Gag Grouper (*Mycteroperca microlepis*) Reproductive Parameters in Support of the SEDAR 71 Assessment

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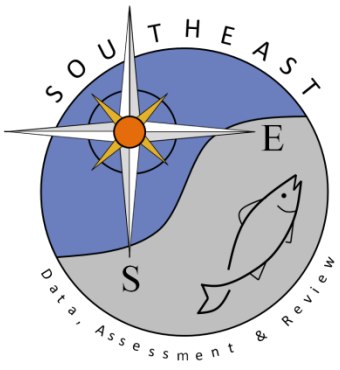

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SUMMARY

Gag grouper (*Mycteroperca microlepis*) samples used here for SEDAR71 were collected via fishery-dependent and fishery-independent methods during 1979-2019. Sampling was conducted by the Marine Resources Monitoring Assessment and Prediction (MARMAP) program from 1979 to 2009, and then by the collaborative Southeast Reef Fish Survey (SERFS) from 2010 to 2019. SERFS consists of 3 components: MARMAP, the Southeast Area Monitoring and Assessment Program, South Atlantic (SEAMAP-SA), and the Southeast Fisheries Independent Survey (SEFIS). MARMAP and SEAMAP-SA are housed at the South Carolina Department of Natural Resources (SCDNR), whereas SEFIS is housed at the Southeast Fisheries Science Center (SEFSC), Beaufort. All specimens collected for life history were measured, weighed, and processed following standard MARMAP and SERFS protocols (Smart *et al.*, 2015). The purpose of this working paper is to provide reproductive analyses and parameters in support of the SEDAR 71 Gag grouper assessment.

METHODS

Sample Collection

Gag grouper were collected by MARMAP and SERFS via fishery-independent sampling or sampling of commercial and recreational catches from fishermen. The specimens were caught mainly with snapper reels, chevron traps, and bottom longlines. For details on samples collected from commercial and recreational catches, see Reichert and Wyanski (2005). For fishery-independent sampling, chevron traps have been used as the standard gear since 1990, while short bottom longlines

are also used. For a full description of fishery-independent sample collection and processing protocols, see Smart *et al.* (2015).

Ageing

Gag grouper otoliths were processed and interpreted to assign increment counts and edge codes following standard protocols described in Reichert *et al.* (2005) and Smart *et al.* (2015). Calendar ages were determined with the rule that if the marginal edge was wide and month of capture was January through August, calendar age was increment count + 1 (see Ostrowski *et al.*, 2020 [SEDAR 71-WP01] for details). All mention of age henceforth will refer to calendar age, which is the age variable selected for the Gag grouper SEDAR71 assessment.

Reproductive Histology

Gonad tissue samples were processed histologically via standard protocols described in Smart *et al.* (2015) and examined to assign sex and reproductive phase. Specimens were classified as female, transitional, or male; and all males were considered mature. Females were classified as immature, early developing (cortical alveolar oocytes), developing (vitellogenic oocytes), actively spawning, regressing, or regenerating (Brown-Peterson et al. 2011). Females were categorized as actively spawning if they had indicators of imminent (oocyte maturation, including germinal vesicle migration and hydration) or recent (postovulatory follicle complexes, POC) spawning. The total duration of spawning indicators was estimated to be 60 h as explained in Gamboa-Salazar *et al*. (2019).

Maturity and Sex Ratio

To estimate female age and length at maturity and sexual transition, generalized linear models were fit to maturity data with four different links (logit, probit, cloglog, and cauchit) and the best fit model was chosen via Akaike's Information Criterion (AIC) values (Akaike, 1978). The maturity analyses were performed with two methods: traditional maturity and functional maturity. The traditional maturity method includes females in the regenerating and early developing phases as mature specimens and includes all months in the year; while the functional maturity method defines maturity to begin at the vitellogenesis stage and includes only the spawning season months – January through May for South Atlantic Gag grouper (Fig. 1). This latter method includes immature and regenerating females, as well as females of uncertain maturity under the immature category, and is the recommended method. Due to previous evidence in shifts in age and length at maturity through time (McGovern *et al*., 1998; Reichert and Wyanski, 2005), the functional maturity analyses were also performed for three different periods. These periods (1979 – 1995; 1996 – 2005; 2006 – 2019) were chosen to align with previously explored data analysis for South Atlantic Gag grouper, while trying to adjust for meaningful sample sizes. In addition, a model with the best-fit link chosen for the overall analyses was also run with 'Period' as an independent variable to determine whether 'Period' was a significant predictor variable in the model.

To estimate sex ratio, immature females were excluded from analyses to restrict the data to the adult population (Coleman *et al.*, 1996). These analyses were also performed with two methods: 1) one including transitional individuals as males because they would have spawned as males in the next spawning season (recommended method; Sadovy and Shapiro, 1987), and 2) one excluding transitional individuals from analyses. For both maturity and sex ratio analyses, total length data in millimeters were rounded to the nearest cm to create 10 mm bins. As this is the official length for the Gag grouper SEDAR 71 assessment, all length measurements henceforth will refer to total length.

Spawning Frequency

Spawning frequency (the number of batches per individual fish) was determined from histological examination of gonad tissue. Data were restricted to include only females from the main spawning season months (January – May, Fig. 1). For each calendar age, the spawning frequency was obtained by multiplying the proportion of actively spawning females by the spawning season duration as described in Gamboa-Salazar *et al*. (2019). To maintain comparable sample sizes, ages 14-19 were pooled in the 14+ age. For the spawning frequency at age model, spawning frequency was related to age via polynomial regression, adding orders in a step-wise process and choosing the best fitting model via AIC values. These analyses were performed with two methods: one including all females in the population (recommended method), and one including only mature females (excluding immature females and females of uncertain maturity).

Fecundity

If Gag ovarian tissue was in a developmental stage suitable for fecundity analysis (undergoing oocyte maturation but with no ovulation), gonads were removed to obtain a total wet weight (±1 g) and a sample of the ovary was then preserved in 10% formalin for later analysis. Batch fecundity was then determined and calculated as described in detail in Reichert and Wyanski (2005). The batch fecundity data were fit to a linear model, a power model with y=0 (2-parameter power), and a 3-parameter power model for each of the independent variables examined: total length, whole weight, and calendar age. For specimens missing a total length value, it was calculated from fork length using TL = 1.0341FL (SEDAR, 2005), and for specimens missing a whole weight value, it was calculated from gutted weight using WW = 1.059GW (SEDAR, 2014). The linear models were fit to compare with previous fecundity analyses for Gag, and to update the regression between batch fecundity and age with the current preferred age-variable (calendar age), as Reichert and Wyanski (2005) fit this regression with increment counts instead. All analyses were completed using R statistical software (R Core Team, 2013).

RESULTS

Sample Collection

The majority of Gag grouper specimens were collected through MARMAP's sampling of commercial catches (75%), while 4% were from recreational catches (Table 1). The source was unknown for 12% of the catches, while 9% were collected by MARMAP and SERFS fishery-independent sampling (Table 1).

Maturity

For the functional maturity method, the Cauchit link had the best fit to estimate female age at maturity (Table 2), and the Logit link provided the best fit for female length at maturity (Table 3; Fig. 2). For the period-based analysis, the Cauchit link also provided the best fit for estimating female age at functional maturity for all periods (Table 4). A model with age and period as predictor variables of maturity reveals that period is a significant variable, as adding period to the model was highly significant ($p<2.2e-16$; Table 5). However, the samples sizes in each period vary, and due to this method selecting only females from the main spawning months, the sample size for the most recent period (2006-2019) is very low (n = 179) and the 95% confidence interval around its A50 value is very large (Table 4C). This shows that confidence in the results of a period-based analysis of age at maturity with the current data

is low. *Thus, the recommended method of overall functional maturity yielded an estimated female age and length at 50% functional maturity of 4.6 years and 744.4 mm (Tables 2 & 3; Fig. 2).*

For the traditional maturity method, the cloglog link provided the best fit to estimate female age at maturity (Table 6), whereas the Logit link provided the best fit for female length at maturity (Table 7; Fig. 3). Here, the estimated female age and length at 50% traditional maturity was 3.9 years and 642.6 mm.

The confidence intervals for the reported overall age and length at 50% maturity values are wide when compared to past period-level analyses, thus it is likely that this reflects some shifts over time, as has been previously documented (McGovern *et al*., 1998; Reichert and Wyanski, 2005).

Sex Ratio

For the method which includes transitional individuals as males, the observed sex ratio for the entire adult population (n= 6426) was 9.5% male and 90.5% female. Here, the logit link was the best fit model for estimating both age (Table 8) and length (Table 9) at sexual transition (Fig. 4). *As the recommended method, this yielded an estimated age and length at sexual transition (to male) of 10.5 years and 1031.4 mm (Tables 8 & 9; Fig. 4).*

For the method which excludes transitional individuals from the analyses, the logit also provided the best fit for estimating both age (Table 10) and length (Table 11) at sexual transition (Fig. 5). Here, the estimated age and length at sexual transition (to male) are 10.7 years and 1035.5 mm.

Spawning Frequency

For both methods, the estimates of spawning frequency had significant dome-shaped relationships with calendar age, with the best-fit models being second order polynomials (Fig. 6). For the method including all females in the population (the recommended method), the model ($y = -14.9303 + 9.3066x - 0.5914x^2$, with *R2* = 0.721, *p* = 0.0004) predicted the highest values of SF at ages 7-8 years (Table 12); and the method including only the mature females in the population ($y = -16.4616 + 10.1349x - 0.6482x^2$, with *R2* =0.715, *p* = 0.0008) had peak values at ages 7-9 years (Table 13).

