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AN UPDATE OF EGG ESCAPEMENT, FISHING MORTALITY, AND SPAWNING STOCK BIOMASS FOR THE CALIFORNIA MARKET SQUID (*DORYTEUTHIS OPALESCENS*) FISHERY FROM 1999 TO 2022

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An update of egg escapement, fishing mortality, and spawning stock biomass for the California market squid (*Doryteuthis opalescens*) fishery from 1999 to 2022

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Table of Contents

Executive Summary

Over the past three decades, the market squid (*Doryteuthis opalescens*) fishery has become one of the most productive and valuable fisheries off California. In 2005, the California Department of Fish and Wildlife established the Market Squid Fishery Management Plan (MSFMP). This management plan implemented several control rules, including: a weekend closure; a restricted access program; a fishing-year catch limit of 107,047 mt; gear restrictions; and a proxy for maximum sustainable yield of 0.30 proportional egg escapement [*(S(F)*]. In this study, we provide an update of the biological and fishery parameters of the egg escapement model that is used to monitor the status of market squid productivity and spawning output off California. Firstly, we derived three new linear models to predict formalin-preserved gonad weights from fresh gonad weights based on laboratory experiments conducted during 2, 4, and 6 weeks of gonad preservation. We found that any one of the 2-, 4-, or 6-week model could be used to convert fresh gonads into formalin-preserved gonads, as all models explained at least 94% of the variability in the data. The 6-week model was selected for computing formalin-preserved gonad weight in this study, for consistency with previous studies and because it had a larger sample size. The application of this model increased efficiency in processing gonad samples and in computing catch fecundity (i.e., the residual number of eggs in harvested market squid females) for the egg escapement model. Secondly, we extended the time series of fishery parameters of the egg escapement model to estimate *S(F),* daily fishing mortality *(F)*, and spawning stock biomass (*SSB*) from 1999 to 2006 through 2022. As in previous studies, these parameters were estimated by quarter in each of the three main regions of the fishery: northern California (Region 1), central California, including around the northern Channel Islands (Region 2), and southern California, including around the southern Channel Islands (Region 3). In all three regions, market squid biomass fluctuated seasonally and interannually, with generally lower *SSB* during and following strong El Niño and/or marine heat wave conditions, particularly in the more southern regions. Over the 23 years of monitoring the fishery, *S(F)* was frequently low in Region 1, highly variable in Region 3, but showed a clear increasing trend in Region 2. We attributed the more positive trends of reproductive outputs in Regions 2 and 3 to differences in the temporal migration and recruitment strength among spawning grounds, which controlled the spatial distribution of fishing effort in the market squid fishery.

1. Introduction

Market squid, *Doryteuthis opalescens*, is a short-lived and semelparous species that is distributed throughout the Alaska and California Current ecosystems from the southern tip of Baja California, Mexico, to southeastern Alaska, U.S. (Anderson, 2000; Chasco et al., 2022; FOC, 2001; Suca et al., 2022). Market squid live less than a year and become mature as soon as four months, with an expected (mean) lifespan estimated to be six months (Butler et al., 1999, 2001; Jackson and Domeier, 2003). There may be considerable uncertainty in age estimates, particularly as ageing errors were not estimated in these previous studies. Market squid have fixed (determinate) fecundity at sexual maturity (Knipe and Beeman, 1978; Macewicz et al., 2004). They are most productive off California during La Niña periods (van Noord & Dorval, 2017), where they typically recruit in spring and summer in northern California and in fall and winter in central and southern California, including along the Channel Islands (Dorval et al., 2013; Foote et al., 2006; Reiss et al., 2004). During El Niño periods and marine heat waves, market squid recruitment tends to shift northward, occupying mostly habitats north of Point Conception from Monterey Bay up to Alaska (Chasco et al., 2022; Suca et al., 2022).

Market squid routinely support the largest commercial fishery in both volume and value in California, with annual catches ranging from 12,377 mt to 130,845 mt from 1999 to 2022, and ex-vessel values from $ 13,515,244 to $ 84,361,914 per year (CDFW, 2021; PFMC, 2022). Small-scale fishing activities began in Monterey during the mid-1800s but expanded in the early 1960s due to a worldwide increase in demand and value for squid products (Doubleday et al., 2016; Rodhouse, 2001). The fishery operates mostly on spawning aggregations in nearshore waters using light boats and round haul vessels that include seine and brail gear (CDFW, 2005). Fishing can expand into Oregon during warm years, but landings in these states are relatively minor compared to those in California (PFMC, 2022). Once mature, market squid recruit into shallow coastal waters, where females deposit egg capsules in clutches for about two or three days and die after spawning (Macewicz et al., 2004). While market squid is included in the Coastal Pelagic Species (CPS) Fisheries Management Plan (PFMC, 2023), the California market squid fishery is primarily managed at the state level under the Market Squid Fishery Management Plan (MSFMP) (CDFW, 2005). Market squid landings, dynamics, and biological characteristics of the population are monitored by state agencies, including the California Department of Fish and Wildlife (CDFW), Oregon Department of Fish and Wildlife (ODFW), and Washington Department of Fish and Wildlife (WDFW). From the 1940s through the mid-1990s, landings were monitored intermittently off Monterey, but beginning in 1999, CDFW implemented a systematic sampling program to estimate biological and fishery parameters (CDFW, 2020; Dorval et al., 2022). In 2016, ODFW developed a sampling program similar to that of CDFW because of increased landings (Pers Comms; Greg Krutzikowsky, ODFW). There is no routine sampling program for market squid off Washington, because there is not an active commercial fishery in this state.

The California market squid fishery is managed assuming one population. Reichow and Smitt (2001) and Gilly (2003) found no significant genetic differentiation among market squid collected on spawning grounds off southern and northern California. Similarly, Cheng et al. (2021) also found no genetic differentiation between northern and southern California, though finer spatio-temporal comparisons uncovered more complex dynamics with the existence of micro-cohorts that were genetically different and that spawned continuously in California.

The MSFMP, adopted by the California Fish and Game Commission in 2005, includes various control rules: a restricted access program; mandatory logbooks; an annual catch limit at 107,047 mt (118,000 short tons); gear restrictions; general habitat closure areas; a two-day weekend closure for uninterrupted spawning; and a proxy for maximum sustainable yield of 0.30 proportional egg escapement (CDFW, 2005; PFMC, 2023). The egg escapement methodology was approved by the Scientific and Statistical Committee and the Pacific Fisheries Management Council in 2001, and included in the CPS FMP to provide the *MSY* proxy for the market squid fishery as required by the Magnuson Stevens Act (MSA). Subsequently, the management authority was delegated to CDFW, therefore market squid fishery has been managed under the MSFMP since 2005 (CDFW, 2005).

CDFW applies the egg escapement model to monitor the population dynamics of market squid by fishing season (April 1 to March 31) statewide, based on the final model developed in Dorval et al. (2013). Initial egg escapement models were developed by Macewicz et al. (2004) and Maxwell et al. (2005), but Dorval et al. (2009) and Dorval et al. (2013) extended these models to compute spawning stock biomass (*SSB*) in addition to proportional egg escapement [*S(F)*] from fishery-dependent and fishery independent data (see list of symbols in Table 1). As stated by Dorval et al. (2013), the egg escapement model was "*founded on classical per-recruit theory (Beverton and Holt 1957; Gabriel et al., 1989; Sissenwine and Shepherd 1987), coupled with the assumption that catch fecundity (θ, the number of oocytes and ova in the ovaries and oviducts of harvested females) is related to daily-based fishing mortality (F) and can be used to develop proxies for F-based biological reference points.*" A key biological parameter in the model is potential fecundity (E_p), which is defined as the "standing stock of oocytes of all stages in the ovary of mature pre-ovulatory female market squid just prior to the first ovulation and is estimated from histological analysis of the ovaries" (Dorval et al. 2013; Macewicz et al., 2005). The knowledge of both E_p and θ allows the computation of the proportion of eggs spawned by mature market squid before capture (Maxwell et al., 2005, Dorval et al., 2013). Based on the recruitment dynamics of market squid, mature individuals are vulnerable to the fishery for only a few days. Therefore, the egg escapement model was developed based on a daily time-step (Dorval et al., 2013; Macewicz et al., 2004; Maxwell et al., 2005). However, Dorval et al. (2013) modeled mortality rates (*F, M*) and egg laying rate (*v*) on a daily time scale, but for monitoring purposes, they computed final *F*, *S(F)*, and *SSB* estimates by quarter and fishing region. While the initial approach of the egg escapement model aimed to perform in-season fishery management, this was found to be unpracticable due to logistical constraints in collecting and processing fishery and biological data on such a short timescale (Dorval et al. 2013).

The egg escapement model was last updated by Ralston et al. (2018) to include new methods developed by McDaniel et al. (2015) to increase the efficiency of biological data collection and processing. In prior studies, the mantle condition index *(MC)* was estimated using mantles that were dried for 14 days at 56°C. However, from experimental data, McDaniel et al. (2015) found that market squid mantles dried for 1 to 4 days at temperatures varying from 60°C to 76°C provided *MC* estimates that were not significantly different from those dried for 14 days at 56°C. Therefore, in September 2014, CDFW began drying mantle punches for three days at 60°C. In addition, CDFW stopped preserving squid gonads in formalin in July 2010, providing instead fresh gonad weights, which can be measured at the time of collection, thus greatly reducing the time for processing and producing gonad data for the egg escapement model.

Table 1. Description of symbols used in this paper.

Notation*	Description
a	Adult
C	Total catch in number
CI	Confidence interval
f	Females
i	Day in which a cohort becomes mature
j	Juvenile
k	Number of females sampled per sampling units
L	Total landings (mt)
m	males
MC	Mantle condition index
ML	Mantle length
n	Number of sampling units
q	Quarter
r	Fishing region
t	Day in the fishery
t_{max}	Maximum age in the fishery
t_{min}	Minimum age in the fishery
τ	The upper α/2 of the student's *t* distribution
Variables	
ε	Residual fecundity
E	Number of eggs spawned
$E(F)$	Eggs-per-recruit at a given *F*
G_0	Fresh gonad weight at the time of collection
G_y	Formalin-preserved gonad weight
G_w	Predicted formalin-preserved gonad weight
MC	Mantle condition index
p	proportion
W	Market squid body weight (g)
Parameters	
E_p	Potential fecundity
F	Instantaneous daily fishing mortality
M	Instantaneous daily natural mortality
$S(F)$	Proportional egg escapement
SSA_f	Spawning stock abundance of females in number
SSB	Spawning stock biomass (males and females) in metric ton
v	Daily egg laying rate
σ	Standard deviation
θ^{mod}	Mean catch fecundity computed from model runs
θ^{bio}	Mean catch fecundity computed from market squid biological characteristic

Note: * indicates that symbol notation and description were adapted from Dorval et al. (2013), but some notations were added to take account of updated information in this paper.

