Predicting market squid (*Doryteuthis opalescens*) landings from pre-recruit abundance

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Abstract

The fishery for market squid (*Doryteuthis opalescens*) in California is typical of many of the world's cephalopod fisheries, in that a very short life span and the effect of environmental forcing on recruitment result in enormous interannual variability in catches and population size. We evaluate the utility of a pre-recruit index of squid abundance that is based on midwater trawl sampling in the 3-5 months preceding the onset of the fishery as a basis for predicting landings. Catches in the survey largely represent squid in the 30-50 mm dorsal mantle length size range, representing individuals 30-90 day old. Catch-per-unit-effort statistics are derived from simple two-factor Δ-Generalized Linear Models, with year and station as main effects and numbers per tow as the dependent variable. Regional models for northern and southern squid populations are developed. Pre-recruit indices, as well as indices of squid prey (krill) abundance are compared with landings data, as well as estimates of squid spawning stock biomass derived from an egg escapement model. Our results show that the abundance of pre-recruit market squid and krill sampled in the survey tracks both catches and overall population size, providing the potential to forecast landings. Our findings are consistent with a sparse but growing literature showing the potential utility of pre-recruit surveys to inform fisheries participants and managers.

Keywords: market squid, krill, pre-recruit, landings, forecast

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1. Introduction

Globally, commercial fisheries for cephalopods are among the largest invertebrate fisheries in the world, and most of these target populations that are fast growing, highly variable ecological opportunists, with low predictability in population dynamics (O'dor and Webber, 1986; Arkhipkin et al., 2015; Doubleday et al., 2016). The commercial fishery for market squid (*Doryteuthis opalescens*) is no exception, as the stock is characterized by a high population turnover rate, with high plasticity in life-history characteristics, resulting high variability in abundance and catches. This fishery ranks among the State of California's top commercial fisheries in terms of volume and value; between 2000 and 2015 the fishery was the largest single species fishery in the State by volume for all but three years and was the largest in terms of ex-vessel value for over half of those years. The 2010-2014 period was particularly productive, with landings and ex-vessel revenue averaging more than 110,000 (mt) and $70 million per year, respectively (Porzio, 2015).

As with most well studied cephalopod populations (Boyle and Rodhouse, 2005; Rodhouse et al., 2014), previous research on this species has demonstrated that environmental factors have a strong influence on market squid recruitment, growth, abundance, and distribution (McInnis and Broenkow 1978; Jackson and Domeier, 2003; Reiss et al., 2004; Koslow and Allen, 2011), with corresponding volatility in abundance and catches associated with El Niño events and anomalous ocean conditions (Zeidberg et al., 2006; van Noord and Dorval, 2017). For example, landings dropped from an average of 75,000 mt in 1996-1997 to less than 3,000 mt in 1998 in response to the strong 1997-1998 El Niño. Landings subsequently increased by over 30-fold, with 1999 and 2000 catches averaging more than 100,000 mt. Such volatility seems to be driven by high sensitivity to variable ocean conditions combined with very high turnover in the population, as most individuals are thought to live no more than 6-9 months (Butler et al., 1999; Jackson and Domier, 2003).

Although the commercial fishery for market squid has existed since the late 1800s (Fields, 1965; Vojkovich, 1998), demand for squid increased markedly in the 1990s, leading to growth of the fishery; landings volatility has seemed to increase as the fishery grew. In particular, participation and landings increased rapidly during the El Niño and subsequent La Niña events of the late 1990s that saw dramatic fluctuations in landings and apparent abundance (Pomeroy and Fitzsimmons, 2001; Zeidberg et al., 2006). Management measures for the fishery at the time of this manuscript include an annual catch limit of 107,048 mt (based on the highest catches reported prior to adoption of the management plan), limited entry into the fishery, weekend closures to provide for periods of uninterrupted spawning, lighting restrictions, and development of monitoring programs that include port sampling and logbooks (Leos, 1998; CDFW, 2005). Port sampling data have been used to assess the magnitude of fishing mortality and spawning population abundance based on an egg-escapement method, in which the relative fraction of potential oocytes (eggs) released from fishery-captured females harvested on their spawning grounds is compared to the spawning potential had no squid been captured (Macewicz et al., 2004; Maxwell et al., 2005; Dorval et al., 2013). While these methods lead to insights that can provide a strong overall basis for management, results are not available until well after the fishery is prosecuted. Given the volatile nature of the resource and the fishery, it could be of considerable value to both the fishing industry and to fisheries managers to have some predictive capability of near term population abundance.

We develop indices of abundance of pre-recruit market squid, as well as a key market squid prey item (krill), based on data collected in a midwater trawl survey that was designed to estimate the abundance of young-of-the-year pelagic juvenile rockfish (Ralston et al., 2013), but using methods comparable to those used to implement pre-recruit surveys in other cephalopod fisheries (e.g., Kidokoro et al., 2014). We evaluate their potential to inform near-term forecasts of squid abundance by comparing the indices to regional catches and to biomass estimates that were hind-casted using the egg escapement method of Dorval et al. (2013). Our objective is to evaluate whether survey indices are sufficiently informative as to provide some value as a pre-recruit index for either fishery participants or fisheries managers relative to near term expectations of resource productivity.

2. Materials and methods

We obtained commercial landings of market squid from California Department of Fish and Wildlife (CDFW) fish ticket reports to provide the spatial and temporal context of the fishery. These were summarized to provide landed weights (mt) of market squid by: year (1990-2014), major port (Eureka, Fort Bragg, Bodega Bay, San Francisco, Monterey, Morro Bay, Santa Barbara, Los Angeles, and San Diego; Fig. 1), and quarter (Jan-Mar, Apr-Jun, Jul-Sep, and Oct-Dec).

