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Changes in biological characteristics of the California market squid (*Doryteuthis opalescens*) from the California commercial fishery from 2000–01 to 2012–13

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The commercial market squid (*Doryteuthis opalescens*) fishery began in Monterey, California during the mid-1800s. In the 1990s, increased market demand emerged overseas, primarily in Europe and Asia, and caused the fishery to grow substantially over the past two decades, and eventually becoming California's top commercial fishery in terms of value and volume. Biological data were obtained through the California Department of Fish and Wildlife sampling program for commercial landings of market squid. Commercial samples were collected at ports from San Francisco to southern California, from the 2000–01 to 2012–13 seasons. This study examines the spatial and temporal trends in biological aspects of captured market squid to determine if dorsal mantle length, whole mass, and sex ratios have significantly changed through time, and if these variables presently differ among seasons, geographic region, or by sex. The length and mass of market squid have fluctuated from season to season, and there were significant differences between regions. Likewise, there are statistically significant interactions between season, region, and sex for both the length and mass of market squid. Specifically, the length and mass of squid depends on the combined interactions of season, region, and sex. Monitoring these biological trends can help inform management about the health of the current stock.

Key words: Squid, coastal pelagic species, commercial fishery, cephalopod, *Doryteuthis (Loligo) opalescens*

Commercial fishing for market squid (*Doryteuthis opalescens*) began in Monterey Bay during the 1860s when Chinese fishermen used torches to attract squid into their nets (Pomeroy and Fitzsimmons 1998). The squid was then dried and exported to China. Starting in the 1990s, increased demand for squid, mainly in Asia, made the California market squid fishery one of the most valuable commercial fisheries in the state (Porzio 2013). In the 2012–13 season, approximately 96,000 metric tons (mt) of squid were landed in California

(Figure 1). Oceanic squid are commonly the largest biomass of all commercially harvested invertebrates globally, and California has one of the largest nearshore squid fisheries in the world (Jereb et al. 2010).

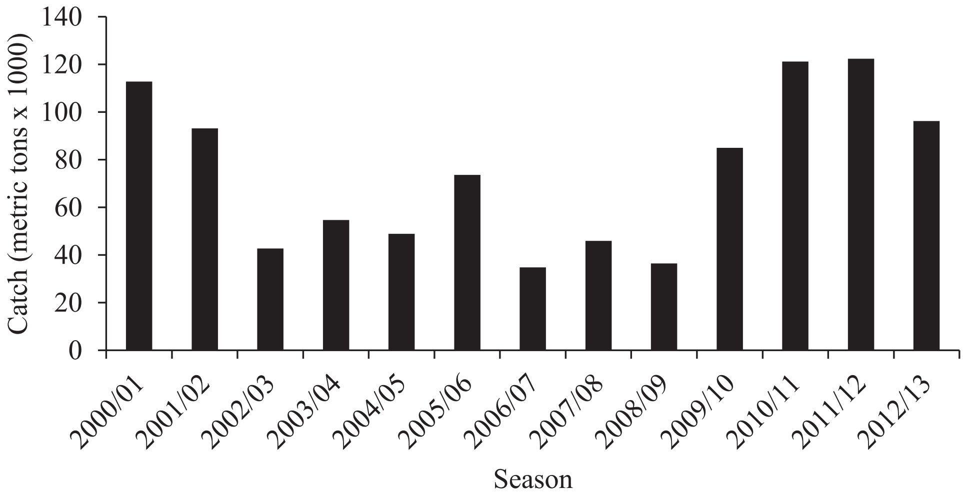

Figure 1.— Statewide commercial landings of California market squid by fishing season, from 2000–2001 to 2012–2013. The commercial fishing season runs from 1 April to 31 March the following year.