Accordingly, Ralston et al. (2018) used the equation ($G_y = 1.8980 \times G_0 - 0.5186$) from McDaniel et al. (2015) to convert fresh gonad weights (G_0) to preserved gonad weights (G_y) for all biological samples collected since July 21, 2010.

The first objective of this paper was to derive a new relationship between fresh and preserved market squid gonad weights. The McDaniel et al. (2015) regression model was derived from formalin-preserved gonads over two weeks and thus had considerable uncertainty that might affect egg escapement estimates depending on market squid size. In this study, we collected additional gonads and derived regression models for gonads preserved during two, four, and six weeks. A new fresh to formalin-preserved relationship based on 6-week preservation of gonads was used to update the egg escapement parameters estimates from July 2010 to December 2022. Secondly, we updated the Dorval et al. (2013) time series of the egg escapement model to provide quarterly estimates of fishing mortality, egg escapement and spawning stock biomass (*SSB*) for the southern, central and northern California regions of the fishery from January 1999 to December 2022.

2. **Methods and Materials**

2.1. *Fishery Data*

Market squid catch information came from mandatory landing receipts reported to CDFW processors. For this study, all catch data were updated from January 1999 to December 2022. Following standard protocols (CDFW, 2020), landings were sampled in three major port complexes: Monterey, Santa Barbara, and Los Angeles. At each port complex, CDFW attempted to collect market squid samples at least 25 days per month from 1999 to 2003, but sampling effort was reduced to 12 randomly selected days per month beginning in 2004. Infrequently, market squid was also collected in Eureka, Half Moon Bay, and San Francisco, but collected samples in these areas were excluded from this study as they were not consistent with the sampling design implemented across the three major ports. In each major port, during each sampling day, vessels were randomly selected, and from each vessel 30 individual market squid were collected randomly (CDFW, 2020). Each individual squid was measured for mantle length (*ML*) in millimeters (mm), and body weight in grams (g); and beginning in July 2010, fresh gonad weight (GW_f) was also measured to the nearest milligram (mg) from the first five females. The sex of each individual market squid was determined visually. From 1998 to June 2001, a maturity stage was assessed using the classification system established by Macewicz et al. (2004) for gross anatomical characteristics of the reproductive system of female market squid (i.e., including nidamental gland, oviduct, and ovary). Thereafter, the presence of clear oocytes in the ovary and oviduct was documented and a sub-sample of six market squid (the first male and first five females) was randomly selected for additional maturity assessment at the CDFW laboratory and for catch fecundity estimation.

Dorval et al. (2013) found that "the three port complexes are not always a good representation of mutually exclusive fishing areas in the market squid fishery, given vessels from different ports often operate in the same general vicinity." Therefore, Dorval et al. (2013) assigned an explicit fishing area using the CDFW commercial fishing blocks (10 miles × 10 miles). Further, Dorval et al. (2013) sub-sampled the collected data based on the following spatial framework (Figure 1):

Region 1: South of Bodega Bay to Point Piedras (CDFW blocks 430-570);

Region 2: Santa Barbara, Los Angeles, and the northern Channel Islands (CDFW blocks 571-736); and

Region 3: San Diego and the southern Channel Islands (CDFW blocks 737-900).

As in Dorval et al. (2013), all randomly selected samples from 1999 to 2022 were analyzed by season (i.e., calendar year quarter) within each region, with a sampling unit defined as a boat trip selected in a given region.

2.2. Gonad Weight Experiment

As indicated previously, the egg escapement model was originally developed based on preserved gonad weights (G_y), a parameter that is critical for the estimation of catch fecundity. Because CDFW stopped preserving gonads and began weighing them fresh in July 2010, McDaniel et al. (2015) developed a regression model to estimate formalin-preserved weight from fresh gonad weights so that the time series of all model parameters can be extended beyond the

Dorval et al. (2013) time series of data, while preserving the consistency and integrity of the estimation of biological parameters from the original models. However, McDaniel et al. (2015) used gonads preserved in formalin for only two weeks, and these samples, collected in June-October 2014, did not fully reflect the expected range of all possible gonad weights observed in mature market squid from past studies. Therefore, CDFW collected additional gonad samples (*N*= 336, Table 2) from September 2015 through August 2017 and from June 2019 through September 2019 to develop new relationships based on fresh gonads preserved in formalin for two, four, and six weeks. Fresh gonads were dissected from mature female market squid collected during standard port sampling in Monterey and Los Angeles ports. Mature female market squid were selected based on five 20 mm *ML* bins: 80-100 mm; 101-120 mm; 121-140 mm; 141-160 mm; and 161-180 mm. Gonads (ovary, oviduct, and oocytes/eggs) were extracted and weighed fresh to the nearest milligram. Each gonad was preserved in an 8-ounce jar filled with 10% buffered formalin solution. After each time period (two, four, and six weeks) we removed the gonads and all loose eggs from the jars, decanting all remaining formalin solution using a sieve. The gonads and any loose eggs were then weighed to the nearest milligram. Gonads with completely broken ovaries and oviducts were removed from the data used in the modeling process. Preserved gonad samples that were not measured within two days of the target date of measurement (due to staffing issues and closure of the of the lab during weekends and holidays) were also removed from the analysis.

Linear regressions were used to determine conversion factors for predicting preserved formalin weight from known fresh gonad weight after two, four, and six weeks of preservation. Although there were small differences in parameter estimates among the three regression models, we selected the 6-week model for computing biological and fishery parameters in this study, not only because it had a much larger sample size (*n*= 121) compared to the 2- and 4-week models (Table 2), but also because after four weeks of preservation in formalin, CPS gonad weights tends to level off (Dorval et al., unpublished data). Further, the 6-week model may have

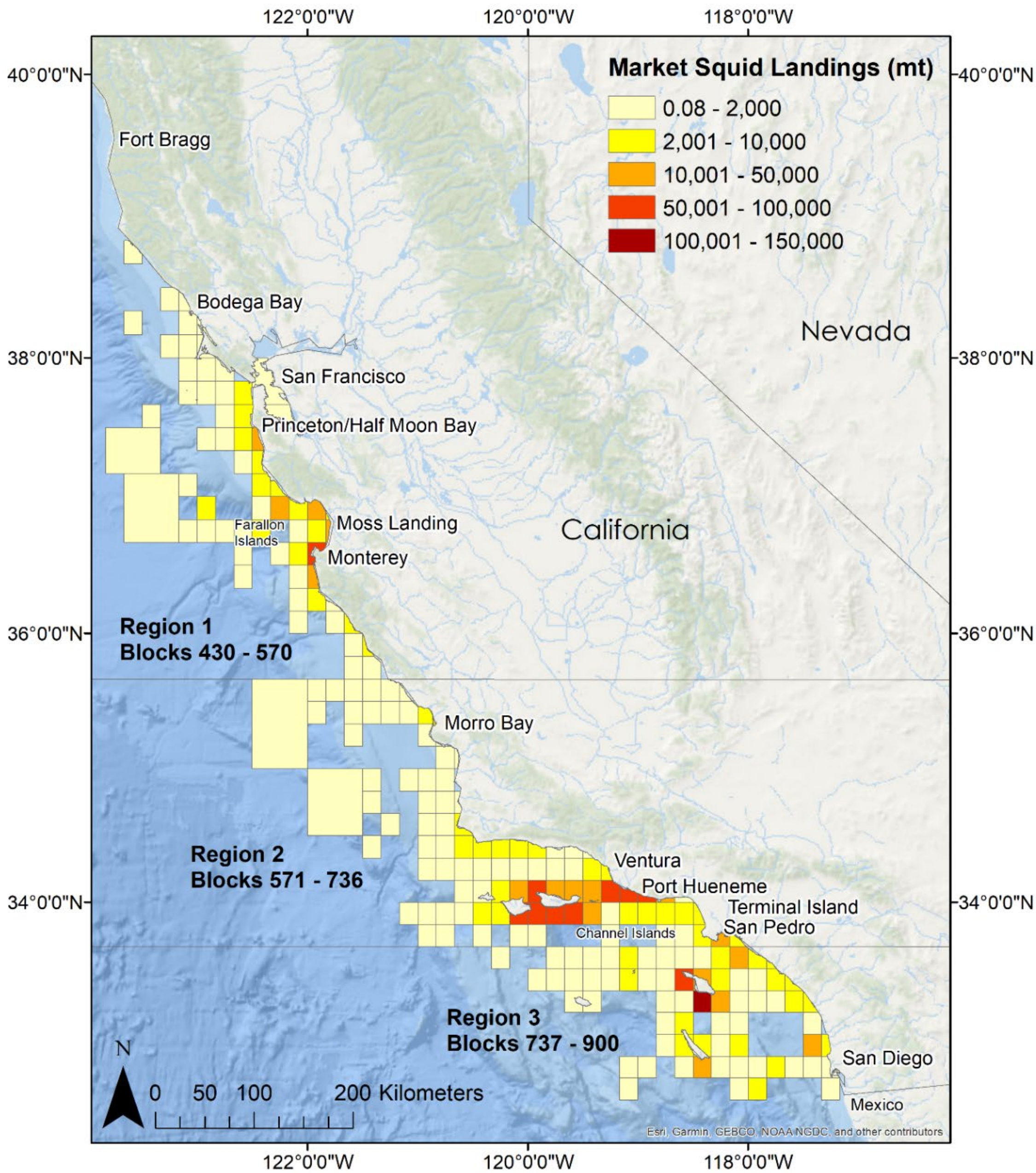

Figure 1. Spatial variability of market squid landings (mt) across California fishing blocks and three major spawning regions from 1999 to 2022.

better reflected the conditions of preserved gonads used in Dorval et al. (2013), in that most of these gonads were measured after more than a month. All models included at least 20 samples in the first three 20 mm bins (Table 2), but only 16 to 18 samples for the fourth targeted bin length (141-160 mm). No female market squid > 160 mm were collected during the time of the experiment, although they have been observed in fishery samples. To account for the predicted interval, i.e. the deviation of fresh gonad weight from the predicted line, we computed gonad weight by adding an error term to the slope and intercept of the 6-week model. For each parameter, the error term was added by resampling from a normal distribution with the mean equal to the parameter estimate and its standard deviation. All model parameters and uncertainties were estimated using codes developed by the authors in R software (R Core 2020).

2.3. *Model Parameterization Summary*

The egg escapement model, as applied to the market squid fishery by Dorval et al. (2013), accounts for recruitment dynamics, growth, maturity schedule, and mortality of market squid coupled with classical per-recruit theory (Gabriel et al., 1989). The model assumes that market squid recruit to the fishery at a minimum of 120 days of age (t_{min}) and a maximum longevity of 360 days (t_{max}). The fishery does not target juvenile squid, because they have no market value. Incidental catches of juveniles may occur, but in general they are less than 5% of the sampled market squid (Dorval et al., 2013). Therefore, in all model scenarios, vulnerability of immature and mature market squid was fixed to 0 and 1, respectively. The model further assumes that a maturity threshold is reached by all females at 100 mm *ML*, after which they stop growing. Growth trajectory of immature market squid follows a natural exponential function with 2 parameters:

$$ML_t^j = 3 \times e^{0.019 \times t}, \tag{1}$$

where *j* indexes individual juvenile market squid at age *t,* and × is the multiplication sign. The growth parameters (α =3 and β = 0.019) were estimated by Maxwell et al. (2005) from market squid age-at-length collected during fishery-independent and fishery-dependent surveys (Butler et al.,1999; CDFW, 2001; Jackson and Domeier, 2003).

