WORKING DOCUMENT

Batch fecundity and an attempt to estimate spawning frequency of king mackerel (*Scomberomorus cavalla*) in U.S. waters

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Introduction

Previous fecundity estimates for king mackerel (Finucane et al. 1986) assumed a determinate spawning pattern. This approach is known to underestimate fecundity in fishes that actually exhibit indeterminate oocyte development reflected in multiple spawnings over a season (Murua et al. 2003). Thus our objective in this report is to provide batch fecundity estimates based upon directed sampling during 2005-2007.

Methods

Efforts were made to obtain lengths (mm), weights (kg), gonads and otoliths from commercial and recreational fisheries, from the Gulf of Mexico and U.S. South Atlantic. However, reproductive samples were only commonly available from the east coast of Florida (hereafter Atlantic) and northeastern Gulf of Mexico (northwest Florida and Alabama; hereafter Gulf). All reproductive sampling was from gear categorized as handline, whether from commercial or recreational boats (charterboats and headboats). Beginning in 2005 a cooperative research program (CRP) directed at stock delineation (William Patterson, PI, University of West Florida) expanded sampling efforts to provide reproductive samples throughout the spawning season. Based upon a call for batch fecundity estimates for king mackerel (SSC, SAP and SEDAR 5 reports) efforts to identify and collect ovaries from hydrated females was deemed important and thus samples were taken as opportunities allowed during age-structure sampling associated with routine port collections and the previously mentioned CRP project. Spawning duration was estimated by looking at the distribution of hydrated females over time. Differences in duration were examined between the Atlantic and Gulf sampling areas and between years based upon the number of available samples.

While most of the king mackerel females sampled for fecundity were haphazardly selected based upon hydrated ovary appearance, estimation of spawning frequency requires random sampling and distinguishing mature non-spawning females from those in active spawning condition. There were periods in which three port samplers made this distinction; two samplers working in the northeastern Gulf in 2006 and 2007 and one working in east Florida in 2007.

Batch Fecundity

Batch fecundity was determined using the hydrated oocyte method. Ovarian tissue samples were cross-sectioned, weighed to the nearest 0.001 g and placed in a vial along with 33% glycerol to separate oocytes for the purpose of counting (Collins et al. 1998). Hydrated oocyte counts were expressed as 1) oocyte density or the number of hydrated oocytes per gram of ovarian tissue, 2) relative fecundity or the number of hydrated oocytes per gram of female body weight, without ovary (see Dickerson et al. 1992) and 3) batch fecundity; calculated by multiplying the final hydrated ooctye estimate by the whole ovary weight, and the product was divided by the weight of the sample (Dickerson et al. 1992, Collins et al. 1998). For most hydrated ovaries, samples were also taken to prepare histological slides (by Louisiana State University School of Veterinary Medicine). Evidence of recent post-ovulatory follicles (POF) in any histological section, suggesting the female may have partially spent her current batch, could then be used as a criterion to eliminate that sample from the fecundity estimates.

A two-factor ANOVA testing for location differences was based upon sampling six regions of the ovary (anterior, middle, and posterior of left and right lobes); each region sampled from the periphery and center portion of a cross-section (from three females) (EXCEL 2007). Based upon the results of the ovary location test, a tissue sample was taken from each hydrated ovary collected by port agents, randomly selected from the 6 possible ovary regions and 2 cross section positions. Batch fecundity was regressed on Fork length (FL), whole weight (Wt), and age for all hydrated females (Collins et al. 1998, 2002). An ANOVA of hydrated oocyte density was conducted to examine the effects of month (Apr-Aug), year (2005-2007) and geographic region (Gulf and Atlantic) (XLSTAT version 7.5). A Tukey (HSD) test was used to compare means within categories.

Spawning frequency

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

Results

Batch fecundity location test

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

Batch fecundity sample summary

A total of 178 females were sampled and macroscopically confirmed as hydrated females after ovaries were preserved (Table 2, Appendix 1). Most samples were collected in 2006 (n=100), most came from the Atlantic (east Florida, n=146) and most were taken in August (n=85) followed by June and May (n = 43 and 44 respectively). In the Atlantic, hydrated females tended to be encountered in two periods; April-June and again in August with no hydrated females detected in July (Figure 1). In the Gulf, hydrated females were encountered in 2006 and 2007 and over a shorter duration from May to July (40 and 62 d; Figure 1). The smallest hydrated female was 602 mm FL with most females greater than 700 mm FL (Figure 1).

Test of oocyte density by month, year and region

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

Batch fecundity regressions

Based upon the trends for oocyte density, regressions for the two geographic regions, and for early season (Apr-May) and late season (Jun-Aug) in the Atlantic are shown in Figure 3. The resulting relationships for the Gulf (all data available) and for June-August data for the Atlantic are very similar with slopes of the fecundity-FL relationships equal to 3220 and 3111 respectively (having a common intercept = -2E+06). In contrast the fecundity-FL slope for Apr-May South Atlantic shows a slope of 1459. The best-fit length relationships were for the Gulf (all data) and for the Atlantic (Jun-Aug) with r^2 = 0.68 and 0.70 respectively.

Like the fecundity-length regressions, the fecundity-age fits also reflected a region-month trend for the Atlantic. The Gulf (all data available) and June-August data for the Atlantic resulted in similar equations with slopes of 19032 (r^2=0.761) and 19302 (r^2=0.469) respectively (Figure 4). All the data combined for the Atlantic resulted in a much lower fit (r^2=0.179) and a visual examination of the age-fecundity plot suggested more than one relationship may exist in the Atlantic.

Spawning frequency

Spawning frequency was estimated based upon 83 trips (collections) made during May – August 2006 and 2007; 13 trips in the Atlantic and 60 trips in the Gulf (Table 4). Based upon these random trips, most hydrated females, and thus the highest spawning fraction, were encountered in May and June in the Atlantic and June in the Gulf. Annual estimates were 7.1% and 7.2% spawning fractions or 2.9 and 4.5 total spawning events on average in the Gulf for 2006 and 2007 respectively and 11.5% spawning fraction or 5.7 total spawns on average in the Atlantic in 2007 (Table 4).

