Reproductive maturity of striped marlin, *Kajikia audax*, in the central North Pacific off Hawaii

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Abstract

Declining trends in the population biomass of striped marlin, *Kajikia audax*, in the western and central North Pacific, have led to recent assessments of this regional stock. As part of the data inputs into these assessments, information on reproductive biology supports the evaluation of stock productivity. The lack of reproductive information for the central North Pacific area led to this study on reproductive maturity and spawning dynamics. This study relied on observer sampling of striped marlin gonad tissues collected onboard Hawaii-based pelagic longline vessels and the exclusive use of gonad histology to confirm gender and derive a first estimate of female length (eye-to-fork) at 50% maturity ($♀L_{EF50}$), spawning patterns, and sex ratios in the central North Pacific around Hawaii. Our estimate of $♀L_{EF50}$ (160.4 cm) was substantially smaller than estimates reported from the western North Pacific around Taiwan (181 cm; Chang et al., 2018) and western-central South Pacific (178.4 cm; Kopf et al., 2012). Female spawning period was May-July with peak spawning in May-June. Sex ratios were biased toward males during the spawning season for much of the size distribution but this lessened and shifted toward females during the August-April non-spawning period. Fish ≥180 cm EFL were infrequently caught for both sexes. The central North Pacific around Hawaii appears to represent a spawning, nursery, and young adult habitat from which fish emigrate as they grow.

Introduction

In the North Pacific, genetic evidence and fisheries data support recognition of two stocks north of the equator consisting of the western and central North Pacific Ocean (WCNPO) west of 140° W longitude and the eastern Pacific Ocean (EPO) east of 140° W (McDowell and Graves, 2009; Purcell and Edmans, 2011; Lee et al., 2012). A recently completed international

assessment update of the WCNPO stock has concluded it currently remains in an overfished state and overfishing persists (Chang et al., 2015). The present status of the WCNPO stock has been exacerbated by below-average recruitment since the 1990s (Piner et al., 2013). The resilience of a stock to recover can be assessed by modelling the steepness of the stock-recruitment relationship. Brodziak et al. (2015) used model simulations to determine the distribution of stock-recruitment steepness and reported that reproductive maturity can have a significant influence on steepness.

The current sources of reproductive information for WCNPO stock assessment studies rely on recent studies conducted in the western North Pacific and western South Pacific. No reproductive parameter estimates for recent WCNPO assessments have been available from the central North Pacific. This information gap may be limiting our current understanding of the stock status and reproductive potential within a substantial portion of the WCNPO stock. The focus of this study is to provide an estimate of female reproductive maturity and associated spawning characteristics based on the histological analysis of gonad samples collected at-sea from the Hawaii-based pelagic longline fishery. Results will provide first-time estimates of reproductive parameters for striped marlin inhabiting the central North Pacific.

Materials and methods

Sample collection

Contracted fishery observers trained and monitored by the NOAA Pacific Islands Regional Office in Honolulu, Hawaii, collected sub-samples of striped marlin gonads at-sea onboard Hawaii-based commercial pelagic longline vessels. The collection period ranged from January

2008 through October 2011 and included 399 vessel fishing trips for which collected gonads were evaluated in this study. The capture locations of sampled fish of both sexes over the nearly 5-year sampling period show a similar spatial pattern largely concentrated between 22-32° North latitude and 150-170° West longitude. This area of sample concentration aligns with waters immediately north and adjacent to the Hawaiian Archipelago from the mid-portion of the Northwestern Hawaiian Islands extending to above the Main Hawaiian Islands. A smaller concentration of samples occurred in an area southwest of the Main Hawaiian Islands and just east of Johnston Atoll centered around 15° N, 165° W. Observers were instructed to sample across a range of sizes during each trip and across all months.

Gonad sampling involved the excision of an approximately 1.5 cm x 2.5 cm section from the middle portion of either lobe of the ovary and testis including a portion of the gonad wall. Excised gonads were preserved fresh at sea (52.4%) in individual 100 ml plastic bottles containing the histological preservative Shandon Glyo-Fixx RTU (Thermo Scientific); the remainder (47.6%) were stored frozen. Each sampled fish was measured for length (posterior margin of the orbit to the central edge of the caudal fin, EFL) to the nearest cm. Other recorded data associated with each sampled fish included deployment and haul back position (latitude and longitude) of each longline set and date of capture.

Sample preparation

Gonad tissues were processed in the laboratory in preparation for histology. Fresh samples preserved at-sea in Shandon Glyo-Fixx RTU (Thermo Scientific) were removed from bottles and a cross-sectioned subsample that included the gonad wall was removed, placed in histology cassettes, and stored in a container of fresh preservative. Frozen samples were thawed, then

similarly subsampled, placed in histology cassettes, and stored in a container of 10% neutrally-buffered Formalin. The preparation of hematoxylin stained, eosin counterstained histology slides was conducted through a contract with the Histology Core facility of the John A. Burns School of Medicine, University of Hawaii, Manoa. All gonads examined and evaluated in this study were based exclusively on these histological preparations.

Histological evaluation

All gonad histology slide preparations were examined with a compound microscope over a range of magnifications (40-600x). Each slide was evaluated microscopically to identify gender. This data was used to determine female sex ratio, defined as the ratio of females to the total number of females and males combined. All ovary samples were further evaluated microscopically to document all oocyte developmental stages present. Other cellular features recorded included relative ovary wall thickness, presence of vascularized connective tissue, atresia and developmental stages of atretic oocytes, and presence of residual hydrated oocytes. The standardized terminology proposed by Brown-Peterson et al. (2011) to classify phases of the reproductive cycle of females and their associated developmental stages was adopted in this study (see Table 1). Females were classified as mature if the most advanced group of oocytes attained at least the secondary vitellogenic stage (Vtg2) or if ovaries contained oocytes in more advanced development stages including the presence of post-ovulatory follicles. Females were also classified as mature if specific ovarian structural features associated with previous spawning (thickened ovarian wall and the presence of residual hydrated oocytes) were observed. Among mature individuals, females were classified as actively spawning if the most advanced group of oocytes included developmental stages from germinal vesicle migration to hydration. Females were classified as immature if none of these latter developmental stages and structural features

were present and if the most advanced group of oocytes were restricted to primary growth, cortical alveoli, or primary vitellogenic stage (Vtg1) oocytes.