In addition, mature females are assumed to have a mean potential fecundity of 3,705 eggs (*SE*=165) (see Dorval et al. 2013) and to deposit eggs at a constant daily rate (*v= 0.45*) (Macewicz et al., 2004). From histological analyses of market squid ovaries, Macewicz et al. (2004) found that a *v*= 0.45 corresponded to female market squid laying eggs cases approximately two days before dying. Based on these assumptions, the model performs simulations based on three daily natural mortality scenarios (*M* = 0.01; *M* = 0.15; *M* = 0.30). Following Dorval et al. (2013), the model based on *M*= 0.15 and *v*= 0.45 was selected as the most plausible scenario (hereafter termed "best case scenario") for estimating fishery parameters in the market squid fishery. In each scenario, *M* was fixed in order to derive fishing mortality (*F*) and estimate the following parameters:

a) The model catch fecundity:

$$\theta_{i,t}^{mod} = \frac{\varepsilon_{i,t} \times (F+M^{a})(1-e^{-(v+F+M^{a})})}{(v+F+M^{a})(1-e^{-(F+M^{a})})}, \tag{2}$$

where, $\varepsilon_{i,t}$ is the residual fecundity of female market squid that matured on day *i* at age *t*; *a* is an index for adult. It is important to note that based on their reproductive biology, it is assumed that market squid females never spawned out all their potential fecundity (see Macewicz et al., 2004). Therefore, at *F*= 0, there is still a positive residual fecundity in squid ovaries, which varies with *v* and M scenarios. This residual fecundity needs to be accounted for when estimating $\theta_{i,t}^{mod}$, preventing catch fecundity to go down to 0 in absence of fishing during simulation modeling [see Figure 4 in Dorval et al., (2013)].

b) The number of spawned eggs-per-recruit at a given fishing mortality:

$$E(F) = \frac{\sum_{t=t_{min}}^{t_{max}} \sum_{i=t}^{t_{max}} E_{i,t}}{N_{t_{min}}^{j}}, \tag{3}$$

where $E_{i,t}$ is the number of eggs actually spawned during day t by a maturity cohort i, $N_{t_{min}}^{j}$ is the number of juvenile j that recruit at the minimum age of 120 days in the fishery.

c) The proportional egg escapement at a fishing mortality greater than zero:

$$S(F) = \frac{E(F>0)}{E(F=0)} \tag{4}$$

Table 2. Sample size of market squid gonads used in each regression model by dorsal mantle length (*ML*) bin.

ML bin (mm)	Model sample size		
	2-week	4-week	6-week
80-100	20	20	21
101-120	32	32	33
121-140	39	38	50
141-160	18	16	17
161-180	0	0	0
Total	109	106	121

2.4. Estimation of Fishery Parameters

2.4.1. Biological Catch Fecundity

As defined in Table 1, the biological catch fecundity is the residual number of oocytes estimated from harvested female market squid. The estimation process includes two variables: a) a mantle condition index (MC_y) derived from mantle punches collected from female market squid; and b) gonad weights (ovary plus oviduct, G_y) measured from formalin-preserved gonads.

Mantle punches were collected from female market squid using a number 11 cork borer (area of 251.65 mm^2) to standardize their area across all samples. Samples from 1999 to 2006 were processed following Macewicz et al. (2004) method, which required mantle punches be dried in a convection oven for 14 days at 56°C. However, McDaniel et al. (2015) developed a new model, which consisted of drying mantle punches for three days at 60°C. This new procedure not only saved time, but also increased the efficiency of computing biological and fishery parameters from the egg escapement model (McDaniel et al., 2015).

In Dorval et al. (2013), gonad weights were measured directly from formalin-preserved gonads, and fresh gonads were not measured before preservation. Starting in July 2010, CDFW began weighing fresh female gonads, with no preservation in formalin. Thus, in this study we used the 6-week regression model to predict formalin-preserved gonad weights (G_y) from fresh gonad weights (G_0) for data collected after July 21, 2010 (see section 3 below). Therefore, the mean catch fecundity (θ^{bio}) in harvested females (from laboratory analysis of gonad samples) was estimated following the equation below:

$$\theta_{r,q}^{bio} = \frac{1}{n}\left(\sum_{u=1}^{n}\left(\frac{1}{5}\sum_{y=1}^{k=5}\left(378.28 \times e^{\left(2.33\times MC_y+0.245\times G_y-0.24\times MC_y\times G_y\right)}\right)\right)\right), \tag{5}$$

where *bio* indicates that catch fecundity was computed from biological characteristics of market squid samples, *k* is the number of females sub-sampled for estimating catch fecundity per sampling unit, and *n* is the number of sampling units per region *r* and quarter *q*. All parameters used in equation 5 were derived by Macewicz et al. (2004) using analysis of ovary histological data and dried mantle weight data. Note that prior to July 21, 2010, G_y was equal to formalin-preserved weight measured in the laboratory, but beginning on this date G_y was equal to the predicted gonad weight (G_w) from the 6-week model.

Further the 95% *CI* interval of θ^{bio} was computed as:

$$\theta_{r,q}^{bio} \pm \tau \times \frac{\sigma}{\sqrt{n}}. \tag{6}$$

where τ is the upper $\alpha/2$ of the Student's *t* distribution with *n*-1 degrees of freedom.

Quarterly mean catch fecundity estimated from harvested market squid was derived from the model catch fecundity to infer $F_{r,q}$ and estimate $S(F_{r,q})$ per each region *r* and quarter *q*. When the model and laboratory catch fecundity did not match exactly, a smooth spline function was used to interpolate fishing mortality rates. Similarly, corresponding confidence intervals for these two parameters were determined based on the 95% *CI* of θ^{bio}.

2.4.2. Spawning Stock

For each region and quarter, mean proportion and mean weight of market squid were estimated for each sex from port sampling data. These statistics were used to compute the number of females in the catch as in the equation below:

$$C_{f,r,q} = \frac{L_{r,q}}{\bar{p}_{f,q} \times \bar{w}_{f,q} + \bar{p}_{m,q} \times \bar{w}_{m,q}} \times \bar{p}_{f,q}, \tag{7}$$

where $L_{r,q}$ is the total landing in region *r* and quarter *q*, *f* indexes female, *m* indexes male, *w* is bodyweight, and *p* is the proportion of females or males in the landings.

Thereafter, the Baranov's catch equation (Quinn & Deriso, 1999), was used to compute the spawning stock abundance of females in number based on the following equation:

$$SSA_{f,r,q} = \frac{(M_{r,q}^{a}+F_{r,q}) \times C_{f,r,q}}{F_{r,q}\times\left(1-e^{\left(M_{r,q}^{a}-F_{r,q}\right)}\right)}. \tag{8}$$

where $M_{r.q}^{a}$ is the natural mortality assumed for adult market squid *a* in region *r* and quarter *q*, and $F_{r,q}$ is the mean daily fishing mortality rate estimated in region *r* and quarter *q*.

Similar equations to 7 and 8 were used to compute quarterly catch and abundance in number of market squid males. Then, total *SSB* was computed by summing the abundance of females and males in weight instead of number. All fishery parameters were estimated based on equations 5 to 8 as in Dorval et al. (2013). For further details on the derivation and the rationale underlying all biological parameters see also Macewicz et al. (2004), Maxwell et al. (2005), and Dorval et al. (2013). All statistics in this paper were estimated using the R software (R Core Team 2000) based on codes developed in previous studies (Dorval et al. 2013; Maxwell et al., 2005).

It is also important to note that the COVID-19 pandemic and subsequent staffing shortages interrupted routine CDFW sampling efforts from 2020 to 2022, leading to small sample sizes in some quarters (see Appendices I and II). Thus, during this timeframe, biological and fishery parameter estimates, and estimated uncertainty, may have been affected by inadequate sampling effort. Unfortunately, potential bias introduced by these events remain unknown as they could not be addressed in this study.

3. **Results**

3.1. Gonad Weight Models

Three new regression models were developed to predict formalin-preserved gonad weight from fresh gonad weight, based on two, four, and six weeks of preservation. In all models, the range of fresh gonad weights varied from 0.485 g to 8.607 g. The 2-week model explained slightly less variability in the data (94.4%) than the 4-week (95.6%) and 6-week models (94.7%) (Figure 2). Across all observations the 4-week model had the lowest predicted interval (1.3 g to 1.4 g) compared to the 2- week (1.5 g to 1.6 g) and 6-week (1.6 g) models. Any one of the 2-week, 4-week or the 6-week model could be used for computing formalin-preserved gonad weights for the egg escapement model, but as stated in *section 2.2* the 6-week model was selected in this study because of the larger sample size (Table 2).

3.2. Catch Variability and Composition

Market squid catches were highly variable temporally and spatially. Across years and regions, the largest landings were from the Channel Islands, Malibu, and Monterey areas (Figure 1). Port landings in all regions were systematically sampled following the same design established in 1999, though the monthly target number of samples for each port region was reduced in 2004. Catches were landed in all years for all regions, but given patterns in market squid distribution and abundance, landings were concentrated in spring and summer in Region 1, and in fall and winter in Regions 2 and 3 (Figure 3). In Region 1, quarterly landings peaked in spring 2002 (17,298 mt) and 2014 (19,688 mt), and in summer 2013 (19,417 mt) and 2014 (30,966 mt). Region 2 recorded the largest quarterly landings, with catches peaking in the fall of 1999 (49,710 mt), 2000 (56,999 mt), 2009 (52,559 mt), 2010 (53,024 mt), and 2011 (48,440 mt). In Region 3, landings peaked in winter 2002 (26,272 mt) and 2006 (33,925 mt), and in the fall of 2005 (26,373 mt) and 2010 (40,467 mt).

The market squid fishery primarily targeted mature individuals during the 1999-2022 period. During this study period, 95.4% of females (out of n= 68,161) were staged as mature based on visual assessment of ovaries. Mature females measured from 75 mm to 185 mm (*ML*), with body weights ranging from 3.7 g to 134.3 g. Immature females varied from 47 mm to 162 mm, and from 4.2 g to 72.3 g in body weight. Males collected from 1999 to 2022 had a minimum length of 53 mm and maximum length of 200 mm, with their body weights ranging from 5.4 g to 143.8 g.