Fecundity

The specimens for fecundity analyses were collected during 1996-2005 (n=105) and ranged in length from 661 to 1159 mm, from 3,670 to 21,020 g in whole weight, and from 3 to 10 years in calendar age. For the linear models, significant relationships were found between batch fecundity and total length, whole weight, and calendar age (Table 14A; Fig. 7). Significant relationships with batch fecundity were also found for all three independent variables when using 2-parameter and 3-parameter power models (Table 14 B & C; Fig. 8).

The 2-parameter power function is the recommended model, based on discussions from previous assessments (Bubley and Wyanski, 2017) and because of the assumption that fecundity is a function of volume instead of length. This is supported by the plots of raw data indicating non-linear relationships with batch fecundity (Figs. 7 & 8), and the estimates of Z having lower standard error values relative to Z (Table 14). *Thus, the following equations are recommended for batch fecundity: with total length (TL) BF = 0.008 * TL ^ 2.647; with whole weight (WW) BF = 8.958 * WW ^ 1.198; and with calendar age (CA) BF = 40869.167 * CA ^ 1.334.*

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TABLES

Table 1. Specimens collected by the MARMAP program and Southeast Reef Fish Survey (SERFS) that were available for South Atlantic Gag Grouper analyses by year and fishery source. FI = Fishery-independent, COM = Commercial, REC = Recreational, U= Unknown origin.

Year	FI	COM	REC	U	Total
1979	3	1	0	423	427
1980	12	0	0	209	221
1981	16	0	0	233	249
1982	34	4	0	77	115
1983	19	0	0	9	28
1984	18	0	0	1	19
1985	27	0	0	0	27
1986	15	0	0	1	16
1987	0	0	0	2	2
1988	21	0	0	10	31
1989	2	0	0	18	20
1990	29	0	0	22	51
1991	16	0	0	6	22
1992	10	0	0	3	13
1993	9	59	0	62	130
1994	57	599	209	6	871
1995	77	4394	193	40	4704
1996	16	100	7	0	123
1997	6	14	0	1	21
1998	4	0	0	0	4
1999	9	0	0	0	9
2000	11	19	0	1	31
2001	4	64	0	0	68
2002	3	66	0	0	69
2003	1	54	0	0	55
2004	2	311	0	7	320
2005	9	1280	0	0	1289
2006	2	0	0	0	2
2007	12	0	0	0	12
2008	5	2	0	0	7
2009	13	300	0	0	313
2010	27	11	0	0	38
2011	43	0	0	0	43
2012	72	7	0	1	80
2013	56	0	1	0	57
2014	51	2	1	0	54

2015	26	8	0	0	34
2016	43	13	0	0	56
2017	25	0	0	0	25
2018	28	0	1	0	29
2019	48	0	2	0	50
Total	881	7308	414	1132	9735

Table 2. Female age at functional maturity for South Atlantic Gag Grouper during 1979-2019. *This is the recommended model for female age at maturity.*

Distribution	Link	N	A50 (yr)	Lower 95% CI (yr)	Upper 95% CI (yr)
Logistic	Cauchit	3185	4.637	3.687	5.830

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-5.49278	0.32558	-16.87	<2e-16
Age	1.18447	0.06789	17.45	<2e-16

Calendar Age (yr)	N	Prop. Mature (observed)	Prop. Mature (predicted)
1	7	0.00	0.07
2	45	0.04	0.10
3	165	0.14	0.15
4	760	0.29	0.29
5	832	0.63	0.63
6	614	0.83	0.82
7	409	0.88	0.89
8	191	0.93	0.92
9	82	0.89	0.94
10	41	0.93	0.95
11	17	0.88	0.96
12	10	1.00	0.96
13	5	1.00	0.97
14	1	1.00	0.97
15	1	1.00	0.97
16	2	1.00	0.98
17	1	1.00	0.98
18	1	1.00	0.98
19	1	0.00	0.98

Table 3. Female total length at functional maturity for South Atlantic Gag Grouper during 1979-2019. *This is the recommended model for female total length at maturity.*

Distribution	Link	N	L50 (mm)	Lower 95% CI (yr)	Upper 95% CI (yr)
Logistic	Logit	5501	744.42	663.47	835.02

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-1.33E+01	3.98E-01	-33.27	<2e-16
Length	1.78E-02	5.09E-04	34.98	<2e-16

Total Length (cm)	N	Prop. Mature (observed)	Prop. Mature (predicted)
29	1	0.00	0.00
30	0	NA	0.00
31	0	NA	0.00
32	1	0.00	0.00
33	0	NA	0.00
34	0	NA	0.00
35	0	NA	0.00
36	0	NA	0.00
37	1	0.00	0.00
38	3	0.00	0.00
39	0	NA	0.00
40	1	0.00	0.00
41	0	NA	0.00
42	2	0.00	0.00
43	3	0.00	0.00
44	2	0.00	0.00
45	1	0.00	0.01
46	2	0.00	0.01
47	2	0.00	0.01
48	4	0.00	0.01
49	4	0.00	0.01
50	8	0.00	0.01
51	6	0.00	0.02
52	15	0.00	0.02
53	12	0.00	0.02
54	19	0.00	0.03
55	17	0.00	0.03
56	34	0.00	0.04
57	23	0.00	0.04
58	37	0.03	0.05
59	32	0.00	0.06
60	61	0.07	0.07

61	40	0.00	0.08
62	78	0.04	0.10
63	45	0.02	0.12
64	68	0.09	0.13
65	56	0.16	0.16
66	85	0.13	0.18
67	69	0.17	0.21
68	87	0.23	0.24
69	58	0.34	0.28
70	97	0.34	0.31
71	78	0.38	0.35
72	109	0.45	0.39
73	85	0.52	0.44
74	128	0.48	0.48
75	134	0.55	0.52
76	182	0.45	0.57
77	142	0.65	0.61
78	217	0.66	0.65
79	171	0.75	0.69
80	287	0.73	0.73
81	206	0.87	0.76
82	290	0.78	0.79
83	217	0.85	0.82
84	317	0.88	0.85
85	213	0.89	0.87
86	231	0.90	0.89
87	187	0.91	0.90
88	217	0.90	0.92
89	170	0.92	0.93
90	142	0.89	0.94
91	101	0.94	0.95
92	113	0.94	0.96
93	73	0.95	0.96
94	105	0.96	0.97
95	42	0.86	0.97
96	69	0.91	0.98
97	31	0.97	0.98
98	43	0.95	0.99
99	29	1.00	0.99
100	42	0.93	0.99
101	17	0.94	0.99
102	25	0.96	0.99
103	12	1.00	0.99

104	30	1.00	0.99
105	7	0.86	1.00
106	20	0.95	1.00
107	14	1.00	1.00
108	8	0.88	1.00
109	5	1.00	1.00
110	3	1.00	1.00
111	1	1.00	1.00
112	6	1.00	1.00
113	1	1.00	1.00
114	2	1.00	1.00
115	2	1.00	1.00
116	2	1.00	1.00
117	0	NA	1.00
118	0	NA	1.00
119	0	NA	1.00
120	0	NA	1.00
121	0	NA	1.00
122	0	NA	1.00
123	0	NA	1.00
124	0	NA	1.00
125	0	NA	1.00
126	0	NA	1.00
127	0	NA	1.00
128	1	1.00	1.00

Table 4. Period-based analysis of female age at functional maturity for South Atlantic Gag Grouper during 1979-2019.

A. Period: 1979-1995

Distribution	Link	N	A50 (yr)	Lower 95% CI (yr)	Upper 95% CI (yr)
Logistic	Cauchit	1595	3.960	2.716	5.740

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-5.1581	0.5031	-10.25	<2e-16
Age	1.3025	0.1178	11.06	<2e-16

Calendar Age (yr)	N	Prop. Mature (observed)	Prop. Mature (predicted)
1	6	0.00	0.08
2	31	0.06	0.12
3	100	0.18	0.21
4	302	0.51	0.52
5	442	0.82	0.80
6	328	0.89	0.89
7	181	0.85	0.92
8	114	0.94	0.94
9	47	0.94	0.95
10	21	0.95	0.96
11	7	0.71	0.97
12	7	1.00	0.97
13	3	1.00	0.97
14	1	1.00	0.98
15	1	1.00	0.98
16	1	1.00	0.98
17	1	1.00	0.98
18	1	1.00	0.98
19	1	0.00	0.98

B. Period: 1996-2005

Distribution	Link	N	A50 (yr)	Lower 95% CI (yr)	Upper 95% CI (yr)
Logistic	Cauchit	1411	5.237181	3.732621	7.342

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-8.1937	0.6968	-11.76	<2e-16
Age	1.5645	0.1361	11.5	<2e-16

Calendar Age (yr)	N	Prop. Mature (observed)	Prop. Mature (predicted)
1	0	NA	NA
2	6	0.00	0.06
3	57	0.09	0.09
4	444	0.14	0.15
5	363	0.40	0.39
6	246	0.77	0.78
7	187	0.90	0.89
8	52	0.90	0.93
9	26	0.85	0.95
10	20	0.90	0.96
11	8	1.00	0.96
12	2	1.00	0.97

C. Period: 2006-2019

Distribution	Link	N	A50 (yr)	Lower 95% CI (yr)	Upper 95% CI (yr)
Logistic	Cauchit	179	4.631	1.631	12.725

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-4.6579	1.3255	-3.514	0.000441
Age	1.0058	0.2578	3.902	9.55E-05

Calendar Age (yr)	N	Prop. Mature (observed)	Prop. Mature (predicted)
1	1	0.00	0.09
2	8	0.00	0.12
3	8	0.00	0.17
4	14	0.50	0.32
5	27	0.59	0.61
6	40	0.75	0.80
7	41	0.90	0.87
8	25	0.96	0.91
9	9	0.78	0.93
10	0	NA	0.94
11	2	1.00	0.95
12	1	1.00	0.96
13	2	1.00	0.96
14	0	NA	0.97
15	0	NA	0.97
16	1	1.00	0.97

Table 5. Model of overall functional maturity at age with age and period as predictor variables. These p values for period represent comparisons to the earliest period (1979-1995).