Statistical analysis

All histology derived data that recorded microscopy evaluation of each sample were digitized for statistical analysis, including gender, reproductive phase, oocyte developmental stages present including atretic oocytes, observations on additional gonadal structures present, and preservation method. Histology data for each sample were linked to the observer collection data that included sample identification number, capture date and location (latitude and longitude), and EFL. Female length distributions were evaluated by month, maturity status, latitude and longitude of capture.

Logistic regression, which is the appropriate form of generalized linear model for a binary response variable such as maturity state, was applied to estimate the intercept ($♀L_{\mathrm{EF50}}$) and the slope of a logistic maturity ogive (β_1), where the probability that a fish is mature (p) is a function of its length (EFL) as $p = \frac{1}{1+\exp\left(-\beta_1\left[EFL - L_{EF\,50}\right]\right)}$. Two hypotheses about female maturation as a function of length were examined with alternative regression models. These were: (i) the probability that a fish was mature was solely a function of fish length (Model 1); and (ii) the probability that a fish was mature was a function of fish length and the month sampled, that is, there was a seasonal effect on observed maturity state (Model 2). In this context, fish length was a continuous predictor and month was a factor variable. Parameters of the logistic ogive models were fit with the R language (R Core Team, 2018) using the glm() function and cross-checked using the lrm() function in the package "rms". Estimates of the median length at

maturity ♀L_{EF50}, the 95th percentile of length at maturity ♀L_{EF95}, and their standard errors were calculated using the dose.p() function in the package "MASS".

Results

Histology samples

Histological determination of gender, reproductive development stage, and maturity status was successfully conducted on 1,324 gonad histology preparations yielding 697 female and 627 male samples. Ovaries and testes were collected from all months of the calendar year during the January 2008-October 2011 sampling period. Histological preparations for 91 and 58 of these ovary and testis samples, respectively, were later found to have unrecorded length data. The resulting n=606 ovary and n=569 testes samples where used to determine length related metrics including ♀L_{EF50}, length distributions, and sex ratio. The timing of the n=606 ovary collections by both month and day of month appears random. Cumulative monthly ovarian sample sizes ranged from 28 to 115.

Length at maturity

The two hypotheses about maturity as a function of length were strongly supported by the data (Appendix). Both logistic regression models were highly statistically significant ($P < 0.001$). Model 2, the logistic regression model that utilized EFL and month together as factor variables, yielded a maturity ogive that estimated ♀L_{EF50} at 160.4 cm (Figure 1). This two-variable model provided a slightly lower ♀L_{EF50} estimate but substantially better model fit (AIC=365) to the data than the single variable (EFL only) Model 1 (AIC=427) which estimated ♀L_{EF50} at 161.9 cm.

The smallest mature female was 146 cm EFL and the smallest actively spawning female was 151 cm EFL.

The two-factor logistic model formulation and parameter value estimates of the female maturity ogive to predict the proportion mature (p) at length (EFL) are:

$$p = \frac{1}{1+\exp\left(-0.1415\left[EFL-160.4\right]\right)}$$

where $♀L_{EF50}$=160.4 and β_1=0.1415

Our sample size (n=606) used to determine the maturity ogive and $♀L_{EF50}$ estimate substantially exceeded female sample sizes reported in recent maturity studies conducted in the western North Pacific (n=228) by Chang et al. (2018) and in the western-central South Pacific (n=186) by Kopf et al. (2012).

Spawning patterns

The median spatial distribution of our ovary sample collections was centered at 25.5° N latitude and 160.3° W longitude. In terms of maturity status, immature and mature females tended to be collected at similar median longitudes (160.6° W and 159.7° W, respectively). However, mature females tended to occur at a higher median latitude than immature females (27.1° N and 24.5° N, respectively).

Immature (never spawned) females were the predominant monthly reproductive phase (54-92%) present throughout most of the calendar year (August-March) and remained a major component (20-45%) in each of the remaining months (Figure 2). Mature spawning capable females (Vtg2-3 stages most advanced group of oocytes present) were first encountered in March

and persisted through July. Active spawning females first appeared two months later in May and lasted through July with a single last observation recorded in August. Active spawners $\geq ♀L_{EF50}$ (n=35, 161-188 cm) were observed throughout the spawning season, however, active spawners of length $< ♀L_{EF50}$ (n=6, 151-160 cm) were observed only during the early portion (May, n=5 and June, n=1). Regenerating females persisted throughout each month of the calendar year with peak occurrences during January and March (26%) and in the spawning season months of June-July (29-34%).

Length distribution and sex ratio

The length composition of both sexes sampled in the Hawaii-based pelagic longline fishery had similar length ranges and medians (females: 87-192 cm EFL, median 154 cm EFL; males: 68-193 cm EFL, median 150 cm EFL). Both sexes also displayed truncated length distributions for fish ≥180 cm EFL (Figure 3). Relative to maturity status, the lengths of immature females were broadly distributed (see Figure 4) spanning the entire range of total females sampled (87-192 cm EFL, median 141 cm EFL) in contrast to mature females (146-190 cm EFL, median 167 cm EFL).

