocytes for the purpose of counting (Collins *et al.* 1998). Hydrated oocyte counts were expressed as:

i) Oocyte density or the number of hydrated oocytes per gram of ovarian tissue,

ii) Relative fecundity or the number of hydrated oocytes per gram of female body weight, without ovary (see Dickerson *et al.* 1992) and

iii) Batch fecundity; calculated by multiplying the final hydrated ooctye estimate by the whole ovary weight, and the product was divided by the weight of the sample (Dickerson *et al.* 1992, Collins *et al.* 1998).

For most hydrated ovaries, samples were also taken to prepare histological slides (by Louisiana State University School of Veterinary Medicine). Evidence of recent post-ovulatory follicles (POF) in any histological section, suggesting the female may have partially spent her current batch, could then be used as a criterion to eliminate that sample from the fecundity estimates.

A two-factor ANOVA was used to test for differences among regions of the ovary (n = 6; anterior, middle, and posterior of left and right lobes) and between locations within those regions (periphery versus interior of a cross-section) (n=3 females) (EXCEL 2007). No significant differences were found in either factor; therefore one tissue sample was taken from a randomly selected ovary region and location within each hydrated ovary. Regression was used to examine relationships between batch fecundity and fork length (FL), whole weight (Wt), and age for all hydrated females (Collins *et al.* 1998, 2002). An ANOVA of hydrated oocyte density was conducted to examine the effects of month (Apr-Aug), year (2005 - 2007) and geographic region (Gulf and Atlantic) (XLSTAT version 7.5). A Tukey (HSD) test was used to compare means within categories.

Spawning Frequency

Spawning frequency (batch interval) was estimated based on the average daily spawning fraction of mature females showing hydrated ova (assumed day-0 proportion), out of the total mature (active) females (determined macroscopically). The inverse of the spawning fraction yields the average expected interval in days between spawning events. The overall spawning season duration in days divided by the average interval yielded the expected number of spawns per female per annual reproductive season (Fitzhugh *et al.* 1993, Nieland *et al.* 2002, Murua *et al.* 2003).

RESULTS

Batch Fecundity Location Test

We found no significant differences in batch fecundity by ovarian region or cross-section position (Table 1). About 98% of the variance was unaccounted for by the model ($r^2 = 0.022$), indicating that most of the variation in batch fecundity occurred between females rather than among ovarian locations within a female.

Batch Fecundity Sample Summary

A total of 178 females were sampled and macroscopically confirmed as hydrated females before ovaries were preserved (Table 2). Most samples were collected in 2006 (n = 100), most came from the Atlantic (east Florida, n = 146) and most were taken in August (n = 85) followed by June and May (n = 43 and 44, respectively). In the Atlantic, hydrated females tended to be encountered in two periods; April-June and again in August with no hydrated females detected in July (Figure 1). In the Gulf, hydrated females were encountered in 2006 and 2007 and over a shorter duration from May to July (40 and 62 d; Figure 1).

The smallest hydrated female was 602 mm FL with most females greater than 700 mm FL (Figure 1).

Test of Oocyte Density by Month, Year and Region

An analysis of variance of oocyte density (hydrated oocytes/g ovarian tissue) among months, years, and geographic region revealed significant differences by month only (Table 3). A Tukey HSD test further revealed the significant difference occurred for the contrast between August (highest oocyte density) and April (lowest density). However the sample size was low for April, only two females in spawning condition were sampled from east Florida (Atlantic). The general trend in the Atlantic was for oocyte density to be lower in the early part of the season (April-May; mean = 1709) than in the later (June – August; mean = 2689; Figure 2). Sample sizes and overall densities were lower for the Gulf, and no apparent monthly trend was evident (means = 1980, 2182, and 1739 for May, June, and July respectively; Figure 2). Over all, mean oocyte density was 2351 hydrated oocytes/g ovarian wt (sd = 723) in contrast to relative fecundity which equaled 140 hydrated oocytes/ g of ovary-free body wt (sd = 63).

Table 1. Raw data for hydrated oocyte density from 3 females; two-way analysis of variance by 6 ovarian regions and two

Region Sample

Core location	A	B	C	D	E	F
inner	1387	1457	1587	1360	1491	1633
	1444	2336	2101	1644	1238	639
	3912	3280	3600	3324	3685	3573
outer	1325	1744	1305	1419	1430	1713
	1824	1798	1733	1931	1671	1348
	3610	3872	3795	3885	3373	3360

Source of Variation	SS	df	MS	F	P-value
XS position (inner vs outer core)	57979.01119	1	57979.01	0.039046	0.845022
Regions (A - F)	542016.6981	5	108403.3	0.073004	0.995749
Interaction	188514.4195	5	37702.88	0.025391	0.999665
Within	35637576.74	24	1484899		
Total	**36426086.87**	**35**			

Table 2. Distribution of fecundity samples (number of hydrated females) by region, month and year. n = 178 female king mackerel.