As stated in the methods section, fresh gonads were not weighed from female market squid collected from January 1999 to July 2010. Fresh gonads collected from July 21, 2010, to December 21, 2022, across the three regions measured from 0.012 g to 12.577 g. However, out of 8,031 fresh gonads extracted from mature females during this period, 1.2% (*n*=94) of gonads weighed < 0.485 g, and 1.8% (*n*=145) weighed > than 8.607 g. Thus, only ~ 3% (n= 239) of fresh gonads collected over 48 quarters had values that were outside of the prediction range of gonad weights used in the 6-week model.

During the 1999-2022 period, quarterly mean proportion of females varied from 0.25 to 0.55 in Region 1, 0.24 to 0.61 in Region 2, and 0.27 to 0.62 in Region 3 (Figure 4). Thus, in most quarters, male market squid were predominant. Females were more abundant than males in 10% of quarterly catches landed in Region 1, and in 15% of quarterly landings in Regions 2 and 3. Mean proportion of females was 0.50 in 6%, 3%, and 8% of quarterly catches, respectively in Regions 1, 2, and 3.

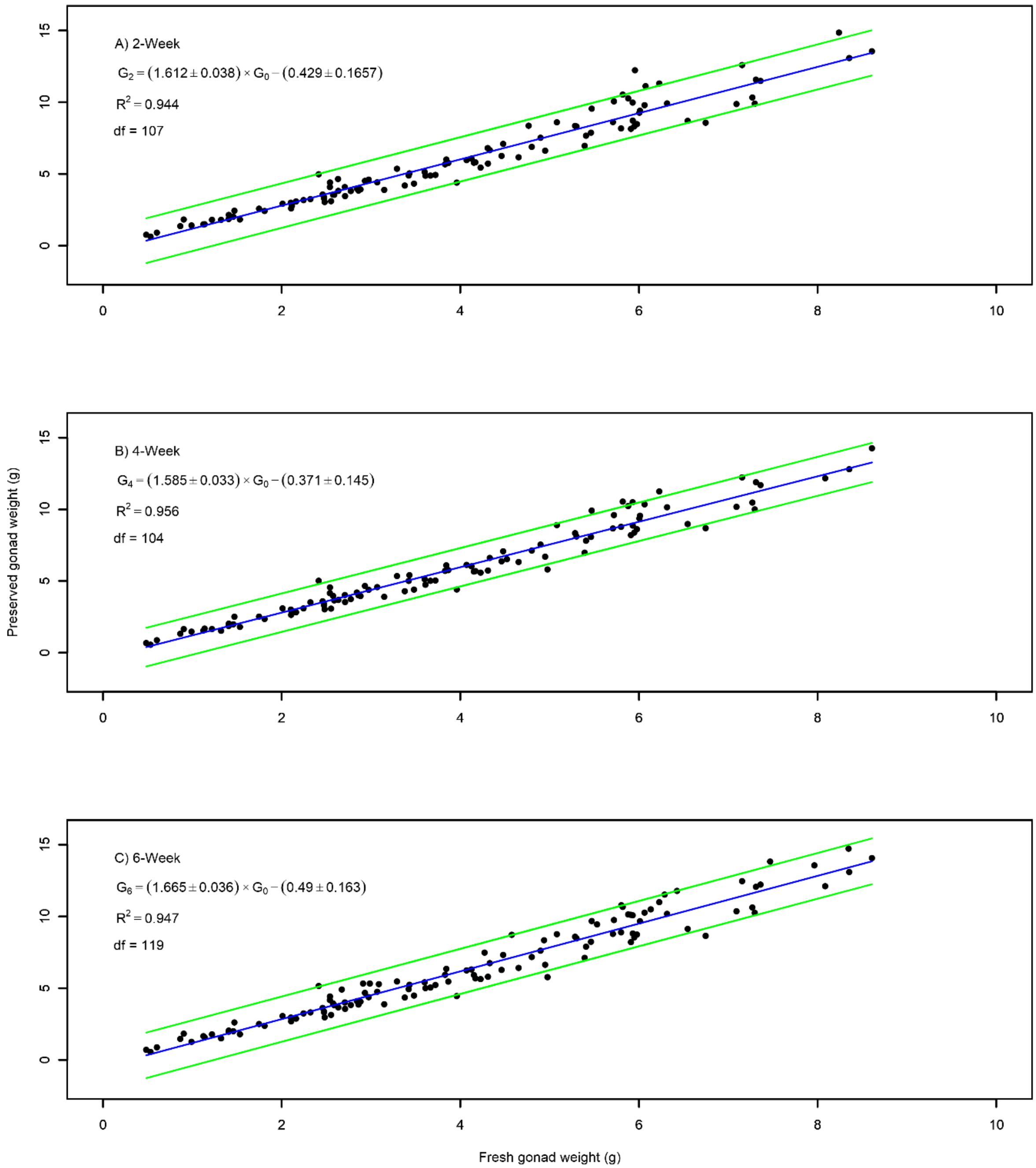

Figure 2. Relationships between female market squid fresh gonad weight (g) and formalin-preserved gonad weight (g) based on three linear models: 1) 2-week model, including gonads preserved in formalin for 2 weeks (Panel A); 4-week model, including gonads preserved in formalin for 4 weeks (Panel B); and 6-week model, gonads preserved in formalin for 6 weeks (Panel C). In each regression, the blue line indicates the predicted values, whereas the green lines show the predicted interval based on the observed samples.

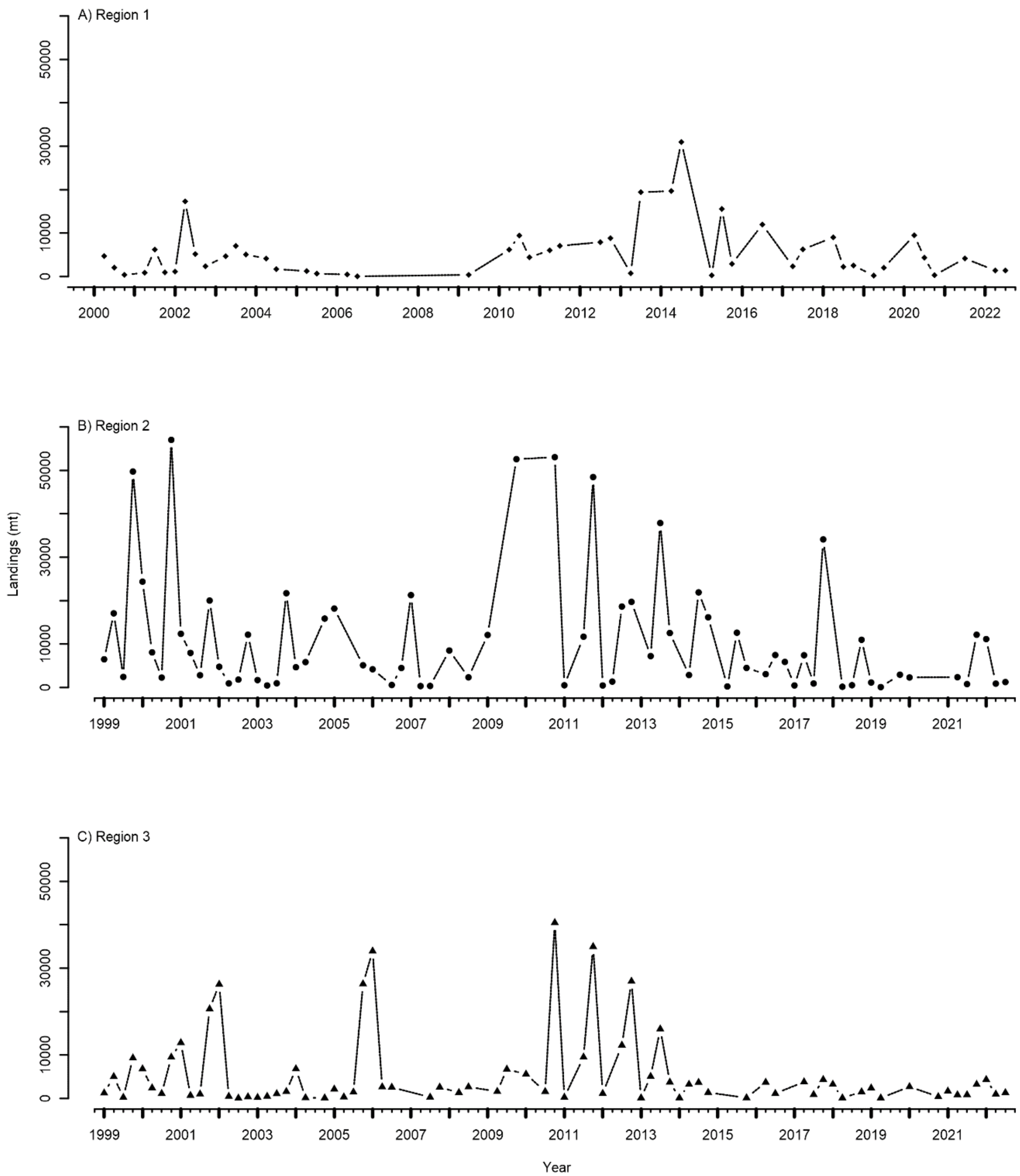

Figure 3. Commercial port landings (mt) of market squid in California by region and quarter from 1999 to 2022.