The overall female sex ratio (proportion of females to the total number of females and males) was 0.53 female based on total samples sizes of 697 females and 627 males without respect to length. Examination of sex ratio with respect to length (EFL) and female non-spawning versus spawning season revealed fluctuations between seasons (see Figures 5 and 6). During the non-spawning season, the proportion of females trended between 0.4-0.6 across the middle of the length distribution (120-170 cm EFL classes) while the smaller and larger length classes were

typically higher (~0.7). The approximately ~0.5 female trend within the middle of the length distribution changed to highly male during the female spawning season when the proportion of females dipped to 0.2-0.3 within the 145-155 cm length classes. The proportion of females in length classes at the tails of the distribution (≤130 cm and ≥160 cm) remained relatively similar between seasons.

Discussion

Length at maturity

The ♀L_{EF50} derived in this study provides the first available length at maturity estimate for striped marlin sampled directly from the Hawaii-based pelagic longline fishery in the central North Pacific. The earliest maturity studies on North Pacific striped marlin were conducted in the eastern North Pacific by Kume and Joseph (1969) and Eldridge and Wares (1974) providing preliminary ♀L_{EF50} estimates of ≥160 cm and 155-165 cm, respectively. Although these latter studies provide estimates similar to ours the methodology was not based on gonad histology. However, the two recent studies conducted in the western Pacific did use gonad histology and yielded substantially larger ♀L_{EF50} estimates. Based on sampling in the western-central South Pacific, Kopf et al. (2012) derived a ♀L_{EF50} estimate equivalent to 178.4 cm. In the western North Pacific off Taiwan, Chang et al. (2018) reported a similar ♀L_{EF50} estimate of 181 cm EFL. These latter studies used similar histology criteria to distinguish mature from immature females; the most advanced group of oocytes present had developed to at least the yolked/vitellogenic stages. In the present study, the developmental stage threshold for assigning a female as mature

was slightly more conservative (oocyte development to at least the secondary vitellogenic stage, Vtg2).

The disparity in $♀L_{EF50}$ estimates between the western and central Pacific is not without precedence. Estimates of $♀L_{EF50}$ for another billfish species (swordfish, *Xiphias gladius*) studied between the same Pacific regions revealed a less pronounced but similar pattern where estimates for the central North Pacific off Hawaii were smaller (144 cm EFL; DeMartini et al. 2000) compared to the western North Pacific off Taiwan (150.7 cm EFL, Wang at el. 2003) and substantially smaller than the western South Pacific off eastern Australia (161.5 cm EFL, Farley et al. 2016). The causative factors behind these lower billfish $♀L_{EF50}$ estimates in the central North Pacific remain unknown.

A recent evaluation by Fitchett (2019) of various growth models based on tagging data and unpublished dorsal spine and otolith age readings collected from the central North Pacific indicates that our $♀L_{EF50}$ estimate corresponds to an age of 2-3 years. In relation to the age and growth results reported in Sun et al. (2011) for western North Pacific striped marlin sampled off Taiwan, our $♀L_{EF50}$ estimate corresponds to age 3.

Spawning pattern

The May-July female spawning season revealed in our study generally coincides with previous results that spawning coincides with late spring to early summer months elsewhere in the North Pacific. In the western North Pacific, spawning females were previously reported during May and June off the Ogasawara Islands of Japan (Ueyanagi and Wares 1974) and April to August off Taiwan (Chang et al. 2018). In the eastern North Pacific, Eldridge and Wares

(1974) and Kume and Joseph (1969) reported spawning in June-July and May-June, respectively. Advances in our knowledge of billfish spawning patterns originate not only from investigating the gonadal development of longline sampled juveniles and adults but also from the field capture of larvae and eggs. By utilizing both lines of inquiry, an improved understanding of spawning patterns can be achieved.

Larval captures largely confirm known spawning seasons based on gonad reproductive studies but also provide a different perspective that can be informative. Evidence of striped marlin spawning in waters adjacent to the main Hawaiian Islands remained unknown until 2005 when seven larvae were collected off the Kona Coast of Hawaii Island in late May (Hyde et al. 2006). Previous to this finding, extensive surface tow collections adjacent to and offshore of Hawaii Island yielded no larval (Matsumoto and Kazama 1974) or egg stages (Hyde et al. 2005). What is most remarkable about the eventual discovery of the striped marlin larvae (n=7) reported by Hyde et al. (2006) is their rare occurrence compared to the other three billfish species known to spawn in Hawaiian waters (Hyde et al. 2005). Large scale surface tow sampling off the Kona Coast that targeted billfish eggs and larvae during 1997-2006 (Humphreys, NMFS unpubl. data) have collected several hundred larvae and eggs of swordfish, blue marlin, and shortbill spearfish. Although our gonad histology results reveal spawning in the offshore vicinity north of Hawaii, there remains little evidence of active spawning immediately adjacent to the islands unlike other billfish and other large pelagic teleosts.

The present study indicates that in offshore waters around Hawaii in the area within range of the local longline fleet, spawning is highly seasonal, of short duration, and that female spawners consist of fish <190 cm EFL. The observed absence of spawners ≥190 cm EFL around Hawaii and the annual summer decline in the catch of striped marlin in the Hawaii-based longline fleet

(Royce1957) remains an enigma. The opportunity to resolve these questions will require future international cooperation among shipboard field researchers to target and acquire sufficient samples from these remote oceanic areas in the central North Pacific.

Sex ratio and size distribution

The preponderance of males observed among striped marlin sampled during the female spawning season has been previously reported from the other regions in the North Pacific. In the subtropical western North Pacific, Nakamura et al. (1953) reported that the ratio of males rapidly declines by the end of the spawning season. Sex ratio data reported in Kume and Joseph (1969) from 1960s longline catches in the eastern North Pacific showed a similar male-biased sex ratio during the spawning season. This phenomenon was recently observed from the same region off the near-continental eastern Pacific area off Mexico, a location that is associated with spawning (Shimose et al. 2013). These similar results suggest an influx of males during the spawning season. Whether the males are coming in from surrounding waters and/or afar remains unknown.