Distribution	Link	N
Logistic	Cauchit	3185

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-5.58061	0.36575	-15.26	<2e-16
Age	1.40299	0.08502	16.5	<2e-16
Period 1996-2005	-1.79138	0.13251	-13.52	<2e-16
Period 2006-2019	-1.0937	0.29319	-3.73	1.91E-04

Table 6. Female age at maturity (traditional method) for South Atlantic Gag Grouper during 1979-2019.

Distribution	Link	N	A50 (yr)	Lower 95% CI (yr)	Upper 95% CI (yr)
Logistic	cloglog	4099	3.895	3.311	4.577

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-4.32436	0.19599	-22.06	<2e-16
Age	1.11032	0.04525	24.54	<2e-16

Calendar Age (yr)	N	Prop. Mature (observed)	Prop. Mature (predicted)
1	37	0.00	0.04
2	124	0.09	0.11
3	283	0.33	0.31
4	870	0.66	0.68
5	1007	0.98	0.97
6	800	1.00	1.00
7	534	1.00	1.00
8	244	1.00	1.00
9	101	1.00	1.00
10	55	1.00	1.00
11	21	1.00	1.00
12	10	1.00	1.00
13	5	1.00	1.00
14	1	1.00	1.00
15	1	1.00	1.00
16	2	1.00	1.00
17	1	1.00	1.00
18	2	1.00	1.00
19	1	1.00	1.00

Table 7. Female total length at maturity (traditional method) for South Atlantic Gag Grouper during 1979-2019.

Distribution	Link	N	L50 (mm)	Lower 95% CI (yr)	Upper 95% CI (yr)
Logistic	Logit	6482	642.57	558.36	739.14

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-19.9215	0.728438	-27.35	<2e-16
Length	0.031	0.001084	28.59	<2e-16

Total Length (cm)	N	Prop. Mature (observed)	Prop. Mature (predicted)
25	1	0.00	0.00
26	0	NA	0.00
27	3	0.00	0.00
28	2	0.00	0.00
29	4	0.00	0.00
30	0	NA	0.00
31	2	0.00	0.00
32	5	0.00	0.00
33	2	0.00	0.00
34	5	0.00	0.00
35	2	0.00	0.00
36	1	0.00	0.00
37	3	0.00	0.00
38	9	0.00	0.00
39	1	0.00	0.00
40	5	0.00	0.00
41	2	0.00	0.00
42	6	0.00	0.00
43	4	0.00	0.00
44	8	0.00	0.00
45	6	0.00	0.00
46	9	0.00	0.00
47	5	0.00	0.00
48	11	0.00	0.01
49	11	0.00	0.01
50	18	0.00	0.01
51	15	0.07	0.02
52	24	0.08	0.02
53	23	0.04	0.03
54	25	0.00	0.04
55	19	0.11	0.05

56	40	0.13	0.07
57	27	0.26	0.10
58	44	0.09	0.13
59	41	0.27	0.16
60	77	0.30	0.21
61	28	0.18	0.27
62	81	0.30	0.33
63	49	0.24	0.40
64	71	0.39	0.48
65	54	0.52	0.56
66	75	0.57	0.63
67	72	0.72	0.70
68	100	0.73	0.76
69	65	0.78	0.81
70	104	0.88	0.86
71	73	0.90	0.89
72	118	0.95	0.92
73	93	0.91	0.94
74	143	0.97	0.95
75	155	0.95	0.97
76	201	1.00	0.97
77	157	0.97	0.98
78	261	0.99	0.99
79	196	0.99	0.99
80	343	0.99	0.99
81	238	1.00	0.99
82	337	1.00	1.00
83	246	1.00	1.00
84	367	1.00	1.00
85	246	1.00	1.00
86	275	1.00	1.00
87	219	1.00	1.00
88	267	1.00	1.00
89	203	1.00	1.00
90	178	1.00	1.00
91	120	1.00	1.00
92	142	1.00	1.00
93	91	1.00	1.00
94	128	1.00	1.00
95	64	1.00	1.00
96	80	1.00	1.00
97	45	1.00	1.00
98	55	1.00	1.00

99	39	1.00	1.00
100	57	1.00	1.00
101	24	1.00	1.00
102	29	1.00	1.00
103	15	1.00	1.00
104	33	1.00	1.00
105	11	1.00	1.00
106	22	1.00	1.00
107	16	1.00	1.00
108	10	1.00	1.00
109	6	1.00	1.00
110	4	1.00	1.00
111	2	1.00	1.00
112	6	1.00	1.00
113	1	1.00	1.00
114	2	1.00	1.00
115	2	1.00	1.00
116	2	1.00	1.00
117	0	NA	1.00
118	0	NA	1.00
119	0	NA	1.00
120	0	NA	1.00
121	0	NA	1.00
122	0	NA	1.00
123	0	NA	1.00
124	0	NA	1.00
125	0	NA	1.00
126	0	NA	1.00
127	0	NA	1.00
128	1	1.00	1.00

Table 8. Female age at sexual transition to male (logit link) for South Atlantic Gag Grouper during 1979-2019. Transitional individuals are included as males. *This is the recommended model for female age at sexual transition (sex ratio).*

Distribution	Link	N	A50 (yr)	Lower 95% CI (yr)	Upper 95% CI (yr)
Logistic	Logit	3790	10.553	9.005	12.396

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-8.22392	0.29941	-27.47	<2e-16
Age	0.77927	0.03514	22.18	<2e-16

Calendar Age (yr)	N	# Female	# Male	Prop. Male (observed)	Prop. Male (predicted)
2	11	11	0	0.00	0.00
3	94	92	2	0.02	0.00
4	574	573	1	0.00	0.01
5	993	984	9	0.01	0.01
6	808	798	10	0.01	0.03
7	560	533	27	0.05	0.06
8	290	242	48	0.17	0.12
9	149	101	48	0.32	0.23
10	92	55	37	0.40	0.39
11	63	21	42	0.67	0.59
12	36	10	26	0.72	0.76
13	29	5	24	0.83	0.87
14	21	1	20	0.95	0.94
15	13	1	12	0.92	0.97
16	12	3	9	0.75	0.99
17	11	1	10	0.91	0.99
18	7	2	5	0.71	1.00
19	9	1	8	0.89	1.00
20	5	0	5	1.00	1.00
21	3	0	3	1.00	1.00
22	3	0	3	1.00	1.00
23	3	0	3	1.00	1.00
24	0	0	0	NA	1.00
25	2	0	2	1.00	1.00
26	1	0	1	1.00	1.00
27	0	0	0	NA	1.00
28	0	0	0	NA	1.00
29	0	0	0	NA	1.00
30	0	0	0	NA	1.00
31	1	0	1	1.00	1.00

Table 9. Female total length at sexual transition to male (logit link) for South Atlantic Gag Grouper during 1979-2019. Transitional individuals are included as males. *This is the recommended model for female total length at sexual transition (sex ratio).*

Distribution	Link	N	L50 (mm)	Lower 95% CI (yr)	Upper 95% CI (yr)
Logistic	Logit	6311	1031.416	908.130	1171.958

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-23.1495	0.73319	-31.57	<2e-16
Length	0.02244	0.00075	29.97	<2e-16

Total Length (cm)	N	# Female	# Male	Prop. Male (observed)	Prop. Male (predicted)
51	1	1	0	0.00	0.00
52	2	2	0	0.00	0.00
53	1	1	0	0.00	0.00
54	0	0	0	NA	0.00
55	2	2	0	0.00	0.00
56	5	5	0	0.00	0.00
57	7	7	0	0.00	0.00
58	4	4	0	0.00	0.00
59	11	11	0	0.00	0.00
60	23	23	0	0.00	0.00
61	7	5	2	0.29	0.00
62	24	24	0	0.00	0.00
63	12	12	0	0.00	0.00
64	28	28	0	0.00	0.00
65	28	28	0	0.00	0.00
66	44	43	1	0.02	0.00
67	52	52	0	0.00	0.00
68	72	72	0	0.00	0.00
69	51	51	0	0.00	0.00
70	91	91	0	0.00	0.00
71	66	66	0	0.00	0.00
72	111	111	0	0.00	0.00
73	85	85	0	0.00	0.00
74	137	137	0	0.00	0.00
75	148	148	0	0.00	0.00
76	198	198	0	0.00	0.00
77	154	153	1	0.01	0.00
78	260	257	3	0.01	0.00
79	195	194	1	0.01	0.00
80	342	338	4	0.01	0.01
81	238	237	1	0.00	0.01

82	339	337	2	0.01	0.01
83	250	246	4	0.02	0.01
84	370	366	4	0.01	0.01
85	245	245	0	0.00	0.02
86	278	275	3	0.01	0.02
87	222	218	4	0.02	0.03
88	272	267	5	0.02	0.03
89	213	202	11	0.05	0.04
90	184	178	6	0.03	0.05
91	125	120	5	0.04	0.06
92	148	141	7	0.05	0.08
93	96	91	5	0.05	0.09
94	148	128	20	0.14	0.11
95	73	64	9	0.12	0.14
96	93	80	13	0.14	0.17
97	60	44	16	0.27	0.20
98	75	55	20	0.27	0.24
99	58	38	20	0.34	0.28
100	92	57	35	0.38	0.33
101	46	24	22	0.48	0.38
102	62	29	33	0.53	0.44
103	39	15	24	0.62	0.49
104	72	33	39	0.54	0.55
105	35	11	24	0.69	0.60
106	57	22	35	0.61	0.66
107	44	16	28	0.64	0.70
108	35	11	24	0.69	0.75
109	30	6	24	0.80	0.79
110	25	4	21	0.84	0.82
111	20	2	18	0.90	0.85
112	23	6	17	0.74	0.88
113	15	1	14	0.93	0.90
114	16	2	14	0.88	0.92
115	13	2	11	0.85	0.93
116	9	2	7	0.78	0.95
117	7	0	7	1.00	0.96
118	7	0	7	1.00	0.97
119	2	0	2	1.00	0.97
120	5	0	5	1.00	0.98
121	3	0	3	1.00	0.98
122	2	0	2	1.00	0.99
123	0	0	0	NA	0.99
124	2	0	2	1.00	0.99

125	0	0	0	NA	0.99
126	0	0	0	NA	0.99
127	0	0	0	NA	1.00
128	1	1	0	0.00	1.00
129	0	0	0	NA	1.00
130	0	0	0	NA	1.00
131	0	0	0	NA	1.00
132	0	0	0	NA	1.00
133	0	0	0	NA	1.00
134	0	0	0	NA	1.00
135	0	0	0	NA	1.00
136	0	0	0	NA	1.00
137	0	0	0	NA	1.00
138	0	0	0	NA	1.00
139	0	0	0	NA	1.00
140	1	0	1	1.00	1.00

Table 10. Female age at sexual transition to male (logit link) for South Atlantic Gag Grouper during 1979-2019. Here, transitional individuals are excluded from analyses.

