Revised analyses of the reproductive maturity of female 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 our first study on female reproductive maturity and spawning dynamics based on gonad histology from observer sampling of the Hawaii-based pelagic longline fleet (Humphreys and Brodziak, 2019). Past genetic studies and recent results from a current study indicate stock intermingling within the fleet's striped marlin catch. In this study, we re-analyze the length distribution and reproductive data to minimize potential external stock individuals in our dataset. Our working hypothesis is that the occurrence of extra-stock females during the central North Pacific spawning season would be best identified as regenerating individuals since they would be reproductively out-of-phase. Logistic regression model runs using standard and robust GLM approaches were applied to all data and portions of the dataset based on spawning/non-spawning season and inclusion/exclusion of regenerating phase females. The robust GLM model approach using length as the single variable provided the two best maturity ogive fits to the data. Our new estimates of female L_{50} (152.2 and 153.6 cm EFL) are based on best fits to portions of the data restricted to the spawning season and exclusion of regenerating females within the spawning season, respectively. These revised L_{50} estimates are lower than our previous estimate of 160.4 cm EFL for the central North Pacific. The central North Pacific around Hawaii represents a very dynamic region that functions as a spawning, nursery, and young adult habitat from which fish emigrate and immigrate to as they grow and mature.

Introduction

In the North Pacific, recent assessments of striped marlin have been conducted under a two-stock scenario that partitions the western and central North Pacific Ocean (WCNPO) stock from the eastern North Pacific Ocean (ENPO) stock at 150° W longitude with the equator as the southernmost boundary for both stocks. A recently completed international assessment update of the WCNPO stock has concluded it currently remains in an overfished state and overfishing persists (ISC Billfish Working Group 2019; Sculley 2021). 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.

Previous sources of reproductive information for WCNPO stock assessment studies relied on distant regional studies conducted in the western North Pacific (Chang et al., 2018) and western-central South Pacific (Kopf et al., 2012). New reproductive parameter estimates based on ovarian histology from samples collected onboard vessels of the Hawaii pelagic longline fishery (Humphreys and Brodziak, 2019) were input into the recent WCNPO assessment (ISC Billfish Working Group 2019). However, recent published genetic studies (Purcell and Edmands, 2011; Mamoozadeh et al., 2019) and unpublished data from an on-going study indicate individuals from an external stock are also caught on the central North Pacific fishing grounds off Hawaii and are present during the female spawning season. The intent of this paper is to reanalyze both the female reproductive and length frequency data to provide a revised maturity ogive and L_{50} estimate that minimizes potential influence from stock intermingling. Our current working hypothesis is the South Pacific is the source of

external stock influx into the central North Pacific fishing grounds. Therefore, when present during the May-July spawning period, these South Pacific females are not reproductively active as their respective spawning season in the southern hemisphere is offset by ~6 months (Kopf et al., 2012).

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 March 2008 through July 2012 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 5-year sampling period show a similar spatial pattern 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 a 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 were 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. Regenerating 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, and/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, reproductive phase, and latitude and longitude of capture.

Based on the previous work with these sample collections and new genetic data (Tim Lam, unpublished data) that showed that striped marlin from genetically distinct Western Central North Pacific and South Pacific spawning groups were mixing within our Hawaii longline fishery study area, we investigated whether there were differences in the length frequency distributions of female striped marlin collected by spawning season and maturity stage. This

investigation was a natural follow-up to our finding in our 2019 working paper (Humphreys and Brodziak 2019) that showed that the best fit for a length-based female maturity ogive using the entire female striped marlin data set include a significant month effect. Here the interpretation that the probability of maturity was substantially influenced by the month of sample collection was consistent with the potential for stock mixing on the Hawaii longline fishing grounds in the North Pacific. In particular, different size classes of maturity stage would be expected to be observed in our sample collection if fish spawned in the austral summer from the South Pacific spawning group were mixing with fish spawned in the North Pacific spawning season of May-July on the Hawaii longline fishing grounds. Here one might expect a change in the mean size of mature stage striped marlin in the non-spawning season (August-April) due to an increase in the fraction of fish from the South Pacific spawning group on feeding migrations that were about ½ year older than the most recent North Pacific spawning group cohort. Given this potential dynamic, we analyzed the striped marlin length frequency data using two data sets. The first data set was comprised of the entire collection of female striped marlin in our Hawaii longline fishery sample. In this case, analyzing the first data set of all samples (n=598) for maturity corresponded to an assumption that the primary maturity signal in the data were from North Pacific spawning group fish. The second data set was comprised of all female striped marlin in our Hawaii longline fishery sample that were not in a regenerating reproductive phase (Table 1). In this case, one might expect that if there were any South Pacific spawning group fish in the maturity data then these fish would be in a mature but inactive reproductive state. The second data set was identical to the first except for 94 female fish in regenerating stage that were excluded in the second data set of all non-regenerating samples (n=505). We summarized empirical statistics of the length distributions of females by spawning season and calculated length composition densities for both data sets to examine whether mean sizes were markedly different. Here the length composition

densities were calculated using 10,000 nonparametric bootstrap replicates and fitted using the function density in the R language. In the empirical comparisons of mean lengths, we considered mean lengths by sampling group to be similar if there was some overlap in the 95% confidence intervals of the means. Here we note that the calculated standard errors of the mean lengths were likely underestimated based on an assumption that the length data were effectively independent samples, i.e., that cluster sampling had a negligible effect on calculated standard errors.

As in our previous analyses of these maturity data (Humphreys and Brodziak 2019), we applied logistic regression to estimate the intercept (L_{50}) and the slope of a logistic maturity ogive (β_1), where the probability that a fish is mature (p) is a function of its eye-fork length (EFL) as $p = \frac{1}{1+\exp\left(-\beta_1\left[EFL - L_{50}\right]\right)}$. In this context, fish length was a continuous predictor and month was a factor variable. Given the uncertainty about the potential for having a mixture of maturity samples from different genetic stocks with different maturity schedules, we applied a robust logistic regression approach based on M-estimates (Huber 1981, Cantoni and Ronchetti 2001) to compute maturity ogive parameters. We also applied a standard maximum likelihood-based logistic regression approach as was done in our previous work (Humphreys and Brodziak 2019). The logistic regression models were fit with the R language (R Core Team, 2021) using the glmrob() (Cantoni 2004) and glm() functions to compute the M-estimates and MLEs of the maturity ogive parameters.

As in our previous analyses of these data, 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

(Model 2), that is, there was a month factor effect on observed maturity state assumed in Model 2. Differences in the goodness of fits of models 1 and 2 under the robust and standard logistic regression models were evaluated using Wald's robust test and analysis of deviance, respectively. Estimates of the median length at maturity L_{50}, the 95th percentile of length at maturity L_{95}, and the slope of the ogive β_1, and their standard errors were calculated using the dose.p() function in the R packages "MASS" and "robustbase", respectively.

Results

Histology samples

Histological determination of gender, reproductive phase, and maturity status was successfully conducted on 1,128 gonad histology preparations yielding 598 female and 530 male samples with complete measurement and capture data. Ovaries and testes were collected from all months of the calendar year during the sampling period. The resulting n=598 ovary samples were used to determine length related metrics including L_{50} and length distributions. The timing of the ovary collections by both month and day of month appears random. Cumulative monthly ovarian sample sizes ranged from 27 to 115.