The length frequency distributions from Hawaii sampled females and males in this study show a similar truncation in the frequency of larger fish. Annual sex-pooled length distributions from the Hawaii-based pelagic longline fishery were analyzed by Courtney (2011) and Sculley (2019) and confirm our results that large fish >175 cm EFL are relatively rare. In western Pacific longline fisheries where the largest fish encountered approach ~220 cm EFL, these larger fish are usually females (Kopf et al., 2012; Chang et al., 2018). These data strongly suggest that the striped marlin inhabiting the central North Pacific area off Hawaii represents primarily a nursery area with spawning conducted by recently matured individuals. Our understanding of central North Pacific striped marlin within the recognized western and central North Pacific stock

remains confounded. What remains problematic toward improving our understanding of the population dynamics within the central North Pacific is 1) the apparent emigration of larger fish to unknown locations, 2) the seasonal increase of males associated with spawning, and unresolved genetic evidence (Purcell and Edmands, 2011) that suggests the co-occurrence of two distinct populations associated with immature and mature sized fish.

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Table 1. Histological characteristics used to assign maturity status and reproductive phase used to evaluate ovary samples (n=606) of striped marlin. Terminology follows that proposed by Brown-Peterson et al. (2011). Key to abbreviations of ovarian developmental stages used in last column: (CA = cortical alveoli; GVBD = germinal vesicle breakdown; GVM = germinal vesicle migration; PG = primary growth; POFs = postovulatory follicles; Vtg1 = primary vitellogenic; Vtg2 = secondary vitellogenic; Vtg3 = tertiary vitellogenic).

MATURITY STATUS	REPRODUCTIVE PHASE	SAMPLE SIZE	GENERAL DESCRIPTION	HISTOLOGIC CHARACTERISTICS
Immature	Immature (never spawned)	346	Virgin	Only oogonia and PG oocytes present. No atresia or muscle bundles. Thin ovarian wall.
Immature	Developing	51	Ovaries begin to develop, but not functionally ready to spawn.	Vtg1 most advanced group of oocytes present. PG and CA also present.
Mature	Spawning Capable	50	Fish are physiologically and functionally able to spawn in this cycle.	Vtg2 and/or Vtg3 oocytes most advanced group of oocytes present. Atretic vitellogenic oocytes may be present. POFs may be present.
Mature	Actively Spawning	41	Spawning is either eminent or underway.	Most advanced group of oocytes include GVM, GVBD, hydrated, or ovulated oocytes.
Mature	Regressing	20	Cessation of spawning; spent.	Vitellogenic and more advanced oocytes stages present are mostly atretic. POFs may be present.
Mature	Regenerating	98	Sexually mature but reproductively inactive. Resting.	Signs of previous spawning may include the presence of enlarged blood vessels in muscle bundles, thick ovarian walls, old degenerating atretic oocytes and residual hydrated oocytes. Oogonia and PG most numerous oocytes present.

LIST OF FIGURES

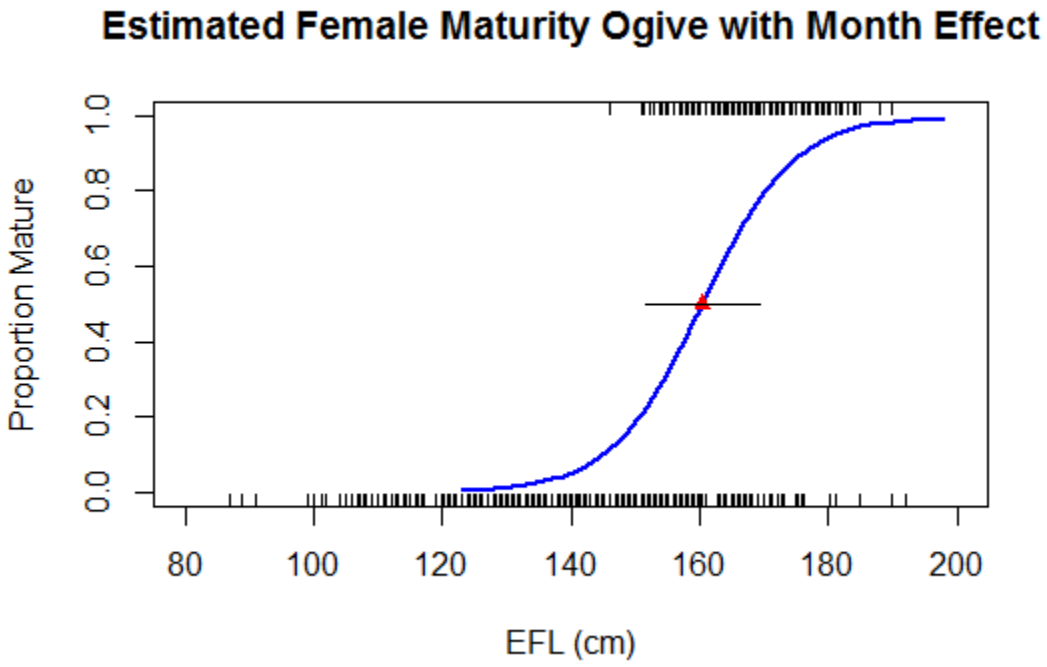

Estimated Female Maturity Ogive with Month Effect
Proportion Mature
0.0
0.2
0.4
0.6
0.8
1.0
80
100
120
140
160
180
200
EFL (cm)

Figure 1.