Field and analytical methods of the National Marine Fisheries Service, Southwest Fisheries Science Center (SWFSC) rockfish recruitment and ecosystem assessment survey (RREAS) have been presented in considerable detail in previous publications (cf., Ralston et al., 2015; Sakuma et al., 2016). In brief, midwater trawl sampling occurs at night in May-June at a series of fixed station locations with a modified-Cobb trawl that has a 9.5 mm mesh cod-end liner and is effective at retaining epipelagic micronekton (free swimming organisms generally < 200 mm). The net is towed for 15 minutes and quantitative sampling is obtained by deploying 85 m of trawl warp and adjusting the speed of the vessel in real time to maintain a targeted headrope depth of 30 m.

The contents of the trawl are sorted to the lowest taxon possible and enumerated. Starting in 1990, a concerted effort was made to improve and standardize abundance estimates of a variety of taxa, including market squid, and we limit our consideration to that year forward. Moreover, starting in 2004 trawl-specific length compositions of market squid catches were collected (dorsal mantle length (DML) mm), allowing for a description of the life-history stages of captured squid and an understanding of variation in their sampling. The RREAS was also expanded spatially in 2004 to cover all of southern and central California, i.e., lat. 32º30'—39º50' N (Sakuma et al., 2006). Prior to that year the survey was limited to the core portion of the latter region (lat. 36º30'—38º20' N).

For this study, the enumerated catch of market squid from each trawl[1] was treated as catch-per-unit-effort (CPUE) abundance data ($n \cdot tow^{-1}$). CPUE data from standard trawl survey stations were summarized using delta-generalized linear models (Δ-GLM) (Stefánsson, 1996; Dick, 2004; Maunder and Punt, 2004). With this approach, the data were fitted separately to a binomial presence/absence model and a lognormal model with zero catches removed. Estimated effects from the two models were then combined multiplicatively. Aside from the dependent variables, link functions, and error distributions, both models were identically structured, including only main effects for year and station. This modeling approach was applied to subsets of the survey data that were regionally stratified north and south of Point Conception, a major zoogeographic faunal break separating regional squid fisheries (CDFW, 2005).

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[1] All catch and length information is publicly available at https://coastwatch.pfeg.noaa.gov/erddap/index.html

As the survey also encounters considerable amounts of adult krill, which are known to dominate the diet of market squid (Fields, 1965; Karpov and Cailliet, 1979), we applied the same Δ-GLM approach to adult krill catches from the survey to evaluate whether prey abundance (krill) is related to squid catches or abundance. The two dominant krill species captured in the survey are *Euphausia pacifica*, which tends to have an offshore distribution, and *Thysanoessa spinifera*, which is more abundant over the shelf (Santora et al., 2011), and is thus more likely to reflect prey availability for market squid. However, species-specific identifications of krill in the survey did not start until 2002 (Sakuma et al. 2016). Consequently we developed time series of "krill" abundance from 1990-2015 for the core region and 2004-2015 for the southern region.

The Δ-GLM models provided separate time series of both squid and krill CPUE by region, offering a basis for evaluating factors that might affect squid population abundance and landings. However, as both our survey indices and associated landings data and biomass estimates demonstrated significant autocorrelation, it was necessary to apply time series methods to the input time series to ensure stationarity (constant mean and equal variance) and remove the effects of autocorrelation that can lead to spurious correlations based on temporal dependencies. We followed the approach of Shumway and Stoffer (2011) by fitting an autoregressive integrated moving average (ARIMA) model to the input time series (survey cpue indices), applying the parameters from the ARIMA model to the output (third quarter landings, biomass estimates) time series, and running a cross correlation function on the resulting residuals. The resulting pre-whitened cross correlation coefficients represent the appropriate statistical relationships between the predictive and observed time series. Due to our interest in evaluating near term fishery potential in the fall based on spring squid or krill catches, only cross correlations with no time lags were reported here.

Market squid "station" estimates of CPUE from a coastwide Δ-GLM model were mapped to depict the overall spatial distribution of market squid sampled in the trawl survey. An Inverse Distance Weighted (IDW) interpolation in ArcGIS was used to contour model estimates in $\log_e$-space. We contoured using 2-5 neighbors and stations where squid were never captured were treated as null values. Lastly, we clipped a 30 nautical mile (nm) buffer around each station to visualize the final IDW estimates. We also assessed concordance between the spatial distribution of squid encountered by the survey and regions of high squid landings to evaluate whether the survey effectively samples the squid stock. To do so we paired midwater trawl station locations with the nine major ports in the State (see above) by minimizing the absolute differences in their latitudes. We then correlated the logarithm of the station effect with the logarithm of cumulative landings of squid at each major port over the 1990-2014 period.

Dorval et al. (2013) developed a method for estimating the spawning stock biomass (SSB) (mt) of market squid by: (1) measuring the realized spawning potential per recruit (SPR) on the fishing grounds, (2) translating the observed SPR into a fishing mortality rate (F_{SPR}) using life-history information, and (3) combining estimated F_{SPR} values with known landings to infer SSB. Their approach required specific assumptions about the natural mortality (M = 0.01, 0.15, and 0.30 d^{-1}) and the egg laying rate (v = 0.45 d^{-1}). This approach also required the measurement of formalin preserved gonad weight of individual squid to estimate the residual number of oocytes in harvested females (Macewicz et al., 2004). Using this approach, in instances where sufficient data were available, they estimated market squid SSB in three regions of California on a year × quarterly basis. Results spanning 1999-2006 are updated here to include eight more years of SSB estimates (2007-2014). To increase the efficiency of data collection and processing the CDFW stopped preserving squid gonads in formalin in August 2010, providing instead fresh gonad weights for the egg escapement model. We therefore used the equation ($W_p = 1.8980 \times W - 0.5186$) from McDaniel et al. (2015) to convert fresh (W_f) to preserved (W_p) gonad weights for all biological samples collected after July 2010. Along with the landings statistics, these SSB estimates were the response variables for the cross correlation analysis with both the krill and squid survey indices.