Length at maturity

A total of 24 logistic regression runs were fitted to sampling data with respect to spawning/non-spawning season and inclusion/exclusion of regenerating phase females (see Appendix for details). The working hypothesis that maturity ogive is best determined by accounting for the latter two factors and that maturity is best described as a function of a single (eye-fork length) variable (Model 1) were strongly supported by the data. Two logistic regression models were highly statistically significant ($P < 0.001$); both applied a robust

GLM approach. One of these logistic regression models was based on an analysis of all females sampled during the spawning season (m1.fem.sp.rob; n=227) while the other excluded regenerating females from the spawning season (m1.nrfem.sp.rob; n=181). These two derived maturity ogives yielded L_{50}estimates of 152.2 and 153.6 cm EFL (Figure 4). Other robust Model 1 logistic regression runs that included total females sampled or those collected during the non-spawning season yielded L_{50}estimates typically >160 cm EFL. Logistic regressions that utilized the standard GLM approach performed less well compared to the robust GLM approach.

The sample size used to determine the maturity ogive and L_{50} estimate based on spawning season females (n=227) and excluding regenerating females from the spawning season (n=181) are comparable to 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 160.2° W longitude. In terms of maturity status, immature and mature females tended to be collected at similar median longitudes (160.5° W and 159.6° W, respectively). However, mature females tended to occur at a higher median latitude than immature females (27.0° N and 24.4° N, respectively).

Immature (virgin) females composed the single largest reproductive phase (57.7%) in the total female sample followed by the regenerating phase (15.6%). Furthermore, virgin females were the predominant reproductive phase (23-94%) in all months of the calendar year (except June) when regenerating females were greatest (Figure 5). 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. Regressing females were almost exclusively observed during the spawning season and last occurred in August. Regenerating females persisted throughout each month of the calendar year with peak occurrences during February-April (12-20%) and in the spawning and post-spawning months of June-September (17-32%).

Length distribution

Density plots of length composition consisting of those females sampled from the Hawaii-based pelagic longline fishery displayed a sharp decline in females ≥180 cm EFL regardless of season, maturity status, or regenerating phase (Figures 1-3). Immature females occupied the entire length range of sampled females including the distribution of mature individuals regardless of spawning/non-spawning season or the exclusion of regenerating females despite the greater mean length of mature females within each of these comparisons (Tables 2 and 3). Differences in mean female length within immature and mature fish were small when contrasting spawning and non-spawning season and inclusion/exclusion of regenerating individuals. However, seasonal shifts in modal length were observed, primarily among immature individuals. In the spawning season, immature females displayed a bimodal profile at ~130 cm EFL (larger peak) and at ~170 cm EFL (smaller peak) while mature females showed a single peak at 165-170 cm EFL. In the non-spawning season, the larger mode for immatures increased to 150-155 cm EFL, the smaller mode declined to ~110 cm EFL, while the modal length of mature individuals differed little from the spawning season.

Discussion

Length at maturity

The revised ♀ L_{50}estimates (152.2 and 153.6 cm EFL) derived in this study provide the first length at maturity analysis conducted to account for potential stock intermingling; in this case, for striped marlin sampled 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_{50} estimates of ≥160 cm and 155-165 cm, respectively. Although these latter studies provide similar estimates, their methodology was not based on gonad histology. However, the two recent studies conducted in the western Pacific did use gonad histology and yielded larger ♀ L_{50} estimates. Based on sampling in the western-central South Pacific, Kopf et al. (2012) derived an L_{50} estimate equivalent to 178.4 cm EFL. In the western North Pacific off Taiwan, Chang et al. (2018) reported a similar L_{50}estimate of 181 cm EFL. These latter studies used similar histology criteria to distinguish mature from immature females, i.e., the most advanced group of oocytes present had developed to at least the yolked/vitellogenic stage. 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_{50} estimates between the western and central Pacific is not without precedence. Estimates of $L_{50}$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 et al.. 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_{50} 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 revised female L_{50} estimates correspond to an age of ~2 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_{50} estimate lies between ages2-3.

Spawning pattern

The May-July female spawning season in the central north Pacific coincides with previous results that spawning occurs from late spring to early summer 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 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). Before 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 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 primarily of fish <180 cm EFL. The observed rarity of spawners ≥180 cm EFL around Hawaii and the annual summer decline in the catch of striped marlin in the Hawaii-based longline fleet (Royce 1957) 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.

Length distribution

The truncated distribution of individuals ≥180 cm EFL shown among Hawaii sampled females in this study has been reported in from other datasets as well. Annual sex-pooled length distributions from the Hawaii-based pelagic longline fishery analyzed by Courtney (2011) and Sculley (2019) support our results that large fish ≥180 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 by both this apparent lack of larger individuals and recent evidence supporting the occurrence of stock intermingling. What remains problematic toward improving our understanding of the population dynamics within the central North Pacific is 1) the destination of "home-grown" fish that emigrate off the Hawaii fishing grounds both seasonally and permanently upon reaching a larger size, and, 2) the extent of stock intermingling and how best to identify extra-stock individuals so that future life history studies are not compromised by mixed stock samples.

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Table 1. Histological characteristics used to assign maturity status and reproductive phase used to evaluate ovary samples (n=598) 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)	345	Virgin	Only oogonia and PG oocytes present. No atresia or muscle bundles. Thin ovarian wall.
Immature	Early Developing	30	Ovaries begin to develop but not functionally ready to spawn.	CA most advanced group of oocytes present. PG also present.
Immature	Late Developing	19	Ovaries further develop, achieve start of vitellogenesis, 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 sometimes 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	93	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 predominate.

Table 2 Mean length distributions of female striped marlin by sample collection season (All Months, Spawning Season [May-July], Non-Spawning Season [August-April]) and maturity stage (Both Immature and Mature, Immature, Mature) for all females samples (n=598) including sample size (N), mean fish length (Mean, eye-fork length in cm), standard error of mean length (Sterr), standard deviation of length (Stdev) and coefficient of variation of length (CV).

Sample Collection Season and Maturity Stage	**N**	**Mean**	**Sterr**	**Stdev**	**CV**
All Months and Both Stages	598	148.9	0.9	22.1	15%
All Months and Immature Stages	394	138.9	1.0	20.5	15%
All Months and Mature Stages	204	168.1	0.5	7.7	5%
Spawning Season and Both Stages	227	157.7	1.3	19.1	12%
Non-Spawning Season and Both Stages	371	143.5	1.1	22.0	15%
Spawning Season and Immature Stages	82	138.9	2.1	19.0	14%
Spawning Season and Mature Stages	145	168.4	0.6	7.5	4%
Non-Spawning Season and Immature Stages	312	138.9	1.2	20.8	15%
Non-Spawning Season and Mature Stages	59	167.5	1.1	8.3	5%

Table 3 Mean length distributions of female striped marlin by sample collection season (All Months, Spawning Season [May-July], Non-Spawning Season [August-April]) and maturity stages (Both Immature and Mature, Immature, Mature) for all female non-regenerating

samples (n=505) including sample size (N), mean fish length (Mean, eye-fork length in cm), standard error of mean length (Sterr), standard deviation of length (Stdev) and coefficient of variation of length (CV).