Discussion

Our batch fecundity estimates indicate king mackerel have a greater reproductive potential than that suggested by Finucane et al. (1986). Based upon the fecundity-length relationship for NW Florida in their Table 4 (Finucane et al., 1986) the expected annual fecundity of an 800 mm FL female would be 1,644,805 ova. However, we estimated that a single batch should equal 560,000 ova for a female this size and thus 3 spawning events could exceed the egg production of the earlier estimate. Although the fecundity method Finucane et al. used assumed a determinate oocyte development pattern, they found consistent ratios of oocytes in different development stages across a protracted spawning period of several months and concluded that multiple spawning was occurring. Given our improved understanding of fecundity patterns (e.g. Murua et al. 2003), the oocyte development pattern described by Finucane et al. supports the conclusion that fecundity is indeterminate in king mackerel. This is also a common finding for other scombrids and mackerel-like carangids as well (Dickerson et al. 1992, Karlou-Riga and Economidis 1997, Abaunza et al. 2003, Mackie et al. 2005).

Our estimated relative fecundity for king mackerel of 140 hydrated oocytes/g gonad free body weight is approximately the middle of the range of estimates for other scombrids and mackerel-like carangids. Other species estimates include: 28-55 oocytes/g (*Scomber scomber*; Dickerson et al. 1992), 112 oocytes/g (*Trachurus symmetricus*, Macewicz and Hunter 1993), 168-278 oocytes/g (*Scomber japonicas*; Dickerson et al. 1992), and 205 oocytes/g (*Trachurus trachurus*; Karlou-Riga and Economidis 1997).

We chose not to eliminate any of the fecundity estimates which showed histological evidence of recent POFs because almost all (88%) of the hydrated females examined exhibited both old and recent POFs suggesting high spawning frequency. We would only have been able to retain 19 of the remaining 152 samples had we used this criterion. We also received some fecundity samples too late to be histologically processed for this report (or were missing, N = 26 out of 178). In the king mackerel fishery we sampled, fishing was reported to occur at all times of day and night; and most of the fecundity sampling was from fish where time of catch was unspecified. It has been noted that king mackerel exhibit a "night-time bite" during "runs" in May and August in east Florida (M. Gamby, unpublished observations). Thus partially spawned gonads may have been sampled, possibly increasing the variance of the fecundity relationships. We cannot clarify this possibility further without knowing more about the time of catch relative to spawning and more about the time involved in the degeneration of post-ovulatory follicles (e.g., was a recent POF from an hour ago or last night?). We assume that once the fish is killed and put on ice, physiological changes such as final oocyte maturation and POF degeneration are arrested. For other fishes, where capture commonly occurs during the day and spawning occurs at night, the issue is less involved.

It was interesting to note that the batch fecundity relationships for the June and August Atlantic data and Gulf data were very similar (slopes and intercepts). However, the very negative values for the intercepts of the fecundity-length relationship (-2E+06) suggests that the regressions would return biased low values for smaller-sized mackerel. Using the fecundity-age relationships is recommended due to the reasonably good correlation coefficients and the "nearer to zero" intercepts. The slopes for the June-August Atlantic and Gulf fecundity-age relationships were also nearly equal. The finding that April-May Atlantic data was best fit by a fecundity relationship with a notably lower slope raises an interesting question. Does the difference signal multiple populations or components, a seasonal effect, or perhaps an artifact from lower sample sizes early in the season?

Certainly, our findings indicate king mackerel spawning is variable in time (monthly and annually) and location. There was an apparent hiatus in spawning in July offshore of east Florida, and only one hydrated female was encountered in August 2007 where they were commonly encountered in August 2005 and 2006. A bi-modal spawning pattern is thought to be the norm for east Florida (M. Gamby, unpublished observations). In NW Florida, routine age-length sampling over the past 15 years has yielded virtually no females in spawning condition (D. DeVries, unpublished observations). Several females in hydrated condition were noted in 2005 and again in 2006 and 2007. In general, few spawning females were detected relative to the number routinely examined during port sampling. Similar notations of finding few spawning adults and variation in time and location of spawning of king mackerel have been made by other workers (Beaumariage 1973, Finucane et al. 1964, Sturm and Salter 1989, Figuerola-Fernández et al. 2007). Such patchy spawning behavior has also been noted for other scrombrids (Dawson 1986, Dickerson, et al. 1992, Mackie et al. 2005). These authors suggested that such a pattern arises when different age-size components within a stock move and spawn at different times and areas. One conclusion is that spawning frequency is easily underestimated in fishes with this trait (Dickerson et al. 1992).

The fact that samplers can only detect visibly hydrated females to estimate spawning fraction probably returns a further underestimate of spawning frequency (Mackie et al. 2005). Hydration is typically a brief phase (hours) of final oocyte maturation on the day of spawning. Therefore, during the relatively short phase of final oocyte maturation, visibly hydrated females are detectable via macroscopic observations during an even smaller window of time. The assumption that visibly hydrated females can be detected over a period of about a day (day-0 proportion) is likely not met. Our finding that 88% of the histologically assessed fecundity samples contained both old and more recent post-ovulatory follicles further suggests that spawning frequency is much higher than estimated by observing the frequency of visibly hydrated females.

Others have indicated the difficulties in estimating spawning frequency in scombrids, particularly in making contrasts among age classes (Dickerson et al. 1992, Mackie et al. 2005, Figuerola-Fernández et al. 2007). A more formal sampling design would be needed to account for variation among regions and across time. Only a large scale random sampling program delivering thousands of gonads to be examined histologically could expand the window of time to detect spawning females (including the migratory nucleus and post-ovulatory stages as well as hydrated oocytes). Perhaps a well designed sampling plan would minimize the number of costly histological preparations needed. But obvious sampling gaps need to be addressed first. The western Gulf was not sampled, and larval abundance data suggests it is a main region of king mackerel spawning in U.S. waters (Grimes et al. 1990, Gledhill and Lyczkowski-Shultz. 2000).