3. Results

The fishery for market squid in the State of California varies spatially and seasonally. Although the fishery originated in Monterey Bay, total landings, summarized over the 25 year period from 1990-2014, show that Southern California ports (Santa Barbara, Los Angeles, and San Diego), representing the region south of Point Conception accounted for 84% of the total catch during that time (Table 1). Landings tend to occur at very different times of the year in the two regions. In particular, landings in the south peak during the fall and winter months (1st and 4th quarters), when 82% of that region's catch is taken. In contrast, the fishery in the north peaks during spring and summer months (2nd and 3rd quarters), accounting for 86% of total landings. Moreover, the proportion of annual statewide landings taken in the two regions has fluctuated widely (Fig. 1). As illustrated in Fig. 1, less than 5% of the total catch was taken in the northern fishery from 2005-2009. Since then, however, the northern share of total landings has risen steadily, reaching 54% in 2014. A very high percentage of statewide landings also occurred in the north in 1992, an El Niño year. These findings support our regional approach to modeling squid abundance north and south of Point Conception.

Annual catch-weighted length distributions of the market squid sampled by the midwater trawl survey are summarized in Fig. 2. It is apparent from Fig. 2 that the great preponderance of the catch is larger than the paralarval stage of roughly 7.6 mm, but less than 50 mm DML, which corresponds to juvenile squid 30 to 90 days old. Very few individuals that are of commercial size are sampled, quite possibly due to significant net avoidance by large squid (DML > 100 mm), consistent with the findings of Kidokoro et al. (2014). Moreover, annual variation in these distributions is not marked, although some minor differences are apparent. In particular, there was a moderate increase in the size of squid taken by the survey in 2012, when the median size increased to 44 mm DML, which has been maintained at somewhat higher values in the 2012-2015 period. Also apparent are somewhat large swings in the 95th length percentile, which is indicative of occasional minor catches of large squid (e.g., 2005 and 2008).

Contoured station effects from the coastwide Δ-GLM model are shown in Fig. 3. Numerical values of "Squid estimate" in the figure represents expected $\log_e(n \cdot tow^{-1})$, averaged over the 2004-2015 time period. Station locations included in the contouring are shown as circles. It is apparent from Fig. 3 that two primary centers of abundance occur within the survey region, which correspond well with those ports of landing that account for over 95% of market squid landings (Monterey, Santa Barbara, and Los Angeles). Moreover, model estimates of the abundance of squid at RREAS trawl stations were significantly correlated ($r = 0.41$, $P < 0.01$) with cumulative landings over the 1990-2014 period at adjacent ports (see Table 1). We therefore conclude that the market squid sampled in the survey are pre-recruits to the California fishery.

Due to the seasonally asynchronous nature of landings, catch-rate data from the survey were evaluated separately north and south of Pt. Conception, resulting in two Δ-GLM models for each taxon (squid and krill). Time series of the logarithm of year effects from the models, with their standard error estimates, are presented in Table 2 and results for squid are plotted in Fig. 4. An examination of residuals showed no patterns that would raise concern that assumptions of the model were violated. Recall that 2004 was the first year that RREAS sampling occurred south of Point Conception. Moreover, no southern sampling was conducted in 2011 due to a lack of shiptime. Our findings show that squid catch rates exhibit substantial interannual variability, with $\log_e$-scale estimates ranging 0.4-6.2 in the north and 4.0-8.2 in the south.

We present updated SSB estimates of market squid based on the approach of Dorval et al. (2013) in Supplementary Appendix A. These estimates are subdivided by quarter and management region (Fig. 3). Region 1 effectively coincides with Monterey Bay, whereas Region 2 represents the preponderance of southern California. While eight new years of data are provided here, there are still many missing values in the table.

Spatially stratified survey catch rates of squid and krill sampled in May-June were positively associated with squid landings and regional estimates of spawning stock biomass in the third quarter (July, August, September) of the same year (Figs 5 and 6). Cross correlation functions provided a means of evaluating how robust the signals from the survey data are relative to observed third quarter landings and biomass estimates, stratified by region. There were positive correlations in all eight comparisons, indicating considerable promise for using survey squid and/or krill CPUE indices to inform managers regarding the pending availability of market squid to the fishery (Figs 5-6). Cross correlations ranged from 0.34 to 0.99 across the different variables and regions (Table 3). Note that only three of the eight comparisons were statistically significant ($\alpha = 0.05$), largely because in some instances there were single outliers (e.g., the southern squid-landings comparison) and in addition the CPUE time series were typically quite short. Interestingly, time series of krill CPUE tended to be as good, if not better, than market squid CPUE with respect to predicting both third quarter landings and biomass.

4. Discussion

High population turnover rates, combined with noisy relationships between spawning stock abundance and recruitment (typically presumed to be in response to high sensitivity to environmental conditions) are widely recognized challenges associated with the assessment and management of cephalopod populations throughout the world (Boyle and Rodhouse, 2005; Rodhouse et al., 2014; Arkhipkin et al., 2015). While an improved understanding of the environmental processes that drive interannual variation in abundance and productivity of such populations would clearly be beneficial, a forecast model based on empirical estimates of abundance immediately prior to the prosecution of major fisheries could be of greater near-term practical utility to both fishermen and resource managers. Our results provide the foundation for a more robust exploration of the utility of such a forecast model, as they demonstrate that standardized abundance estimates of pre-recruit market squid from the May-June RREAS midwater trawl survey are positively associated with both region-specific landings and spawning biomasses in the following months. Similar results have been found by Kidokoro et al. (2014), who documented a strong correlation between an index of abundance of survey trawl-caught juvenile Japanese common squid (*Todarodes pacificus*) and subsequent stock size estimates, although they also reported considerable observation error.

Our results are consistent with previous studies that indicate that juvenile indices are likely to be more appropriate for informing near term fisheries potential in cephalopod populations than paralarval surveys, as paralarval abundance indices tend to relate more strongly to spawning stock biomass (reviewed in Rodhouse et al., 2015, and consistent with Koslow and Allen, 2011; Perretti and Sederat, 2016; van Noord and Dorval, 2017). Stige et al. (2013) drew similar conclusions for finfish with respect to larval and juvenile abundance indices. They also found that inclusion of environmental correlates helped to explain additional recruitment variation relative to models that focused on juvenile indices alone, a result consistent with that of Koslow and Allen (2011) for market squid. The correlations observed here between the abundance of krill and that of market squid imply that environmental factors could be mediated through their influence on prey abundance. Thus, continued evaluations of the variable growth, distribution and productivity of market squid, using methods such as structural equation modeling or stable isotope analysis (e.g., Stewart et al., 2014; Xavier et al., 2014; Thorson et al., 2015), could help disentangle the interacting effects of environmental factors and trophic pathways, and help researchers better understand the likely oceanographic and trophic drivers of variable production in this population. Such efforts would complement the development of statistical models that explored the combination of juvenile abundance indices and environmental factors to accurately predict regional market squid availability to the fishery.