Distribution	Link	N	A50 (yr)	Lower 95% CI (yr)	Upper 95% CI (yr)
Logistic	Logit	3752	10.661	9.046	12.592

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-8.82362	0.33517	-26.33	<2e-16
Age	0.82768	0.03837	21.57	<2e-16

Calendar Age (yr)	N	# Female	# Male	Prop. Male (observed)	Prop. Male (predicted)
2	11	11	0	0.00	0.00
3	93	92	1	0.01	0.00
4	574	573	1	0.00	0.00
5	987	984	3	0.00	0.01
6	807	798	9	0.01	0.02
7	548	533	15	0.03	0.05
8	283	242	41	0.14	0.10
9	147	101	46	0.31	0.20
10	86	55	31	0.36	0.37
11	62	21	41	0.66	0.57
12	35	10	25	0.71	0.75
13	29	5	24	0.83	0.87
14	21	1	20	0.95	0.94
15	13	1	12	0.92	0.97
16	12	3	9	0.75	0.99
17	11	1	10	0.91	0.99
18	7	2	5	0.71	1.00
19	9	1	8	0.89	1.00
20	5	0	5	1.00	1.00
21	2	0	2	1.00	1.00
22	3	0	3	1.00	1.00
23	3	0	3	1.00	1.00
24	0	0	0	NA	1.00
25	2	0	2	1.00	1.00
26	1	0	1	1.00	1.00
27	0	0	0	NA	1.00
28	0	0	0	NA	1.00
29	0	0	0	NA	1.00
30	0	0	0	NA	1.00
31	1	0	1	1.00	1.00

Table 11. Female total length at sexual transition to male (logit link) for South Atlantic Gag Grouper during 1979-2019. Here, transitional individuals are excluded from analyses.

Distribution	Link	N	L50 (mm)	Lower 95% CI (yr)	Upper 95% CI (yr)
Logistic	Logit	6227	1035.520	901.488	1189.989

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-26.8800	0.932400	-28.83	<2e-16
Length	0.025960	0.000937	27.69	<2e-16

Total Length (cm)	N	# Female	# Male	Prop. Male (observed)	Prop. Male (predicted)
51	1	1	0	0.00	0.00
52	2	2	0	0.00	0.00
53	1	1	0	0.00	0.00
54	0	0	0	NA	0.00
55	2	2	0	0.00	0.00
56	5	5	0	0.00	0.00
57	7	7	0	0.00	0.00
58	4	4	0	0.00	0.00
59	11	11	0	0.00	0.00
60	23	23	0	0.00	0.00
61	6	5	1	0.17	0.00
62	24	24	0	0.00	0.00
63	12	12	0	0.00	0.00
64	28	28	0	0.00	0.00
65	28	28	0	0.00	0.00
66	43	43	0	0.00	0.00
67	52	52	0	0.00	0.00
68	72	72	0	0.00	0.00
69	51	51	0	0.00	0.00
70	91	91	0	0.00	0.00
71	66	66	0	0.00	0.00
72	111	111	0	0.00	0.00
73	85	85	0	0.00	0.00
74	137	137	0	0.00	0.00
75	148	148	0	0.00	0.00
76	198	198	0	0.00	0.00
77	154	153	1	0.01	0.00
78	258	257	1	0.00	0.00
79	194	194	0	0.00	0.00
80	340	338	2	0.01	0.00
81	237	237	0	0.00	0.00
82	338	337	1	0.00	0.00

83	246	246	0	0.00	0.00
84	367	366	1	0.00	0.01
85	245	245	0	0.00	0.01
86	277	275	2	0.01	0.01
87	219	218	1	0.00	0.01
88	271	267	4	0.01	0.02
89	206	202	4	0.02	0.02
90	182	178	4	0.02	0.03
91	121	120	1	0.01	0.04
92	146	141	5	0.03	0.05
93	93	91	2	0.02	0.06
94	140	128	12	0.09	0.08
95	71	64	7	0.10	0.10
96	87	80	7	0.08	0.12
97	58	44	14	0.24	0.15
98	73	55	18	0.25	0.19
99	54	38	16	0.30	0.23
100	89	57	32	0.36	0.28
101	42	24	18	0.43	0.34
102	57	29	28	0.49	0.40
103	38	15	23	0.61	0.46
104	71	33	38	0.54	0.53
105	35	11	24	0.69	0.59
106	55	22	33	0.60	0.65
107	43	16	27	0.63	0.71
108	33	11	22	0.67	0.76
109	30	6	24	0.80	0.80
110	24	4	20	0.83	0.84
111	20	2	18	0.90	0.87
112	23	6	17	0.74	0.90
113	15	1	14	0.93	0.92
114	16	2	14	0.88	0.94
115	13	2	11	0.85	0.95
116	9	2	7	0.78	0.96
117	7	0	7	1.00	0.97
118	7	0	7	1.00	0.98
119	2	0	2	1.00	0.98
120	5	0	5	1.00	0.99
121	3	0	3	1.00	0.99
122	1	0	1	1.00	0.99
123	0	0	0	NA	0.99
124	2	0	2	1.00	1.00
125	0	0	0	NA	1.00

126	0	0	0	NA	1.00
127	0	0	0	NA	1.00
128	1	1	0	0.00	1.00
129	0	0	0	NA	1.00
130	0	0	0	NA	1.00
131	0	0	0	NA	1.00
132	0	0	0	NA	1.00
133	0	0	0	NA	1.00
134	0	0	0	NA	1.00
135	0	0	0	NA	1.00
136	0	0	0	NA	1.00
137	0	0	0	NA	1.00
138	0	0	0	NA	1.00
139	0	0	0	NA	1.00
140	1	0	1	1.00	1.00

Table 12. Observed and predicted values of spawning frequency (SF, number of batches per individual fish) at calendar age for South Atlantic Gag Grouper during 1979-2019, including all females in the population. Predicted values are from second-order polynomial regression models, with sample size (N) at each age. Ages 14-19 were pooled. *This is the recommended model for spawning frequency at age.*

Model equation	$y = -14.9303 + 9.3066x - 0.5914x^2$		
	$\boldsymbol{b_0}$	$\boldsymbol{b_1}$	$\boldsymbol{b_2}$
Standard Error	5.0932	1.5621	0.1013

Calendar Age	**Observed SF**	**Predicted SF**	**N**
1	0.00	-6.22	7
2	0.50	1.32	45
3	0.95	7.67	165
4	7.77	12.83	760
5	17.29	16.82	832
6	20.61	19.62	614
7	21.62	21.24	409
8	26.26	21.67	191
9	26.12	20.92	82
10	16.39	18.99	41
11	22.00	15.88	17
12	1.60	11.58	10
13	3.20	6.10	5
14+	3.54	-0.56	7

Table 13. Observed and predicted values of spawning frequency (SF, number of batches per individual fish) at calendar age for South Atlantic Gag Grouper during 1979-2019, including only mature females in the population. Predicted values are from second-order polynomial regression models, with sample size (N) at each age. Ages 14-19 were pooled.