Market squid habitat ranges from Alaska to Baja California along the west coast of North America (Okutani and McGowan 1969, Jackson 1998). Typically, seine or brail gear, combined with the use of lights as an attractant, are used to capture shallow spawning populations in nearshore areas (Recksiek and Frey 1978). Spawning can occur year-round; however, the fishery is typically most active from April to October in Monterey and from October to May in the Channel Islands (Vojkovich 1998). In the last three years, however, substantial landings have occurred during the summer in southern California. Declines in overall commercial squid catch and paralarva densities occur after El Niño events, which suggests that environmental changes have strong influences on squid population size and abundance, as well as on recruitment (McInnis and Broenkow 1978, Jackson and Domeier 2003, Reiss et al. 2004, Koslow et al. 2011).

Management of the California market squid fishery focuses on evaluation of squid using the "egg escapement method" (Macewiz et al. 2004, CDFG 2005). Market squid are terminal spawners, and spawning occurs multiple times over their last few days of life (Fields 1965). Market squid usually live four to nine months, reproduce at the end of their lifespan, and are harvested on spawning grounds; for the fishery to be sustainable, it is critically important that an adequate number of eggs are spawned prior to harvest (CDFG 2005).

Biological data were developed and initially collected by Fields (1965) from 1946 until 1962. Biological samples were again collected in 1972 when morphometric comparisons were made between squid from the Monterey Bay and southern California (Evans 1976). Monterey port sampling was initiated in 1989 to re-establish a database of biological information from locally caught market squid (Leos 1998). The sampling design has changed slightly over the years, with the current sampling design adopted in

2000. The current California Department of Fish and Wildlife (CDFW) fishery-dependent sampling program was designed to monitor biological characteristics of the proportion of the population allowed to spawn (escape) prior to capture by the fishery (CDFG 2005). This "egg escapement method" (Macewicz et al. 2004) is used to evaluate the population dynamics of the species (Dorval et al. 2013).

Spatial and temporal trends in biological aspects of market squid collected in the current CDFW sampling regime (2000–01 to 2012–13) were examined to determine if length and mass have changed through time and if these variables differ between geographic regions or by sex. Sex ratios were also examined to determine if they have changed through time or differ by geographic region.

Materials and Methods

Dorsal mantle length (DML, mm), mass (whole body, g), and sex ratios for California market squid samples (30 individuals) collected between 2000–01 and 2012–13 were compared spatially, temporally, and by sex. We categorized the samples used in these analyses geographically as northern California (NCA, north of Point Piedras Blancas) or southern California (SCA, south of Point Piedras Blancas) (Figure 2). Data were eliminated from analyses if the sex was undetermined.

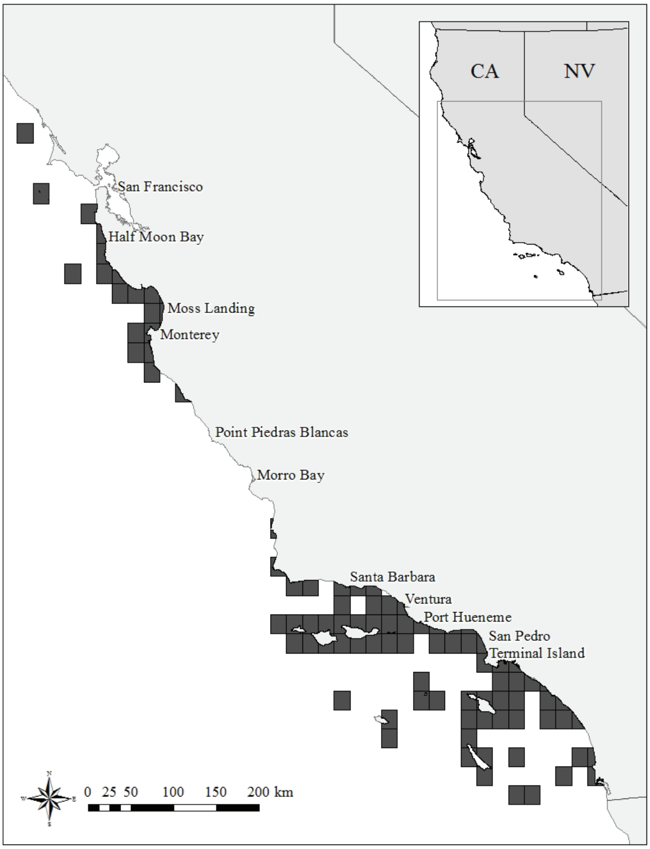

Figure 2.— Commercial landing locations for California market squid from from the 2000–2001 to the 2012–2013 fishing seasons sampled by CDFW fishing blocks (displayed in dark grey). Each block measures 10 × 10 minutes. The commercial fishing season runs from 1 April to 31 March the following year.