Recommendations

1) Apply batch fecundity relationships (whether length or age-related) to estimate female reproductive potential until age-based spawning frequency estimates can be incorporated. Recognize the possibility that annual differences in population reproductive potential may occur even at equivalent levels of stock biomass (see Marshall et al. 2003).
2) Establish clear priorities for added reproductive information as expanded work would involve considerable costs for a long-term sampling program.
3) If made a priority, more precisely determine 1) the extent of hydration that can be determined via routine observations in the field and 2) the timing of this phase relative to final oocyte maturation and spawning and 3) calibration of the degeneration of post-ovulatory follicles. This is needed to account for and correct a likely bias in spawning frequency estimates.
4) If made a priority, design and implement a reproductive sampling program (in concert with age sampling) on an annual basis that expands and intensifies spatial and temporal coverage (particularly adding the western Gulf of Mexico). A goal would be to provide annual estimates of spawning frequency. This would include regular training of port agents and scientific observers in macroscopic methods and additionally include a quality control component of random sub-sampling for histological comparisons.

Acknowledgments

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

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

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

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

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

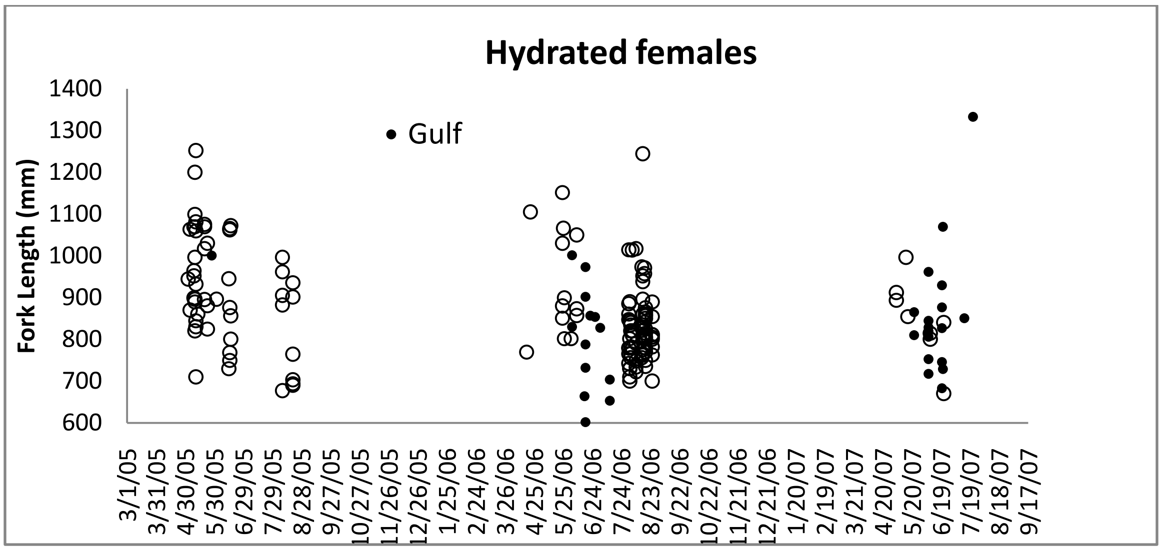

Figure 1. Dates captured and lengths of hydrated females. Atlantic data are represented by open circles and Gulf data by closed circles. The estimated spawning season duration in days based upon earliest and latest appearances of hydrated females; Atlantic 2005-103d, 2006-131d, 2007-50d; Gulf 2006-40d, 2007-62d.

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

Source	df	SS	MS	F	Pr > F
Month	4	30997977.565	7749494.391	22.587	< 0.0001
Year	2	844854.342	422427.171	1.231	0.295
Mackerel Region	1	300340.162	300340.162	0.875	0.351
Month*Mackerel Region	1	811453.266	811453.266	2.365	0.126
Month*Year*Mackerel Region	6	3664615.971	610769.328	1.780	0.106

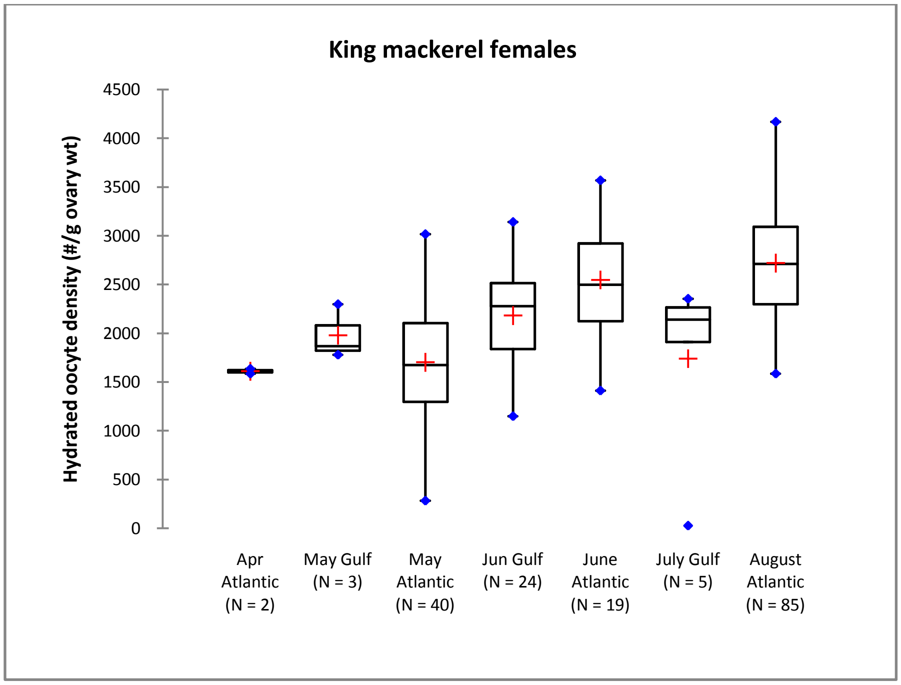

Figure 2. Box plots of hydrated oocyte density by month and geographic region. The center line of each box represents the median and cross-hairs indicate the mean. The minimum and maximum values are shown.

