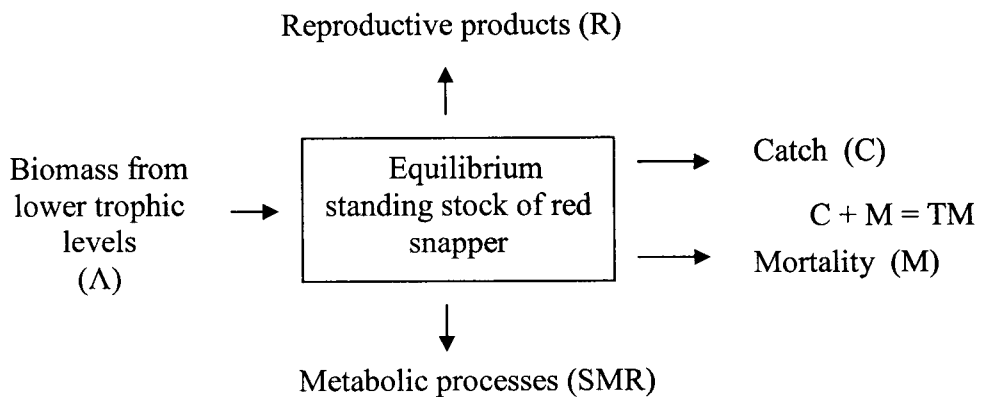


Estimation of prey biomass necessary to maintain the equilibrium standing stock biomass of red snapper (*Lutjanus campechanus*), at various levels, in the Gulf of Mexico.

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In 1999 the Gulf of Mexico red snapper stock assessment concluded that the spawning biomass of red snapper (*Lutjanus campechanus*) at maximum sustainable yield (B_{MSY}) ranged from two to four billion pounds. However, it was determined the current spawning stock biomass is significantly less than the B_{MSY} estimates. The purpose of the following analysis was to determine the energetic input from lower trophic levels necessary to support a B_{MSY} of red snapper at two, three and four billion lbs. taking into account the energetic expense of reproduction and metabolism as well as negative growth associated with harvest and bycatch. The model used to estimate input from lower trophic levels needed to support an equilibrium standing stock of a given size is graphically represented by:



In equation form:

$$\Lambda = (R + TM + SMR) / AE$$

Where:

Λ = Biomass from lower trophic levels; includes total weight of prey consumed by red snapper and subsequently utilized for SMR, development of tissues associated with reproduction, and somatic growth. For the stock to be stable somatic growth must equal TM.

R = Energy allocated for the development of reproductive products

TM = Total mortality equals the sum of fishing (C) and natural mortality (M)

SMR = Standard metabolic rate. This value is calculated multiplying the sum of R and Z by a respiration coefficient.

AE = Constant equaling 0.65 which represents an assimilation efficiency of 65% of ingested biomass.

Further explanation of parameter estimates

Reproductive products (R)

To estimate the energetic expense associated with reproductive products three values, 7.5, 10, and 12.5% of B_{MSY} were utilized. To select the range of values age based fecundity data from red snapper was analyzed. For the purposes of this analysis only the energetic expense incurred by females was considered as males devote significantly less energy to reproduction than do females. For example, Schafer (1998) estimated that the energetic cost of reproduction for female yellowfin tuna (*Thunnus albacares*) is approximately double that incurred by males. Applying the greater energetic expense incurred by females to both sexes results in a higher estimate of this energetic output in the model. Collins et al. (1996) presented age based fecundity estimates for red snapper, collected in the eastern Gulf of Mexico (Appendix 1). Age estimates were based on the analysis of sagittal otoliths, with estimates ranging 3 to 12 years. Annual fecundity estimates (AFE) ranged from 11,613 (age 5 individual) to 59,665,760 (age 12 individual) hydrated oocytes (Figure 1). Analysis of variance indicated that there was a statistically significant relationship between age and AFE ($n = 54$, d.f. = 7,46, $p < 0.01$). To test for differences in AFE among age classes Fisher's least significant difference procedure was employed ($\alpha = 0.05$). There was no significant difference in mean AFE values for the 3 to 6 and 6 to 9 age classes. However, age classes 10 and 12 were significantly different from one another as well as the younger age classes (Table 1).