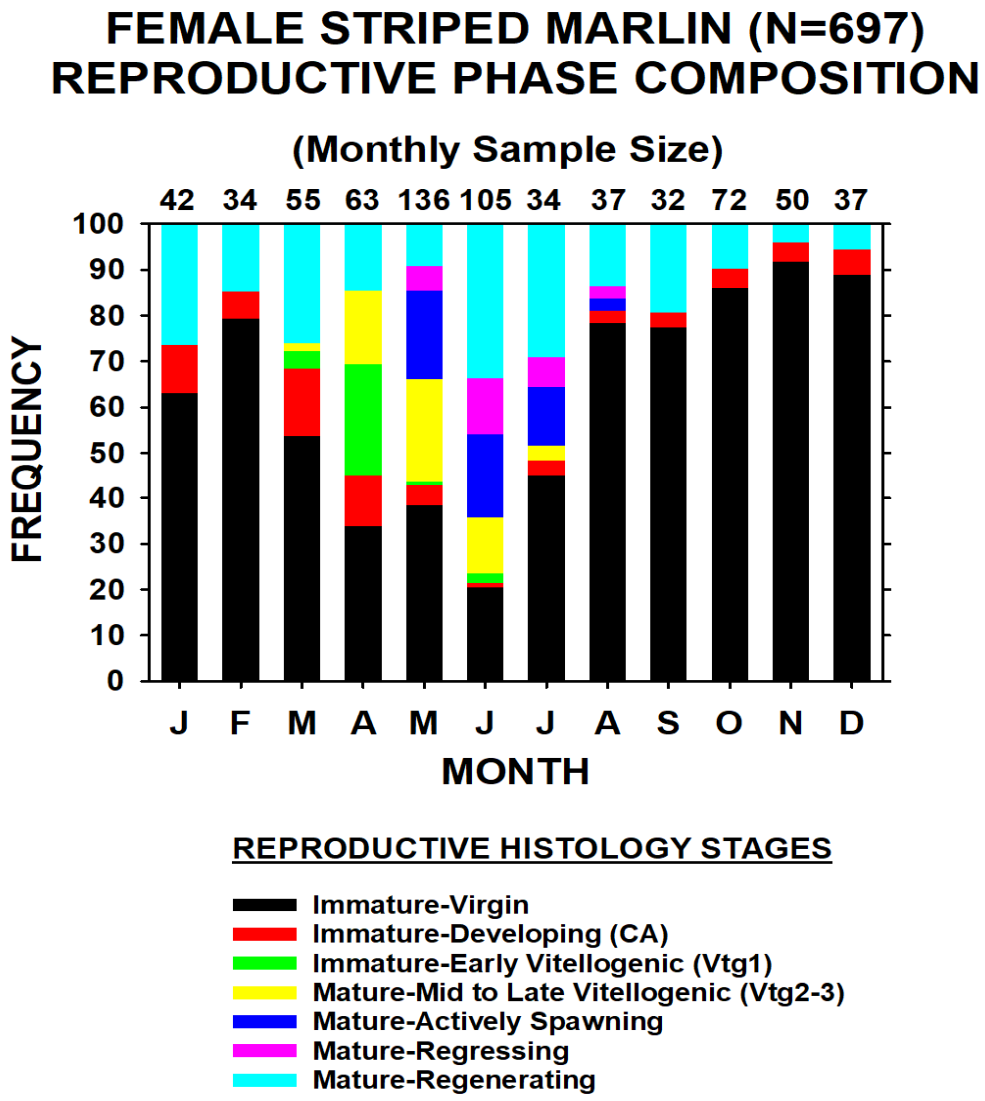

FEMALE STRIPED MARLIN (N=697)
REPRODUCTIVE PHASE COMPOSITION
(Monthly Sample Size)
42 34 55 63 136 105 34 37 32 72 50 37
FREQUENCY
100
90
80
70
60
50
40
30
20
10
0
J F M A M J J A S O N D
MONTH
REPRODUCTIVE HISTOLOGY STAGES
Immature-Virgin
Immature-Developing (CA)
Immature-Early Vitellogenic (Vtg1)
Mature-Mid to Late Vitellogenic (Vtg2-3)
Mature-Actively Spawning
Mature-Regressing
Mature-Regenerating

Figure 2.

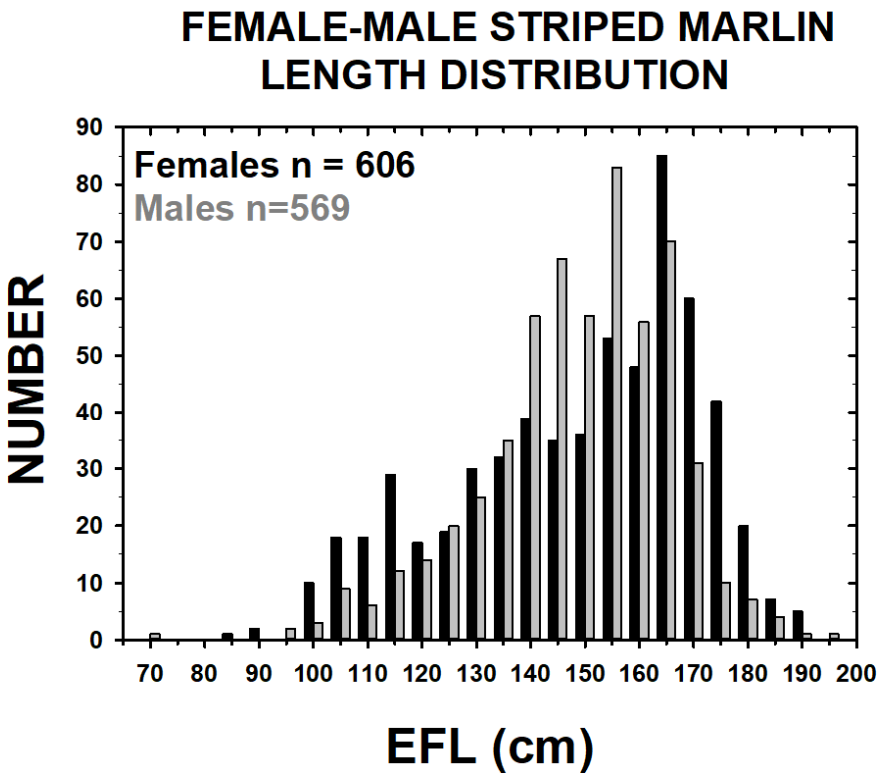

FEMALE-MALE STRIPED MARLIN
LENGTH DISTRIBUTION
Females n = 606
Males n=569
NUMBER
0
10
20
30
40
50
60
70
80
90
70
80
90
100
110
120
130
140
150
160
170
180
190
200
EFL (cm)

Figure 3.