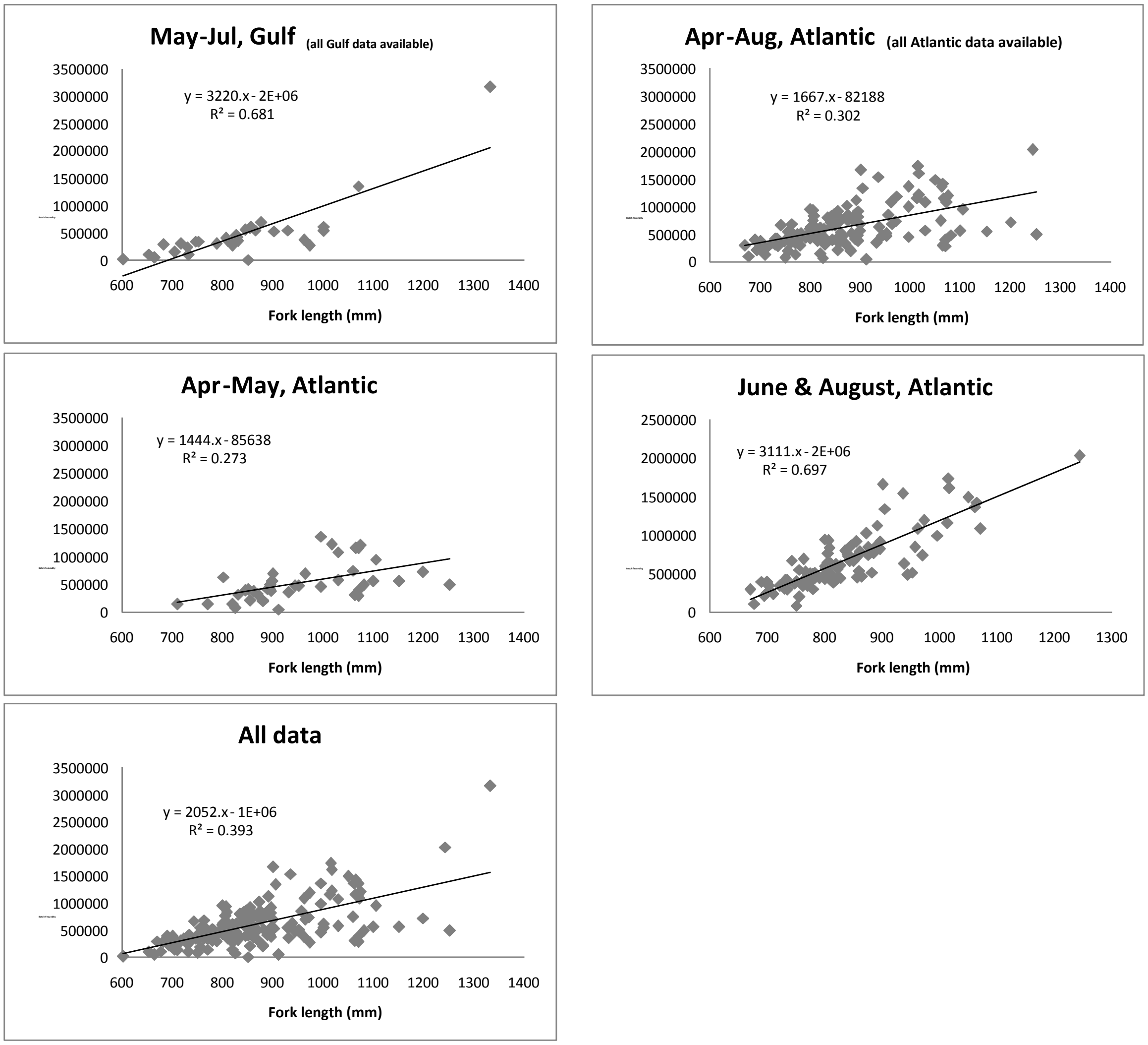

Figure 3. Batch fecundity- fork length regressions for combinations of month and geographic region.