CDFW sampling procedure. — The regulatory season for the commercial market squid fishery in California is 1 April through 31 March of the following year. CDFW commercial fishery sample collection methods (2000–01 to 2012–13) were based on a stratified random sampling design. In January of 2000, sampling goals were set to 25 monthly samples. In 2004, the sampling protocol was reduced to 12 samples per month, following the previously established guidelines already used by the CDFW to collect Pacific sardine and Pacific mackerel samples. When the market squid fishery was active, 12 days were randomly sampled within each month and at each each of the following ports: Monterey—Moss Landing, Ventura—Port Hueneme, and Terminal Island—San Pedro (Figure 2).

Samples consisted of 30 squid selected randomly from a single commercial fishery landing. Squid were collected throughout the offloading process using a hand held dip net. Landing information was obtained from the captain of each sampled vessel, and included sample date, a landing number based on the number of annual commercial squid landings, sample number, vessel name and Fish and Game number (FGN), captain's estimate of landing weight (short tons), net set location (FG block number), number of sets, gear used, whether a light boat was used, light boat name and FGN, port, dealer's name, and landing receipt number. In the lab, each squid was laid out to drain for at least five minutes before being measured for DML and mass, and sex was determined. A sub-sample of one male and six females was sampled for gonad weight, and a mantle-punch sample and statoliths were removed for egg escapement determination and ageing, respectively (CDFG 2005). Data for ageing and egg escapement were not analyzed in this study.

Data analysis. —All statistical analyses were performed using R software (Version 3.0.0). One sample, consisting of 30 individual squid, was considered to be a sampling unit. DML and mass of a sample each was calculated using the average DML and mass of all squid in each sample. A 3-way analysis of variance (ANOVA) was used to examine the main effects and interactions of season, region, and sex for DML and mass. The assumptions of normality and homogeneity of variance were tested through visual inspection of a Residuals and Fitted Values plot and a Normal Q-Q plot; data met all assumptions. ANOVA results were supported by interaction plots, which were used to inspect significant interactions. A Pearson's Chi-squared test was used to compare sex ratios among and within seasons separated by region (NCA and SCA). Based on Fields' (1965) findings, the expected sex ratio was 1:1 for all Chi-squared analyses. Values are expressed as means ± 1 standard deviation (*SD*).

Results

A total of 50,744 individual male (3,092 samples) and 41,277 individual female (3,088 samples) squid were collected from each region from 2000–01 to 2012–13. Throughout the state, male DML averaged 128.4 mm (± 9.6 mm) and female DML averaged 125.2 mm (± 7.7 mm), with average masses of 44.8 g (± 9.7 g) and 35.9 g (± 7.0 g), respectively. Overall, more males were collected than females, and males were, on average, larger than females (Table 1). Statewide sex ratios pooled by all seasons were dominated by males (1.2:1). Although sex ratios differed slightly among regions, they were similar (NCA 1.3:1; SCA 1.2:1).

Mean DML and mass of males and females experienced similar fluctuations over the past 13 seasons (Figure 3). Statewide and across seasons, the lowest mean DML was

	Male	Female
Number of samples	3,092	3,088
Number of squid	50,744	41,277
Average DML (mm)	128.4	125.2
Range	93.5-158.3	94.0-159.0
SD	9.6	7.7
Average mass (g)	44.8	35.9
Range	20.4-82.4	14.8-61.0
SD	9.7	7.0

Table 1.—Length and mass of male and female squid collected from the California market squid fishery during commercial fishing seasons from 2000–2001 to 2012–2013. The commercial fishing season runs from 1 April to 31 March the following year.