Sample Collection Season and Maturity Stage	N	Mean	Sterr	Stdev	CV
All Months and Both Stages	505	145.4	1.0	22.1	15%
All Months and Immature Stages	394	138.9	1.0	20.5	15%
All Months and Mature Stages	111	168.3	0.7	7.6	4%
Spawning Season and Both Stages	181	155.0	1.5	20.2	13%
Non-Spawning Season and Both Stages	324	140.0	1.2	21.3	15%
Spawning Season and Immature Stages	82	138.9	2.1	19.0	14%
Spawning Season and Mature Stages	99	168.3	0.7	7.4	4%
Non-Spawning Season and Immature Stages	312	138.9	1.2	20.8	15%
Non-Spawning Season and Mature Stages	12	168.3	2.6	8.9	5%

LIST OF FIGURES

Figure 1. Estimated length frequency densities (blue lines) with 95% confidence intervals (gray areas) for female striped marlin samples collected in all months by maturity stage ([All]

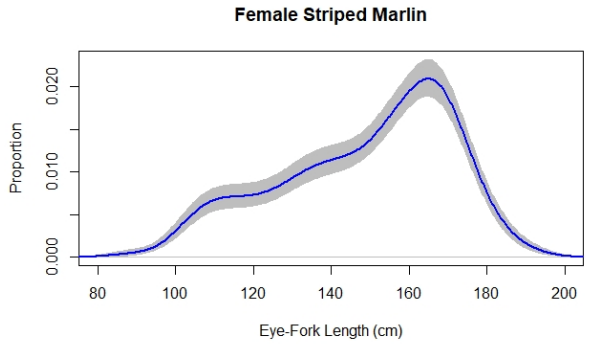
Females, Immature Females and Mature Females) with regenerating fish (left panels) and without regenerating fish (rights panels).

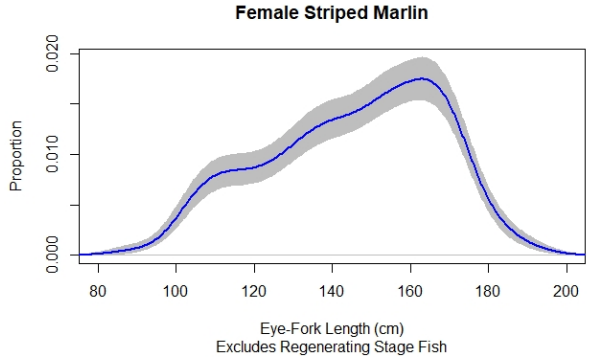
Figure 2. Estimated length frequency densities (blue lines) with 95% confidence intervals (gray areas) for female striped marlin samples collected during the spawning season (May-July) by maturity stage ([All] Females, Immature Females and Mature Females) with regenerating fish (left panels) and without regenerating fish (rights panels).

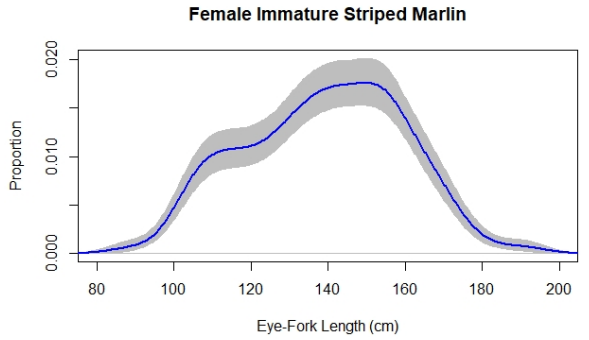
Figure 3. Estimated length frequency densities (blue lines) with 95% confidence intervals (gray areas) for female striped marlin samples collected during the non-spawning season (August-April) by maturity stage ([All] Females, Immature Females and Mature Females) with regenerating fish (left panels) and without regenerating fish (rights panels).

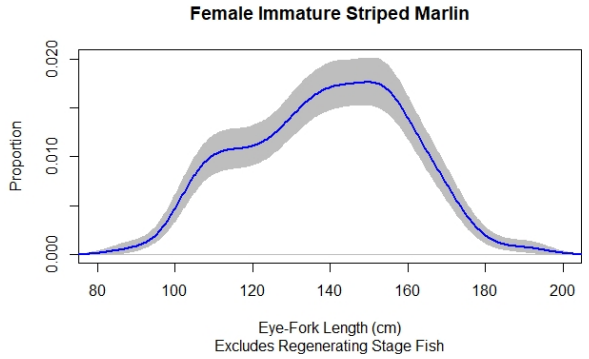
Figure 4. The two best fit maturity ogives derived from logistic regression using length as the single variable (Model 1) and a robust GLM approach. Data was restricted to females collected during the spawning season (May-July). Ogive displayed in black is for all spawning season females (n=227) while the ogive displayed in dark grey excluded regenerating phase females within the spawning season (n=181). . The color-coded dashed intersecting lines converge on the L_{50} values analyzed for all spawning season females (dashed lines in black) and where regenerating females were excluded from analysis (dashed grey lines).

Figure 5. Monthly composition of maturity status and specific reproductive phases present for female striped marlin based on microscopic evaluation of histology preparations.


Female Striped Marlin
Proportion
0.000
0.010
0.020
80
100
120
140
160
180
200
Eye-Fork Length (cm)


Female Striped Marlin
Proportion
0.000
0.010
0.020
80
100
120
140
160
180
200
Eye-Fork Length (cm)
Excludes Regenerating Stage Fish


Female Immature Striped Marlin
Proportion
0.000
0.010
0.020
80
100
120
140
160
180
200
Eye-Fork Length (cm)


Female Immature Striped Marlin
Proportion
0.000
0.010
0.020
80
100
120
140
160
180
200
Eye-Fork Length (cm)
Excludes Regenerating Stage Fish

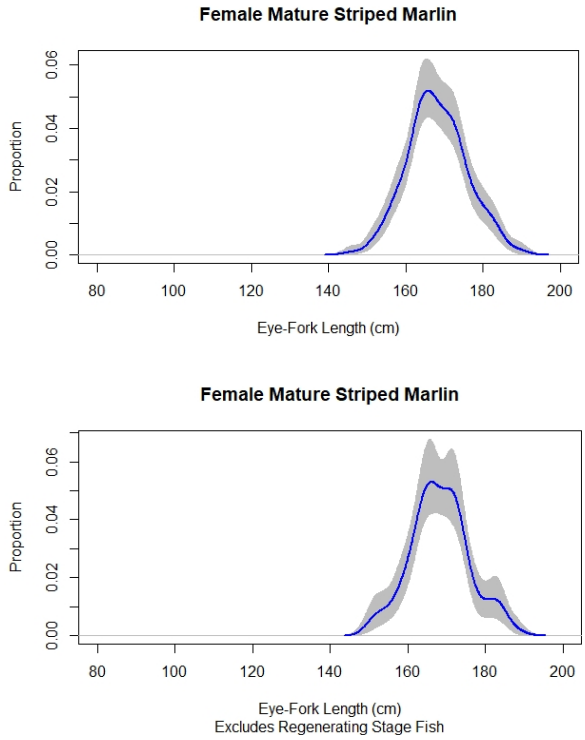

Female Mature Striped Marlin
Proportion
0.00
0.02
0.04
0.06
80
100
120
140
160
180
200
Eye-Fork Length (cm)
Female Mature Striped Marlin
Proportion
0.00
0.02
0.04
0.06
80
100
120
140
160
180
200
Eye-Fork Length (cm)
Excludes Regenerating Stage Fish

Figure 1.