		Apr	May	June	July	August
	2005		1			
Gulf	2006			10	3	
	2007		2	14	2	
	2005		29	11		11
Atlantic	2006	2	7	4		74
	2007		4	4		
	Total	**2**	**43**	**43**	**5**	**85**

Table 3. Analysis of variance of hydrated oocyte density among months, years and geographic regions.

Source	df	SS	MS	F	Pr > F
Month	4	30997977.565	7749494.391	22.587	< 0.0001
Year	2	844854.342	422427.171	1.231	0.295
Mackerel Region	1	300340.162	300340.162	0.875	0.351
Month*Mackerel Region	1	811453.266	811453.266	2.365	0.126
Month*Year*Mackerel Region	6	3664615.971	610769.328	1.780	0.106
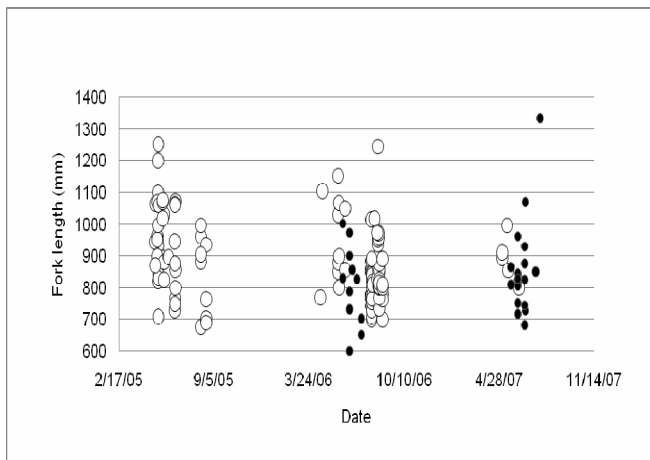
Figure 1. Capture dates and lengths of hydrated female king mackerel. Atlantic data are represented by open circles and Gulf data by closed circles. The estimated spawning season duration in days based upon earliest and latest appearances of hydrated females; Atlantic 2005-103d, 2006-131d, 2007-50d; Gulf 2006-40d, 2007-62d.
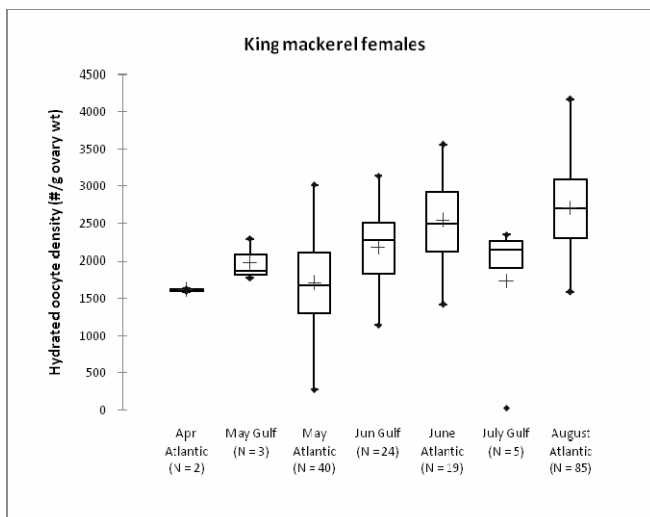
Figure 2. Box plots of hydrated oocyte density by month and geographic region. The center line of each box represents the median and cross-hairs indicate the mean. The minimum and maximum values are shown.

Batch Fecundity Relationships

The fecundity-length relationships for the Gulf (all data) and Atlantic (June and August) were very similar and appeared to be linear with slopes of 3220 and 3111, respectively (Figure 3). These relationships had r^2s of 0.68 and 0.70 and had a common intercept of -2E+06. In contrast, the fecundity-FL relationship for the early season Atlantic data (Apr-May), also linear, had a much lower slope of 1459 (Figure 3).