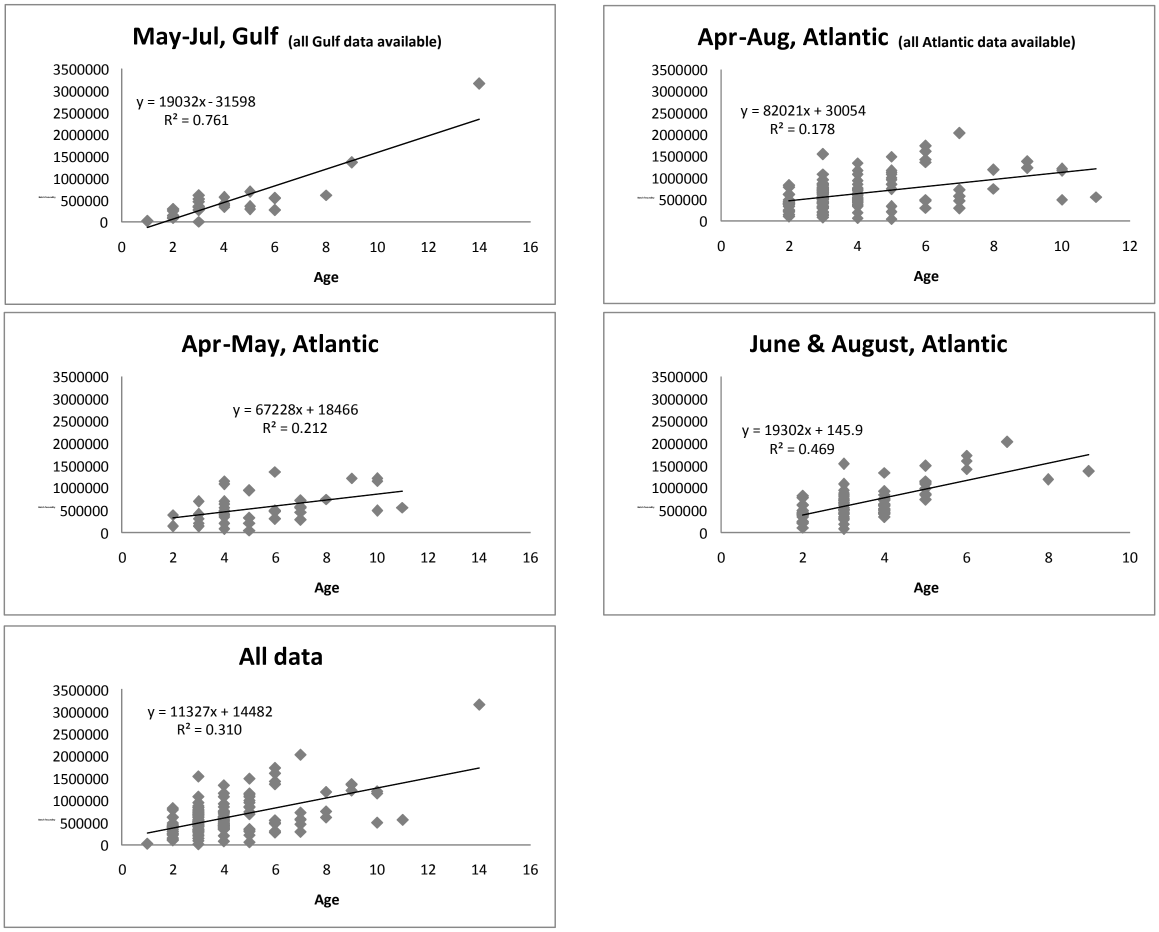

Figure 4. Batch fecundity-age regressions for combinations of month and geographic region.

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

		May				**June**				**July**				**August**							
	Year	# Trips or collections	# Active females	# H	H Spawning interval (d)	# Trips or collections	# Active females	# H	H Spawning interval (d)	# Trips or collections	# Active females	# H	H Spawning interval (d)	# Trips or collections	# Active females	# H	H Spawning interval (d)	Average daily spawning fraction	Annual average spawning interval (d)	Estimated season duration (d)	H-based estimate of annual spawns
Gulf	2006	2	13	0		26	192	16	12.00	8	89	4	22.25	7	36	0		7.12%	14.05	40	2.85
	2007	6	30	1	30.00	13	81	7	11.57	6	27	0		2	12	0		7.21%	13.88	62	4.47
Atlantic	2007	3	53	8	6.63	5	50	6	8.33	2	12	0		3	28	1	28.00	11.45%	8.73	50	5.73

Appendix 1. Batch fecundity data

Year	PC #	KMK #	Date	Capture Location	Final Age	FL (mm)	Body wt (g)	Gonad wt in Formalin (g)	Sample wt (g)	H count	Oocyte density (H ova/g ovary wt)	Batch fecundity (per female)	Rel Batch fecundity (per g body wt)
2005	4	573	5/3/2005	Palm Beach	4	944		449.21	0.0749	79	1054.74	473800	
2005	15	593	5/5/2005	Palm Beach	5	870	4040	205.75	0.0749	120	1602.14	329640	81.59
2005	16	594	5/5/2005	Palm Beach	6	1064		230.01	0.0751	99	1318.24	303209	
2005	24	596	5/9/2005	Palm Beach	4	964		413.3	0.0752	126	1675.53	692497	
2005	24	597	5/9/2005	Palm Beach	6	952		332.67	0.0752	107	1422.87	473347	
2005	24	598	5/9/2005	Palm Beach	4	899		388.73	0.0748	108	1443.85	561268	
2005	25	600	5/9/2005	Martin	7	1070		253.75	0.0751	85	1131.82	287200	
2005	26	601	5/10/2005	Palm Beach	7	1200	13740	342.83	0.0751	158	2103.86	721267	52.49
2005	26	602	5/10/2005	Palm Beach	2	820		65.63	0.0748	165	2205.88	144772	
2005	26	603	5/10/2005	Palm Beach	7	996	4090	227.69	0.0751	151	2010.65	457805	111.93
2005	26	604	5/10/2005	Palm Beach	4	896	3360	147	0.0748	194	2593.58	381257	113.47
2005	26	605	5/10/2005	Palm Beach	4	890	2720	173.49	0.0749	180	2403.20	416932	153.28
2005	27	607	5/10/2005	Palm Beach		1070	8610	254.14	0.0748	117	1564.17	397518	46.17
2005	27	608	5/10/2005	Palm Beach	7	1100	9750	574.65	0.0747	73	977.24	561572	57.60
2005	28	609	5/11/2005	Palm Beach	3	710	2310	105.08	0.0749	97	1295.06	136085	58.91
2005	28	610	5/11/2005	Palm Beach	6	1081	8840	292.76	0.075	126	1680.00	491837	55.64
2005	28	611	5/11/2005	Palm Beach	3	830	3580	172.21	0.0752	138	1835.11	316024	88.27
2005	28	612	5/11/2005	Palm Beach	10	1252	16960	407.31	0.0749	91	1214.95	494863	29.18
2005	28	614	5/11/2005	Palm Beach	2	845	4490	251.04	0.075	118	1573.33	394970	87.97
2005	28	615	5/11/2005	Palm Beach	4	932	4890	168.95	0.0748	156	2085.56	352356	72.06
2005	28	616	5/11/2005	Palm Beach	8	1060	8610	478.22	0.0748	117	1564.17	748018	86.88
2005	29	617	5/13/2005	Martin		861		131.61	0.075	214	2853.33	375527	
2005	54	625	5/20/2005	Palm Beach	4	895	4580	208.65	0.075	175	2333.33	486850	106.30