An ovary mass to body mass ratio was calculated for each sample. The mean of this ratio was 0.02 (n = 65, S.D. = 0.17, range = 0.02-0.10). Because of the high degree of variability between ovary mass to body mass ratio and age (Figure 1) and absence of AFE data from all age classes the maximum calculated ovary to body mass ratio X 100 of 10% was used in subsequent calculations as the percent of energy allocated to reproduction in the model. Further justification for using this value was provided by the estimate of age 20+ red snapper being the most fecund (AFE of 60,000,000) age class in the previous red snapper stock assessment. This AFE value was approximately the same as reported for by Collins et al. for an age 12+ individual (AFE = 59,665,760) (Figure 2). Wilson and Nieland (2001) estimated ages, analyzing of sagittal otoliths, up to 52.6 years. However, Wilson and Nieland (2001) also concluded that growth in both sexes of red snapper slows considerably after age 8 – 10 years. Therefore, the estimate of ovary weight being 10% of total body weight may be an underestimate. To include a degree of variability in the analysis values of 7.5% and 12.5% were also employed.

The use of 10% as the output of energy to reproduction was compared with published estimates of allocation of energy for reproductive purposes in other marine and freshwater fishes. Total annual energy dedicated, in terms of percent of energy budget, to reproduction varied from 3.1 to 9.8% in Gila topminnows (*Poeciliopsis occidentalis*) (Constantz 1979), 7 to 16% in pike (*Esox lucius*) (Diana 1983), 7.5 % in American plaice (*Hippoglossoides platessoides*) (MacKinnon 1972, 1973) and 1.3 to 12% in cod (*Gadus morhua*) (Dann 1975) (the above references to energy budgets cited in Wooten 1985). Essington (2003) determined that >10% of the energetic budget of skipjack tuna (*Katsuwonus pelamis*) was dedicated to reproduction while <5% of the budget was utilized by albacore (*Thunnus alauunga*) for reproduction. By comparing the estimate of energetic allocation to reproduction for red snapper calculated in this study to the aforementioned published values for other fishes it appears that the 10% value is well within the bounds of reason. No adjustment with regards to age/size related senescence was applied to the model. It should be noted that preliminary analyses by Melissa Woods (NMFS, Panama City Laboratory) that the AFE for age 9+ red snapper can be as high as 80 million to 106 million ova per year (G. Fitzhugh, pers. comm.), therefore, the 10% estimate utilized in this study might underestimate the energetic expense of reproduction for this species. However, since recent data indicates that the variability in batch fecundity ranges from 8 million hydrated ova in a 13 + year old fish to less than 1 million hydrated ova for fishes in 20++ age classes (G.Fitzhugh, pers. comm.) the use of the 10% estimate of energetic allocation to reproduction seems justified.

Mortality (TM = C + M)

Three levels of fishing mortality (C) were used in the analysis. The model was calculated under three harvest scenarios; 10 million, 50 million and 100 million lbs. Annual mortality (A) was calculated using the following equation (Ricker 1975):

$$(1-A) = S = e^{-z}$$

Where:

A = annual mortality

S = annual survival rate

Z = instantaneous mortality

The estimate for Z reported by Henwood et al. (2004) of 0.1289 was used in the calculation. The resulting estimate for A was 0.1209. Therefore, the natural and bycatch mortality estimate used in the analysis was 12% of the equilibrium standing stock at two, three and four billion lbs.