Like the length-based linear regressions, the fecundity-age fits also reflected a region-month trend for the Atlantic. Slopes of the Gulf (all data) and June- and August Atlantic relationships were similar; 19032 ($r^2 = 0.761$) and 19302 ($r^2 = 0.469$), respectively (Figure 4). The fecundity-age relationship for all Atlantic data combined had a much lower fit ($r^2 = 0.179$), and an examination of the plotted data suggested more than one relationship may exist in the Atlantic.

Spawning Frequency

King mackerel in the Gulf were estimated to spawn, on average, every 2.9 and 4.5 da (7.1% and 7.2% spawning fractions) in 2006 and 2007, respectively; while those in the Atlantic spawned every 5.7 da (11.5% spawning fraction) in 2007 (Table 4). Spawning frequency was estimated based upon 83 trips (collections) made during May – August 2006 and 2007; 13 trips in the Atlantic and 60 trips in the Gulf (Table 4). Most hydrated females, and thus the highest spawning fraction, were encountered in May and June in the Atlantic and June in the Gulf.

DISCUSSION

Our batch fecundity estimates indicate king mackerel have a greater reproductive potential than that suggested by Finucane *et al*. (1986). Based upon the fecundity-length relationship for NW Florida in their Table 4 (Finucane *et al*., 1986) the expected annual fecundity of an 800 mm FL female would be 1,644,805 ova. However, we estimated that a single batch should equal 560,000 ova for a female this size (linear regression) and thus three spawning events could exceed the egg production of the earlier estimate. Although the fecundity method Finucane *et al*. used assumed a determinate oocyte development pattern, they found consistent ratios of oocytes in different development stages across a protracted spawning period of several months and concluded that multiple spawning was occurring. Given our improved understanding of fecundity

patterns (e.g. Murua *et al.* 2003), the oocyte development pattern described by Finucane *et al.* supports the conclusion that fecundity is indeterminate in king mackerel. This is also a common finding for other scombrids and mackerel-like carangids as well (Dickerson *et al.* 1992, Karlou-Riga and Economidis 1997, Abaunza *et al.* 2003, Mackie *et al.* 2005). Our estimated relative fecundity for king mackerel of 140 hydrated oocytes/g gonad free body weight is approximately the middle of the range of estimates for other scombrids and mackerel-like carangids. Other species estimates include: 28-55 oocytes/g (*Scomber scomber*; Dickerson *et al.* 1992), 112 oocytes/g (*Trachurus symmetricus*, Macewicz and Hunter 1993), 168-278 oocytes/g (*Scomber japonicas*; Dickerson *et al.* 1992), and 205 oocytes/g (*Trachurus trachurus*; Karlou-Riga and Economidis 1997).