The development and implementation of forecast models to inform the fishery should be considered with some caution, however, as previous studies have found that considerable predictive power is needed to mitigate the risk of imprecise predictions misinforming management. For example, De Oliveira and Butterworth (2005) showed that an environmental index would have to explain at least 50% of recruitment variability before the added benefit to management outweighed the risk of erroneous recruitment forecasts. Although not all of our cross-correlation function results meet that threshold with respect to the relationship to either landings or biomass, we are confident that as the time series lengthen, more robust methods of addressing the mechanistic nature of the relationship as well as evaluating and addressing the effects of autocorrelation on the inferred results can be applied. Moreover, as their study focused on a short-lived anchovy species, albeit one with a considerably longer lifespan than market squid, exploration of the requisite level of information content would presumably need to be evaluated rigorously in the context of the unique characteristics of this fishery.

For example, Kidokoro et al. (2014) noted that the high observation error in their juvenile index biased their relationship between juvenile abundance and stock size towards one with lower slope and higher intercept, which could inflate the estimated abundance or fishery potential during low productivity years. If not explicitly accounted for in a forecast model, through either a non-linear predictor or threshold based control rule, biases such as this could potentially lead to greater risk of overharvest. Although cephalopod populations have typically been characterized as resilient, market squid are also among the most frequently encountered forage species in California Current predator studies (Lowry et al., 1999; Szoboszlai et al., 2015), which could lead to some concerns about destabilization of the ecosystem if the squid stock was depleted by overexploitation. Similarly, the prospect of regional management was discussed in Dorval et al. (2013), although such an approach would require an analysis of the biological and socioeconomic impacts to both the fishery and the management system, which are also topics well beyond the scope of this paper.

From a more global perspective, the need to develop the means of improving management of cephalopod fisheries through forecast models based on either environmental or empirical data has long been recognized (Boyle and Rodhouse, 2005; Koslow and Allen, 2011; Xavier et al., 2015). Likewise, the potential to use pre-recruit abundance data from fishery-independent surveys has shown considerable practical potential (Kidokoro et al., 2014; Rodhouse et al., 2015). Our hope is that our findings can provide a foundation for developing a rigorous forecast model for market squid through simulation study. Such an approach could determine both the information content necessary to develop a statistically robust predictive model and should also explore the consequences of implementing a forecast-based approach to augment the current management regime.

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Table 1. Seasonal and spatial variation in the market squid fishery. Presented are aggregated total landings (mt) from 1990-2014, by major port and quarter. The dashed line represents ports north (above) and south (below) of Point Conception.

Major Port	Jan-Mar	Apr-Jun	Jul-Sep	Oct-Dec	Total	Percentage
Eureka	0	1	1,455	761	2,217	0.1%
Fort Bragg	0	0	0	0	0	0.0%
Bodega Bay	0	0	41	0	41	0.0%
San Francisco	0	450	30,939	4,423	35,812	2.1%
Monterey	1,698	85,034	100,290	29,141	216,162	12.7%
Morro Bay	0	651	8,706	1,038	10,396	0.6%
Santa Barbara	209,867	55,597	104,624	472,216	842,303	49.5%
Los Angeles	169,417	27,003	78,022	319,777	594,219	34.9%
San Diego	27	0	0	1	28	0.0%

Table 2. Time series of market squid and krill CPUE ($n \cdot tow^{-1}$) calculated from midwater trawl survey data collected north and south of Point Conception. Presented are estimates of $\log_e$(CPUE) derived from regional Δ-GLM models with associated standard errors of the estimates in parentheses.

Year	Squid North	Squid South	Krill North	Krill South
1990	3.89 (0.33)	.	11.72 (0.26)	.
1991	3.44 (1.12)	.	12.25 (0.29)	.
1992	5.08 (0.28)	.	10.90 (0.40)	.
1993	3.61 (0.55)	.	12.22 (0.32)	.
1994	3.39 (0.48)	.	12.13 (0.30)	.
1995	3.93 (0.34)	.	11.55 (0.35)	.
1996	2.77 (0.51)	.	10.31 (0.33)	.
1997	4.25 (0.29)	.	11.15 (0.36)	.
1998	0.74 (1.20)	.	8.60 (0.34)	.
1999	1.75 (0.96)	.	10.93 (0.28)	.
2000	3.22 (0.59)	.	12.36 (0.30)	.
2001	4.64 (0.35)	.	12.71 (0.30)	.
2002	4.11 (0.30)	.	9.92 (0.34)	.
2003	2.57 (0.63)	.	11.79 (0.29)	.
2004	3.14 (0.61)	4.57 (0.57)	10.91 (0.26)	8.31 (0.48)
2005	1.72 (0.77)	4.63 (0.31)	10.72 (0.29)	9.02 (0.33)
2006	0.41 (1.23)	4.04 (0.33)	11.28 (0.29)	9.90 (0.43)
2007	1.00 (1.14)	4.63 (0.37)	11.82 (0.27)	10.28 (0.51)
2008	1.90 (0.90)	4.32 (0.35)	13.30 (0.25)	11.25 (0.45)
2009	3.19 (0.34)	5.79 (0.48)	12.61 (0.29)	11.02 (0.45)
2010	2.70 (0.68)	4.54 (0.47)	12.30 (0.24)	10.06 (0.49)
2011	3.53 (0.50)	.	12.47 (0.29)	.
2012	4.73 (0.29)	8.20 (0.41)	12.70 (0.34)	11.24 (0.49)
2013	5.28 (0.24)	5.67 (0.36)	13.27 (0.26)	11.86 (0.45)
2014	6.15 (0.19)	7.21 (0.55)	13.54 (0.26)	11.79 (0.48)
2015	5.50 (0.27)	5.45 (0.31)	10.68 (0.30)	8.87 (0.49)

Table 3: Cross correlation function results for squid and krill indices as related to third quarter (Q3) market squid landings and biomass estimates (results significant at 0.05 level are shown in bold).