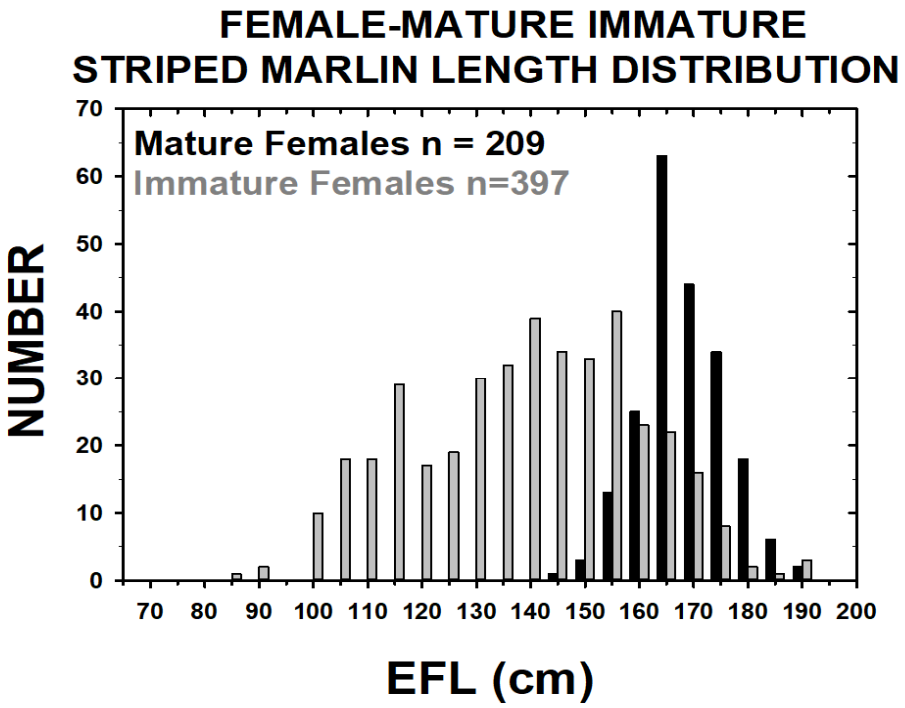

FEMALE-MATURE IMMATURE
STRIPED MARLIN LENGTH DISTRIBUTION
Mature Females n = 209
Immature Females n=397
NUMBER
EFL (cm)
0
10
20
30
40
50
60
70
70
80
90
100
110
120
130
140
150
160
170
180
190
200

Figure 4.

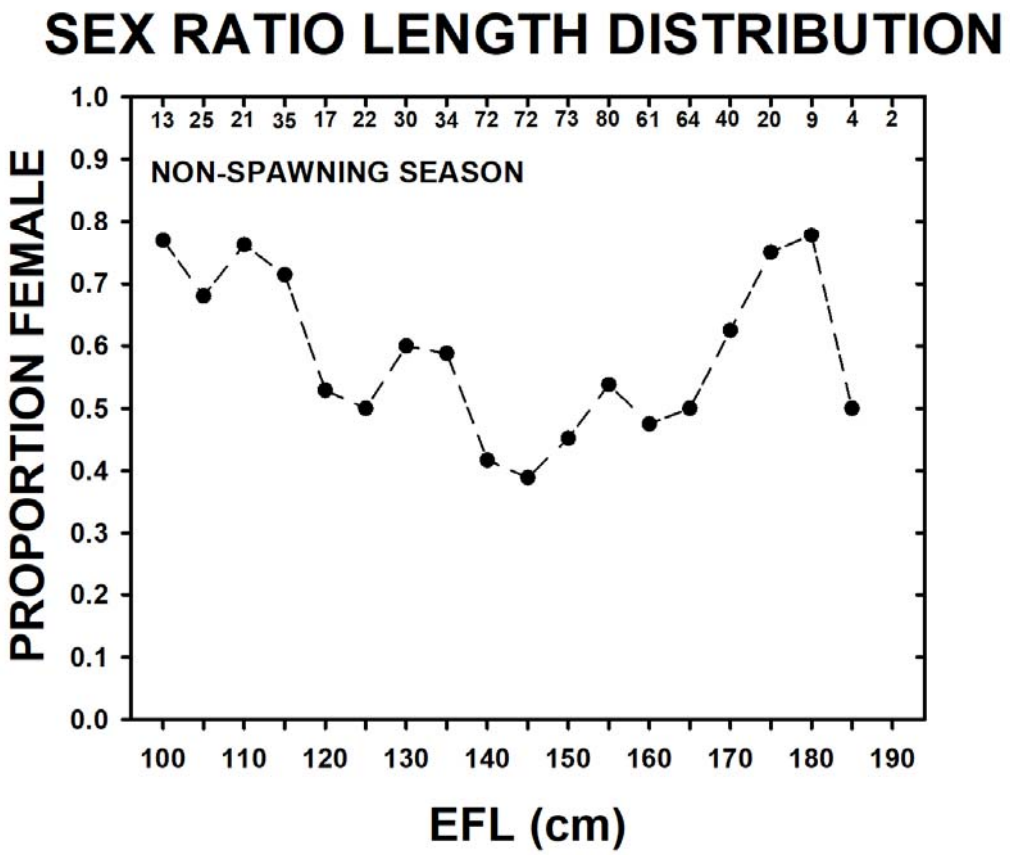

SEX RATIO LENGTH DISTRIBUTION
13 25 21 35 17 22 30 34 72 72 73 80 61 64 40 20 9 4 2
NON-SPAWNING SEASON
PROPORTION FEMALE
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
100 110 120 130 140 150 160 170 180 190
EFL (cm)

Figure 5.