Model equation	$y = -16.4616 + 10.1349x - 0.6482x^2$		
	$\boldsymbol{b_0}$	$\boldsymbol{b_1}$	$\boldsymbol{b_2}$
Standard Error	6.670	1.881	0.115

Calendar Age	**Observed SF**	**Predicted SF**	**N**
2	4.48	1.22	5
3	2.56	8.11	61
4	14.34	13.71	412
5	18.49	18.01	778
6	20.78	21.01	609
7	21.62	22.72	409
8	26.26	23.13	191
9	26.12	22.25	82
10	16.39	20.07	41
11	23.38	16.59	16
12	1.60	11.82	10
13	3.20	5.75	5
14+	3.54	-1.62	7

Table 14. Regression coefficients for the relationships between batch fecundity and total length (TL), whole weight, and calendar age using a linear model fit (A), a 2-parameter power fit (B), and a 3-parameter power fit (C). Specimens were collected during 1996-2005. *The 2-parameter power fit (B) is the recommended model for each variable.*

A

	Batch fecundity = a + bX							
Independent Variable (X)	**Range**	**a**	**SE_a**	**b**	**SE_b**	**Adjusted R^2**	**F**	**n**
TL (mm)	661-1159	-902956.4	214444.6	1587.7	245.7	0.28	41.75	105
Whole Weight (g)	3670-21020	-114500	66150	67.540	7.295	0.48	85.71	93
Calendar Age (yr)	3-10	-141164	119747	98695	18905	0.22	27.25	92

B

Batch Fecundity	**Batch fecundity = b*X^Z**					
Independent Variable (X)	**Range**	**b**	**SE_b**	**Z**	**SE_z**	**n**
TL (mm)	661-1159	0.008	0.021	2.647	0.397	105
Whole Weight (g)	3670-21020	8.958	9.476	1.198	0.114	93
Calendar Age (yr)	3-10	40869.167	20236.705	1.334	0.258	92

C

	Batch fecundity = a + (b*X^Z)							
Independent Variable (X)	**Range**	**a**	**SE_a**	**b**	**SE_b**	**Z**	**SE_z**	**n**
TL (mm)	661-1159	-825600	2474000	1012	15320	1.058	1.956	105
Whole Weight (g)	3670-21020	-70970	271400	33.050	152.6	1.070	0.453	93
Calendar Age (yr)	3-10	136400	254700	10900	35950	1.858	1.361	92

FIGURES

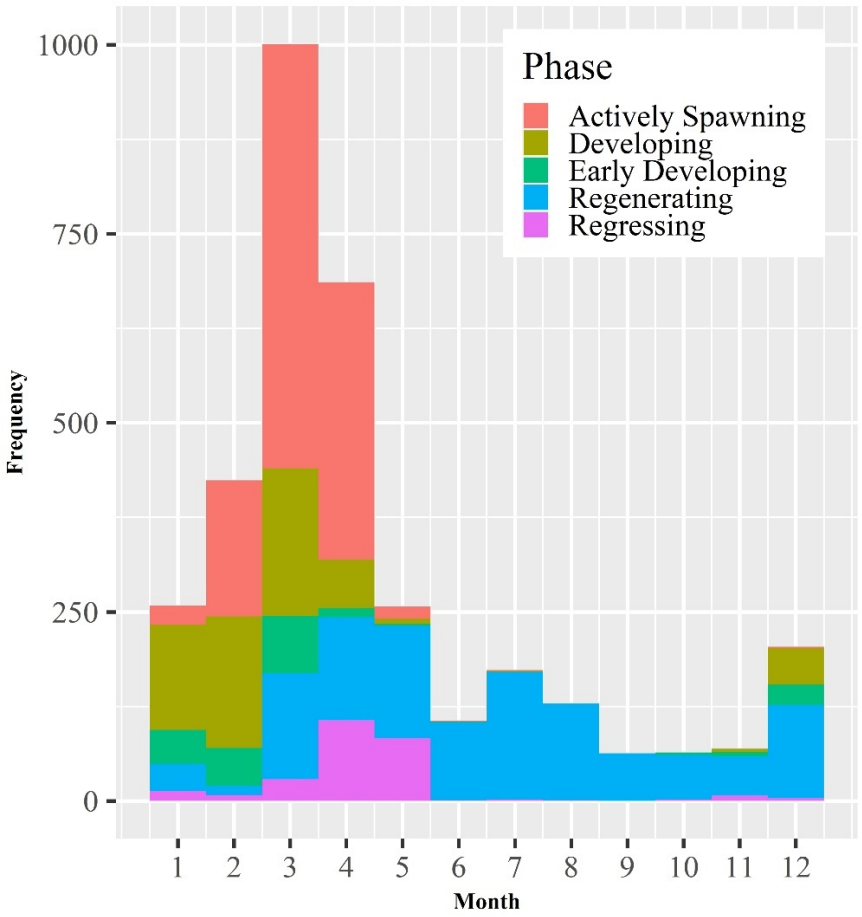
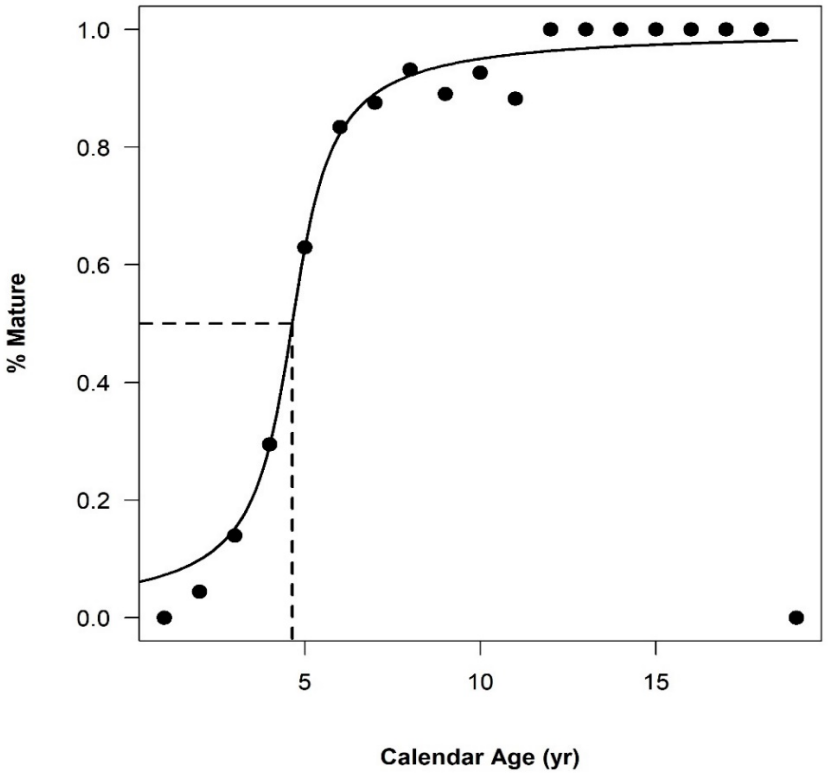


Figure 1. South Atlantic Gag Grouper reproductive phase by month for the period of 1979-2019.



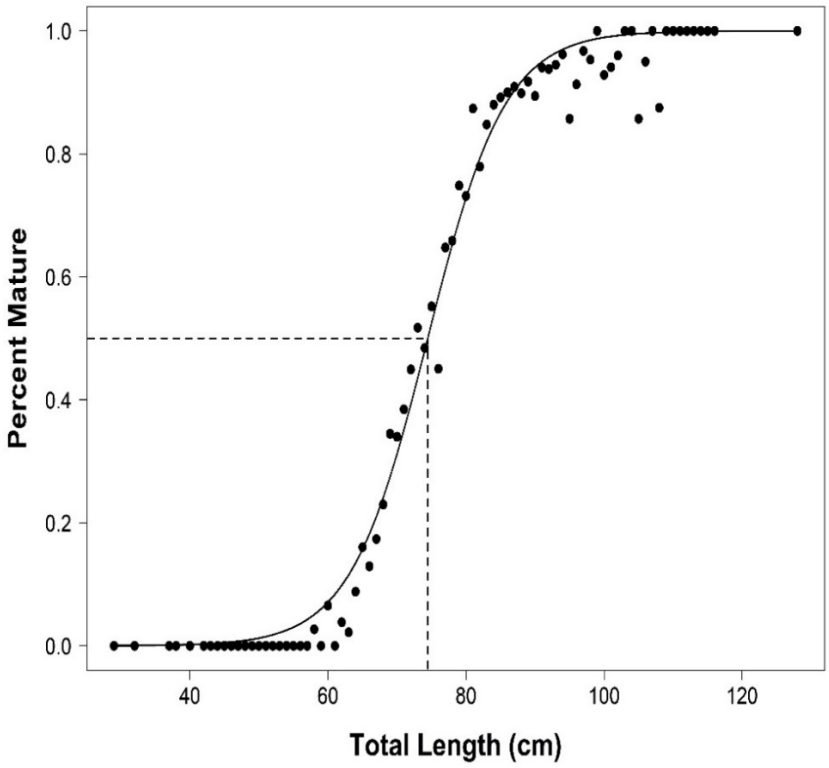
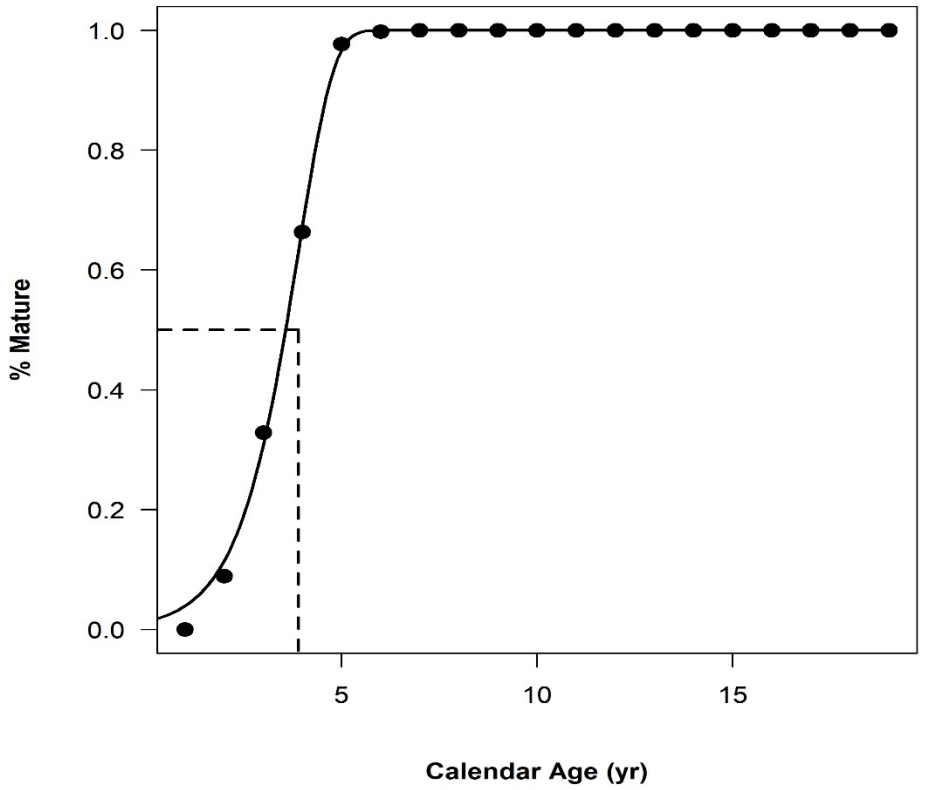