Northern region

	krill cpue	squid cpue
Q3 landings	0.337 (25)	0.357 (25)
Biomass	**0.637 (11)**	0.503 (11)

Southern region

	krill cpue	squid cpue
Q3 landings	**0.880 (10)**	0.479 (10)
Biomass	0.692 (6)	**0.997 (6)**

List of Figure Captions

Figure 1. Spatial fluctuation of total landings in the market squid fishery over the last 25 years.

Figure 2. Annual variation in length-frequency distributions of market squid taken in the midwater trawl survey. The 5th (p05), 25th (p25), 50th (median), 75th (p75), and 95th (p95) percentiles of survey catches are depicted by year.

Figure 3. Contour plot of $\log_e$(CPUE) station effects from a coastwide market squid Δ-GLM model. Trawl stations with at least one positive catch are shown as '○' symbols, whereas stations where no squid have been taken are shown as a '+'. The three CDFW reporting regions described in Dorval et al. (2013) and listed in Supplementary Appendix A are depicted.

Figure 4. Annual variation in the abundance of market squid in the midwater trawl survey. Plotted are the year effects from the two area-specific models for north and south of Point Conception (error bars ± 1.0 standard error).

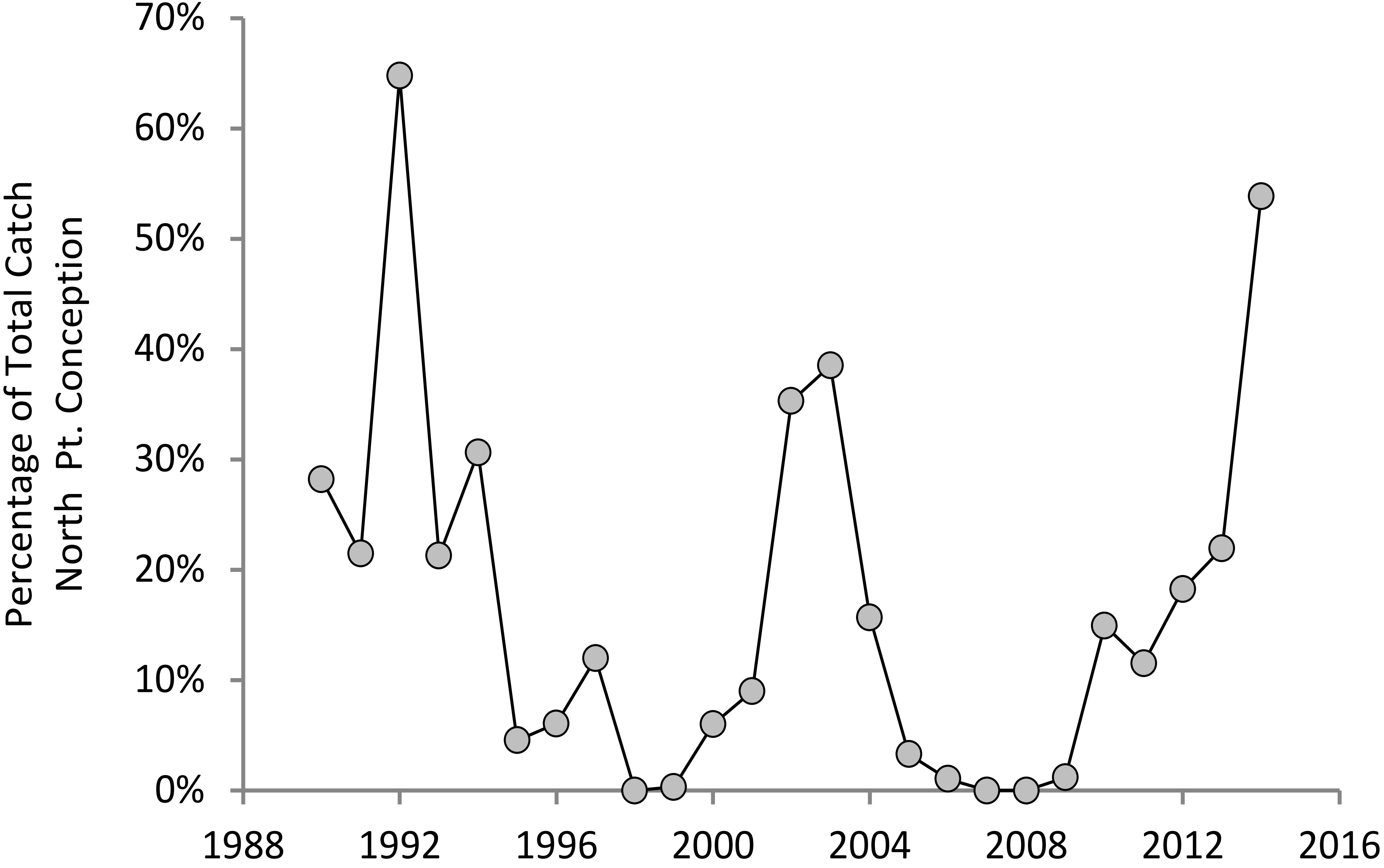
Figure 5. Relationships among midwater trawl survey CPUE estimates for krill (left) and market squid (right) from stations sampled north of Point Conception in comparison to third quarter landings (above) and spawning stock biomass (below) in the northern region. Numbers enclosed within symbols are the last two digits of the survey year.