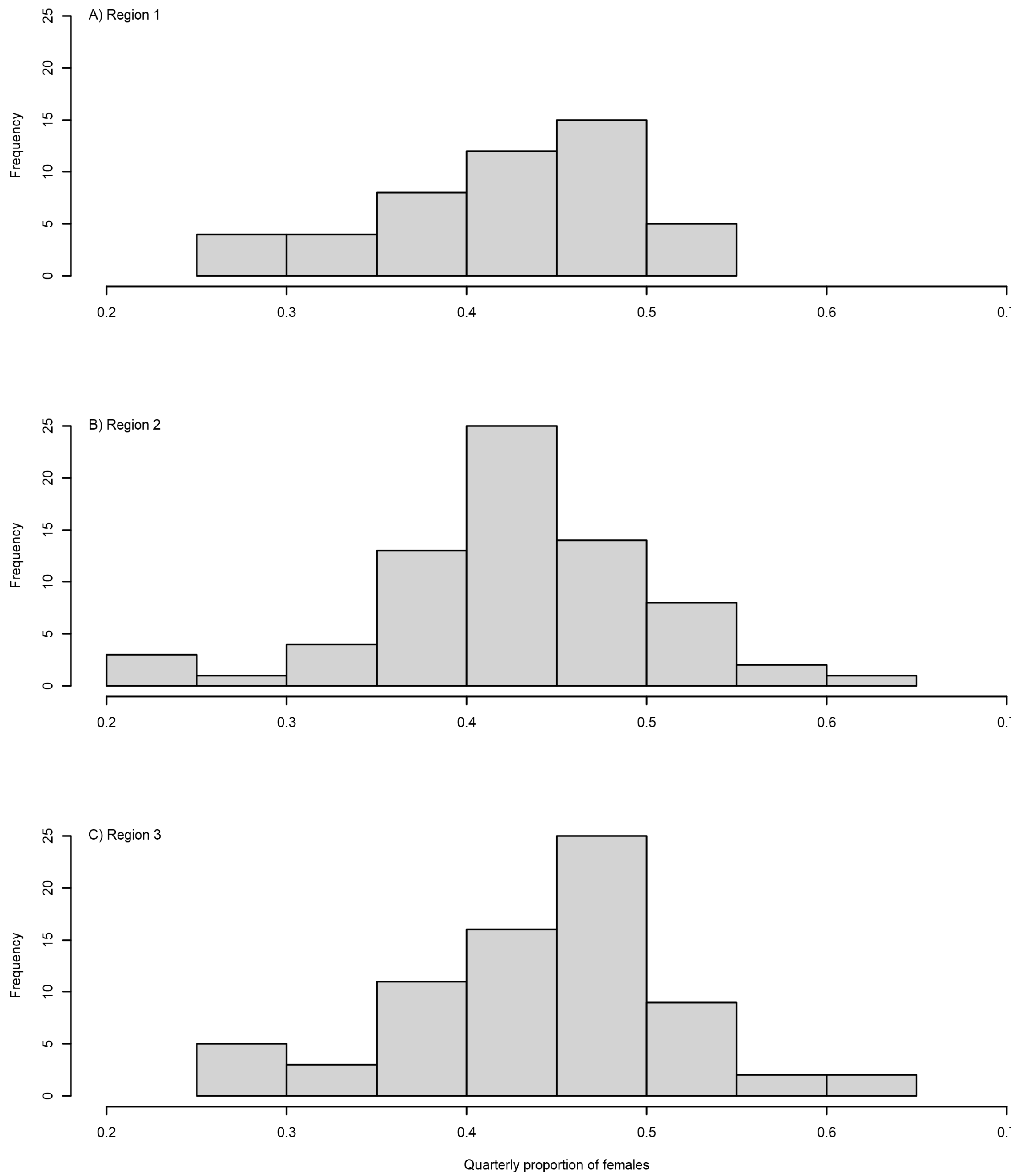

Figure 4. Frequency of mean proportion of females estimated from market squid samples collected in California by region and quarter from 1999 to 2022.

3.3. Biological Catch Fecundity

On average, mature females collected in each quarter and region had a chance to spawn prior to harvest, showing partially emptied ovaries and clear oocytes in their oviduct. Quarterly mean catch fecundity measured from port sampling ranged from 1935 eggs (*CV*= 8.4%) to 5,702 (*CV*= 21.1%) in Region 1, from 1,271 eggs (CV = 26%) to 3,868 eggs (*CV*= 33.4%) in Region 2, and from 1,139 eggs (*CV*= 19.3%) to 4,918 eggs (*CV*=21%) in Region 3. Given the *CV* values, all quarterly mean estimates were within the range of expectation based on the assumed potential fecundity and uncertainty used to parameterize the egg escapement model.

3.4. Daily Fishing Mortality

In all regions, quarterly mean of daily fishing mortality derived from the egg escapement model was highly variable throughout the 1999-2022 period. Compared to Regions 2 and 3, Region 1 experienced the highest fishing rates on average (Figure 5). Mean *F* per quarter ranged from 0.34 to 6 in Region 1, from 0.09 to 6 in Region 2, and from 0.05 to 6 in Region 3. Further, mean *F* in Region 1, 2, and 3 was lower than 1.0 in 13.7%, 51.4% and 52.1% of the sampled quarters, respectively.

3.5. Proportional Egg Escapement

As spawning output is inversely related to fishing mortality, *S(F)* in Region 1 was more frequently below 0.30 than in the other two regions (Figure 6). In Region 1, mean quarterly *S(F)* ranged from 0.11 to 0.64, but was below 0.30 in 70.6% of the sampled quarters. In Region 2, mean quarterly *S(F*) varied from 0.11 to 0.88, but was below 0.30 in 27.1% of the sampled quarters. In Region 3, mean quarterly *S(F)* ranged from 0.11 to 0.92, but was below 0.30 in 38% of the quarters. Notably, in the last two years (2021 and 2022), mean *S(F)* (including their 95% *CI*) was below 0.30 in all quarters sampled in Regions 1 and in the last six quarters sampled in Region 3 (Figure 6). In contrast, over these two recent years mean *S(F)* were consistently lower than 0.30 in all quarters sampled in Region 2, although their lower 95% *CI* was below 0.30 in three out of the six sampled quarters. More specific details on *S(F)* estimates and their confidence interval per quarter are provided in Appendix I.

3.6. Abundance and Spawning Stock Biomass

In all regions, model estimates of female market squid abundance fluctuated during the 1999-2022 period, but over this time series, quarterly abundance was, on average, largest in Region 2 and 3 (Figure 7). In Region 1, mean quarterly abundance of females ranged from 1.05 to 308.64 million, with two moderate abundance peaks (> 200 million) occurring in fall 2012 and in summer 2014. In Region 2, mean quarterly female abundance ranged from 2.29 to 1,599.97 million, with four major peaks (> 1 billion) of abundance occurring in winter 2005 and 2007, and in fall 2000 and 2012. In Region 3, mean quarterly abundance of females ranged from 1.40 to 1,515.83 million, with two major peaks (> 1 billion) of abundance occurring in fall 2010 and 2012.

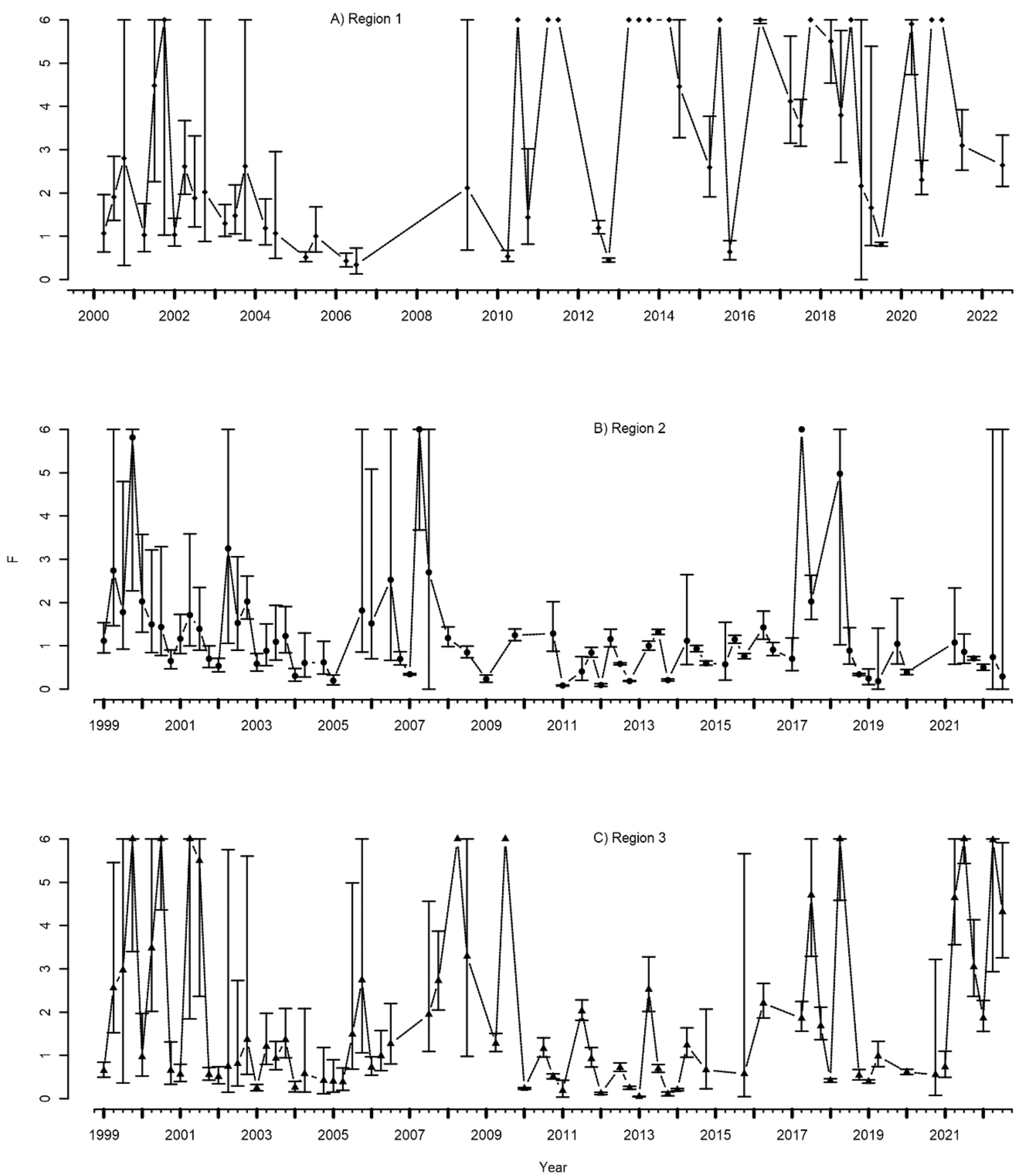

Figure 5. Daily fishing mortality rates (*F*) per region and quarter (Panels A-C) derived from the egg escapement model based on the best-case scenario (M^a =0.15 and v=0.45). Error bars show the upper and lower 95% *CI* of quarterly mean estimates.