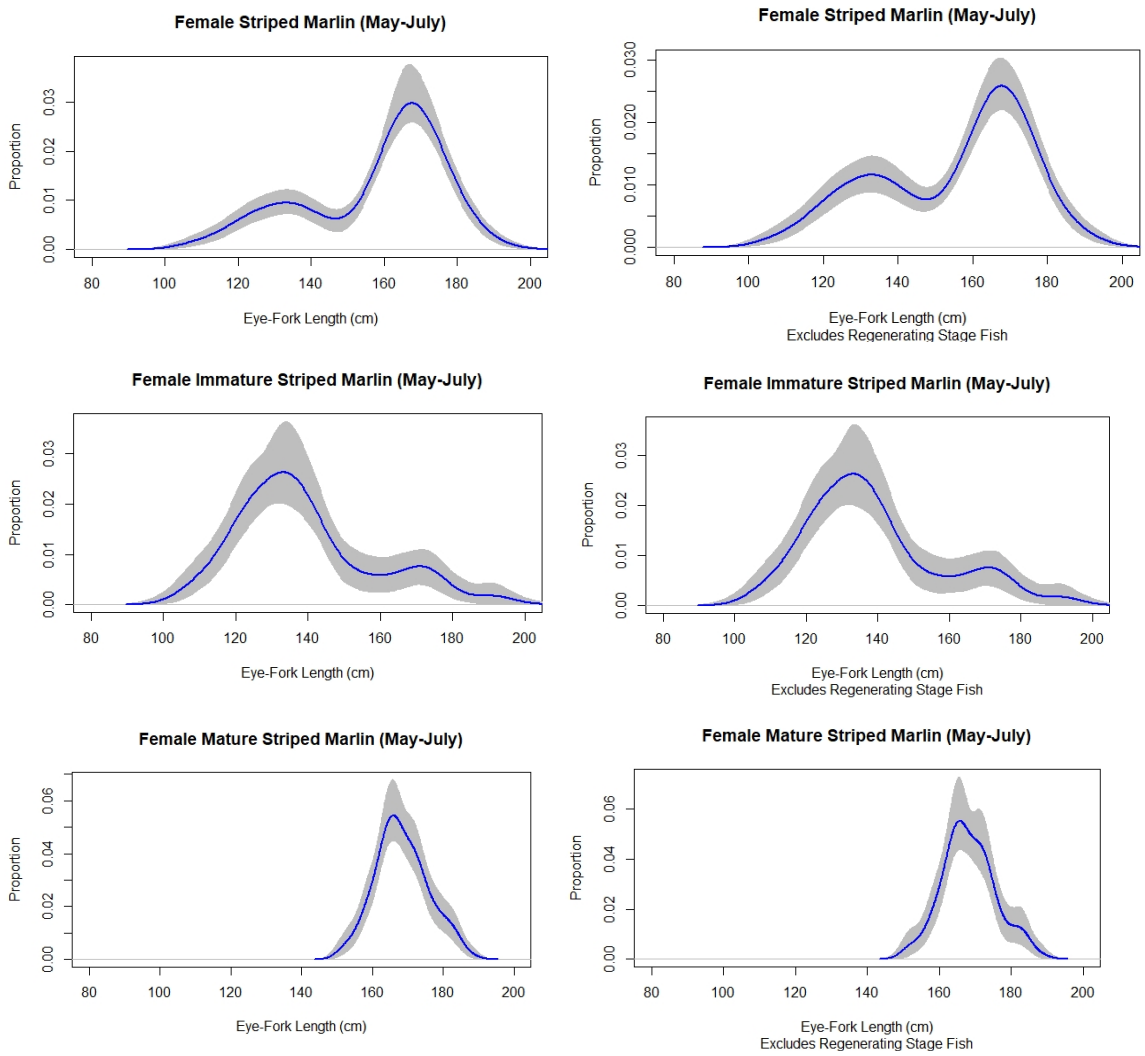
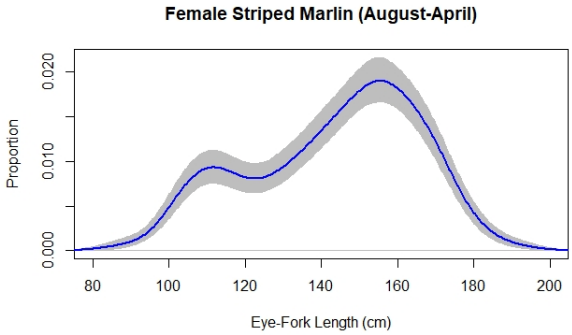
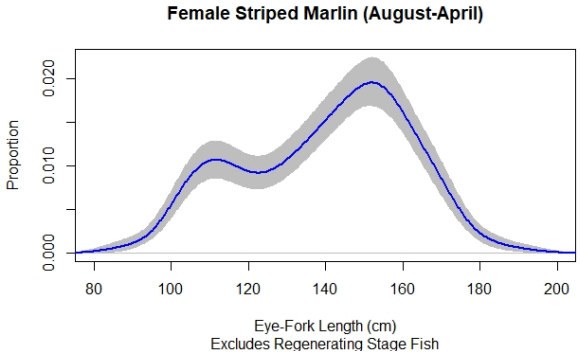
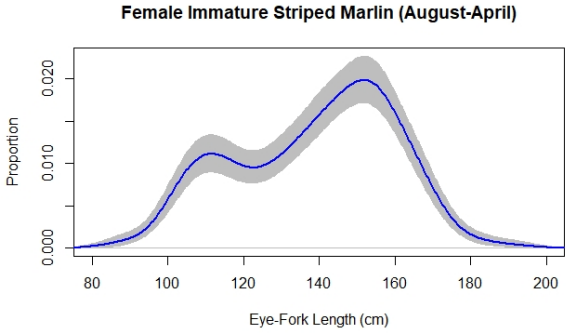
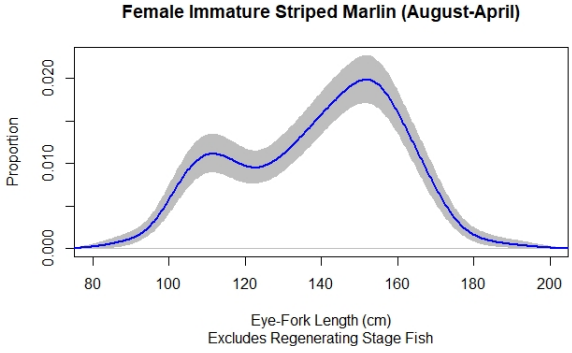

Female Striped Marlin (May-July)
Proportion
0.00
0.01
0.02
0.03
80
100
120
140
160
180
200
Eye-Fork Length (cm)
Female Striped Marlin (May-July)
Proportion
0.000
0.010
0.020
0.030
Eye-Fork Length (cm)
Excludes Regenerating Stage Fish
Female Immature Striped Marlin (May-July)
Eye-Fork Length (cm)
Female Immature Striped Marlin (May-July)
Eye-Fork Length (cm)
Excludes Regenerating Stage Fish
Female Mature Striped Marlin (May-July)
0.00
0.02
0.04
0.06
Eye-Fork Length (cm)
Female Mature Striped Marlin (May-July)
Eye-Fork Length (cm)
Excludes Regenerating Stage Fish

Figure 2.