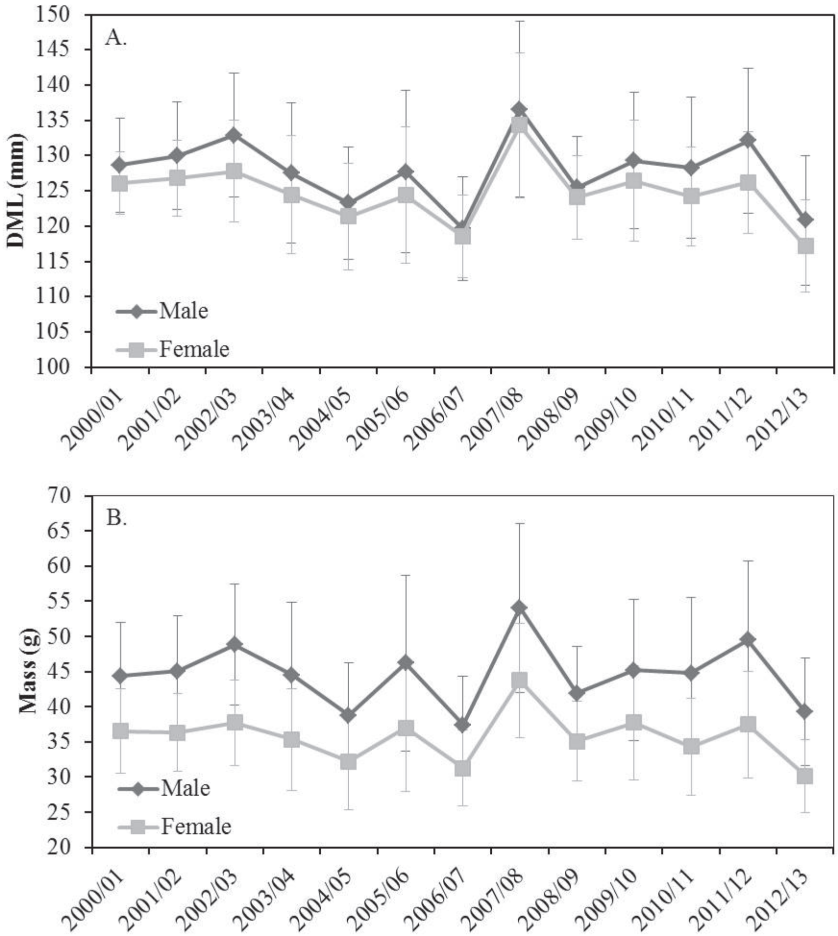

Figure 3.—Mean (±*SD*) dorsal mantle length (DML; A) and mass (B) for male and female California market squid across all regions by commercial fishing season. The commercial fishing season runs from 1 April to 31 March the following year.

119.7 mm (± 7.3 mm) for males and was observed during the 2006–07 season, whereas the lowest DML observed for females was 117.2 mm (± 6.5 mm) during the 2012–13 season. The greatest mean DML for males was 136.6 mm (± 12.5 mm) and the greatest mean DML for females was 134.3 mm (± 10.3 mm), both of which were observed during the 2007–08 season. Mean squid DML varied within 17 mm in the 13 season time period. Minimum and maximum average mass for males occurred in the 2006–07 and 2007–08 seasons and were 37.4 g (± 6.9 g) and 54.1 g (± 12.0 g), respectively. The minimum female mass (30.2 g ± 5.2 g) was observed in the 2012–13 season. Similar to males, maximum female mass (43.7 g ± 8.1 g) was observed in the 2007–08 season.

Results from 3-way ANOVA for DML indicate that the 3-way interaction between season, region, and sex, were not significant ($F_{11, 6130} = 1.44$, $P = 0.15$; Table 2). However, DML is significantly influenced by the interactions between season and region ($F_{11, 6130} = 60.60$, $P < 0.001$), season and sex ($F_{12, 6130} = 2.99$, $P < 0.001$), and region and sex ($F_{11, 6130}$

Table 2.—Results of three-way ANOVA for dorsal mantle length (A) and mass (B) of California market squid collected during commercial fishing seasons from 2000–2001 to 2012–2013 with season, region, and sex as factors. The commercial fishing season runs from 1 April to 31 March the following year.