2005	54	626	5/20/2005	Palm Beach	10	1070	8930	740.6	0.0749	117	1562.08	1156879	129.55
2005	54	627	5/20/2005	Palm Beach	9	1017	6980	493.79	0.0752	186	2473.40	1221342	174.98
2005	54	628	5/20/2005	Palm Beach	10	1075	7930	398.74	0.0749	226	3017.36	1203141	151.72
2005	55	630	5/23/2005	Palm Beach	4	825		186.82	0.0748	29	387.70	72430	
2005	55	632	5/23/2005	Palm Beach	7	1030		296.01	0.0749	145	1935.91	573050	
2005	55	633	5/23/2005	Palm Beach	4	881		274.54	0.0751	54	719.04	197406	
2005	57	2	5/27/2005			1001	6203	287.9	0.075	140	1866.67	537413	86.63
2005	58	713	6/1/2005	Palm Beach	4	896	5210	391.19	0.0747	176	2356.09	921679	176.91
2005	59	731	6/14/2005	Palm Beach	4	945	4940	253.19	0.0748	144	1925.13	487425	98.67
2005	59	732	6/14/2005	Palm Beach	3	730	2580	124.36	0.0751	187	2490.01	309658	120.02
2005	60	779	6/15/2005	Palm Beach	6	1065	7430	426.65	0.0751	251	3342.21	1425954	191.92
2005	60	780	6/15/2005	Palm Beach	9	1062	8340	701.46	0.0749	146	1949.27	1367332	163.95
2005	60	781	6/15/2005	Palm Beach	3	750	2490	59.96	0.0751	106	1411.45	84631	33.99
2005	60	782	6/15/2005	Palm Beach	2	768	2200	163.18	0.0749	187	2496.66	407405	185.18
2005	60	783	6/15/2005	Palm Beach	4	876	4210	208.59	0.0751	268	3568.58	744369	176.81
2005	77	784	6/16/2005	Palm Beach	2	800	3310	146.9	0.0748	222	2967.91	435987	131.72
2005	77	785	6/16/2005	Palm Beach	5	1072	8300	310.95	0.075	261	3480.00	1082106	130.37
2005	77	786	6/16/2005	Palm Beach	3	856	3710	283.49	0.0752	190	2526.60	716265	193.06
2005	130	865	8/8/2005	Palm Beach	4	905	4530	395.78	0.075	254	3386.67	1340375	295.89
2005	130	866	8/8/2005	Palm Beach	3	962	6620	442.37	0.0751	184	2450.07	1083836	163.72
2005	130	867	8/8/2005	Palm Beach	2	677	2440	54.18	0.0749	149	1989.32	107781	44.17
2005	130	868	8/8/2005	Palm Beach	5	996	7540	379.24	0.0747	196	2623.83	995061	131.97
2005	130	869	8/8/2005	Palm Beach	3	882	4490	225.82	0.0748	171	2286.10	516246	114.98
2005	131	891	8/19/2005	Palm Beach	3	764	2810	147.09	0.0749	214	2857.14	420257	149.56
2005	131	893	8/19/2005	Palm Beach	2	690	2260	99.84	0.0752	297	3949.47	394315	174.48
2005	131	894	8/19/2005	Palm Beach	3	936	4890	540.31	0.0751	214	2849.53	1539632	314.85
2005	131	895	8/19/2005	Palm Beach	2	694	2260	68.8	0.0752	233	3098.40	213170	94.32
2005	131	897	8/19/2005	Palm Beach	2	703	2310	100.49	0.0751	254	3382.16	339873	147.13
2005	131	898	8/19/2005	Palm Beach		901	4980	529.94	0.0752	236	3138.30	1663110	333.96
2006	6	491	4/17/06	Jupiter	3	770	3170	89.32	0.0750	119	1586.67	141721	44.71
2006	7	494	4/21/06	Palm Beach	5	1105	10890	580.4	0.0753	123	1633.47	948064	87.06
2006	21	593	5/24/06	Palm Beach	4	1030	7390	570.71	0.0750	142	1893.33	1080544	146.22
2006	21	595	5/24/06	Palm Beach	3	851	4440	218.7	0.0750	138	1840.00	402408	90.63
2006	21	596	5/24/06	Palm Beach	3	880	4080	146.46	0.0750	110	1466.67	214808	52.65
2006	21	597	5/24/06	Palm Beach	11	1152	8700	285.59	0.0751	147	1957.39	559011	64.25
2006	24	606	5/25/06	Palm Beach	4	1066	7390	661.44	0.0748	131	1751.34	1158404	156.75