We chose not to eliminate any of the fecundity estimates which showed histological evidence of recent POFs because almost all (88%) of the hydrated females examined exhibited both old and recent POFs suggesting high spawning frequency. We would only have been able to retain 19 of the remaining 152 samples had we used this criterion (26 of 178 fecundity samples were unavailable for histological processing). In the king mackerel fishery we sampled in the Atlantic, fishing occurred at all times of day and night; and for most samples, time of catch was unspecified. Given that fish were caught throughout the day and night, at least some partially spawned gonads very likely were sampled, possibly increasing the variance of the fecundity relationships. We cannot clarify this possibility further without knowing more about the time of catch relative to spawning and more about the time involved in the degeneration of post-ovulatory follicles
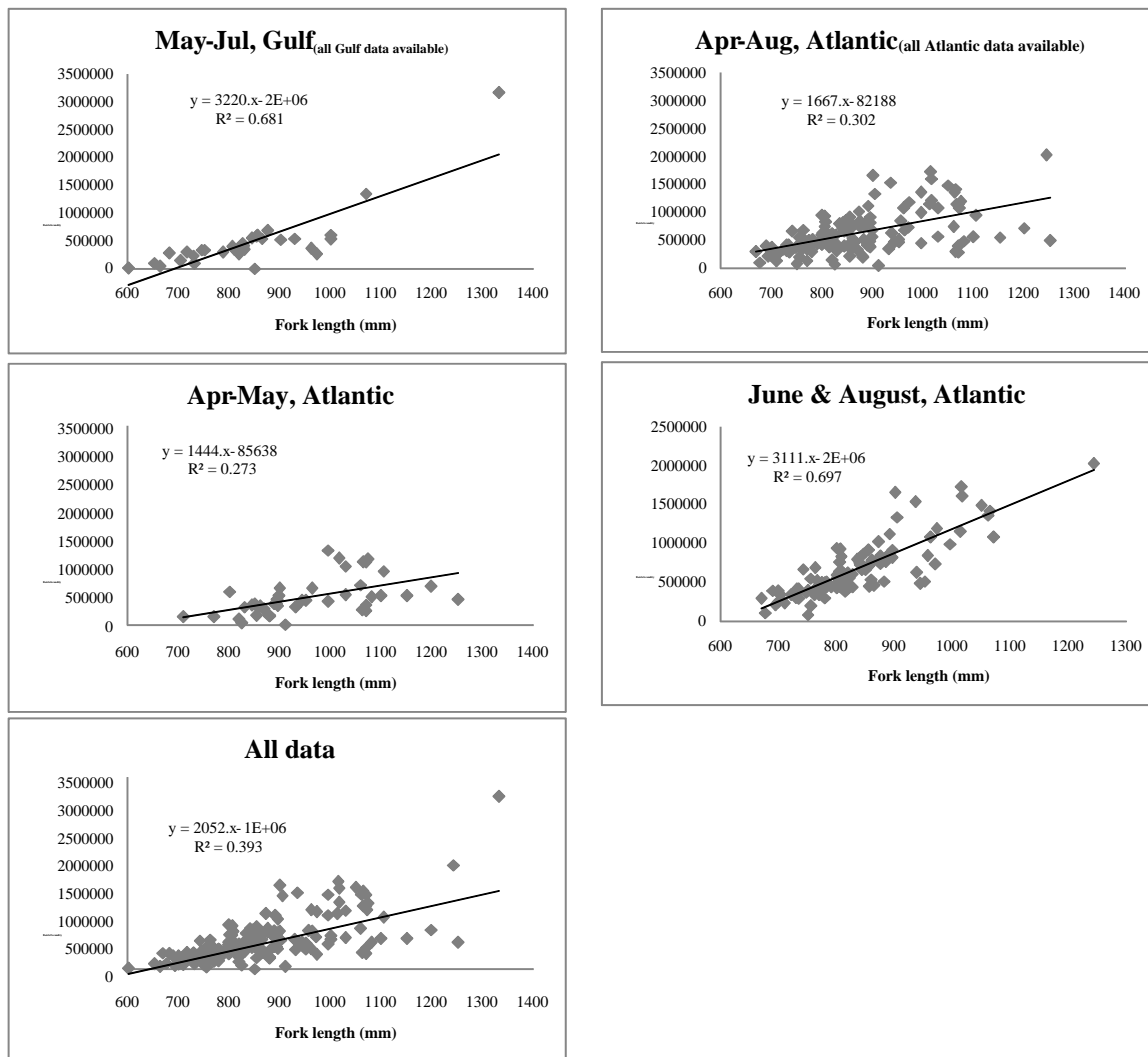
Figure 3. Batch fecundity- fork length regressions for combinations of month and geographic region.