(A) Dorsal Mantle Length

Factor	*df*	Sum of Squares	Mean Square	*F*	*P*
Main Effects					
Season	12	76,080	6,340	113.26	< 0.001
Region	1	3,466	3,466	61.92	< 0.001
Sex	1	16,388	16,388	292.76	< 0.001
Two-way interactions					
Season:Region	11	37,316	3,392	60.60	< 0.001
Season:Sex	12	2,010	167	2.99	< 0.001
Region:Sex	1	2,007	2,007	35.86	< 0.001
Three-way interaction					
Season:Region:Sex	11	889	81	1.44	0.15
Residuals	6,130	343,140	56		

(B) Mass

Factor	*df*	Sum of Squares	Mean Square	*F*	*P*
Main Effects					
Season	12	54,730	4,561	83.10	< 0.001
Region	1	8,468	8,468	154.29	< 0.001
Sex	1	123,451	123,451	2,249.26	< 0.001
Two-way interactions					
Season:Region	11	35,985	3,271	59.60	< 0.001
Season:Sex	12	3,410	284	5.18	< 0.001
Region:Sex	1	1,854	1,854	33.78	< 0.001
Three-way interaction					
Season:Region:Sex	11	2,181	198	3.61	< 0.001
Residuals	6,130	336,447	55		

= 35.85, $P < 0.001$) (Table 2). Plots indicate that the strongest interactions were between season and region (Figure 4A). That is, DML was highly dependent upon the season and region in which the squid were present. Interactions between season and sex (Figure 4B),