Appendix 1 continued. Batch fecundity data

Year	PC #	KMK #	Date	Capture Location	Final Age	FL (mm)	Body wt (g)	Gonad wt in Formalin (g)	Sample wt (g)	H count	Oocyte density (H ova/g ovary wt)	Batch fecundity (per female)	Rel Batch fecundity (per g body wt)
2006	25	607	5/26/06	Palm Beach	4	802	3498	285.84	0.0750	165	2200.00	628848	179.80
2006	25	608	5/26/06	Palm Beach	3	900	4666	265.89	0.0748	194	2593.58	689608	147.78
2006	29	610	6/2/06	Palm Beach		802	3440	196.37	0.0751	193	2569.91	504653	146.70
2006	30	1	6/3/06	Panama City	8	1002		310.53	0.0749	148	1975.97	613597	
2006	30	3	6/3/06	Panama City	5	830		204.86	0.0752	128	1702.13	348698	
2006	40	649	6/8/06	Indian River	3	857	4580	183.97	0.0749	183	2443.26	449486	98.14
2006	40	650	6/8/06	Indian River		873	4800	355.04	0.0747	215	2878.18	1021869	212.89
2006	40	651	6/8/06	Indian River	5	1050	9110	735.18	0.0750	152	2026.67	1489965	163.55
2006	47	2	6/16/06	Panama City		664		37.6	0.0749	86	1148.20	43172	
2006	50	7	6/17/06	Panama City	6	973		115.69	0.0752	177	2353.72	272302	
2006	50	9	6/17/06	Panama City	3	902		230.77	0.0751	173	2303.60	531601	
2006	50	10	6/17/06	Panama City	1	602		13.72	0.0748	100	1336.90	18342	
2006	51	17	6/17/06	Panama City	2	732		62.89	0.0752	113	1502.66	94502	
2006	52	6	6/17/06	Panama City	5	788		129.11	0.0750	172	2293.33	296092	
2006	57	1	6/22/06	Panama City	3	857	4677	324.02	0.0749	141	1882.51	609971	130.42
2006	62	2	6/27/06	Panama City		854		204.58	0.0749	215	2870.49	587246	
2006	64	9	7/2/06	Panama City	4	828	4533	165.64	0.0751	170	2263.65	374951	82.71
2006	71	12	7/12/06	Panama City	2	653		49.18	0.0752	161	2140.96	105292	
2006	71	21	7/12/06	Panama City	2	704		75.38	0.0748	143	1911.76	144109	
2006	84	978	8/1/06	Palm Beach	3	885	4350	320.73	0.0747	179	2396.25	768550	176.68
2006	84	979	8/1/06	Palm Beach	6	1015	8070	640.46	0.0750	203	2706.67	1733512	214.81
2006	84	980	8/1/06	Palm Beach	2	861	4120	314.96	0.0747	186	2489.96	784238	190.35
2006	84	981	8/1/06	Palm Beach	3	780	3080	123.1	0.0751	182	2423.44	298325	96.86
2006	84	982	8/1/06	Palm Beach	3	742	2760	191.64	0.0749	262	3498.00	670356	242.88
2006	84	983	8/1/06	Palm Beach	3	847	4580	282.02	0.0749	232	3097.46	873547	190.73
2006	84	984	8/1/06	Palm Beach	3	765	2990	185.39	0.0748	171	2286.10	423819	141.75
2006	84	985	8/1/06	Palm Beach	3	780	3670	220.25	0.0750	165	2200.00	484550	132.03
2006	86	986	8/2/06	Palm Beach	3	730	2440	115.1	0.0752	225	2992.02	344382	141.14
2006	86	987	8/2/06	Palm Beach	2	731	2990	157.96	0.0749	197	2630.17	415462	138.95
2006	86	988	8/2/06	Palm Beach	3	844	3990	189.08	0.0752	264	3510.64	663791	166.36
2006	86	989	8/2/06	Palm Beach	2	700	2130	83.72	0.0748	219	2927.81	245116	115.08
2006	86	990	8/2/06	Palm Beach	3	802	2990	143.92	0.0749	290	3871.83	557234	186.37
2006	86	993	8/2/06	Palm Beach	5	891	5890	489.44	0.0748	172	2299.47	1125450	191.08
2006	86	994	8/2/06	Palm Beach	2	710	2080	65.76	0.0752	270	3590.43	236106	113.51
2006	88	995	8/3/06	Martin	3	835	3900	259.66	0.0749	229	3057.41	793887	203.56
2006	88	996	8/3/06	Martin	3	756	2260	195.73	0.0750	211	2813.33	550654	243.65
2006	88	997	8/3/06	Martin	4	765	3440	208.96	0.0748	150	2005.35	419037	121.81
2006	88	998	8/3/06	Martin	3	840	4350	295.83	0.0747	183	2449.80	724724	166.60
2006	88	999	8/3/06	Martin	2	782	3220	155.6	0.0752	215	2859.04	444867	138.16
2006	88	1000	8/3/06	Martin	2	820	4260	311.06	0.0751	149	1984.02	617150	144.87
2006	89	1018	8/4/06	Palm Beach	3	780	2850	155.42	0.0749	208	2777.04	431607	151.44
2006	89	1019	8/4/06	Palm Beach	4	810	3990	230.79	0.0748	203	2713.90	626342	156.98
2006	89	1020	8/4/06	Palm Beach	5	1014	7160	426.03	0.0752	204	2712.77	1155720	161.41
2006	89	1021	8/4/06	Palm Beach	3	820	3710	213.59	0.0748	217	2901.07	619639	167.02
2006	90	1023	8/8/06	Palm Beach		790	3220	156.09	0.0749	212	2830.44	441803	137.21
2006	90	1024	8/8/06	Palm Beach		734	2670	154.4	0.0751	200	2663.12	411185	154.00
2006	90	1025	8/8/06	Palm Beach		722	2440	134.14	0.0749	191	2550.07	342066	140.19
2006	90	1026	8/8/06	Palm Beach		748	3040	175.93	0.0750	158	2106.67	370626	121.92
2006	90	1027	8/8/06	Palm Beach	6	1017	3530	475.5	0.0750	254	3386.67	1610360	456.19
2006	93	1047	8/14/06	Palm Beach	4	827	9200	281.09	0.0751	119	1584.55	445402	48.41
2006	93	1048	8/14/06	Palm Beach	8	973	14300	395.75	0.0749	225	3004.01	1188835	83.14
2006	93	1049	8/14/06	Palm Beach	3	756	6000	89.58	0.0752	164	2180.85	195361	32.56
2006	95	1050	8/17/06	Palm Beach	5	957	5620	510.76	0.0751	124	1651.13	843332	150.06
2006	95	1051	8/17/06	Palm Beach	5	971	5570	201.57	0.0751	275	3661.78	738106	132.51
2006	95	1052	8/17/06	Palm Beach	3	780	2990	153.9	0.0750	246	3280.00	504792	168.83
2006	95	1053	8/17/06	Palm Beach	4	805	3440	268.95	0.0751	212	2822.90	759220	220.70
2006	95	1054	8/17/06	Palm Beach	3	800	2990	267.7	0.0749	265	3538.05	947136	316.77
2006	99	1055	8/18/06	Palm Beach		865	4080	165.03	0.0749	210	2803.74	462701	113.41
2006	99	1056	8/18/06	Palm Beach	3	860	4440	311	0.0752	181	2406.91	748551	168.59