Standard metabolic rate (SMR)

Standard metabolic rate was calculated by multiplying the sum of all growth (TM+R) by a respiration coefficient. Lindeman (1941) summarized the findings of several studies and determined that respiratory coefficients for freshwater fishes range from approximately 1 to 1.5. He went on to conclude that the average respiratory coefficient for aquatic predators in general was 1.4. Wakeman et al. (1979) estimated that energy content of increased body weight could be determined by multiplying the body weight (kg) of age 1 and 2 red snapper by 4.5. To determine the respiratory metabolism (kcal/day) of red snapper of the same ages Wakeman et al. (1979) multiplied the body weight (kg) by 6.9. To determine a respiration coefficient for red snapper, as per Lindeman (1942), the estimate of 6.9 for respiratory metabolism was divided by the estimate of 4.5 for the caloric content of the change in body mass. This calculation resulted in a respiratory coefficient estimate of 1.53 for juvenile red snapper. As no literature was located specifically related to this ratio for red snapper and a rough estimate of 1.5 was calculated, based on the results of Wakeman et al. (1979), a range of values were utilized in the analysis. It was felt that the use of a range of values for this parameter estimate would be appropriate as there are ontogenetic shifts in red snapper habitat utilization which would presumably effect the respiration and growth of red snapper due to varying abiotic influences associated with different habitats. Four levels, 1.0, 1.4, 1.5, 1.6, of respiration coefficients were used for the current analysis to provide a range of estimate for Λ at the three levels of B_{MSY} .

Assimilation efficiency (AE)

Assimilation efficiency was held constant at 65% throughout the analysis. Based on the findings of Kitchell et al. (1978), Brown et al. (1992) determined that the mean AE for marine fishes is 65% of total ingested biomass. Wakeman et al. (1979) assumed AE to be 75% in juvenile red snapper, based on the conclusions of Winberg (1956). As cited in Wakeman et al. (1979), Edwards et al. (1972) estimated that AE can be as high as 98.7% in some fishes. Therefore, it is possible that AE values used in this study are lower than actual AE values. It should be noted that juvenile snapper feed primarily on invertebrates while adults predominately feed on other fishes (Moran 1988). As invertebrates are

provide more energy as a food source than do vertebrates (Horn 1998) AE values are likely higher for juveniles than they are for adults. However, this was not taken into account in this analysis.

Equilibrium standing stock

Parameter estimates, were based on standing stock biomasses equaling two, three and four billion lbs.

The results of the analyses are listed in Tables 2, 3 and 4. The final column on each table indicates the total biomass from lower trophic levels that would be needed to support equilibrium standing stocks of two, three and four billion lbs. based on corresponding model parameter values.

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Method: 95.0 percent LSD

Age	Count	Mean	Homogeneous Groups
3	11	1.23384E6	X
4	19	2.65494E6	X
5	11	2.92302E6	X
6	2	9.38222E6	XX
8	7	1.37749E7	X
9	1	1.71621E7	X
10	2	3.4798E7	X
12	1	5.96658E7	X

Contrast	Difference	+/- Limits
3 - 4	-1.4211E6	4.40264E6
3 - 5	-1.68917E6	4.955E6
3 - 6	-8.14837E6	8.93276E6
3 - 8	*-1.25411E7	5.61845E6
3 - 9	*-1.59282E7	1.21372E7
3 - 10	*-3.35642E7	8.93276E6
3 - 12	*-5.84319E7	1.21372E7
4 - 5	-268077.0	4.40264E6
4 - 6	-6.72728E6	8.6386E6
4 - 8	*-1.112E7	5.13791E6
4 - 9	*-1.45071E7	1.19224E7
4 - 10	*-3.21431E7	8.6386E6
4 - 12	*-5.70108E7	1.19224E7
5 - 6	-6.4592E6	8.93276E6
5 - 8	*-1.08519E7	5.61845E6
5 - 9	*-1.42391E7	1.21372E7
5 - 10	*-3.1875E7	8.93276E6
5 - 12	*-5.67427E7	1.21372E7
6 - 8	-4.39272E6	9.31714E6
6 - 9	-7.77987E6	1.42322E7
6 - 10	*-2.54158E7	1.16205E7
6 - 12	*-5.02835E7	1.42322E7
8 - 9	-3.38715E6	1.24229E7
8 - 10	*-2.10231E7	9.31714E6
8 - 12	*-4.58908E7	1.24229E7
9 - 10	*-1.76359E7	1.42322E7
9 - 12	*-4.25037E7	1.64339E7
10 - 12	*-2.48677E7	1.42322E7

* denotes a statistically significant difference.