Figure 2. Female age (Cauchit link) and total length (Logit link) at functional maturity for South Atlantic Gag Grouper during 1979-2019. *These are the recommended models for female age and length at maturity.*



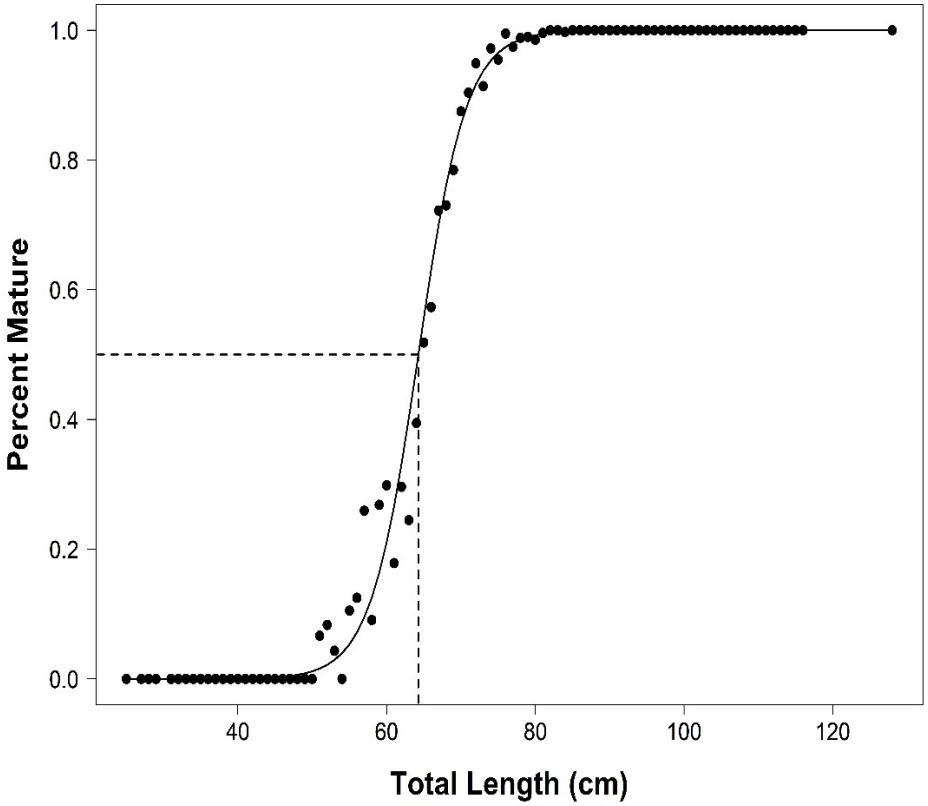


Figure 3. Female age (Cauchit link) and total length (Logit link) at maturity (traditional method) for South Atlantic Gag Grouper during 1979-2019.

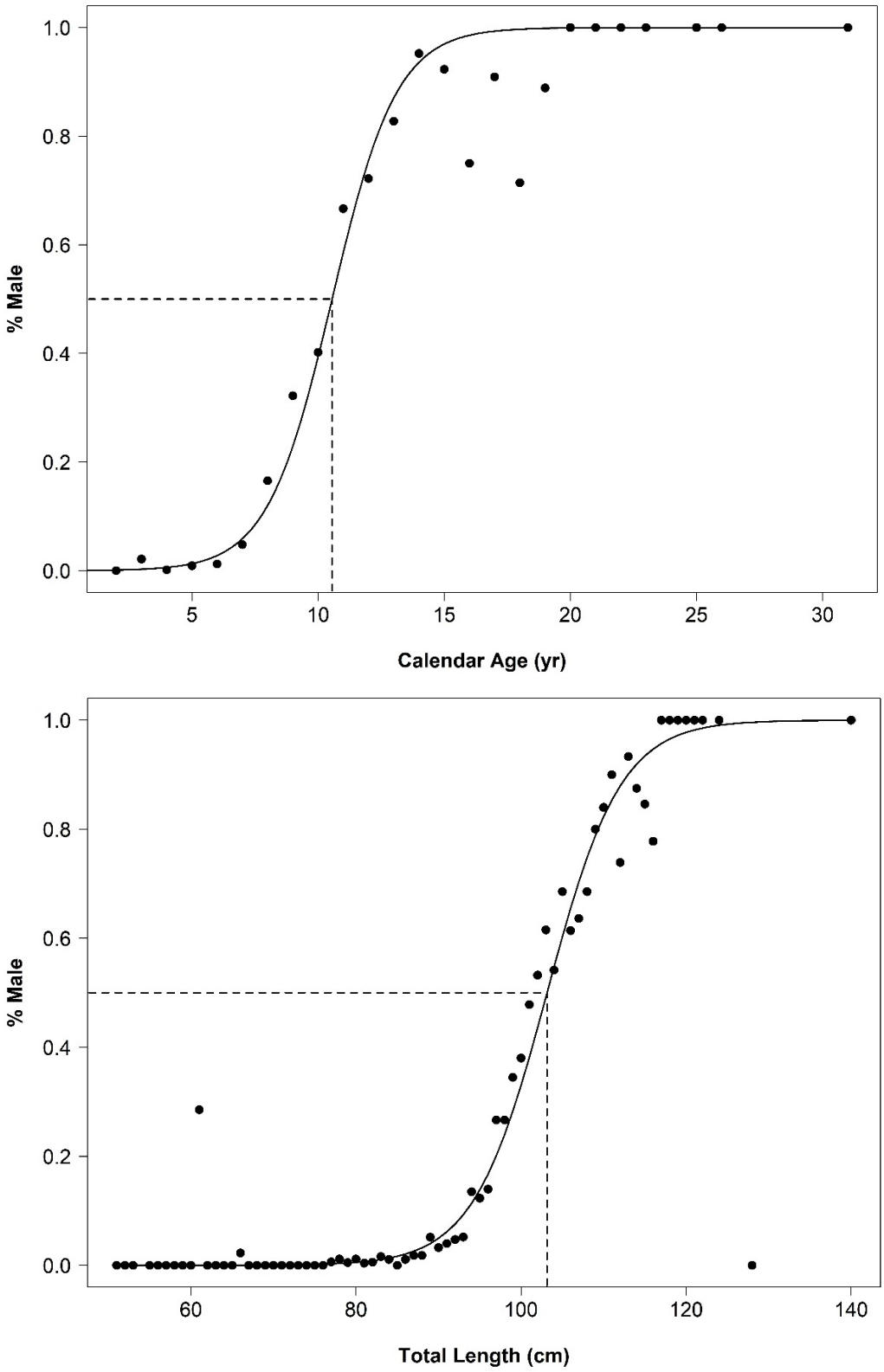


Figure 4. Female age (logit link) and total length (logit link) at sexual transition to male for South Atlantic Gag Grouper during 1979-2019. Transitional individuals are included as males. *These are the recommended models for age and length at sexual transition (sex ratio).*