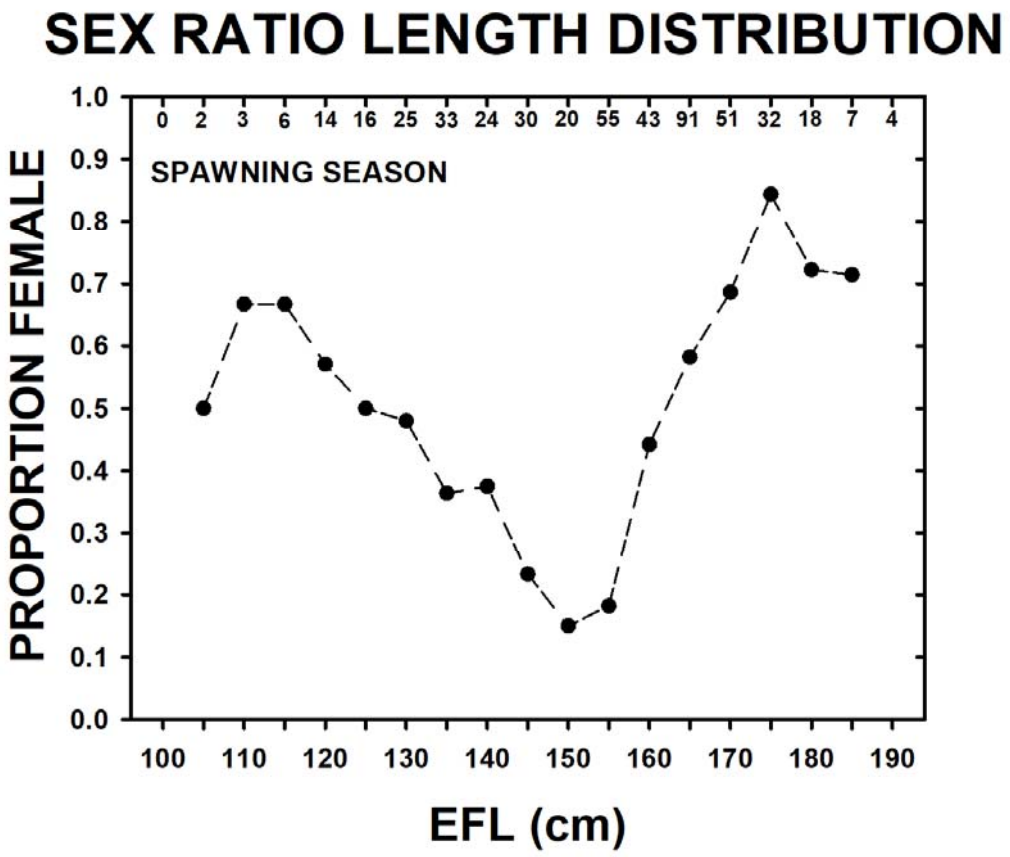

SEX RATIO LENGTH DISTRIBUTION
0 2 3 6 14 16 25 33 24 30 20 55 43 91 51 32 18 7 4
SPAWNING SEASON
PROPORTION FEMALE
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
100 110 120 130 140 150 160 170 180 190
EFL (cm)

Figure 6.

Appendix. Summaries of the logistic regression model fits to the maturity data.

Model 1.

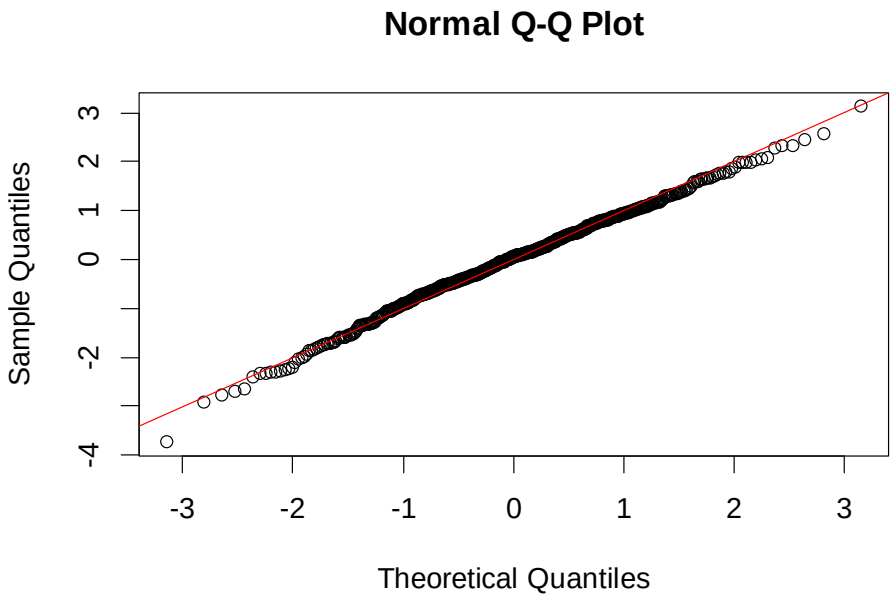
Model 1 is the basic model in which it is assumed that each fish was a random sample from the population and that the only important predictor of female maturity is fish length.

Results for model 1 indicate that there was a highly significant fit to the maturity data. The fish length effect is very important and produces reasonable residual patterns for the QQ-plot of the randomized quantile residuals. The AIC value for the model 1 fit is about AIC=427.0.