Table 1. Results of Fisher's least significant difference procedure examining the relationship between age and annual fecundity estimates. Analysis based on data presented in Collins et al. (1996).

Mortality	Catch	R	RC	SMR	Λ
0.48	0.01	0.30	1.00	0.79	2.43
0.48	0.01	0.30	1.40	1.11	2.92
0.48	0.01	0.30	1.50	1.19	3.04
0.48	0.01	0.30	1.60	1.26	3.16
0.48	0.01	0.40	1.00	0.89	2.74
0.48	0.01	0.40	1.40	1.25	3.29
0.48	0.01	0.40	1.50	1.34	3.42
0.48	0.01	0.40	1.60	1.42	3.56
0.48	0.01	0.50	1.00	0.99	3.05
0.48	0.01	0.50	1.40	1.39	3.66
0.48	0.01	0.50	1.50	1.49	3.81
0.48	0.01	0.50	1.60	1.58	3.96
0.48	0.05	0.30	1.00	0.83	2.55
0.48	0.05	0.30	1.40	1.16	3.06
0.48	0.05	0.30	1.50	1.25	3.19
0.48	0.05	0.30	1.60	1.33	3.32
0.48	0.05	0.40	1.00	0.93	2.86
0.48	0.05	0.40	1.40	1.30	3.43
0.48	0.05	0.40	1.50	1.40	3.58
0.48	0.05	0.40	1.60	1.49	3.72
0.48	0.05	0.50	1.00	1.03	3.17
0.48	0.05	0.50	1.40	1.44	3.80
0.48	0.05	0.50	1.50	1.55	3.96
0.48	0.05	0.50	1.60	1.65	4.12
0.48	0.10	0.30	1.00	0.88	2.71
0.48	0.10	0.30	1.40	1.23	3.25
0.48	0.10	0.30	1.50	1.32	3.38
0.48	0.10	0.30	1.60	1.41	3.52
0.48	0.10	0.40	1.00	0.98	3.02
0.48	0.10	0.40	1.40	1.37	3.62
0.48	0.10	0.40	1.50	1.47	3.77
0.48	0.10	0.40	1.60	1.57	3.92
0.48	0.10	0.50	1.00	1.08	3.32
0.48	0.10	0.50	1.40	1.51	3.99
0.48	0.10	0.50	1.50	1.62	4.15
0.48	0.10	0.50	1.60	1.73	4.32

Table 2. Results of analysis assuming a 4 billion lb. equilibrium standing stock. All values reported in billions of lbs. See text for description of parameter estimates for mortality, catch, energy allocated to reproduction (R), respiration coefficient (RC), and energetic cost of standard metabolic rate (SMR). Values below the column heading ' Λ ' represents the total amount of biomass needed to support an equilibrium standing stock of four billion lbs.