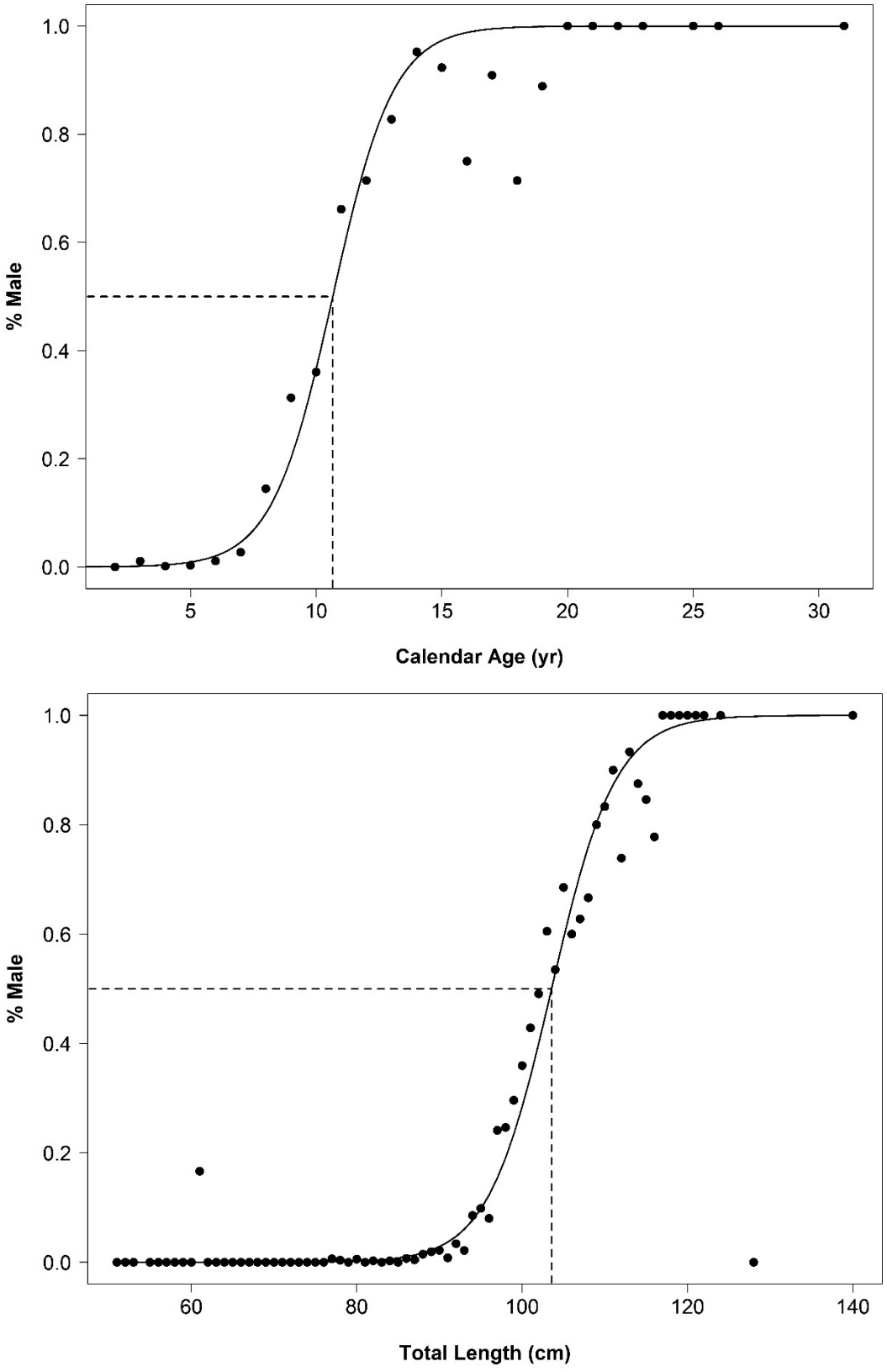
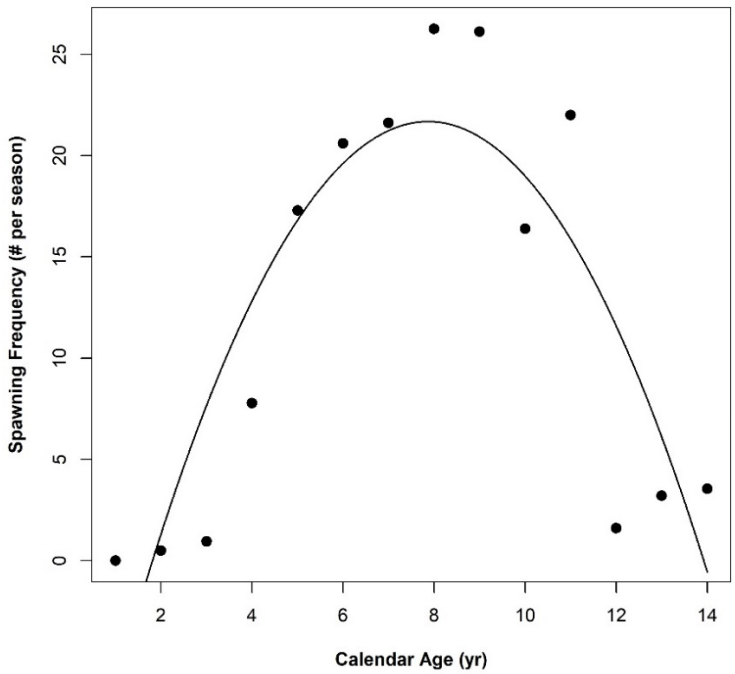


Figure 5. Female age (logit link) and total length (logit link) at sexual transition to male for South Atlantic Gag Grouper during 1979-2019. Transitional individuals excluded from analyses.

A



B

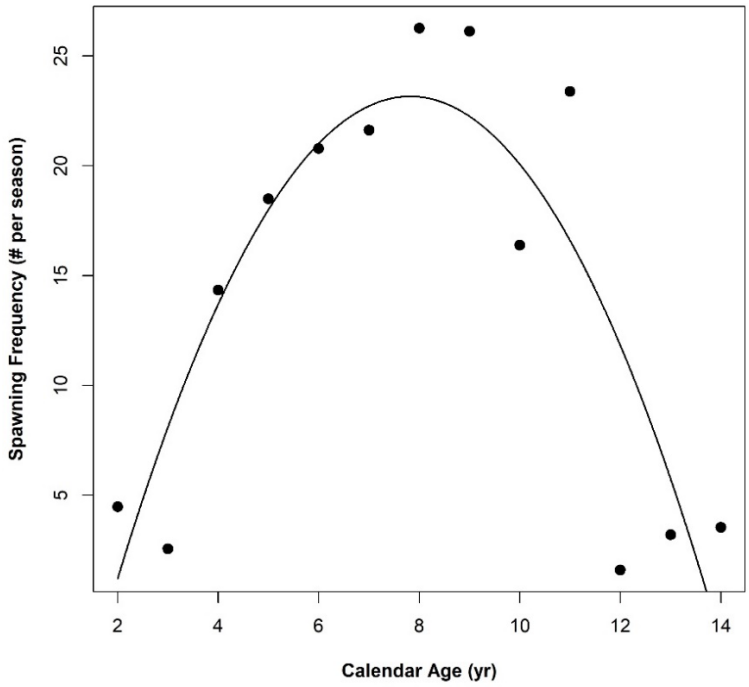


Figure 6. Observed (filled circles) values of spawning frequency at calendar age for South Atlantic Gag Grouper during 1979-2019, for entire female population (A) and for mature females only (B). Second-order polynomial regression models were fitted to the data (solid line). Ages 14-19 were pooled. Model equation $y = -14.9303 + 9.3066x - 0.5914x^2$ for (A), with *R2* = 0.721, *p* = 0.0004 and $y = -16.4616 + 10.1349x - 0.6482x^2$ for (B), with *R2* =0.715, *p* = 0.0008. *Model A is the recommended one for spawning frequency at age.*