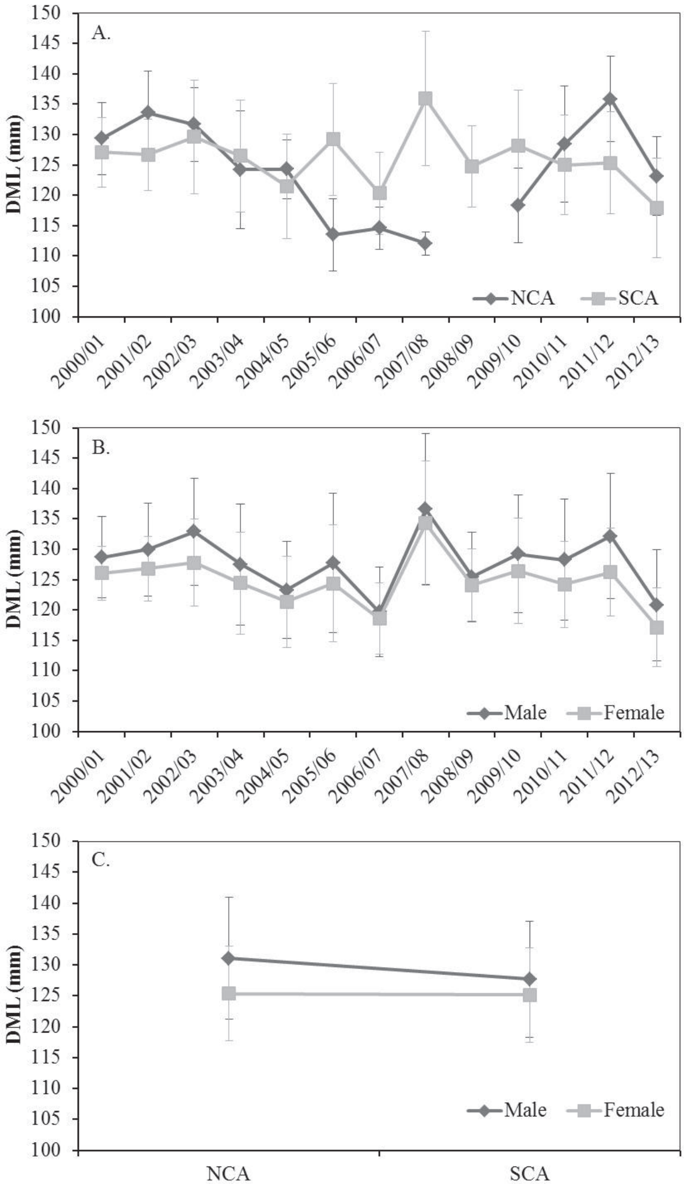

Figure 4.—Mean (±*SD*) dorsal mantle length (DML) by (A) commercial fishing season and geographic region, (B) commercial fishing season and sex, and (C) geographic region and sex. The commercial fishing season runs from 1 April to 31 March the following year.

and region and sex (Figure 4C), while still significant, were moderate and show that, regardless of season or region, male DML is always greater than female DML. The plot of region and sex (Figure 4C) also indicated that DML for males and females in NCA tended to be greater than those squid in SCA. Unlike squid DML, mass was significantly impacted by the combined interactions between season, region, and sex ($F_{11,\ 6130} = 3.61$, $P < 0.001$, Table 2). The interaction plots illustrate that mass fluctuated among seasons as well as between regions and that the pattern of fluctuations was similar for males (Figure 5A) and females (Figure 5B). The pattern of interactions also showed that the scale of fluctuations for males and females differed. Namely, the interaction of season and region on male squid generally resulted in greater mass and more extreme fluctuations than the same interaction on female squid.

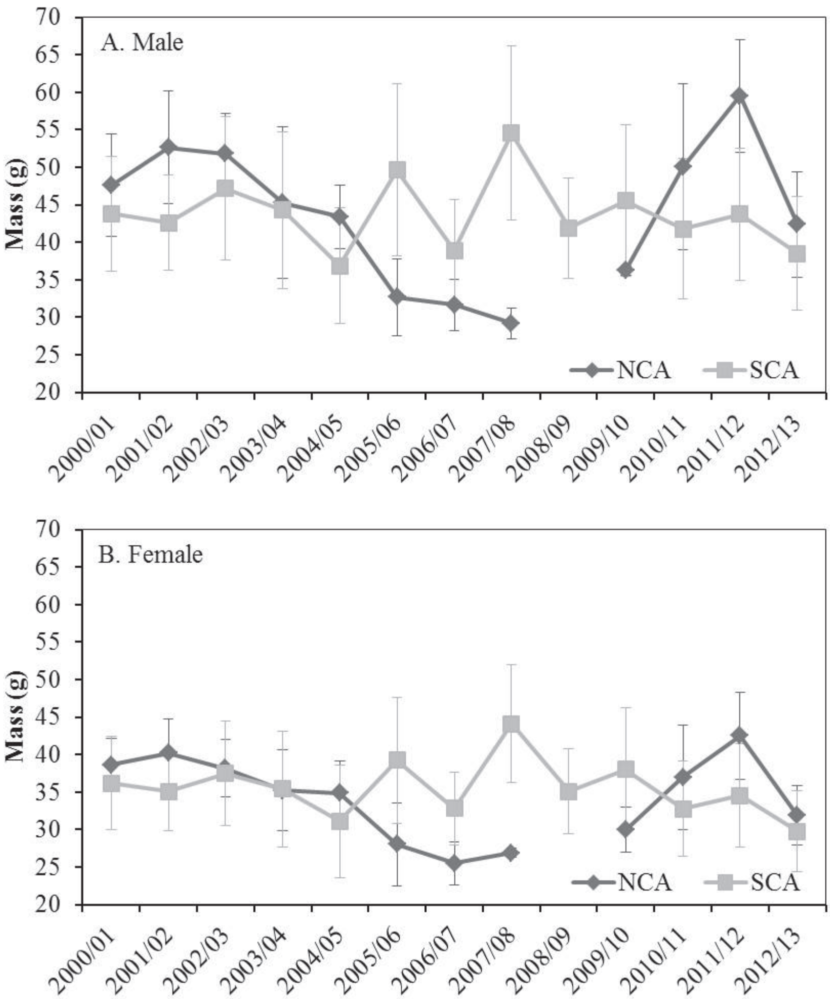

Figure 5.—Mean mass (±*SD*) by commercial fishing season and geographic region for male (A) and female (B) California market squid. No samples were collected in the Northern California Area during the 2008–2009 commercial fishing season. The commercial fishing season runs from 1 April to 31 March the following year.