Female Striped Marlin (August-April)
Proportion
0.000
0.010
0.020
80
100
120
140
160
180
200
Eye-Fork Length (cm)


Female Striped Marlin (August-April)
Proportion
0.000
0.010
0.020
80
100
120
140
160
180
200
Eye-Fork Length (cm)
Excludes Regenerating Stage Fish


Female Immature Striped Marlin (August-April)
Proportion
0.000
0.010
0.020
80
100
120
140
160
180
200
Eye-Fork Length (cm)


Female Immature Striped Marlin (August-April)
Proportion
0.000
0.010
0.020
80
100
120
140
160
180
200
Eye-Fork Length (cm)
Excludes Regenerating Stage Fish

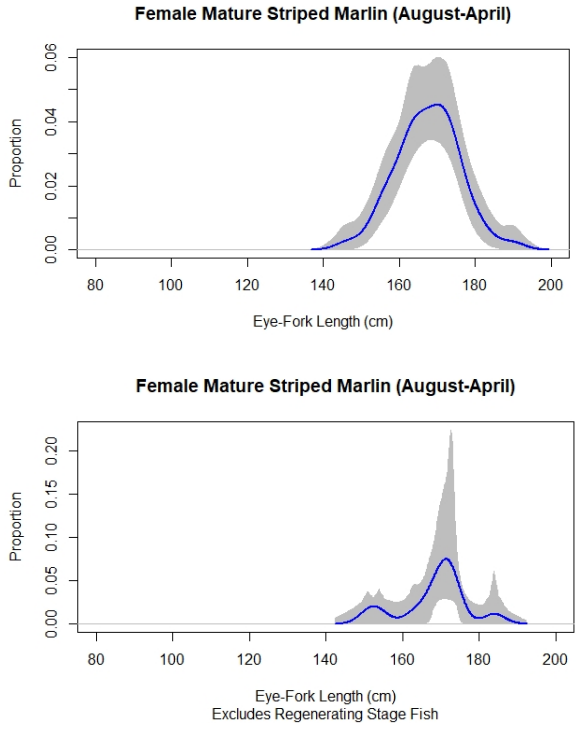

Female Mature Striped Marlin (August-April)
Proportion
0.00
0.02
0.04
0.06
80
100
120
140
160
180
200
Eye-Fork Length (cm)
Female Mature Striped Marlin (August-April)
Proportion
0.00
0.05
0.10
0.15
0.20
80
100
120
140
160
180
200
Eye-Fork Length (cm)
Excludes Regenerating Stage Fish

Figure 3.

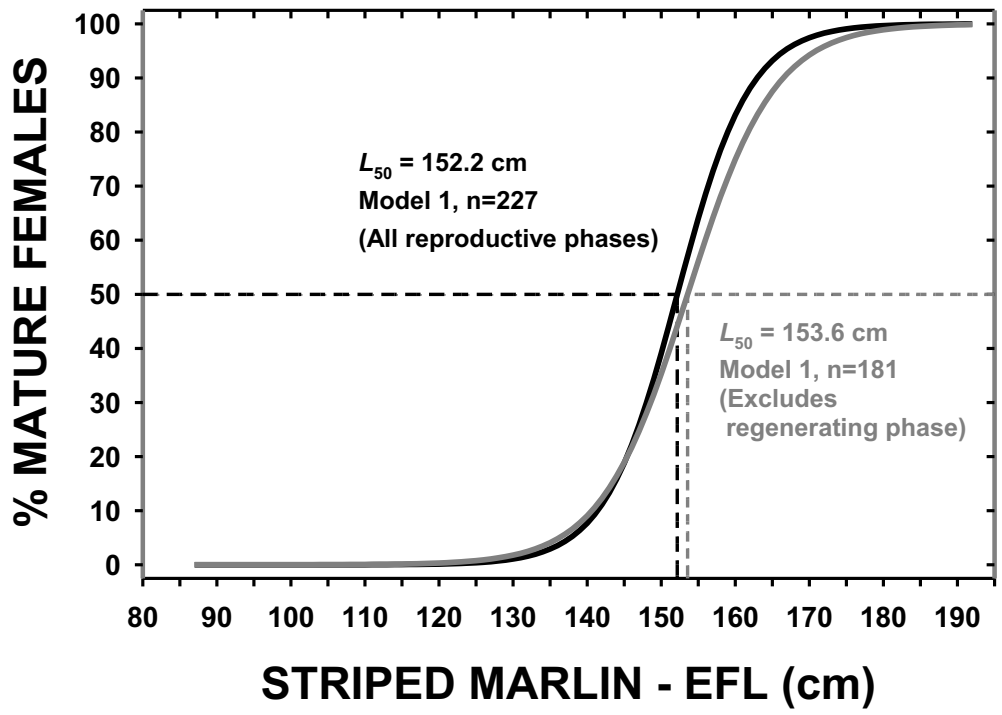

% MATURE FEMALES
100
90
80
70
60
50
40
30
20
10
0
80
90
100
110
120
130
140
150
160
170
180
190
STRIPED MARLIN - EFL (cm)
L_{50} = 152.2 cm
Model 1, n=227
(All reproductive phases)
L_{50} = 153.6 cm
Model 1, n=181
(Excludes
regenerating phase)

Figure 4.