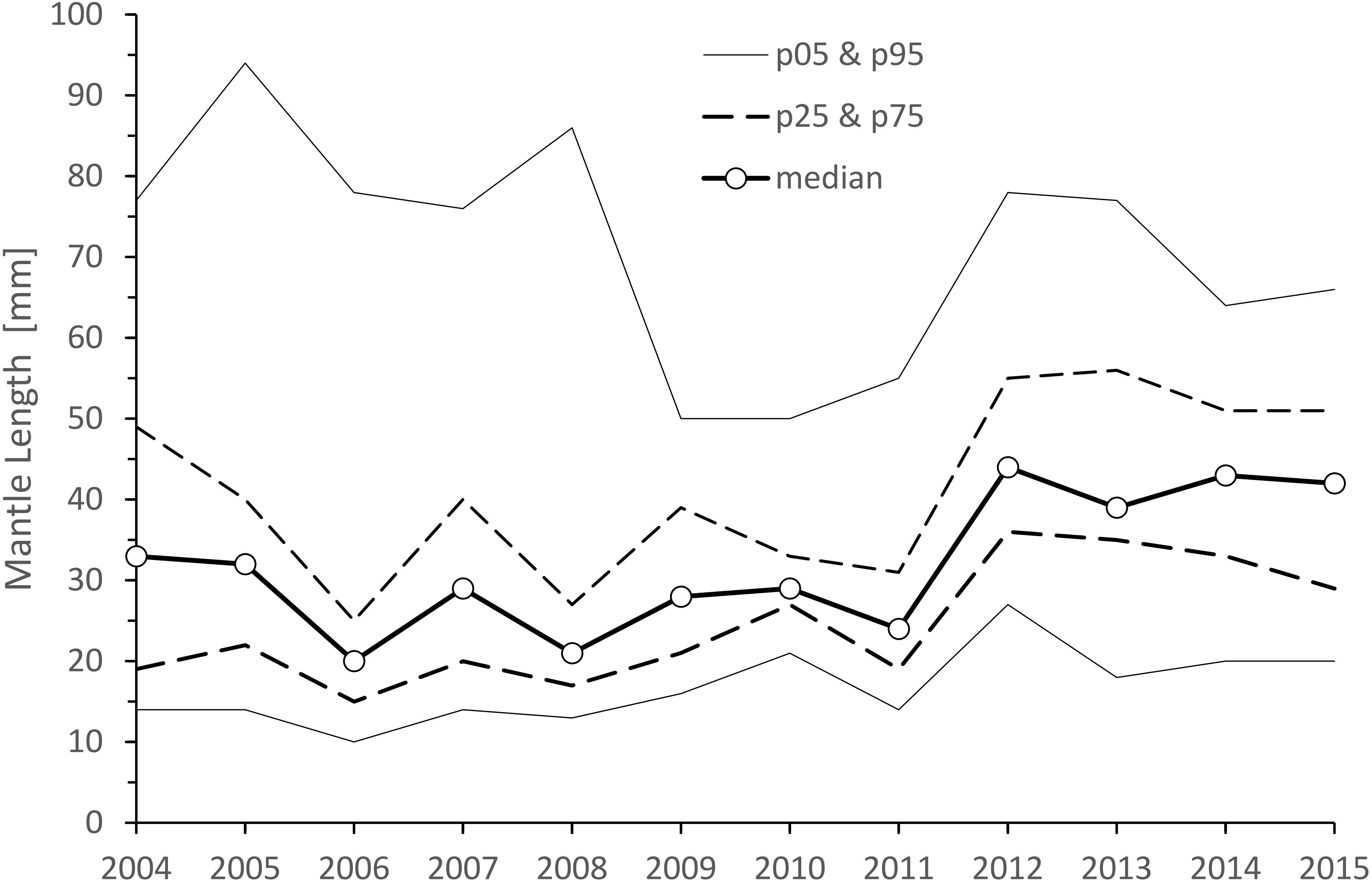
Figure 6. Relationships among midwater trawl survey CPUE estimates for krill (left) and market squid (right) from stations sampled south of Point Conception in comparison to third quarter landings (above) and spawning stock biomass (below) in the southern region. Numbers enclosed within symbols are the last two digits of the survey year.