Mortality	Catch	R	RC	SMR	Λ
0.36	0.01	0.23	1.00	0.60	1.83
0.36	0.01	0.23	1.40	0.83	2.20
0.36	0.01	0.23	1.50	0.89	2.29
0.36	0.01	0.23	1.60	0.95	2.38
0.36	0.01	0.30	1.00	0.67	2.06
0.36	0.01	0.30	1.40	0.94	2.47
0.36	0.01	0.30	1.50	1.01	2.58
0.36	0.01	0.30	1.60	1.07	2.68
0.36	0.01	0.38	1.00	0.75	2.29
0.36	0.01	0.38	1.40	1.04	2.75
0.36	0.01	0.38	1.50	1.12	2.87
0.36	0.01	0.38	1.60	1.19	2.98
0.36	0.05	0.23	1.00	0.64	1.95
0.36	0.05	0.23	1.40	0.89	2.34
0.36	0.05	0.23	1.50	0.95	2.44
0.36	0.05	0.23	1.60	1.02	2.54
0.36	0.05	0.30	1.00	0.71	2.18
0.36	0.05	0.30	1.40	0.99	2.62
0.36	0.05	0.30	1.50	1.07	2.73
0.36	0.05	0.30	1.60	1.14	2.84
0.36	0.05	0.38	1.00	0.79	2.42
0.36	0.05	0.38	1.40	1.10	2.90
0.36	0.05	0.38	1.50	1.18	3.02
0.36	0.05	0.38	1.60	1.26	3.14
0.36	0.10	0.23	1.00	0.69	2.11
0.36	0.10	0.23	1.40	0.96	2.53
0.36	0.10	0.23	1.50	1.03	2.63
0.36	0.10	0.23	1.60	1.10	2.74
0.36	0.10	0.30	1.00	0.76	2.34
0.36	0.10	0.30	1.40	1.06	2.81
0.36	0.10	0.30	1.50	1.14	2.92
0.36	0.10	0.30	1.60	1.22	3.04
0.36	0.10	0.38	1.00	0.84	2.57
0.36	0.10	0.38	1.40	1.17	3.08
0.36	0.10	0.38	1.50	1.25	3.21
0.36	0.10	0.38	1.60	1.34	3.34

Table 3. Results of analysis assuming a three billion lb. equilibrium standing stock. All values reported in billions of lbs. See text for description of parameter estimates for mortality, catch, energy allocated to reproduction (R), respiration coefficient (RC), and energetic cost of standard metabolic rate (SMR). Values below the column heading ‘ Λ ’ represents the total amount of biomass needed to support an equilibrium standing stock of three billion lbs.

Mortality	Catch	R	RC	SMR	Λ
0.24	0.01	0.15	1.00	0.40	1.23
0.24	0.01	0.15	1.40	0.56	1.48
0.24	0.01	0.15	1.50	0.60	1.54
0.24	0.01	0.15	1.60	0.64	1.60
0.24	0.01	0.20	1.00	0.45	1.38
0.24	0.01	0.20	1.40	0.63	1.66
0.24	0.01	0.20	1.50	0.68	1.73
0.24	0.01	0.20	1.60	0.72	1.80
0.24	0.01	0.25	1.00	0.50	1.54
0.24	0.01	0.25	1.40	0.70	1.85
0.24	0.01	0.25	1.50	0.75	1.92
0.24	0.01	0.25	1.60	0.80	2.00
0.24	0.05	0.15	1.00	0.44	1.35
0.24	0.05	0.15	1.40	0.62	1.62
0.24	0.05	0.15	1.50	0.66	1.69
0.24	0.05	0.15	1.60	0.70	1.76
0.24	0.05	0.20	1.00	0.49	1.51
0.24	0.05	0.20	1.40	0.69	1.81
0.24	0.05	0.20	1.50	0.74	1.88
0.24	0.05	0.20	1.60	0.78	1.96
0.24	0.05	0.25	1.00	0.54	1.66
0.24	0.05	0.25	1.40	0.76	1.99
0.24	0.05	0.25	1.50	0.81	2.08
0.24	0.05	0.25	1.60	0.86	2.16
0.24	0.10	0.15	1.00	0.49	1.51
0.24	0.10	0.15	1.40	0.69	1.81
0.24	0.10	0.15	1.50	0.74	1.88
0.24	0.10	0.15	1.60	0.78	1.96
0.24	0.10	0.20	1.00	0.54	1.66
0.24	0.10	0.20	1.40	0.76	1.99
0.24	0.10	0.20	1.50	0.81	2.08
0.24	0.10	0.20	1.60	0.86	2.16
0.24	0.10	0.25	1.00	0.59	1.82
0.24	0.10	0.25	1.40	0.83	2.18
0.24	0.10	0.25	1.50	0.89	2.27
0.24	0.10	0.25	1.60	0.94	2.36