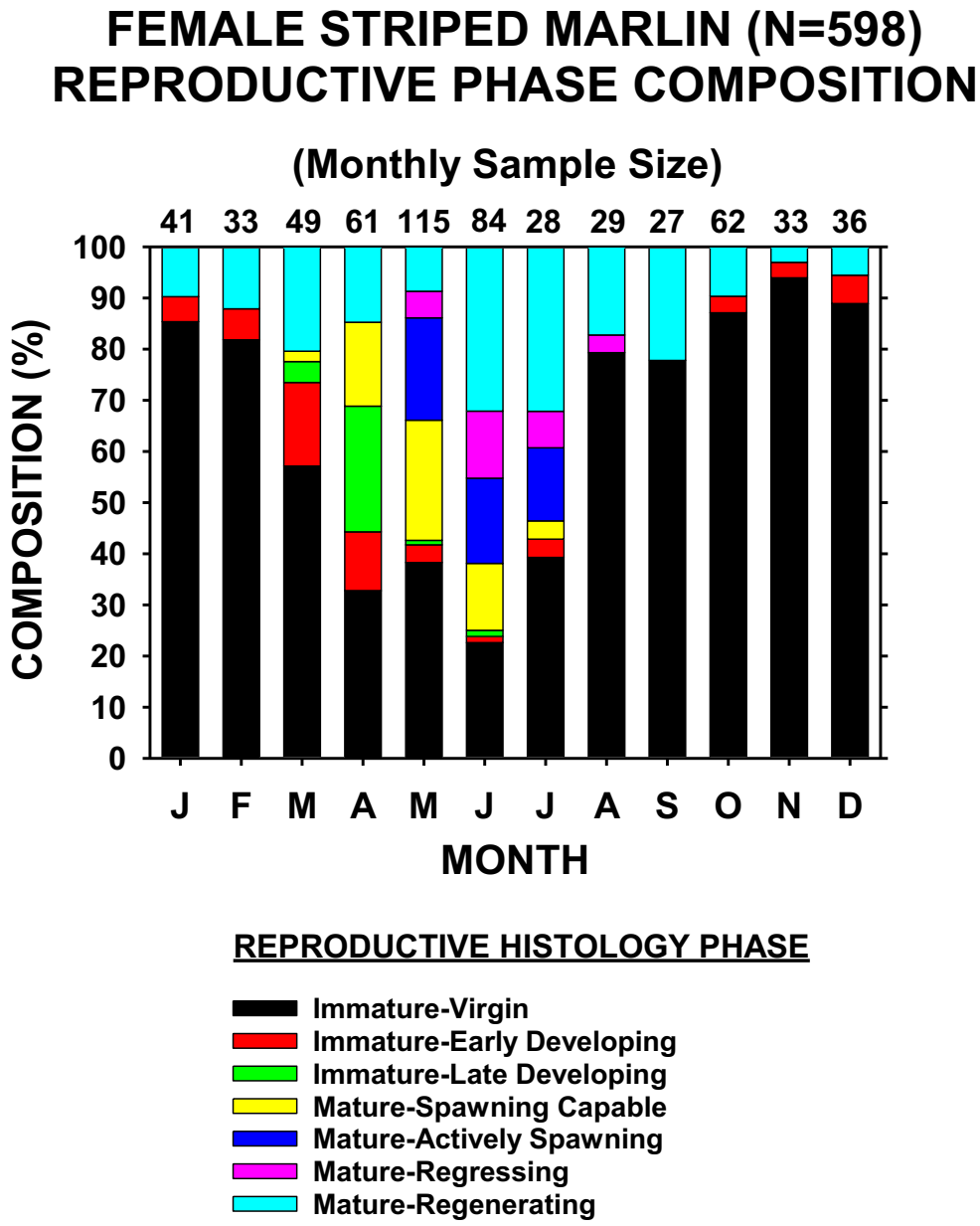


Figure 5.

Appendix. This Appendix includes summaries of the best-fitting robust logistic regression model that were fit to the female striped marlin maturity data collected during the spawning season (May-July) using all samples and using all samples excluding regenerating

fish. This Appendix also includes 4 tables that summarize the results of each of the 24 logistic regression models that were fitted to the female striped marlin maturity data.

Best Fitting Model with All Samples

Model 1 (R model object code is m1.fem.sp.rob) produced the best fit to the female maturity data collected during the spawning season in comparison to Model 2 (R model object code is m2.fem.sp.rob) based on the Robust Wald test results.

> anova(m1.fem.sp.rob,m2.fem.sp.rob,test="Wald")

Robust Wald Test Table

Model 1: mature ~ efl

Model 2: mature ~ efl + month_F

Models fitted by method 'Mqle'

Model	pseudoDf	Test.Stat	Df	Pr(>chisq)
1	225			
2	223	0.56543	2	0.7537

Results for the best fitting model with all samples indicated that there was a highly significant fit to the maturity data ($P < 0.0001$). Fish length was the only significant predictor and Model 1 produced reasonable residual patterns based on the histogram and QQ-plots of the randomized quantile residuals shown below. The estimate of the length at 50% maturity was L_{50} = 152.2 cm with a standard error of 1.8. The estimate of the length at 95% maturity was L_{95} = 165.6 cm with a standard error of 2.2. The estimate of the slope of the maturity ogive was β_1 = 0.204 with a standard error of 0.034. A summary of the best fitting model with all samples is listed below along with the predicted dose responses and the histogram and QQ-plot of the quantile residuals.

> summary(m1.fem.sp.rob)

Call: glmrob(formula = f1, family = binomial, data = MLS.ALL, subset = female.spawn)

Coefficients:

	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-31.07630	5.40086	-5.754	8.72e-09	***
efl	0.20422	0.03423	5.966	2.43e-09	***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Robustness weights w.r * w.x:

212 weights are ~= 1. The remaining 15 ones are summarized as

Min.	1st Qu.	Median	Mean	3rd Qu.	Max.

0.02304 0.12440 0.17760 0.25510 0.31180 0.74180

Number of observations: 227

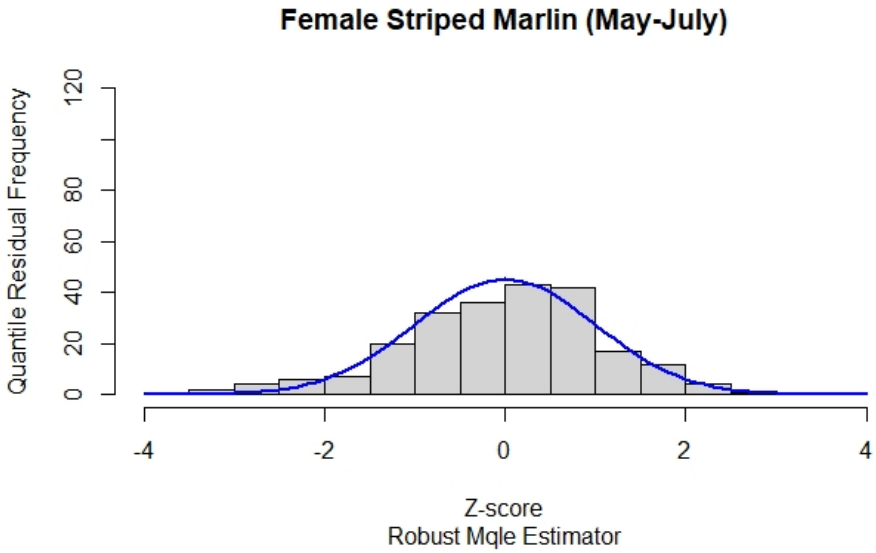
Fitted by method 'Mqle' (in 10 iterations)

(Dispersion parameter for binomial family taken to be 1)

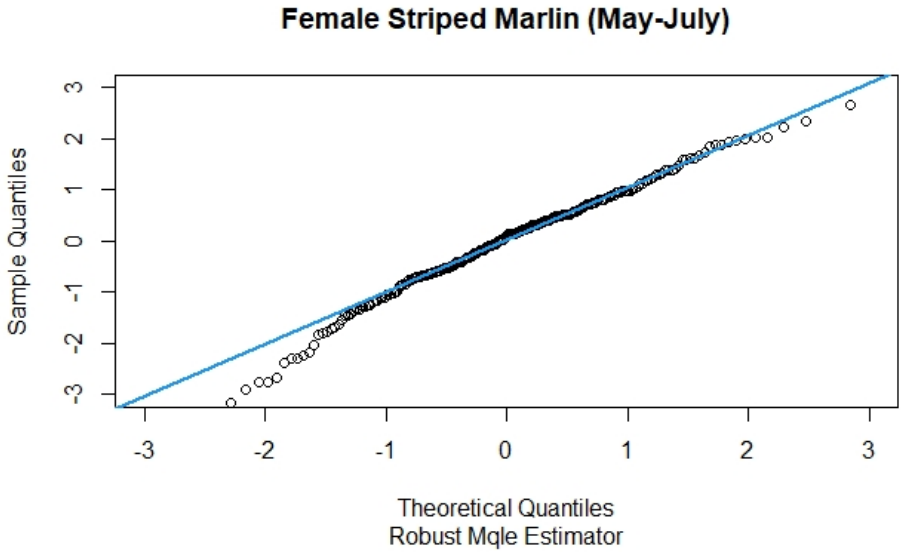
> dose.p(m1.fem.sp.rob, p=matvec)

	Dose	SE
p = 0.010:	129.6708	4.909579
p = 0.025:	134.2324	4.189478
p = 0.050:	137.7537	3.646010
p = 0.100:	141.4126	3.099493
p = 0.250:	146.7922	2.356436
p = 0.382:	149.8161	1.996980
p = 0.500:	152.1718	1.767755
p = 0.618:	154.5274	1.604309
p = 0.750:	157.5514	1.524259
p = 0.900:	162.9310	1.774263
p = 0.950:	166.5899	2.153618
p = 0.975:	170.1112	2.604325
p = 0.990:	174.6728	3.255209

Histogram of randomized quantile residuals



Q-Q plot of randomized quantile residuals



Best Fitting Model with All Samples Excluding Regenerating Fish

Model 1 (R model object code is m1.nr.fem.sp.rob) produced the best fit to the female maturity data collected during the spawning season in comparison to Model 2 (R model object code is m2.nr.fem.sp.rob) based on the Robust Wald test results.