(e.g., was a recent POF from the previous hour or from the previous night?). We assume that once the fish is killed and put on ice, physiological changes such as final oocyte maturation and POF degeneration are arrested. For other fishes, where capture commonly occurs during the day and spawning occurs at night, the issue is less problematic.
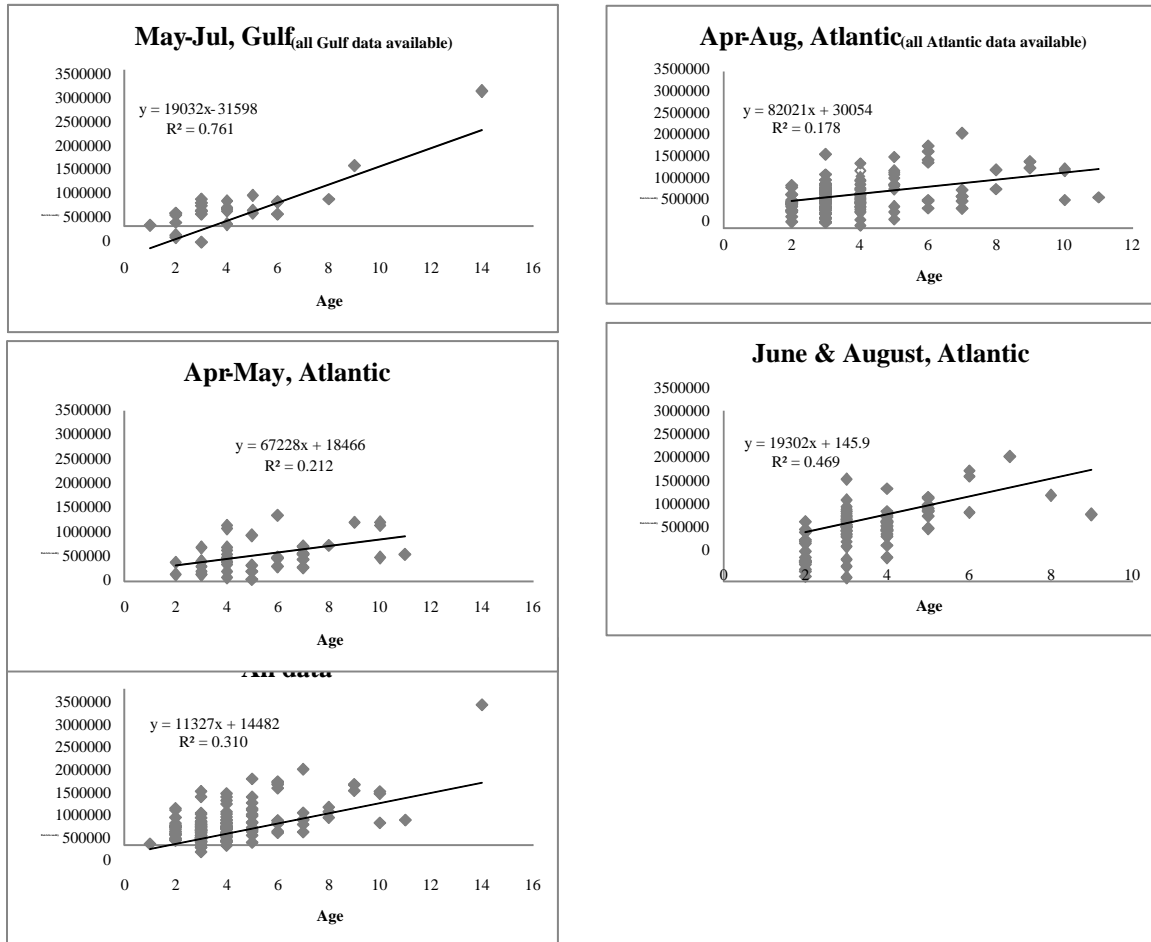

Figure 4. Batch fecundity-age regressions for combinations of month and geographic region.

Table 4. Spawning frequency estimate based upon detecting visibly hydrated (H) females. Annual spawning interval based on those months or periods that have hydrated females; Atlantic 2007 includes May and June (only 1 fish was encountered in hydrated condition in August during random trips). See Figure 1 for estimates of season duration.

	Year	Gulf 2006	Gulf 2007	Atlantic 2007
May	# Trips or collections	2	6	3
	# Active females	13	30	53
	# H	0	1	8
	H Spawning interval (d)	0	30	6.63
June	# Trips or collections	26	13	5
	# Active females	192	81	50
	# H	16	7	6
	H Spawning interval (d)	12	11.57	8.33
July	# Trips or collections	8	6	2
	# Active females	89	27	12
	# H	4	0	0
	H Spawning interval (d)	22.25	0	0
August	# Trips or collections	7	2	3
	# Active females	36	12	28
	# H	0	0	1
	H Spawning interval (d)	0	0	28
	Average daily spawning fraction	0.07	0.07	0.11
	Annual average spawning interval (d)	14.05	13.88	8.73
	Estimated season duration (d)	40	62	50

Certainly our findings indicate king mackerel spawning is variable in time (monthly and annually) and location. There was an apparent hiatus in spawning in July off east Florida, and only one hydrated female was encountered in August 2007 where they were commonly encountered in August 2005 and 2006. A bi-modal spawning pattern is thought to be the norm for east Florida (M. Gamby, Unpublished observations). In NW Florida, routine age-length sampling over the past 15 years has yielded virtually no females in spawning condition (D. DeVries, Unpublished observations). Several females in hydrated condition were noted in 2005 and again in 2006 and 2007. In general, few spawning females were detected relative to the number routinely examined during port sampling.