Table 4. Results of analysis assuming a two billion lb. equilibrium standing stock. All values reported in billions of lbs. See text for description of parameter estimates for mortality, catch, energy allocated to reproduction (R), respiration coefficient (RC), and energetic cost of standard metabolic rate (SMR). Values below the column heading ‘ Λ ’ represents the total amount of biomass needed to support an equilibrium standing stock of two billion lbs.

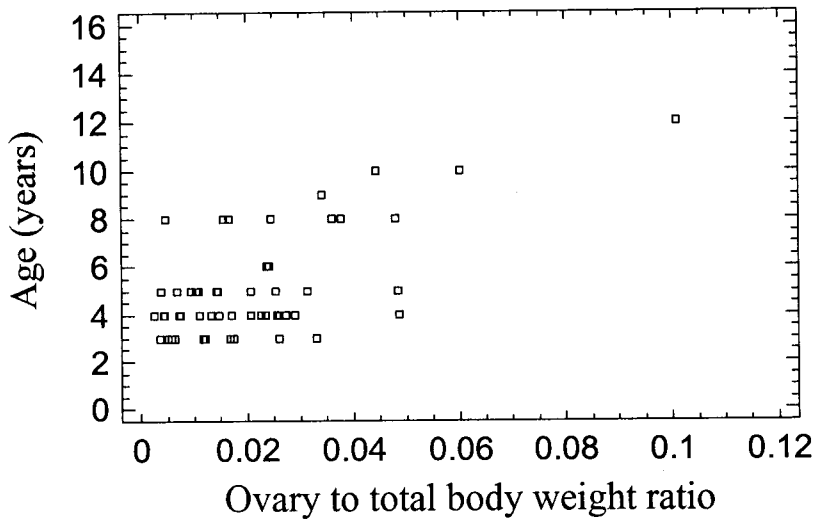


Figure 1. Relationship between age and ovary weight to body weight ratio (n = 54) for red snapper based on data presented in Collins et al. 1996.

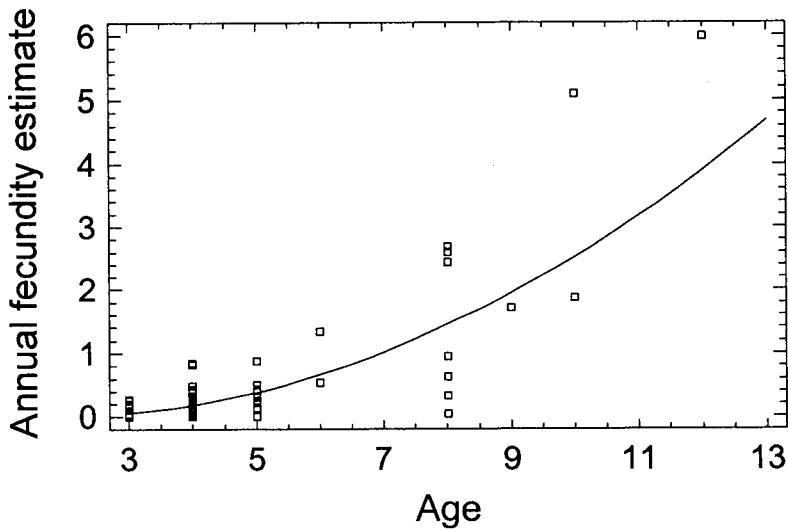


Figure 2. Plot of relationship between age (years) and annual fecundity estimate, based on data reported in Collins et al. (1996). Annual fecundity values reported in millions. $AFE = (-1080.51 + (609.63(\text{Age})))^2$, using the square root-Y regression model ($r^2 = 0.64$).