The estimated length at 50% maturity is L50 = 161.925 with an estimated standard error of 0.805.

```
> summary(model1)
Call:
glm(formula = Mature ~ EFL, family = binomial)

Deviance Residuals:
     Min        1Q    Median        3Q       Max
-3.00650  -0.45036  -0.07089   0.58996   2.22497

Coefficients:
             Estimate Std. Error z value Pr(>|z|)
(Intercept) -24.27445    2.17872  -11.14   <2e-16 ***
EFL           0.14991    0.01345   11.14   <2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for binomial family taken to be 1)

    Null deviance: 780.8  on 605  degrees of freedom
Residual deviance: 423.0  on 604  degrees of freedom
AIC: 427

Number of Fisher Scoring iterations: 6
```

Q-Q plot of randomized quantile residuals



Calculation of predicted lengths (Dose) at 50% and 95% maturity and standard errors (SE)

```
> dose.p(model1,p=matvec)
                Dose        SE
p = 0.025: 137.4870 2.3158365
p = 0.050: 142.2839 1.9179642
p = 0.100: 147.2683 1.5234792
p = 0.250: 154.5967 1.0255636
p = 0.500: 161.9251 0.8048485
p = 0.750: 169.2535 1.0530858
p = 0.900: 176.5819 1.5605789
p = 0.950: 181.5663 1.9575277
```

Model 2.

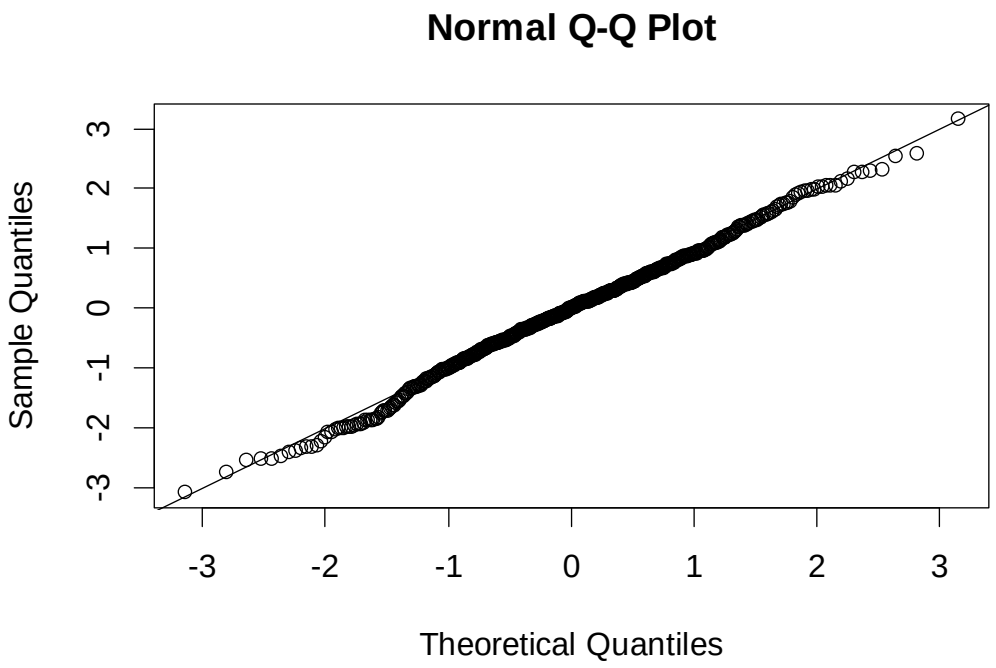
Model 2 is an extension of the sized-based maturity model in which it is assumed that each fish was a random sample from the population and that both fish length and month of sampling have important effects on maturation.

Results for model 2 again indicate that there was a highly significant fit to the maturity data. The fish length effect is very important and produces reasonable residual patterns for the QQ-plot of the randomized quantile residuals (not shown). The month effect is also important, albeit much less important than length, but shows significant summer (month6 is June) and winter (month12 is December) coefficients. The AIC value for the model 2 fit is about AIC=364.6. Given that we are using the same data with different model parameters, the difference in AIC value between model 1 and model 2 is very large and indicates that model 2 provides a substantially better fit to the data, all else being equal.

The estimated length at 50% maturity for model 2 is L50 = 160.427 with an estimated standard error of 4.528.

```
> summary(model2)

Call:
glm(formula = Mature ~ EFL + month, family = binomial)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-3.1730  -0.3513  -0.0799   0.3749   2.5396

Coefficients:
             Estimate Std. Error z value Pr(>|z|)
(Intercept) -22.696625   2.229711 -10.179   <2e-16 ***
EFL           0.141477   0.013800  10.252   <2e-16 ***
month2       -1.466983   0.870805  -1.685   0.0921 .
month3       -1.177189   0.765128  -1.539   0.1239
month4       -1.082994   0.734928  -1.474   0.1406
month5        0.560590   0.700891   0.800   0.4238
month6        1.690067   0.749744   2.254   0.0242 *
month7        1.390844   0.901397   1.543   0.1228
month8       -0.002114   0.959183  -0.002   0.9982
month9       -1.143122   0.904135  -1.264   0.2061
month10      -1.550789   0.840991  -1.844   0.0652 .
month11      -1.742441   1.273665  -1.368   0.1713
month12      -2.027268   1.008289  -2.011   0.0444 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for binomial family taken to be 1)

    Null deviance: 780.80  on 605  degrees of freedom
Residual deviance: 338.57  on 593  degrees of freedom
AIC: 364.57

Number of Fisher Scoring iterations: 7
```

Q-Q plot of randomized quantile residuals



Calculation of predicted lengths (Dose) at 50% and 95% maturity and standard errors (SE)

```
> dose.p(model2,p=matvec)

                Dose       SE
p = 0.025: 134.5316 4.913417
p = 0.050: 139.6146 4.735098
p = 0.100: 144.8961 4.599376
p = 0.250: 152.6614 4.500615
p = 0.500: 160.4268 4.528164
p = 0.750: 168.1921 4.679794
p = 0.900: 175.9574 4.944101
p = 0.950: 181.2390 5.179751
p = 0.975: 186.3220 5.443075
```