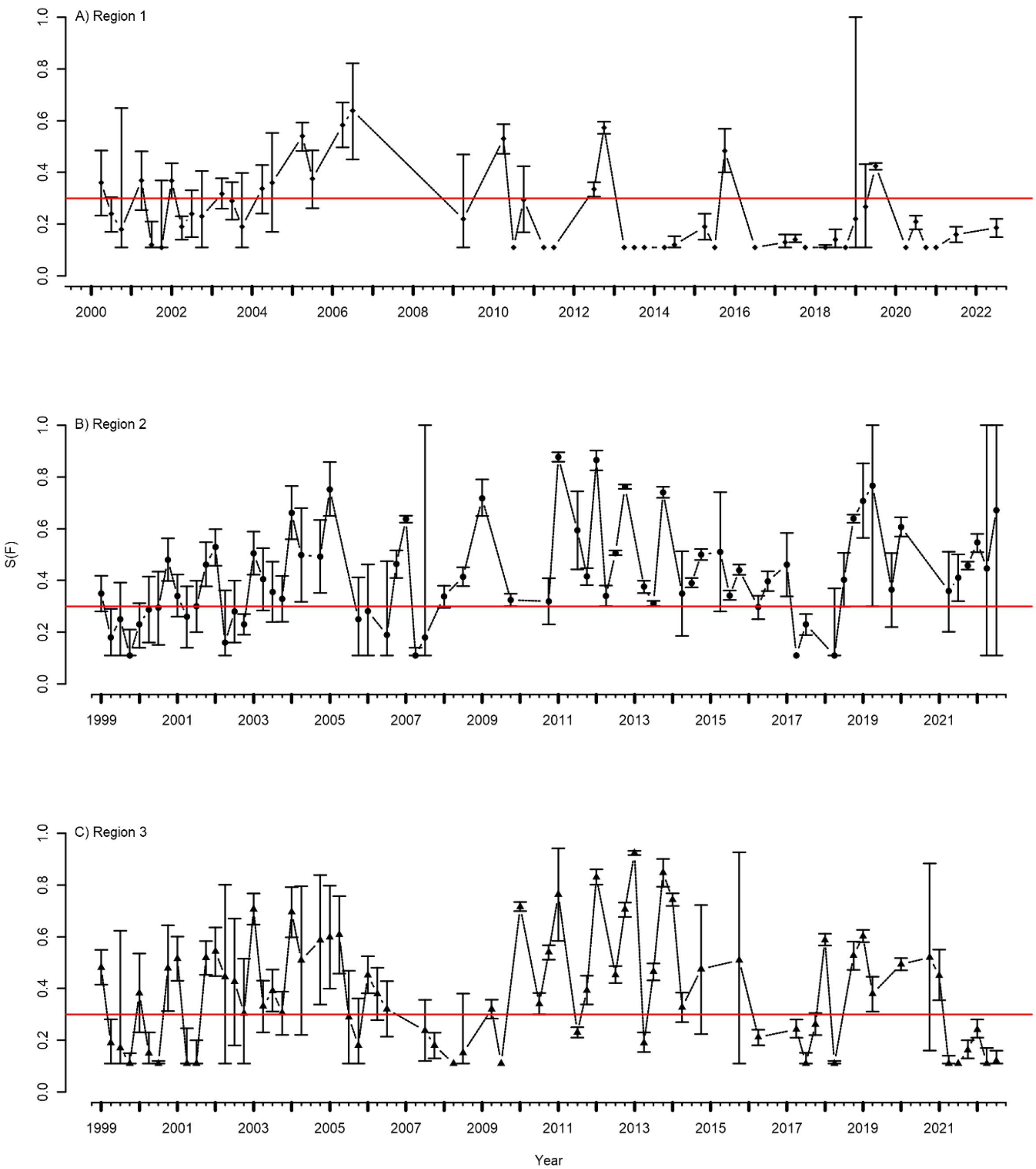

Figure 6. Proportional egg escapement estimated by region and quarter (Panel A-C) based on the best-case scenario (M^a = 0.15 and v= 0.45). Error bars show the upper and lower 95% *CI* of quarterly mean estimates. The red line indicates a proportional egg escapement [*S(F)]* of 0.30.

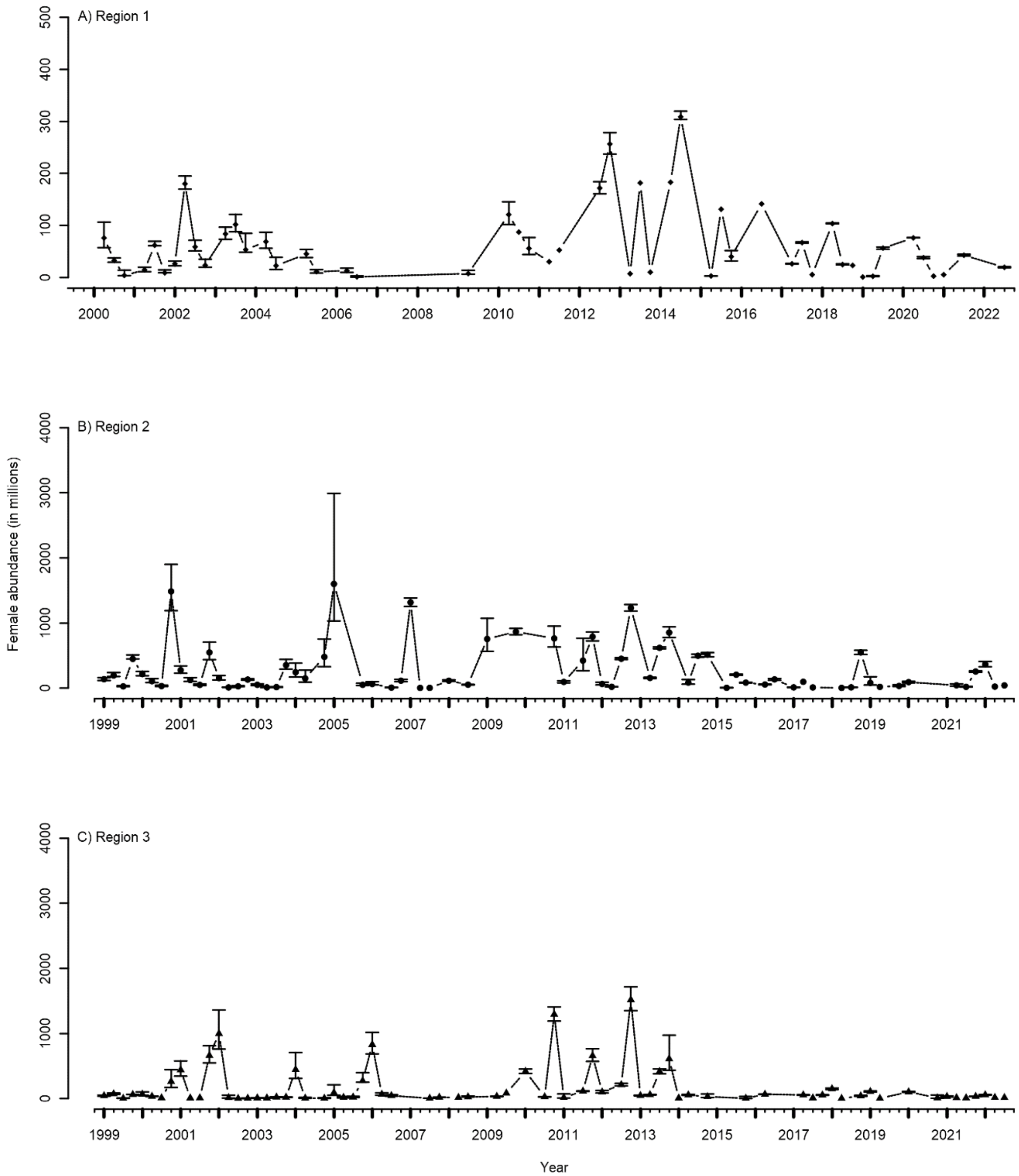

Figure 7. Mean number of mature spawning females estimated by region and quarter (Panel A-C) based on the best-case scenario ($M^a = 0.15$ and $v = 0.45$). Error bars show the upper and lower 95% *CI* of quarterly mean estimates.

Total *SSB*, computed based on the "best case scenario" (M= 0.15 and v= 0.45) and catch data, followed similar trends to female abundance across quarters in all regions (Appendix II). In Region 1, the two moderate peaks of *SSB* were estimated to be 26,122 mt in the fall of 2012 and 32,330 mt in summer 2014. In Region 2, the major peaks of *SSB* were estimated to be 90,652 mt in fall 2011, 108,656 mt in winter 2005, 123,901 mt in fall 2012, and 127,275 in fall 2000. In Region 3, the two major peaks of *SSB* were estimated to be 107,789 mt in fall 2010 and 130,630 mt in fall 2012.

As a sensitivity analysis, *SSB* was also computed based on two other scenarios [*i.e, (*M= 0.01 and v= 0.45*) and (*M= 0.30 and v = 0.45)] provided in Appendix II for comparison to the quarterly estimates from the "best case scenario" (M= 0.15 and v= 0.45). As expected, the scenario with the lowest natural mortality (M= *0.01*) produced the lowest *SSB* estimates across quarters for each region, whereas the scenario with the highest M (0.30) yielded higher *SSB*.

4. Discussion

In this study we presented an update of biological and fishery parameters of the egg escapement model that are used to monitor the California market squid fishery. We extended the 1999 to 2006 time series of *F*, *S(F)*, and *SSB* through to 2022. New and more efficient methods were applied to shorten the laboratory processing time for mantle punch and gonad samples collected from port sampling. As a result, the estimation of all fishery parameters *S(F)* can be completed in a more reasonable amount of time after the completion of fishing in a given quarter, thus shortening the process of monitoring fishing pressure and reproductive outputs in each of the three fishing regions.

4.1. Application of Gonad Weight Models

In this study, three new models were developed to predict formalin-preserved gonad weight from fresh gonad weight. All three models were an improvement compared to the McDaniel et al. (2015) 2-week models, as they included a broader range of gonad weights and more representative samples across all bin sizes (*i.e.*, based on *ML*). For example, fresh gonad weights in McDaniel et al. (2015) ranged from 1.500 g to 8.000 g, whereas in the three new models, fresh gonad weights varied from 0.485 g to 8.607 g. However, as in McDaniel (2015), no samples were found in the 161-180 mm bin in port samples collected during the gonad experiment in 2014 and 2015. This was likely due to continued reduction of the size of market squid that recruited into the fishery (Protasio et al., 2014). Despite that, a small fraction of fresh gonad weights (~3%) measured from landings were outside of the prediction range of the 6-week model. These weights had little effect on the egg escapement model results, not only because these gonads were collected over multiple quarters, but also because estimates of fishery parameters were based on mean values per quarter. Although the smallest (< 0.486 g) and largest fresh gonads (> 8.607 g) were rare in the catches, effort should be made to collect samples from these weight categories to improve the gonad weight models.

Any one of the three gonad models could be used for predicting formalin weight from fresh gonad weight, as all explained at least 94% of the variability of the data. However, we selected the 6-week model because its sample size was larger and better reflected the timing of measurement of formalin-preserved gonads in Dorval et al. (2013). This model allowed new fresh gonad weights to be combined with historical data (i.e., preserved gonad weights) and to consistently update the time series of egg escapement parameters up to 2022. As stated in McDaniel et al. (2015), using fresh gonads is more efficient since there was no longer a need to purchase, transport and dispose of formalin, a hazardous chemical preservative, nor need to wait before weighing the gonads. In converting fresh gonad weight to formalin-preserved weight, the 6-week model had a predicted interval of 1.6 g, which could impact the result of egg escapement. To minimize this uncertainty, a randomly selected error term was added to all predicted values based on the standard error of the slope and intercept of this model (see method section). Likewise, in this study we used a robust model to predict gonad weight and to derive fishery parameters to monitor the market squid fishery.