It was interesting to note that the batch fecundity relationships for the June and August Atlantic data and Gulf data had very similar linear fits (slopes and intercepts). But our finding that April-May Atlantic data was best fit by a fecundity relationship with a notably lower slope again suggests that reproductive output is not constant with respect to either time or location or both. Does the difference signal multiple populations or components, a seasonal effect, or perhaps an artifact from lower sample sizes from the Atlantic early in the season? While these results may be suggestive of spatial-temporal differences, discussions during recent stock assessment workshops noted the paucity of data, especially for the Gulf. No fecundity data were available from the western Gulf. Therefore, a single batch fecundity function was derived from the NE Gulf and Florida Atlantic data for use in the 2008 stock assessment (Figure 5). Also based on the fact that fecundity is a function of the volume of the female, and volume increases exponentially with length, a power function was applied to fit the fecundity-fork length data. Fecundity at length was subsequently converted to fecundity at age using region specific von Bertalanfy growth functions (SEDAR 16 2008).
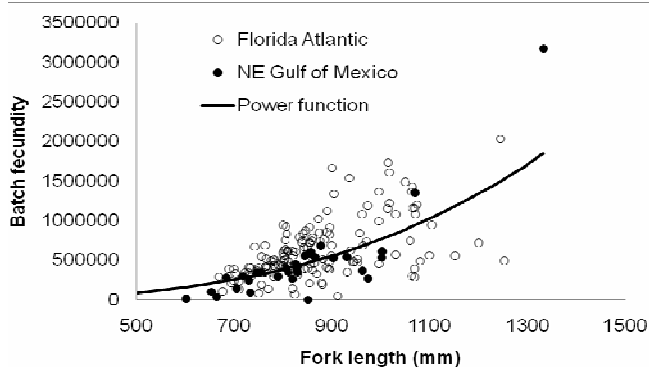
Figure 5. Power function for batch fecundity used as the estimate of reproductive potential for Gulf and Atlantic stocks combined: batch fecundity = $0.00054 * FL^{3.05}$.

Other workers have noted finding few spawning adult king mackerel and variation in time and location of spawning (Beaumariage 1973, Finucane *et al.* 1986, Sturm and Salter 1989, Figuerola-Fernández *et al.* 2007). Such patchy spawning behavior has also been noted for other scrombrids (Dawson 1986, Dickerson, *et al.* 1992, Mackie *et al.* 2005). These authors suggested that such a pattern arises when different age-size components within a stock move and spawn at different times and areas. One conclusion is that spawning frequency is easily underestimated in fishes with this trait (Dickerson *et al.* 1992). The fact that samplers can only detect visibly hydrated females to estimate spawning fraction probably returns a further underestimate of spawning frequency (Mackie *et al.* 2005). Hydration is typically a brief phase (hours) of final oocyte maturation on the day of spawning. Therefore, during the relatively short phase of final oocyte maturation, visibly hydrated females are detectable via macroscopic observations during an even smaller window of time. The assumption that visibly hydrated females can be detected over a period of about a day (day-0 proportion) is likely not met. Our finding that 88% of the histologically assessed fecundity samples contained both old and more recent post-ovulatory follicles further suggests that spawning frequency is much higher than estimated by observing the frequency of visibly hydrated females.

Others have indicated the difficulties in estimating spawning frequency in scombrids, particularly in making contrasts among age classes (Dickerson *et al.* 1992, Mackie *et al.* 2005, Figuerola-Fernández *et al.* 2007). A carefully considered sampling design would be needed to account for variation among regions and across time. A large scale random sampling program delivering thousands of otoliths and gonads to be examined histologically could expand the window of time to detect spawning females (including the migratory nucleus and post-ovulatory stages as well as hydrated oocytes) and enable an age-based contrast of spawning frequency. Thus, additional information is needed on:

i) The extent of hydration that can be determined via routine observations in the field,

ii) The timing of this phase relative to final oocyte maturation and spawning, and

iii) Calibration of the degeneration of post-ovulatory follicles to account for and correct a likely bias in spawning frequency estimates.

Such an expanded approach to collect spawning frequency data by age would certainly be costly, and we think it may be worthwhile to investigate other approaches for determination of reproductive potential in species such as king mackerel. Extrapolating average weight at age to spawning stock biomass estimates would be the least costly approach. But where sufficient data exist for some species, annual differences in population reproductive potential have been found to occur at equivalent levels of stock

biomass (Marshall *et al.* 2003). Fundamentally, we understand that energy gained by food consumed is the primary determinant of egg production (Tyler and Dunn 1976 and references therein). It may become feasible to apply cost-effective methods to measure 'surplus energy' that can serve as a proxy for the energy metabolized by the fish into egg production, rather than to measure the fecundity directly (Marshall *et al.* 1999). Regardless of the approach used, obvious sampling gaps need to be addressed first. There are no batch fecundity data from the western Gulf and larval abundance data suggests it may be the main region of king mackerel spawning in U.S. waters (Grimes *et al.* 1990, Gledhill and Lyczkowski-Shultz. 2000).

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