> anova(m1.nr.fem.sp.rob,m2.nr.fem.sp.rob,test="Wald")

Robust Wald Test Table

Model 1: mature ~ efl

Model 2: mature ~ efl + month_F

Models fitted by method 'Mqle'

Model	pseudoDf	Test.Stat	Df	Pr(>chisq)
1	179			
2	177	0.25113	2	0.882

Results for the best fitting model with all non-regenerating samples indicated that there was a highly significant fit to the maturity data ($P < 0.0001$). Fish length was the single significant predictor and Model 1 produced adequate residual patterns based on the histogram and QQ-plots of the randomized quantile residuals shown below. The estimate of the length at 50% maturity was L_{50} = 153.6 cm with a standard error of 1.9. The estimate of the length at 95% maturity was L_{95} = 170.9 cm with a standard error of 2.7. The estimate of the slope of the maturity ogive was $\beta_1 = 0.170$ with a standard error of 0.028. A summary of the best fitting model with all non-regenerating samples is listed below along with the predicted dose responses and the histogram and QQ-plot of the quantile residuals.

> summary(m1.nr.fem.sp.rob)

Call: glmrob(formula = f1, family = binomial, data = MLS, subset = female.spawn)

Coefficients:

	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-26.14880	4.52141	-5.783	7.32e-09	***
efl	0.17028	0.02846	5.984	2.18e-09	***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Robustness weights w.r * w.x:

166 weights are ~= 1. The remaining 15 ones are summarized as

Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
0.05097	0.20790	0.27980	0.36290	0.44730	0.92160

Number of observations: 181

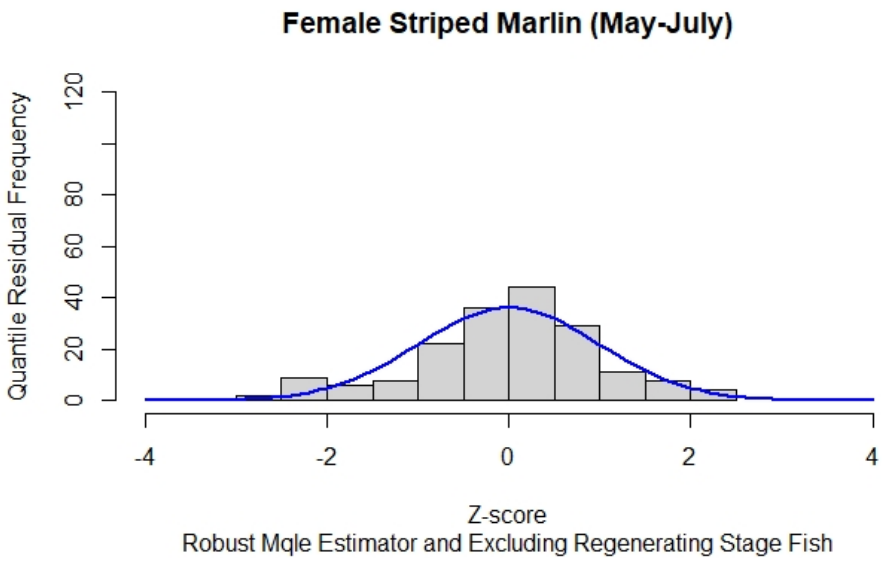
Fitted by method 'Mqle' (in 9 iterations)

(Dispersion parameter for binomial family taken to be 1)

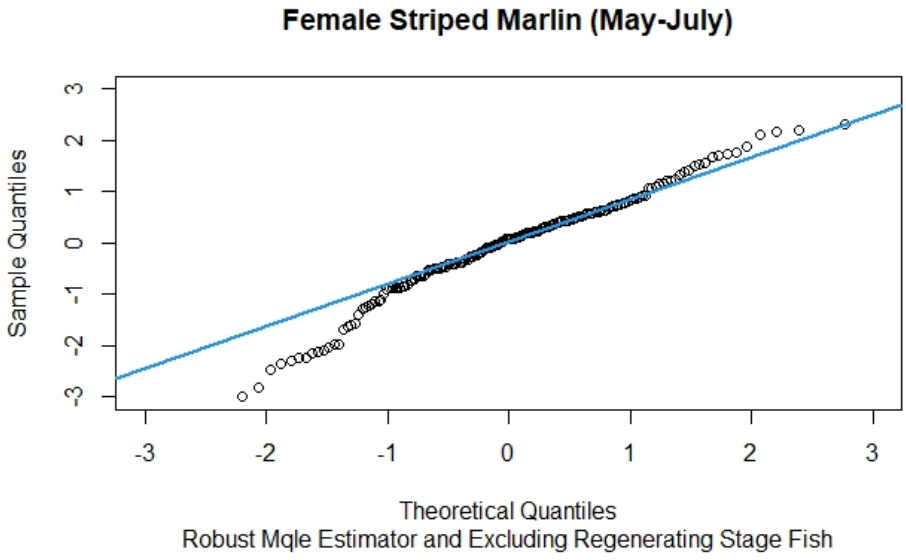
> dose.p(m1.nr.fem.sp.rob, p=matvec)

	Dose	SE
p = 0.010:	126.5747	5.616227
p = 0.025:	132.0453	4.754856
p = 0.050:	136.2684	4.105580
p = 0.100:	140.6564	3.454488
p = 0.250:	147.1081	2.578656
p = 0.382:	150.7346	2.167949
p = 0.500:	153.5597	1.921041
p = 0.618:	156.3848	1.768216
p = 0.750:	160.0113	1.748220
p = 0.900:	166.4630	2.178784
p = 0.950:	170.8510	2.688031
p = 0.975:	175.0741	3.259810
p = 0.990:	180.5447	4.063607

Histogram of randomized quantile residuals



Q-Q plot of randomized quantile residuals



Summary of the Robust Logistic Regression Models Fitted to All Female Samples by Season

Model names with "m1" have eye-fork length as the predictor and with "m2" have eye-fork length and month (as a factor) as predictors noting that the estimated month effect parameters are not shown here for brevity.

Model names with "sp" are fit to data collected during the spawning season and with "nsp" are fit to data collected not during the spawning season.