Trends north of Point Piedras Blancas.—A total of 1,366 samples were collected in NCA, containing 11,669 males and 8,725 females. Examination of season means displayed in the interaction plots reveals that there was a decrease in size (DML and mass) for both sexes from 2001-02 through 2007-08; squid size increased to the largest mean size in 2011-2012 and then decreased the following season (Figure 5A, Figure 5B; DML not shown).

Chi-squared results indicate a significant difference in sex ratios among seasons ($\chi^2_{11} = 23.4$, $P < 0.05$). Chi-square results within seasons show that, for more recent seasons, there was a significant difference in expected (1:1) and observed sex ratios (Table 3). During these seasons, there tended to be at least 1.5 times more males than females.

Table 3.— Sex of California market squid collected from the Northern California Area (A) and Southern California Area (B) during commercial fishing seasons from 2000–2001 to 2012–2013, and results of χ^2 tests with an assumed sex ratio of 1:1. The commercial fishing season runs from 1 April to 31 March the following year.

(A)	Male		Female				
Season	Number	Percent	Number	Percent	χ^2	*df*	*P*
2000/01	1,060	50.8	1,025	49.2	0.03	1	0.87
2001/02	2,170	52.2	1,989	47.8	0.19	1	0.66
2002/03	2,302	57.9	1,675	42.1	2.49	1	0.11
2003/04	1,450	55.0	1,185	45.0	1.01	1	0.31
2004/05	804	61.2	509	38.8	5.05	1	0.02
2005/06	684	63.5	394	36.5	7.24	1	0.01
2006/07	567	72.8	212	27.2	20.77	1	<0.01
2007/08	37	61.7	23	38.3	5.44	1	0.02
2008/09	-	-	-	-	-	-	-
2009/10	53	46.1	62	53.9	0.61	1	0.43
2010/11	908	61.6	567	38.4	5.34	1	0.02
2011/12	999	64.1	560	35.9	7.93	1	<0.01
2012/13	635	54.8	524	45.2	0.92	1	0.34
Total	11,669		8,725				

(B)	Male		Female				
Season	Number	Percent	Number	Percent	χ^2	*df*	*P*
2000/01	6,921	51.9	6,421	48.1	0.14	1	0.71
2001/02	6,447	50.7	6,270	49.3	0.02	1	0.89
2002/03	4,088	56.8	3,112	43.2	1.84	1	0.18
2003/04	4,956	55.2	4,022	44.8	1.08	1	0.30
2004/05	1,740	55.3	1,409	44.7	1.10	1	0.29
2005/06	2,243	53.3	1,967	46.7	0.43	1	0.51
2006/07	1,526	52.0	1,408	48.0	0.16	1	0.69
2007/08	1,788	58.5	1,266	41.5	2.92	1	0.09
2008/09	1,710	58.4	1,219	41.6	2.81	1	0.09
2009/10	1,624	51.1	1,553	48.9	0.05	1	0.82
2010/11	1,476	57.0	1,115	43.0	1.94	1	0.16
2011/12	1,620	59.9	1,086	40.1	3.89	1	0.05
2012/13	2,936	63.3	1,704	36.7	7.05	1	0.01
Total	39,075		32,552				

Trends south of Point Piedras Blancas.—The 4,814 SCA samples were comprised of 39,075 males and 32,552 females. There was no consistent trend in the size (DML and mass) of male and female squid from season to season in SCA (Figure 5A, Figure 5B; DML not shown). Rather, fluctuations were moderate from 2000–01 to 2004–05, increased substantially from 2005–06 to 2007–08, and returned to moderate during the 2008–09 to 2012–13 seasons.