4.2. Fishery Parameters

As expected, *S(F)* was inversely related to *F*, with quarters exhibiting lower fishing pressure yielding higher reproductive outputs in the three fishing regions. In the late 1980s, the market squid fishery was developing, passing largely from an artisanal fishery to a market-driven fishery in response to higher international demands for cephalopod products (Arkhipkin et al., 2015; Doubleday et al., 2016; Rodhouse, 2001). During this time, there was a shift from mainly brail fishing to larger purse seine vessels and participation in the fishery continued to grow leading up to the early development of the MSFMP in the late 1990s (CDFW, 2021). Over the 23 years of monitoring the fishery, *S(F)* was frequently low in Region 1, highly variable in Region 3, but showed a clear increasing trend in Region 2. Environmental drivers such as temperature, upwelling, heat waves (van Noord and Dorval, 2017; Suca et al., 2022; Chasco et al., 2022) that can impact the biological assumptions underlying the egg escapement model have not been fully studied; thus further investigation is required to better understand factors that can explain potential differences across regions in estimated fishery and biological parameters. Particularly, future studies should consider the latitudinal distance and variations in sea surface temperature, upwelling, chlorophyll-a and zooplankton between the fishing sites within- and among-regions.

Interannual and seasonal dynamics of the market squid population and the fishery are different among the three fishing regions, and thus results are variable when considering potential impacts of the MSFMP on egg escapement in each region. For example, market squid tend to shift northward during El Niños and marine heat waves (Chasco et al., 2022; Suca et al. 2022), thus in these years the fishery tends to operate more in the northern region (Region 1) than in the southernmost region (Region 3). Under these dynamics and as suggested by the results of this study, Region 1 tends to experience higher levels of fishing mortality rates regardless of abundance. During El Niño, when Regions 2 and 3 undergo periods of low abundance, fishing pressure may be more impactful to market squid reproductive output in Region 1 where most fishing capacity and efforts are concentrated. Further, in La Niña years, the market squid spawning stock in Regions 2 and 3 was in general one order of magnitude larger than in Region 1. Because the fishery is market driven, fishing will slow in periods of low demand or when freezing capacity is limited. Therefore, the impact of fishing pressure on egg escapement is lower in periods and regions of high biomass, such as in Regions 2 and 3 during the 2011-2014 period (Appendix II).

For the sustainable management of the market squid fishery, CDFW applies the 0.30 proportional egg escapement proxy by fishing season (April 1 to March 31) statewide by computing a weighted-mean across Regions 1, 2, and 3. When monitoring fishery dynamics in the long term, it is important to consider the temporal variability in market squid growth, maturation and recruitment, and the distribution of fishing effort regionally to improve our understanding of fishing pressure under different atmospheric and oceanographic conditions.

Spawning stock biomass (*SSB*) estimated from the egg escapement model often fluctuated by one or two orders of magnitude between regions and seasons. Estimates were likely influenced, in part, by variations in *SST*, chlorophyll-a, zooplankton as controlled by upwelling conditions during events such as ENSO and marine heatwaves (Chasco et al., 2022; Suca et al., 2022; van Noord & Dorval, 2017). Densities of paralarvae typically increase with cool *SST*, moderate zooplankton concentration, and low chlorophyll-*a* concentrations (van Noord & Dorval, 2017) and are significantly correlated with the ENSO index (Koslow and Allen 2011). Particularly, Perretti and Sederat (2016) found that EL Niño conditions were associated with lower survival of late-stage paralarvae. Ralston et al. (2018) also found that the abundance of pre-recruit market squid and its primary prey, krill, was correlated with *SSB*. Across the whole fishery, market squid stock productivity was high during the cold (La Niña) seasons, from summer 2010 to spring 2012 (cooler La Niña conditions), and from spring 2013 to summer 2014 (transition to warmer El Niño conditions, https://www.ncei.noaa.gov/access/monitoring/ enso/soi), which likely led to record peak estimates of *SSB* in the fall of 2012 in Region 2 (123,901 mt) and Region 3 (130,6030 mt) based on the best case scenario. Since the 2014-2016 El Niño event and associated marine heatwaves (Chasco et al., 2022; Suca et al., 2022; Van Noord & Dorval, 2017), *SSB* has remained one or two orders of magnitude lower than the peak biomass observed in Regions 2 and 3 (i.e., around the northern and southern Channel Islands), even with cooler La Niña conditions from 2020 to 2023. Levels of abundance have fluctuated in Regions 1 (Monterey and San Francisco Bay Areas) with no strong temporal trends, although the most recent *SSB* peaks observed in this region were estimated during the transition period to EL Niño in summer 2013 (19,945 mt) and spring of 2014 (20,223 mt). These regional patterns in *SSB* were also consistent with recent findings that showed that market squid recruitment coupled with *SST* and upwelling dynamics likely contributed to regional abundance of juvenile market squid (Suca et al., 2022), and that large shifts in the spatial distribution of the market squid population were associated with marine heatwaves.

Although much research effort has been done to improve the efficiency of sampling, data processing, and parameterization of the egg escapement model, various aspects of this model could benefit from more improvement. As the market squid abundance contracts southward into California and Baja California during La Niñas and expands northward into the U.S. Pacific northwest and eastern Alaska during El Niño and marine heat waves, the collection of biological data across all these spatial and temporal scales could contribute to improve estimation of potential fecundity and the reproductive outputs of this species in low and high abundance periods, and in exploited and non-exploited fishing areas. Particularly, the occurrence of "pre-ovulatory females" is rare in many fishery-independent surveys conducted by National Oceanic and Atmospheric Administration (NOAA) research vessels (Macewicz, 2004; Dorval et al. 2013). As a result, potential fecundity is derived using a limited number of samples (n= 34) collected from a relatively narrow temporal and spatial scale. Additionally, since the publication of Dorval et al. (2013), which included results from past growth studies, to our knowledge no research has been published on the growth dynamics of market squid collected in California and other states. Likewise, increasing and expanding the sample size of pre-ovulatory market squid coast-wide and ageing backlogs of statoliths collected by CDFW could further help improve the parameterization of the egg escapement model while determining the degree to which environmental conditions are driving changes in growth, maturation, and reproductive potential of this species. Improved understanding of the life history of market squid across this larger spatial scale could be also helpful in determining factors that control the resilience of its population to interannual and decadal changes in environmental conditions along the U.S. Pacific coast.

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7. Appendices

Appendix I- Mean proportional egg escapement [*S(F)*] estimated in the market squid fishery from 1999 to 2022 by region and quarter, based on best case scenario of daily natural mortality ($M = 0.15$), and daily egg laying rate ($v = 0.45$.). The letter *n* indicates the number of sampling units. Empty cell indicates that no port samples were recorded in a given quarter, thus *S(F)* could not be computed, whereas. *L95% CI* and *U95% CI* are lower and upper 95% confidence interval of *S(F),* respectively.

Year	**Quarter**	**Region 1 *S(F)***				**Region 2 *S(F)***				**Region 3 *S(F)***			
		n	*S(F)*	*L95% CI*	*U95% CI*	*n*	*S(F)*	*L95% CI*	*U95% CI*	*n*	*S(F)*	*L95% CI*	*U95% CI*
1999	1					32	0.35	0.28	0.42	48	0.48	0.41	0.55
1999	2					26	0.18	0.11	0.29	39	0.19	0.11	0.28
1999	3					9	0.25	0.11	0.39	3	0.17	0.11	0.62
1999	4					29	0.11	0.11	0.21	11	0.11	0.11	0.15
2000	1					30	0.23	0.14	0.31	23	0.38	0.23	0.53
2000	2	18	0.36	0.23	0.48	30	0.29	0.16	0.41	18	0.15	0.11	0.23
2000	3	14	0.24	0.17	0.30	15	0.29	0.15	0.43	10	0.11	0.11	0.12
2000	4	2	0.18	0.11	0.65	57	0.48	0.40	0.56	13	0.48	0.31	0.64
2001	1					32	0.34	0.26	0.42	30	0.52	0.43	0.60
2001	2	14	0.37	0.25	0.48	32	0.26	0.14	0.38	12	0.11	0.11	0.25
2001	3	36	0.12	0.11	0.21	26	0.30	0.20	0.40	18	0.11	0.11	0.20
2001	4	12	0.11	0.11	0.37	41	0.46	0.38	0.55	30	0.52	0.45	0.58
2002	1	19	0.37	0.30	0.44	35	0.53	0.46	0.60	31	0.54	0.45	0.64
2002	2	79	0.19	0.14	0.23	16	0.16	0.11	0.36	5	0.44	0.11	0.80
2002	3	41	0.24	0.15	0.33	21	0.28	0.16	0.40	6	0.43	0.18	0.67
2002	4	12	0.23	0.11	0.41	70	0.23	0.19	0.27	13	0.30	0.11	0.51
2003	1					33	0.50	0.42	0.59	18	0.71	0.65	0.77
2003	2	26	0.32	0.26	0.38	12	0.41	0.28	0.52	22	0.33	0.23	0.43
2003	3	29	0.29	0.22	0.36	13	0.36	0.24	0.47	26	0.39	0.31	0.47
2003	4	13	0.19	0.11	0.40	35	0.33	0.24	0.42	35	0.31	0.22	0.39
2004	1					19	0.66	0.56	0.77	28	0.70	0.60	0.79
2004	2	12	0.34	0.24	0.43	9	0.50	0.32	0.68	6	0.51	0.22	0.80
2004	3	12	0.36	0.17	0.55								
2004	4					12	0.49	0.35	0.63	5	0.59	0.34	0.84
2005	1					7	0.75	0.65	0.86	12	0.60	0.40	0.80
2005	2	12	0.54	0.48	0.59					9	0.61	0.46	0.76
2005	3	12	0.38	0.26	0.48	12				12	0.29	0.11	0.47
2005	4						0.25	0.11	0.41	12	0.18	0.11	0.36

Year	Quarter	Region 1 *S(F)*				Region 2 *S(F)*				Region 3 *S(F)*			
2006	1					7	0.28	0.11	0.46	42	0.45	0.38	0.52
2006	2	21	0.58	0.50	0.67	3				17	0.38	0.28	0.48
2006	3	4	0.64	0.45	0.82	14	0.19	0.11	0.47	19	0.32	0.21	0.43
2006	4					14	0.46	0.41	0.52				
2007	1					33	0.64	0.62	0.65				
2007	2					6	0.11	0.11	0.14				
2007	3					2	0.18	0.11	1.00	5	0.24	0.12	0.36
2007	4									16	0.18	0.13	0.23
2008	1					13	0.34	0.29	0.38				
2008	2									3	0.11	0.11	0.11
2008	3					5	0.41	0.38	0.45	6	0.15	0.11	0.38
2008	4												
2009	1					4	0.72	0.65	0.79				
2009	2	3	0.22	0.11	0.47					12	0.32	0.28	0.36
2009	3									26	0.11	0.11	0.11
2009	4					22	0.32	0.30	0.35				
2010	1									11	0.72	0.70	0.73
2010	2	10	0.53	0.47	0.59								
2010	3	28	0.11	0.11	0.11					17	0.34	0.30	0.38
2010	4	5	0.29	0.17	0.42	7	0.32	0.23	0.41	19	0.54	0.51	0.57
2011	1					14	0.88	0.86	0.90	5	0.76	0.58	0.94
2011	2	14	0.11	0.11	0.11								
2011	3	29	0.11	0.11	0.11	5	0.59	0.44	0.74	28	0.23	0.21	0.25
2011	4					17	0.42	0.38	0.45	13	0.39	0.34	0.45
2012	1					12	0.87	0.83	0.90	7	0.83	0.80	0.86
2012	2					15	0.34	0.30	0.38				
2012	3	19	0.34	0.31	0.36	47	0.51	0.50	0.52	21	0.45	0.42	0.49
2012	4	17	0.57	0.55	0.60	39	0.76	0.75	0.77	13	0.71	0.68	0.73
2013	1									20	0.92	0.92	0.93
2013	2	9	0.11	0.11	0.11	23	0.38	0.35	0.40	14	0.19	0.15	0.23
2013	3	28	0.11	0.11	0.11	50	0.31	0.30	0.32	17	0.47	0.43	0.50
2013	4	4	0.11	0.11	0.11	22	0.74	0.72	0.76	9	0.85	0.79	0.90
2014	1									12	0.74	0.72	0.77
2014	2	14	0.11	0.11	0.11	3	0.35	0.19	0.51	9	0.33	0.27	0.38
2014	3	22	0.12	0.11	0.15	21	0.39	0.37	0.41				
2014	4					23	0.50	0.48	0.52	2	0.48	0.22	0.72
2015	1												