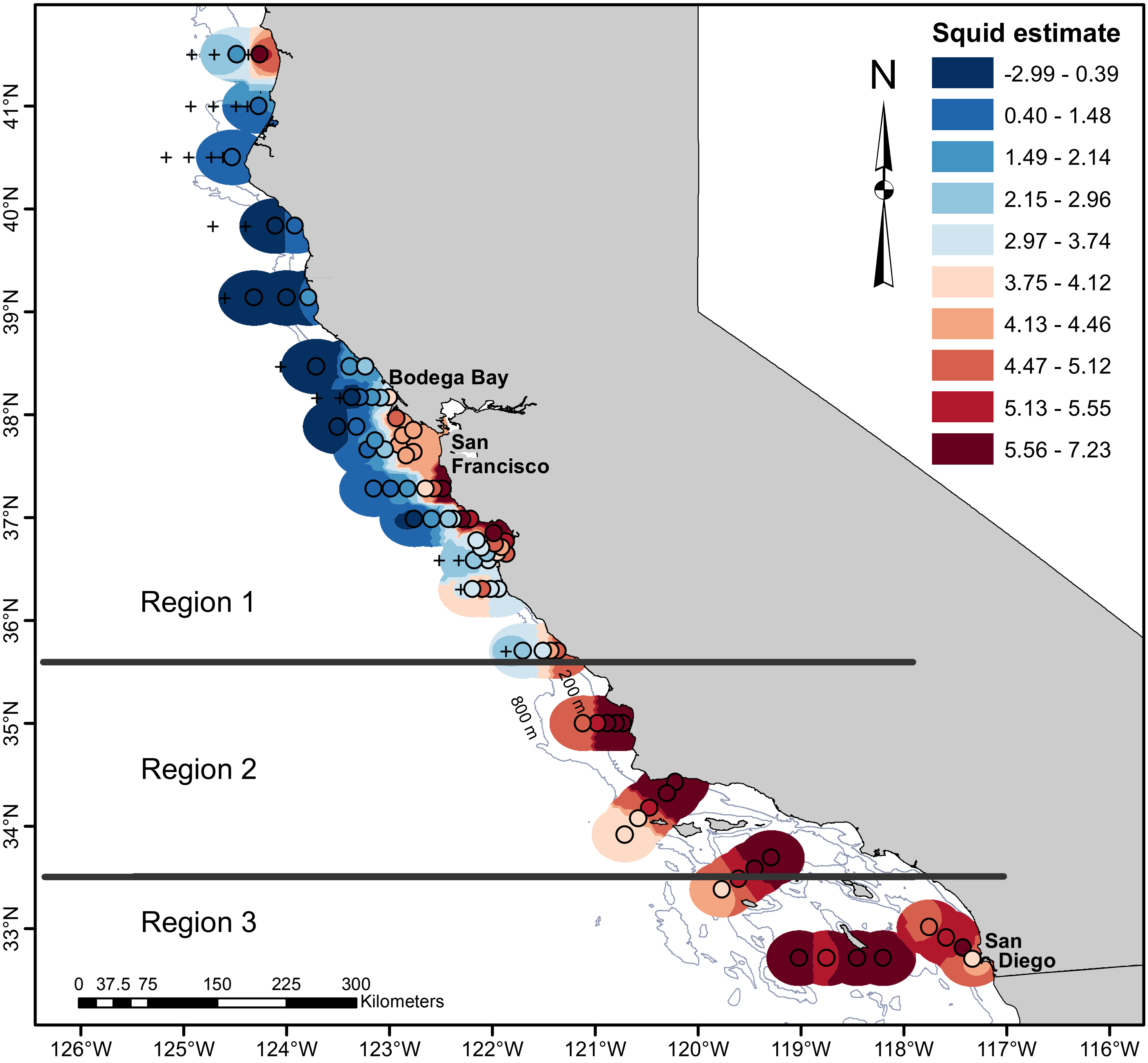
Supplementary Appendices

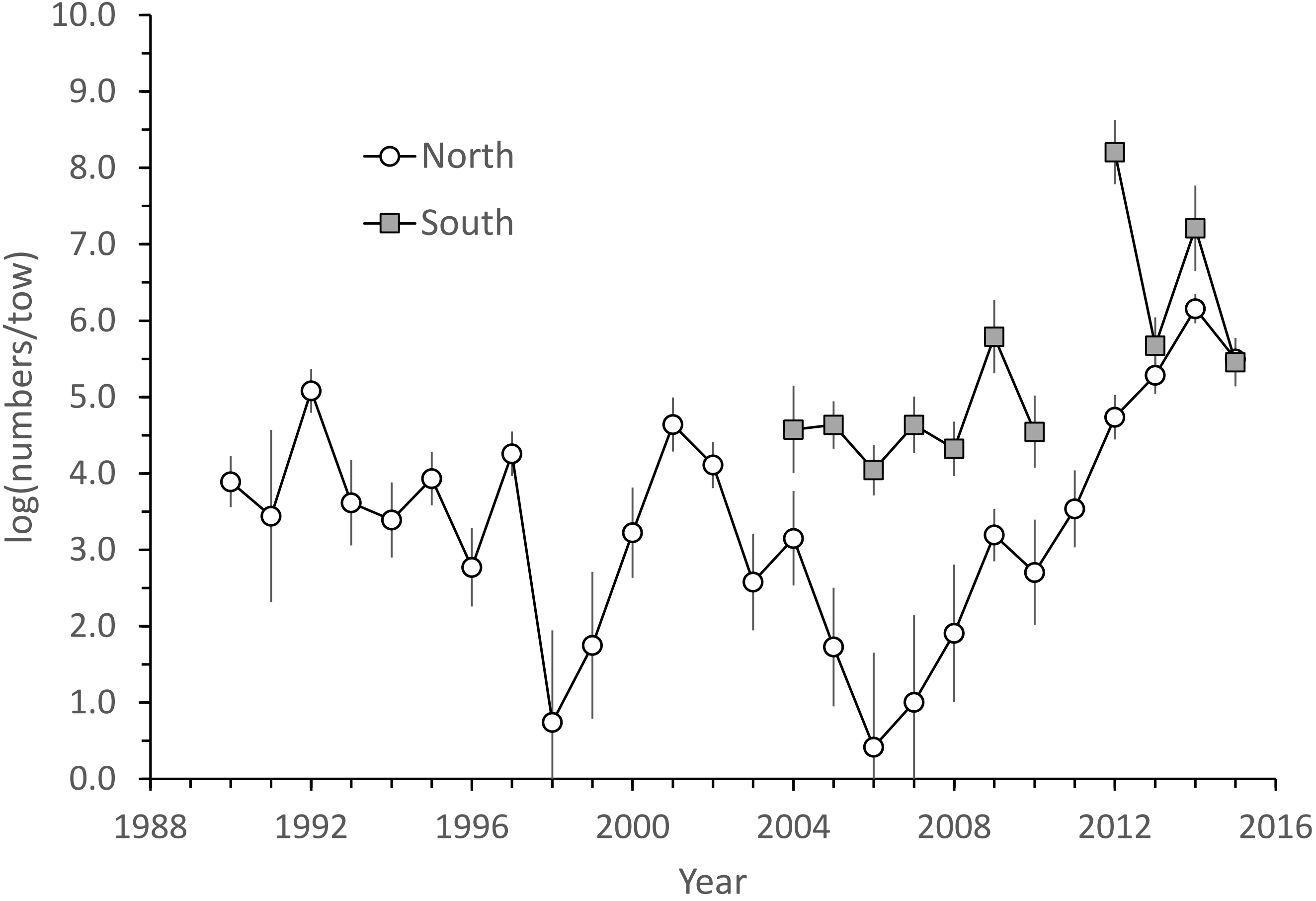
Supplementary Appendix A. Year × quarter estimates of market squid spawning stock biomass [mt] in CDFW management Regions 1, 2, and 3 (see Figure 3). Estimates based on the method of Dorval et al. (2013), assuming a natural mortality rate of **M** = 0.15 and an egg laying rate of **ν** = 0.45.