Appendix 1. Data presented in Collins et al. (1996) used to calculate ovary mass to body mass ratio. 'Age' represents age estimate of individual in years, 'AFE' represents annual fecundity estimate per individual, 'Total weight' represents the total body weight of each individual, 'Ovary weight' represents the weight of ovaries after being excised, and 'OM/BM' ratio represents the ovary to body mass ratio calculated for each sample.

Age	AFE	Total weight (kg)	Ovary weight (g)	OM/BM ratio
4	4046172	2.10	35.7	0.0170
5	3052608	1.30	32.9	0.0253
4	2132000	1.40	32.8	0.0234
3	1926782	1.10	28.6	0.0260
4	3063034	1.40	28.9	0.0206
5	2159378	1.70	24.5	0.0144
3	50700	1.10	3.9	0.0035
3	1959880	1.50	18.1	0.0121
5	4303130	1.60	50	0.0313
3	2687282	1.00	33.1	0.0331
N.R.	182910	0.84	5.4	0.0064
N.R.	7333809	2.00	131.4	0.0657
4	8356698	3.10	150.8	0.0486
3	219576	0.70	4.5	0.0064
8	3220686	4.65	72.2	0.0155
4	3708915	1.70	43.5	0.0256
N.R.	39942	N.R.	4	N.R.
4	2470503	1.22	33.2	0.0272
4	1577058	1.04	27.1	0.0261
9	17162082	8.85	302.1	0.0341
5	4974375	2.90	60	0.0207
3	121086	0.80	4.1	0.0051
6	5336961	3.88	92.1	0.0237
5	11613	1.25	4.9	0.0039
8	25954040	5.00	180	0.0360
N.R.	23692130	5.50	197.7	0.0359
12	59665760	9.00	908.2	0.1009
3	2613415	1.30	22.7	0.0175
5	2462215	1.30	18.5	0.0142
10	18618565	3.80	168.5	0.0443
10	50977465	9.10	546.5	0.0601
4	1876000	1.20	13.4	0.0112
4	219765	1.00	4.2	0.0042
4	4935805	2.40	35	0.0146
4	8192135	3.75	84.4	0.0225
8	26828200	4.60	173.9	0.0378
8	24401055	6.30	302.2	0.0480
4	4297125	1.50	43.6	0.0291
5	8837885	1.50	72.5	0.0483
4	773045	0.90	6.7	0.0074

Age	AFE	Total weight (kg)	Ovary weight (g)	OM/BM ratio
3	1474200	1.00	11.7	0.0117
5	1327200	2.35	16	0.0068
8	9434845	4.80	117.4	0.0245
8	6235635	4.90	81.1	0.0166
3	1712305	0.80	13.5	0.0169
N.R.	18602150	3.80	136.4	0.0359
5	1383375	2.55	26.4	0.0104
N.R.	16030	0.60	1.2	0.0020
4	903980	2.10	15.3	0.0073
4	1571150	1.20	13.4	0.0112
N.R.	122920	0.75	2.9	0.0039
5	1087135	1.20	11.2	0.0093
N.R.	4614610	2.30	36.6	0.0159
N.R.	1948835	1.59	18.6	0.0117
4	476280	1.40	6.3	0.0045
N.R.	3793895	1.36	26	0.0191
N.R.	2482445	1.78	23.5	0.0132
4	197155	1.05	4.6	0.0044
6	13427470	4.90	118.1	0.0241
N.R.	781830	0.60	7.1	0.0118
4	69685	1.30	3.4	0.0026
3	363860	0.70	3.6	0.0051
5	2554265	3.50	38.2	0.0109
4	1577345	2.30	30.5	0.0133
3	443170	1.10	6.3	0.0057
8	350070	5.00	23.1	0.0046