Year	Quarter	Region 1 *S(F)*				Region 2 *S(F)*				Region 3 *S(F)*			
2015	2	5	0.19	0.14	0.24	2	0.51	0.28	0.74				
2015	3	24	0.11	0.11	0.11	32	0.34	0.32	0.36				
2015	4	7	0.48	0.40	0.57	25	0.44	0.42	0.46	2	0.51	0.11	0.93
2016	1												
2016	2					9	0.30	0.25	0.34	11	0.21	0.18	0.24
2016	3	14	0.11	0.11	0.11	12	0.40	0.36	0.44				
2016	4												
2017	1					6	0.46	0.34	0.58				
2017	2	14	0.13	0.11	0.16	15	0.11	0.11	0.11	16	0.24	0.21	0.28
2017	3	34	0.14	0.13	0.16	10	0.23	0.19	0.27	11	0.11	0.11	0.15
2017	4	3	0.11	0.11	0.11					14	0.26	0.22	0.31
2018	1									17	0.59	0.57	0.61
2018	2	28	0.11	0.11	0.12	3	0.11	0.11	0.37	6	0.11	0.11	0.12
2018	3	13	0.14	0.11	0.18	6	0.40	0.30	0.51				
2018	4	13	0.11	0.11	0.11	30	0.64	0.62	0.65	11	0.53	0.47	0.58
2019	1	2	0.22	0.11	1.00	6	0.71	0.56	0.85	12	0.60	0.58	0.63
2019	2	4	0.27	0.11	0.43	2	0.77	0.30	1.00	7	0.38	0.31	0.45
2019	3	29	0.42	0.41	0.44								
2019	4					5	0.36	0.22	0.51				
2020	1					6	0.61	0.57	0.64	19	0.49	0.47	0.52
2020	2	26	0.11	0.11	0.11								
2020	3	22	0.21	0.18	0.23								
2020	4	7	0.11	0.11	0.11					3	0.52	0.16	0.88
2021	1	2	0.11	0.11	0.11					7	0.45	0.35	0.55
2021	2					5	0.36	0.20	0.51	15	0.11	0.11	0.14
2021	3	22	0.16	0.13	0.19	4	0.41	0.32	0.50	4	0.11	0.11	0.11
2021	4					25	0.46	0.44	0.47	12	0.16	0.13	0.20
2022	1					14	0.55	0.51	0.58	20	0.24	0.21	0.28
2022	2					2	0.45	0.11	1.00	6	0.11	0.11	0.17
2022	3	19	0.19	0.15	0.22	2	0.67	0.11	1.00	10	0.12	0.11	0.16

Appendix II. Market squid spawning stock biomass (*SSB*) in metric tons estimated by region and quarter based on three scenarios of daily natural mortality, *M* (0.01, 0.15, 0.30), and a constant daily egg laying rate, $v = 0.45$. The letter *n* indicates the number of sampling units. Empty cells indicate that no landings data were recorded in a given quarter, thus *SSB* could not be computed, whereas * indicates that the denominator of equation 8 was zero, thus value of abundance in number or in biomass was undetermined.

Year	**Quarter**	**Region 1 *SSB***				**Region 2 *SSB***				**Region 3 *SSB***			
		n	0.01	0.15	0.30	*n*	0.01	0.15	0.30	*n*	0.01	0.15	0.30
1999	1					32	9118	10260	10198	48	2305	2803	2605
1999	2					26	18142	19069	19671	39	5408	5704	5882
1999	3					9	2869	3095	3165	3	263	276	285
1999	4					29	49930	51124	52345	11	9351	9566	9796
2000	1					30	27614	29523	30317	23	10215	11695	11463
2000	2	18	6747	7631	7554	30	10077	11019	11180	18	2493	2593	2674
2000	3	14	2366	2539	2603	15	2903	3187	3225	10	1135	1161	1189
2000	4	2	419	440	454	57	104744	127275	118392	13	17394	21114	19659
2001	1					32	17033	19081	19031	30	25503	31831	28884
2001	2	14	1274	1447	1428	32	9477	10252	10469	12	685	701	717
2001	3	36	6277	6473	6654	26	3621	3986	4026	18	1022	1048	1074
2001	4	12	960	982	1005	41	35308	42345	39861	30	41254	51640	46732
2002	1	19	1652	1876	1851	35	9756	12302	11056	31	55341	70594	62760
2002	2	79	18530	19523	20134	16	987	1030	1062	5	812	964	915
2002	3	41	5993	6438	6597	21	2252	2458	2497	6	115	135	129
2002	4	12	2678	2864	2941	70	13785	14738	15135	13	475	523	528
2003	1					33	3340	4137	3781	18	683	1067	780
2003	2	26	6157	6821	6859	12	744	862	836	22	651	727	727
2003	3	29	8820	9656	9789	13	1380	1556	1544	26	1654	1904	1858
2003	4	13	5425	5715	5893	35	29228	32561	32612	35	2069	2281	2302
2004	1					19	12997	18905	14809	28	20656	31635	23561
2004	2	12	5652	6319	6312	9	11185	13775	12656	6	323	401	366
2004	3	12	2445	2766	2738								
2004	4					12	29938	36702	33863	5	283	377	322
2005	1					7	63651	108656	72716	12	5158	6952	5864
2005	2	12	2632	3349	2985					9	823	1120	936
2005	3	12	988	1126	1108	12				12	1821	1992	2021
2005	4						5998	6460	6612	12	28020	29451	30381
2006	1					7	5206	5686	5773	42	58880	70261	66439
2006	2	21	1090	1446	1239	3				17	3941	4501	4421
2006	3	4	116	163	132	14	621	656	676	19	3419	3797	3812

Year	**Quarter**	**Region 1 *SSB***				**Region 2 *SSB***				**Region 3 *SSB***			
2006	4					14	7957	9557	8985				
2007	1					33	55695	78360	138942				
2007	2					6	337	345	353				
2007	3					2	381	401	425	5	330	354	384
2007	4									16	2762	2903	3072
2008	1					13	11657	13038	14935				
2008	2									3	1351	1382	1415
2008	3					5	3752	4371	5310	6	2756	2873	3010
2008	4												
2009	1					4	38887	62093	172169				
2009	2	3	449	479	516					12	2133	2367	2682
2009	3									26	6754	6909	7075
2009	4					22	70367	78276	88993				
2010	1									11	17896	28469	77562
2010	2	10	12666	15985	22224								
2010	3	28	9478	9696	9929					17	2195	2460	2827
2010	4	5	5594	6138	6853	7	70082	77716	87986	19	84704	107789	152244
2011	1					14	2581	6829	*	5	941	1648	8477
2011	2	14	6058	6197	6346								
2011	3	29	7095	7258	7433	5	27810	37329	58946	28	10791	11536	12458
2011	4					17	77739	90652	110280	13	53605	61731	73701
2012	1					12	2267	5623	*	7	4996	10697	7
2012	2					15	1878	2105	2419				
2012	3	19	10777	12039	13767	47	36324	45029	60583	21	21301	25428	32091
2012	4	17	19916	26123	39218	39	70929	123901	620043	13	83809	130630	325406
2013	1									20	735	2808	*
2013	2	9	757	775	793	23	10675	12169	14316	14	5462	5765	6130
2013	3	28	19497	19945	20426	50	49463	54702	61703	17	28425	34171	43617
2013	4	4	1561	1597	1636	22	42739	71319	251530	9	17099	39074	*
2014	1									12	457	767	2801
2014	2	14	19769	20223	20711	3	4026	4530	5231	9	4361	4855	5525
2014	3	22	31345	32330	33455	21	33371	38365	45691				
2014	4					23	31038	38273	51016	2	2492	3017	3897
2015	1												
2015	2	5	298	314	333	2	479	595	806				
2015	3	24	15620	15979	16364	32	17479	19608	22552				
2015	4	7	5390	6568	8575	25	7630	9034	11254	2	280	348	471

Year	Quarter	Region 1 *SSB*				Region 2 *SSB*				Region 3 *SSB*			
2016	1												
2016	2					9	3907	4291	4795	11	4125	4387	4707
2016	3	14	12019	12295	12591	12	11537	13311	15937				
2016	4												
2017	1					6	835	1001	1273				
2017	2	14	2387	2469	2562	15	7461	7632	7816	16	4427	4762	5180
2017	3	34	6428	6682	6976	10	1051	1124	1214	11	894	921	951
2017	4	3	534	546	560					14	5208	5642	6196
2018	1									17	7618	10153	15775
2018	2	28	9070	9299	9556	3	173	178	183	6	120	122	125
2018	3	13	2297	2382	2480	6	831	961	1156				
2018	4	13	2548	2607	2669	30	28873	40716	72640	11	3079	3877	5367
2019	1	2	189	202	217	6	3586	5604	14124	12	5791	7833	12588
2019	2	4	260	282	310	2	356	628	3426	7	156	178	210
2019	3	29	3306	3873	4746								
2019	4					5	4258	4827	5635				
2020	1					6	5659	7689	12487	19	5110	6271	8286
2020	2	26	9538	9763	10011								
2020	3	22	4770	5060	5412								
2020	4	7	305	312	319					3	822	1029	1411
2021	1	2	557	569	583					7	2908	3466	4361
2021	2					5	3387	3827	4447	15	835	860	889
2021	3	22	4348	4545	4776	4	1250	1453	1760	4	846	866	887
2021	4					25	21302	25499	32322	12	3386	3542	3725
2022	1					14	23645	30246	43152	20	5035	5414	5888
2022	2					2	1539	1830	2294	6	1003	1027	1052
2022	3	19	1489	1568	1662	2	3580	5292	10847	10	1343	1387	1437