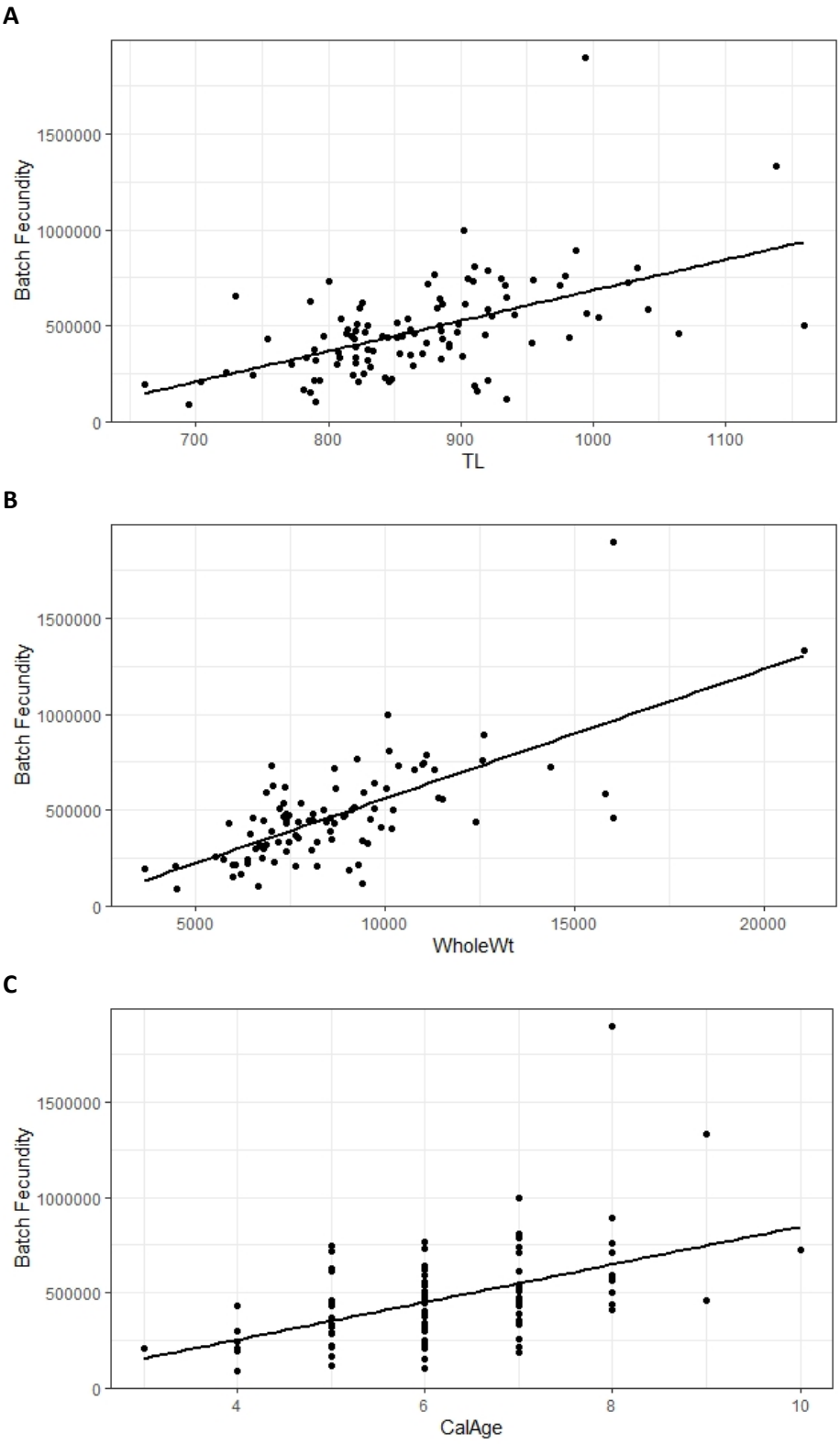
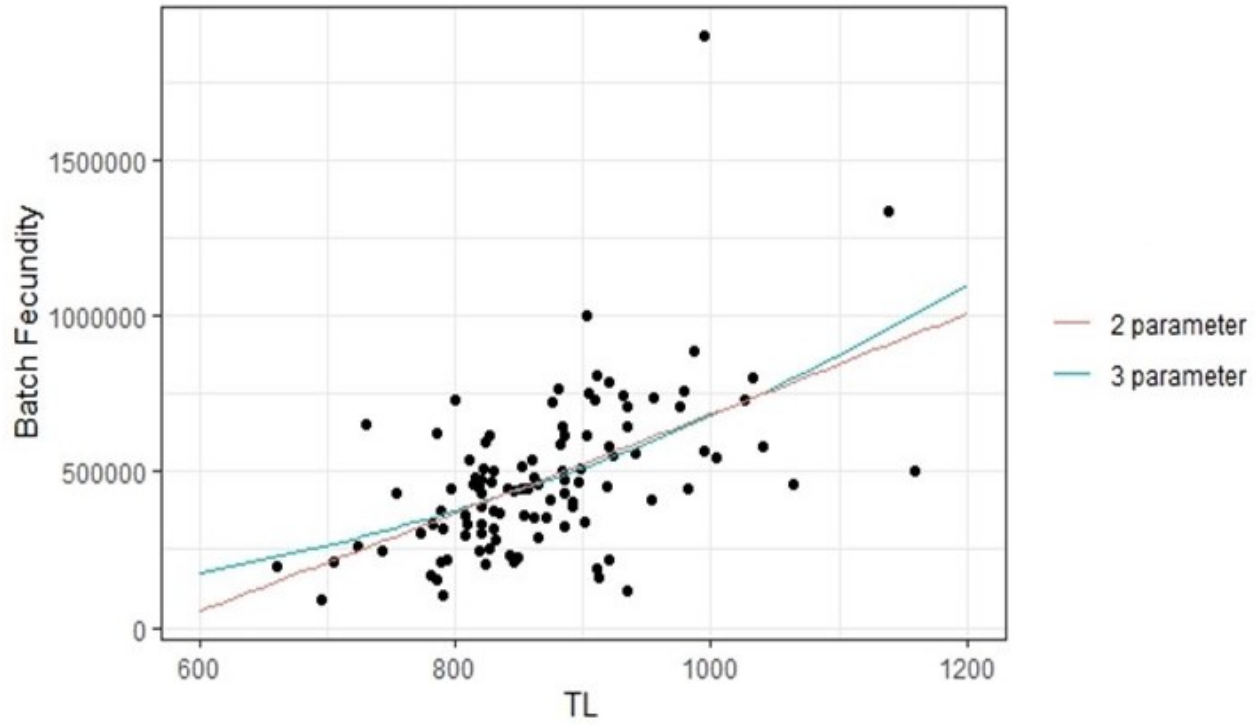
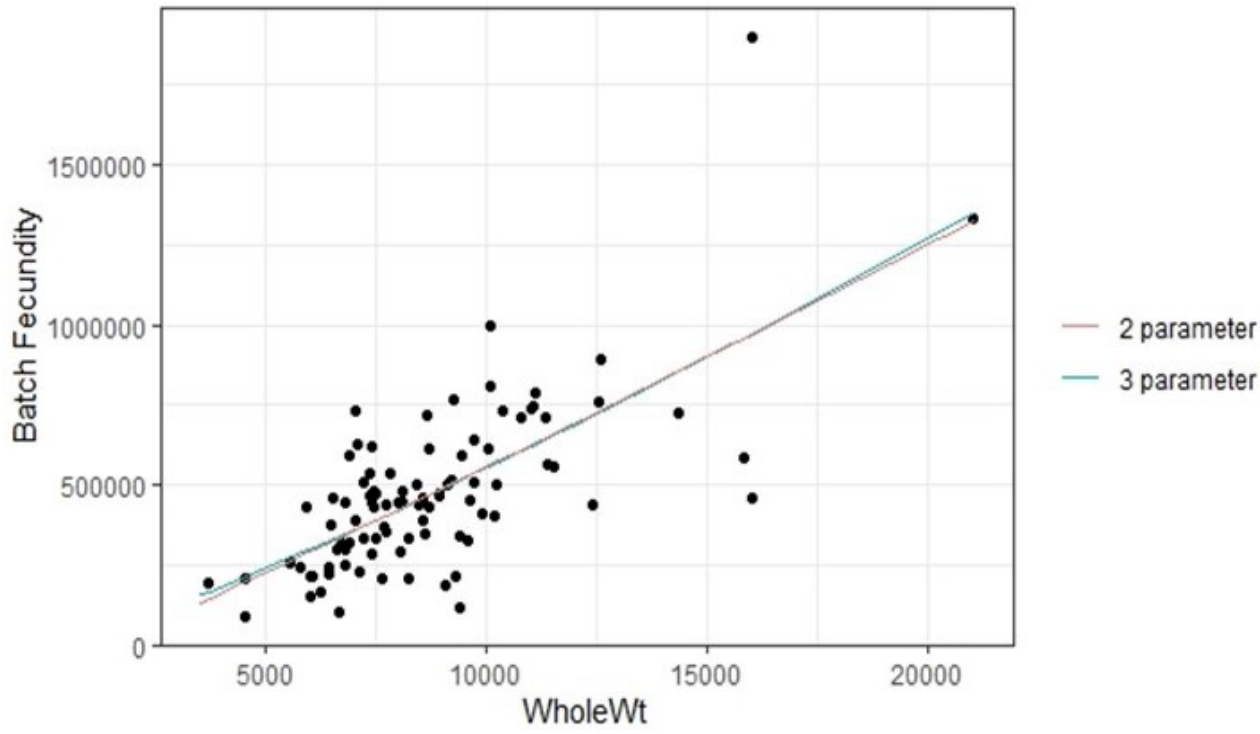


Figure 7. Linear models of batch fecundity (BF) at total length (A; TL, mm), whole weight (B; WholeWt, g), and calendar age (C; CalAge, yr) for Gag grouper collected during 1996-2005 (n=105). BF = a + bX with a = -902956.4 and b = 1587.7 for TL; a = -114500 and b = 67.54 for whole weight; and a = -141164 and b = 98695 for calendar age.

A


Batch Fecundity
1500000
1000000
500000
0
600
800
1000
1200
TL
2 parameter
3 parameter

B


Batch Fecundity
1500000
1000000
500000
0
5000
10000
15000
20000
WholeWt
2 parameter
3 parameter

C

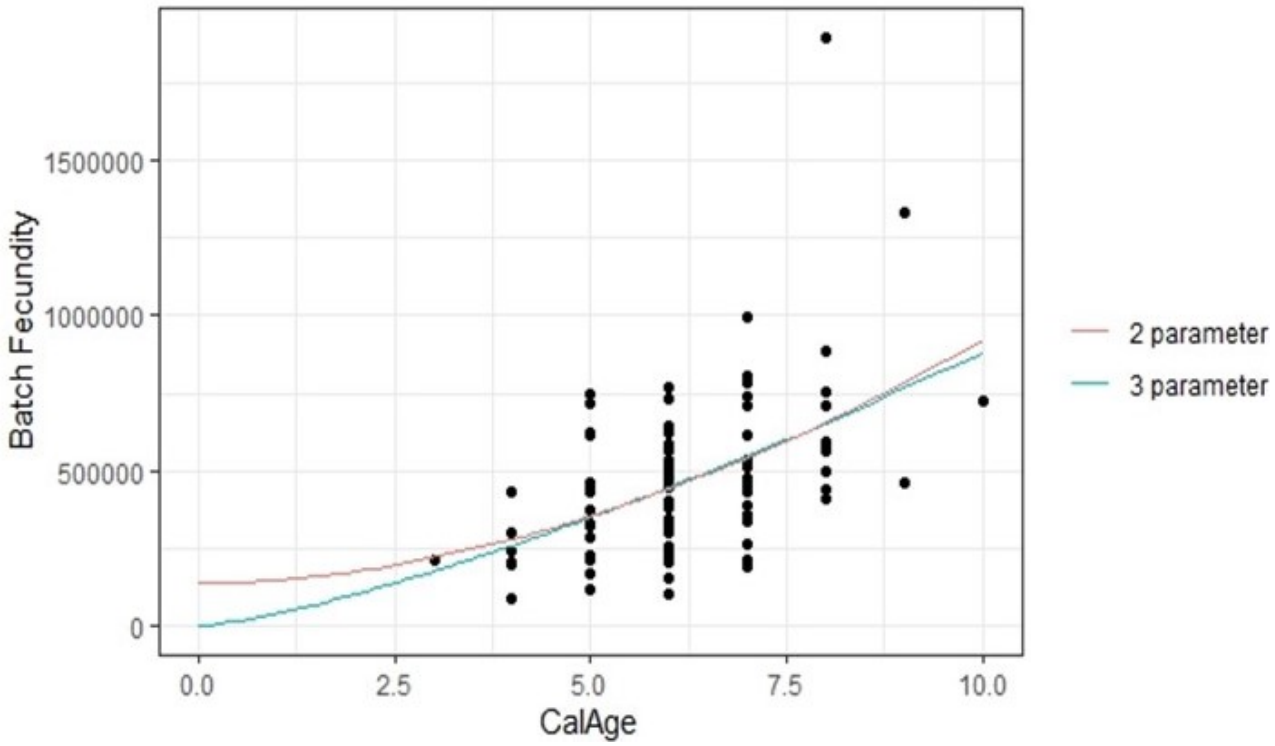


Figure 8. Comparison of 2-parameter (red line) and 3-parameter (blue line) power models of batch fecundity (BF) at total length (A; TL, mm), whole weight (B; WholeWt, g), and calendar age (C; CalAge, yr) for Gag grouper collected during 1996-2005 (n=105). For 2-parameter power fit BF = b * X^Z; for 3-parameter power fit BF = a + (b * X^Z). See Table 14 for model parameter estimates. *The 2-parameter power fit is the recommended model for each variable.*