Appendix 1 continued. Batch fecundity data

Year	PC #	KMK #	Date	Capture Location	Final Age	FL (mm)	Body wt (g)	Gonad wt in Formalin (g)	Sample wt (g)	H count	Oocyte density (H ova/g ovary wt)	Batch fecundity (per female)	Rel Batch fecundity (per g body wt)
2006	99	1057	8/18/06	Palm Beach	4	770	3710	211.8	0.0748	120	1604.28	339786	91.59
2006	99	1058	8/18/06	Palm Beach	4	800	3440	196.2	0.0748	165	2205.88	432794	125.81
2006	99	1059	8/18/06	Palm Beach	4	856	4120	222.27	0.0751	245	3262.32	725115	176.00
2006	99	1060	8/18/06	Palm Beach	4	805	3760	271.33	0.0752	177	2353.72	638636	169.85
2006	99	1061	8/18/06	Palm Beach	3	850	4300	215.35	0.0747	231	3092.37	665942	154.87
2006	99	1062	8/18/06	Palm Beach	4	825	3580	160.69	0.0748	211	2820.86	453283	126.62
2006	99	1063	8/18/06	Palm Beach	3	780	3530	207.33	0.0748	182	2433.16	504466	142.91
2006	99	1064	8/18/06	Palm Beach	3	750	3350	137.36	0.0749	222	2963.95	407128	121.53
2006	99	1065	8/18/06	Palm Beach	3	735	3530	145.38	0.0751	151	2010.65	292309	82.81
2006	99	1066	8/18/06	Palm Beach	4	875	5080	313.1	0.0747	203	2717.54	850861	167.49
2006	99	1067	8/18/06	Palm Beach	4	815	4120	209.07	0.0753	154	2045.15	427580	103.78
2006	116	307	8/15/06	Jupiter	3	762	3098	189.81	0.0748	136	1818.18	345109	111.40
2006	116	308	8/15/06	Jupiter	3	766	3351	210.78	0.0751	186	2476.70	522038	155.78
2006	116	311	8/15/06	Jupiter	3	803	3573	193.17	0.0747	199	2663.99	514603	144.03
2006	116	313	8/15/06	Jupiter	3	808	3501	200.2	0.0748	312	4171.12	835059	238.49
2006	116	314	8/15/06	Jupiter	4	827	4032	229.37	0.0753	200	2656.04	609216	151.11
2006	116	315	8/15/06	Jupiter	3	822	5532	248.05	0.0750	170	2266.67	562247	101.64
2006	116	320	8/15/06	Jupiter	3	938	3451	297.08	0.0749	158	2109.48	626684	181.59
2006	116	321	8/15/06	Jupiter	2	808	2476	269.81	0.0748	171	2286.10	616812	249.08
2006	117	340	8/15/06	Jupiter	7	1244	10755	912.52	0.0750	167	2226.67	2031878	188.92
2006	117	342	8/15/06	Jupiter	4	952	4127	222.1	0.0748	174	2326.20	516650	125.18
2006	117	343	8/15/06	Jupiter	2	896	3819	244.65	0.0749	252	3364.49	823121	215.54
2006	117	353	8/15/06	Jupiter	4	860	3733	227.44	0.0750	178	2373.33	539791	144.62
2006	118	390	8/15/06	Jupiter	3	775	2928	140.38	0.0750	267	3560.00	499753	170.71
2006	118	399	8/17/06	Jupiter	3	842	4775	340.62	0.0750	185	2466.67	840196	175.96
2006	119	1068	8/25/06	Palm Beach	4	800	4080	320.84	0.0748	139	1858.29	596213	146.13
2006	119	1069	8/25/06	Palm Beach	2	700	2350	126.86	0.0747	230	3078.98	390600	166.21
2006	119	1070	8/25/06	Palm Beach	3	782	3530	152.36	0.0750	253	3373.33	513961	145.60
2006	119	1071	8/25/06	Palm Beach		806	4030	391.96	0.0750	178	2373.33	930252	230.83
2006	119	1072	8/25/06	Palm Beach		855	4490	299.08	0.0749	230	3070.76	918403	204.54
2006	119	1073	8/25/06	Palm Beach	3	763	3490	218.11	0.0751	237	3155.79	688310	197.22
2006	119	1074	8/25/06	Palm Beach		811	2990	172.78	0.0751	214	2849.53	492342	164.66
2006	119	1075	8/25/06	Palm Beach	5	890	4260	260.69	0.0750	246	3280.00	855063	200.72
2006	119	1076	8/25/06	Palm Beach	4	811	4120	274.47	0.0752	168	2234.04	613178	148.83
2007	13	681	5/4/2007	Palm Beach	3	894	5903	407.88	0.0749	74	987.98	402979	68.26
2007	13	683	5/4/2007	Palm Beach	5	912	5262	184.37	0.0748	21	280.75	51762	9.84
2007	15	687	5/14/2007	Palm Beach	6	996	6524	467.37	0.0750	219	2920.00	1364720	209.18
2007	18	700	5/16/2007	Palm Beach	5	855	4350	331.19	0.0751	48	639.15	211679	48.66
2007	36	702	6/8/2007	Palm Beach	2	815	5220	175.33	0.0751	164	2183.75	382878	73.35
2007	36	704	6/8/2007	Palm Beach	2	800	4080	235.4	0.0750	155	2066.67	486493	119.24
2007	63	5	6/20/2007	Bay	6	930	5423	206.28	0.0747	197	2637.22	544005	100.32
2007	63	6	6/20/2007	Bay	5	877	5320	218.35	0.0748	235	3141.71	685993	128.95
2007	63	9	6/20/2007	Bay	3	827	3922	186.7	0.0750	184	2453.33	458037	116.80
2007	63	13	6/20/2007	Bay	3	746	2846	139.75	0.0748	185	2473.26	345638	121.44
2007	63	14	6/20/2007	Bay	2	683	2342	102.21	0.0750	210	2800.00	286188	122.18
2007	68	5	6/21/2007	Bay	2	729	2495	89.42	0.0748	204	2727.27	243873	97.74
2007	69	10	6/21/2007	Bay	9	1070	8387	459.86	0.0747	220	2945.11	1354340	161.49
2007	71	705	6/22/2007	Palm Beach		841	3483	282.6	0.0750	200	2666.67	753600	216.38
2007	71	706	6/22/2007	Palm Beach		670	2076	96.38	0.0748	228	3048.13	293779	141.51
2007	147	16	5/22/2007	Dauphin Isle	6	865	4527	306.6	0.0748	133	1778.07	545158	120.43
2007	147	25	5/22/2007	Dauphin Isle	3	810	3459	151.46	0.0749	172	2296.40	347812	100.56
2007	148	33	6/6/2007	Dauphin Isle	4	962	6588	229.07	0.0748	121	1617.65	370554	56.25
2007	148	42	6/6/2007	Dauphin Isle	3	819	4719	230.08	0.0748	86	1149.73	264530	56.05
2007	148	43	6/6/2007	Dauphin Isle	4	845	4234	255.93	0.0747	163	2182.06	558455	131.89
2007	148	47	6/6/2007	Dauphin Isle	4	806	3332	189.64	0.0751	158	2103.86	398976	119.75
2007	148	51	6/6/2007	Dauphin Isle	4	753	2948	152.68	0.0751	170	2263.65	345614	117.24
2007	148	55	6/6/2007	Dauphin Isle	2	718	2857	138.55	0.0751	164	2183.75	302559	105.89
2007	148	58	6/6/2007	Dauphin Isle	4	829	4397	182.3	0.0748	173	2312.83	421630	95.90
2007	158	204	7/13/2007	Orange Beach	3	851	4550	258.62	0.0748	2	26.74	6915	1.52
2007	164	335	7/22/2007	Dauphin Isle	14	1333	21160	1345.5	0.0752	177	2353.72	3166935	149.67