Chi-squared results for SCA indicate that there was no significant difference in sex ratios among seasons (χ^2_{12} = 7.04, P = 0.85). Results from Chi-square tests within seasons show significant differences in the expected (1:1) and observed sex ratios in the 2011–12 and 2012–13 seasons, when the percent of males increased to approximately 60 % (Table 3).

Discussion

Given that market squid are a valuable commodity for California's economy and are a vital forage species, it is important to document biological characteristics of specimens captured in the fishery. Biological characteristics of market squid tend to oscillate over time as shown in seasonal fluctuations of DML and mass from 2000–01 to 2012–13. As evident from this study, seasonal mean DML may fluctuate in excess of 14 mm from season to season in market squid. Research indicates that these differences may be correlated with long-term climatic patterns, such as the El Niño Southern Oscillation (ENSO), influencing nutrients and food sources among seasons and within regions (Jackson and Domeier 2003, Reiss et al. 2004, Koslow and Allen 2011). Growth and development in Cephalopoda are also highly influenced by seasonal fluctuations in temperature (Grist and des Clers 1998, Jackson and Domeier 2003). It has been suggested that growth rates and life cycles of cephalopods can be greatly accelerated by locality and temperature (Jackson et al. 1997).

Resulting size differences could reflect the species' ability to adjust to changing environmental conditions. Specifically, when conditions are not ideal, squid tend to have smaller DML and mass. However, when conditions are preeminent, squid take advantage of the favored conditions and increase in size. Increased biological productivity on spawning grounds may provide a framework for highly productive nursery grounds contributing to larger DML and mass (Ichii et al. 2004). Differences in size could also potentially be attributed to different cohorts. However, since age data have not been analyzed, this cannot be confirmed or denied. The size and "freshness" of squid greatly impacts its economic value. Larger, high quality squid is ideal for market demands and is vital for higher prices paid to fishermen.

Improved metrics of environmental and oceanographic conditions have greatly contributed to the ability to link those conditions to recruitment in squid populations of South America and Japan (Sakurai et al. 2000, Agnew et al. 2002). Statewide, from season to season, the lowest mean DML occurred in 2006–07, and the greatest mean DML was observed in 2002–03. In 2002, biological productivity in the California Current was higher than usual (Schwing et al. 2002), which may have led to larger mean squid size in the 2002–03 season. During the 2005–06 (July to June) season, the California Current experienced a delay in upwelling along with recruitment failure for various marine organisms (Peterson et al. 2006); the smaller market squid size in the 2006–07 fishing season may have been a result of the 2005–06 environmental conditions. Additionally in 2006-07, there was also a late onset of upwelling (Goericke et al. 2007), and market squid spawning activity is usually associated with local and seasonal influxes of nutrients from upwelling or winter mixing events (Zeidberg 2006).

Males have remained the more abundant sex in the fishery. Previous studies have found sex ratios to fluctuate rapidly, although sex ratios tended to be dominated by males (Hanlon et al. 2004). Most observations have not included lone females on mating grounds. Extra males observed on spawning grounds tend to be larger, competitive males or smaller "sneaker" males (Hanlon et al. 2004, Zeidberg 2008). These "sneaker" males insert their spermatophores into the mantle cavity of females mating with larger males. It has been suggested that paired males are able to out compete unpaired sneaker males in other squid species (Janzen and Havenhand 2003). Moreover, skewed operational sex ratios on mating grounds have been found to set up the gradient for sexual selection in cephalopods (Hanlon et al. 2002).

Additionally, differences in squid size from season to season may also reflect the time of year in which the samples were taken. Future research should be conducted to find clearer relationships linking environmental, oceanographic, and biological variables of market squid. Comparison of historical biological datasets and the current CDFW study would provide a clearer representation of how the fishery and the biology have changed through time. Comparing these changes to environmental variability, and on a finer scale, could provide additional insights useful in the management of this short-lived species.

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