ROBUST LOGISTIC REGRESSION ALL FEMALE SAMPLES SUMMARY

Maturity Ogive Results

Model Name	efl	std efl	P value	Test stat	DF	Pr(>Chisq)	AIC
m1.fem.rob	0.165	0.017	<2e-16		596		na
m2.fem.rob	**0.166**	**0.019**	**<2e-16**	**59.683**	**585**	**1.06E-08**	**na**
m1.fem.sp.rob	**0.204**	**0.034**	**2.43E-09**		**225**		**na**
m2.fem.sp.rob	0.197	0.033	3.12E-09	0.565	223	0.754	na
m1.fem.nsp.rob	**0.144**	**0.022**	**1.39E-10**		**369**		**na**
m2.fem.nsp.rob	0.148	0.024	6.23E-10	7.580	361	0.476	na

Model Name	n	L50	L50 std	L95	L95 std	B1	B1 CV
m1.fem.rob	598	160.995	0.798	178.890	1.936	0.165	10.2%
m2.fem.rob	**598**	**159.008**	**3.980**	**176.716**	**4.602**	**0.166**	**11.3%**
m1.fem.sp.rob	**227**	**152.172**	**1.768**	**166.590**	**2.154**	**0.204**	**16.8%**
m2.fem.sp.rob	227	153.359	2.242	168.275	2.582	0.197	16.9%
m1.fem.nsp.rob	**371**	**167.930**	**1.475**	**188.354**	**4.133**	**0.144**	**15.6%**
m2.fem.nsp.rob	371	159.378	4.431	179.315	5.823	0.148	16.2%

Summary of the Robust Logistic Regression Models Fitted to All Nonregenerating Female Samples by Season

Model names with "m1" have eye-fork length as the predictor and with "m2" have eye-fork length and month (as a factor) as predictors noting that the estimated month effect parameters are not shown here for brevity.

Model names with "sp" are fit to data collected during the spawning season and with "nsp" are fit to data collected not during the spawning season.

ROBUST LOGISTIC REGRESSION NO REGENERATING FEMALE SAMPLES SUMMARY

Maturity Ogive Results

Model Name	efl	std efl	P value	Test stat	DF	Pr(>Chisq)	AIC
m1.nr.fem.rob	**0.146**	**0.018**	**<2e-16**				**na**
m2.nr.fem.rob	Model m2.nr.fem.rob did not converge			na	na	na	na
m1.nr.fem.sp.rob	**0.170**	**0.028**	**2.18E-09**		**179**		**na**
m2.nr.fem.sp.rob	0.168	0.029	5.93E-09	0.251	177	0.882	na
m1.nr.fem.nsp.rob	**0.097**	**0.030**	**0.001251**				**na**
m2.nr.fem.nsp.rob	Model m2.nr.fem.nsp.rob did not converge			na	na	na	na

Model Name	n	L50	L50 std	L95	L95 std	B1	B1 CV
m1.nr.fem.rob	**505**	**165.211**	**1.045**	**185.433**	**2.904**	**0.146**	**12.1%**
m2.nr.fem.rob	505	na	na	na	na	na	na
m1.nr.fem.sp.rob	**181**	**153.560**	**1.921**	**170.851**	**2.688**	**0.170**	**16.4%**
m2.nr.fem.sp.rob	181	154.367	2.397	171.884	3.000	0.168	17.2%
m1.nr.fem.nsp.rob	**324**	**186.484**	**7.519**	**216.764**	**16.501**	**0.097**	**31.0%**
m2.nr.fem.nsp.rob	324	na	na	na	na	na	0.000

Summary of the Standard Logistic Regression Models Fitted to All Female Samples by Season

Model names with "m1" have eye-fork length as the predictor and with "m2" have eye-fork length and month (as a factor) as predictors noting that the estimated month effect parameters are not shown here for brevity.

Model names with "sp" are fit to data collected during the spawning season and with "nsp" are fit to data collected not during the spawning season.

STANDARD LOGISTIC REGRESSION ALL FEMALE SAMPLES SUMMARY

Maturity Ogive Results

Model Name	efl	std efl	P value	Test stat	Pr(>Chisq)	Null dev	Resid dev	Percent dev	AIC
m1.fem	0.150	0.014	<2e-16			767.58	414.39	46.0%	418.39
m2.fem	**0.144**	**0.014**	**<2e-16**	**86.737**	**7.25E-14**	**767.58**	**327.65**	**57.3%**	**353.65**
m1.fem.sp	0.139	0.018	1.76E-14			296.97	145.41	51.0%	149.41
m2.fem.sp	**0.143**	**0.019**	**8.69E-14**	**6.903**	**0.032**	**296.97**	**138.50**	**53.4%**	**146.50**
m1.fem.nsp	**0.142**	**0.020**	**5.82E-13**			**325.04**	**197.51**	**39.2%**	**201.51**
m2.fem.nsp	0.144	0.021	4.95E-12	8.363	0.399	325.04	189.15	41.8%	209.15

Model Name	n	L50	L50 std	L95	L95 std	B1	B1 CV
m1.fem	598	161.982	0.814	181.647	1.979	0.150	9.0%
m2.fem	**598**	**160.343**	**4.468**	**180.838**	**5.116**	**0.144**	**9.8%**
m1.fem.sp	227	152.800	1.734	174.003	2.510	0.139	13.0%
m2.fem.sp	**227**	**156.523**	**2.073**	**177.086**	**2.881**	**0.143**	**13.4%**
m1.fem.nsp	**371**	**168.731**	**1.507**	**189.458**	**3.913**	**0.142**	**13.9%**
m2.fem.nsp	371	160.322	4.489	180.737	5.785	0.144	14.5%

Summary of the Standard Logistic Regression Models Fitted to All Nonregenerating Female Samples by Season

Model names with "m1" have eye-fork length as the predictor and with "m2" have eye-fork length and month (as a factor) as predictors noting that the estimated month effect parameters are not shown here for brevity.

Model names with "sp" are fit to data collected during the spawning season and with "nsp" are fit to data collected not during the spawning season.

STANDARD LOGISTIC REGRESSION NO REGENERATING FEMALE SAMPLES SUMMARY

Maturity Ogive Results

Model Name	efl	std efl	P value	Test stat	Pr(>Chisq)	Null dev	Residual dev	Percent dev	AIC
m1.nr.fem	**0.140**	**0.015**	**<2e-16**			**531.92**	**306.30**	**42.4%**	**310.30**
m2.nr.fem	0.127	0.017	3.92E-14	128.600	<2.2e-16	531.92	177.69	66.6%	203.69
m1.nr.fem.sp	**0.129**	**0.018**	**2.11E-12**			**249.32**	**128.35**	**48.5%**	**132.35**
m2.nr.fem.sp	0.132	0.019	7.21E-12	3.284	0.1936	249.32	125.07	49.8%	133.07
m1.nr.fem.nsp	**0.124**	**0.030**	**3.01E-05**			**102.65**	**71.27**	**30.6%**	**75.27**
m2.nr.fem.nsp	0.107	0.036	0.00311	19.000	0.01486	102.65	52.27	49.1%	72.27

Model Name	n	L50	L50 std	L95	L95 std	B1	B1 CV
m1.nr.fem	**505**	**166.417**	**1.087**	**187.476**	**2.848**	**0.140**	**10.8%**
m2.nr.fem	505	301.535	18146.000	324.692	18146.000	0.127	13.2%
m1.nr.fem.sp	**181**	**155.051**	**1.857**	**177.928**	**3.160**	**0.129**	**14.2%**
m2.nr.fem.sp	181	157.513	2.234	179.817	3.401	0.132	14.6%
m1.nr.fem.nsp	**324**	**182.910**	**4.963**	**206.711**	**10.255**	**0.124**	**24.0%**
m2.nr.fem.nsp	324	339.897	37943.060	367.454	37943.080	0.107	33.8%