	Region 1				Region 2				Region 3			
Year	Jan-Mar	Apr-Jun	Jul-Sep	Oct-Dec	Jan-Mar	Apr-Jun	Jul-Sep	Oct-Dec	Jan-Mar	Apr-Jun	Jul-Sep	Oct-Dec
1999	-	-	-	-	10,260	19,069	3,095	51,124	2,803	5,704	276	9,566
2000	-	7,631	2,539	440	29,523	11,019	3,187	127,275	11,695	2,593	1,161	21,114
2001	-	1,447	6,473	982	19,081	10,252	3,986	42,345	31,831	701	1,048	51,640
2002	1,876	19,523	6,438	2,864	12,302	1,030	2,458	14,738	70,594	964	135	523
2003	-	6,821	9,656	5,715	4,137	862	1,556	32,561	1,067	727	1,904	2,281
2004	-	6,319	2,766	-	18,905	13,775	-	36,702	31,635	401	-	377
2005	-	3,349	1,126	-	108,656	-	-	6,460	6,952	1,120	1,992	29,451
2006	-	1,446	163	-	5,686	-	656	9,557	70,261	4,501	3,797	-
2007	-	-	-	-	79,634	345	404	-	7,398	-	356	2,918
2008	-	-	-	-	13,149	-	4,420	-	11,927	1,382	2,879	-
2009	-	483	-	-	63,426	-	-	78,918	17,838	2,388	6,908	6,960
2010	-	36,598	9,695	4,543	-	-	5,093	59,113	31,104	-	1,816	78,156
2011	-	6,169	7,257	-	5,669	-	30,367	68,008	4,045	-	9,781	45,882
2012	-	-	9,402	21,354	4,612	1,732	35,799	101,764	8,418	-	0	109,407
2013	-	775	19,944	1,597	-	9,588	42,729	57,741	2,076	5,204	27,047	30,655
2014	-	20,274	31,806	-	-	3,596	-	-	644	3,335	-	-

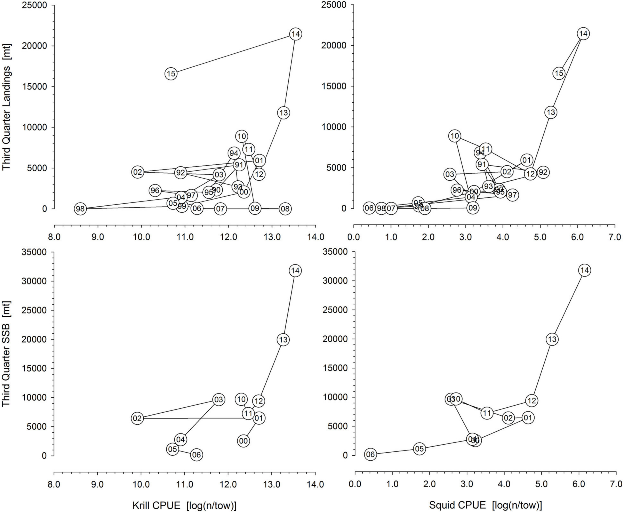

Percentage of Total Catch
North Pt. Conception
70%
60%
50%
40%
30%
20%
10%
0%
1988
1992
1996
2000
2004
2008
2012
2016


p05 & p95
p25 & p75
median
Mantle Length [mm]
0
10
20
30
40
50
60
70
80
90
100
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
2015

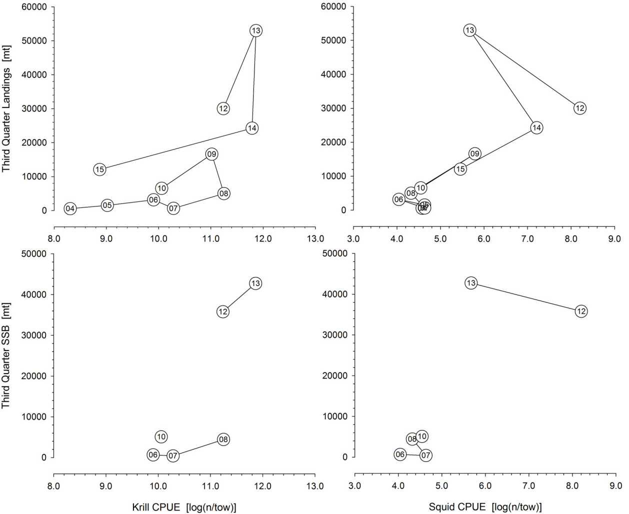

Squid estimate
-2.99 - 0.39
0.40 - 1.48
1.49 - 2.14
2.15 - 2.96
2.97 - 3.74
3.75 - 4.12
4.13 - 4.46
4.47 - 5.12
5.13 - 5.55
5.56 - 7.23
N
Bodega Bay
San Francisco
San Diego
Region 1
Region 2
Region 3
200 m
800 m
0 37.5 75 150 225 300
Kilometers
41°N
40°N
39°N
38°N
37°N
36°N
35°N
34°N
33°N
126°W
125°W
124°W
123°W
122°W
121°W
120°W
119°W
118°W
117°W
116°W



North
South
log(numbers/tow)
10.0
9.0
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0.0
1988
1992
1996
2000
2004
2008
2012
2016
Year



Third Quarter Landings [mt]
25000
20000
15000
10000
5000
0
15
14
13
10
11
94
01
91
02
92
03
12
93
96
90
95
00
04
97
05
99
98
06
07
09
08
Third Quarter SSB [mt]
35000
30000
25000
20000
15000
10000
5000
0
8.0
9.0
10.0
11.0
12.0
13.0
14.0
Krill CPUE [log(n/tow)]
0.0
1.0
2.0
3.0
4.0
5.0
6.0
7.0
Squid CPUE [log(n/tow)]


Third Quarter Landings [mt]
60000
50000
40000
30000
20000
10000
0
Third Quarter SSB [mt]
50000
40000
30000
20000
10000
0
8.0
9.0
10.0
11.0
12.0
13.0
3.0
4.0
5.0
6.0
7.0
8.0
9.0
04
05
06
07
08
09
10
12
13
14
15
Krill CPUE [log(n/tow)]
Squid CPUE [log(n/tow)]