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Dynamic spawning patterns in the California market squid (*Doryteuthis opalescens*) inferred through paralarval observation in the Southern California Bight, 2012-2019

Running title: Market squid spawning dynamics

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Abstract

24 The California market squid is ecologically and economically important to the California Current
25 Ecosystem and coastal communities. However, the population undergoes periodic and large-
26 scale fluctuations on the order of magnitudes, largely as a result of warm ocean temperature and
27 reduced ocean productivity related to cycles in El Niño Southern Oscillation. These fluctuations
28 can lead to cascading trophic effects on the ecosystem, market uncertainty, and substantial
29 revenue losses for fishing communities. In order to investigate the role that spawning behavior
30 may play in mitigating the detrimental environmental effects on the population as well as
31 allowing the species to capitalize during favorable ocean conditions, surveys for market squid
32 paralarvae were conducted three times per hatching season from 2012-2019. The specific
33 objectives were to 1) assess whether there was a large-scale synchronous peak in paralarval
34 abundance each season, 2) investigate whether market squid paralarvae were found at certain
35 locations in similar abundances throughout the duration of a hatching season, and 3) to
36 understand the influence of oceanographic parameters, such as zooplankton availability, sea
37 surface temperature, and chlorophyll-*a* on paralarvae abundance during each hatching season.
38 Adaptable spawning strategies that varied over time were observed. Market squid displayed
39 large-scale synchronous spawning during cool and productive oceanographic conditions;
40 protracted spawning was observed during warm and oligotrophic conditions. No overall site-
41 fidelity was observed across all effort, but during two seasons where habitat compression was
42 possible, market squid consistently spawned in certain areas. Generalized Additive Models were
43 used to explore the effects of a small set of oceanographic variables on paralarval density on a
44 seasonal basis. Sea surface temperature and geographic variables were generally the most
45 important variables. These findings indicate that market squid spawning behaviors and habitat
46 are adaptable and dependent on oceanography and population density.

47

48 **Introduction**

49   The California market squid (*Doryteuthis opalescens*) is ecologically and economically
50 important in the California Current Ecosystem (CCE) and to coastal fishing communities.
51 Market squid are short-lived, semelparous animals with a pronounced life-history plasticity and
52 high metabolic demands (Vidal et al., 2002; Pecl et al., 2004; Pecl & Jackson, 2007), as a result,
53 their populations fluctuate greatly and are acutely susceptible to changes in broad-scale

54 oceanographic patterns, such as the warm and cool phases of the El Niño Southern Oscillation

55 (ENSO) (Reiss et al., 2004; Zeidberg et al., 2006; Koslow & Allen, 2011). Population indices

56 and landings often plummet by orders of magnitude during warm and unproductive

57 oceanographic conditions in the CCE; however, the population's rebound and geographic

58 expansion is equally remarkable (Zeidberg & Hamner, 2002; Reiss et al., 2004; Perretti, 2014).

59 An on-going question remains as to how the population is able to rebound once favorable

60 conditions return, and what role spawning strategies might play in this cycle.

61   Spawning behavior, referring to the spatial and temporal release of offspring into the

62 environment, often develops as a means to mitigate sources of egg or larval mortality (May,

63 1974; Legget & Deblois, 1994). For example, mass spawning inundates predator populations and

64 reduces the impact of predation (Johannes, 1978). Starvation can also be a major source of

65 mortality, and in temperate ecosystems, which exhibit relatively predictable seasonality and

66 productivity cycles, recruitment will be greatest when larval abundance is timed to match the

67 period of greatest plankton abundance, maximizing foraging opportunities and growth while

68 minimizing mass starvation (Cushing, 1969). Spawning animals often migrate substantial

69 distances to ensure their offspring are reared in environments where they have the greatest

70 likelihood of success (Alerstam et al., 2003). Perhaps the most extreme form of this natal

71 philopatry is exhibited by salmon and sea turtles, which return to the rivers or beaches where

72 they were born (Lohmann et al., 2008). Less extreme in example, many species, such as the

73 California market squid, return seasonally to predictable spawning grounds, and these migrations

74 can be influenced by changes in oceanography (Fields, 1965; Chen et al., 2007). During their

75 juvenile and sub-adult phase, market squid disperse widely over the continental shelf throughout

76 the CCE; upon maturation, they migrate to shallow, nearshore habitats where they form large

77 aggregations and spawn, mortality follows post spawning (Fields, 1965; Macewicz et al. 2004;

78 Perretti et al. 2015). Post hatching, these planktonic paralarvae are retained near shallow-water

79 spawning areas for a duration of 13-16 days and up to ~30 days, before dispersing again over the

80 continental shelf and into deeper waters (Zeidberg & Hamner, 2002). During this critical phase

81 of first feeding, paralarval must learn to capture zooplankton before utilizing their egg yolk

82 reserve, the incidence of feeding success has been shown to increase with age in market squid

83 paralarvae (Hurley 1976). Paralarvae also lack strong swimming capabilities during this time and

84 the density and availability of zooplankton food sources would be of critical importance to the

85   survival of these paralarvae in order to satisfy their substantial energetic demands (O'Dor &

86   Webber, 1995). While the population can range from Baja, Mexico to southeast Alaska, USA

87   there are two traditional spawning grounds (commercial fishing targets spawning aggregations)

88   that contribute the vast majority of landings in a given year: the Monterey Bay area (MBA), and

89   the Southern California Bight (SCB, Fig 1). The SCB is geographically larger than the MBR, and

90   under typical conditions, the SCB constitutes approximately 70% - 90% of the total commercial

91   landings (CDFG, 2005; Zeidberg et al., 2006; CDFW 2015). Recruitment to these spawning

92   grounds is temporally off-set and likely a result of differing maturation rates due to discrepancies

93   in water temperature and food availability (McGowan, 1954; Jackson & Domeier, 2003;

94   Forsythe, 2004). Market squid generally recruit to the MBA in summer, and to the SCB during

95   autumn, with paralarvae hatching ~2 months afterwards (Vojkovich, 1998). As semelparous

96   spawners, each "cohort" is annually replaced and the fecundity of an individual or population

97   cannot increase with age. Therefore, the spawning success during each year and the survival and

98   growth of paralarval, which is largely influenced by food availability and feeding success, is of

99   critical importance to the biomass of the population (Cushing 1990).

100   While this general spawning trend is well understood, the fine-scale spawning dynamics

101   and the drivers of those dynamics within a season are unclear. For example, it is unknown if

102   spawning is protracted across weeks or months during the spawning season in relatively similar

103   concentrations. Or conversely, is spawning a singular and synchronized, high-intensity event on

104   a regional scale? Additionally, questions remain as to how market squid utilize the neritic

105   environment during each season. As aggregate spawners for example, are market squid attracted

106   to established egg beds and the presence of squid, resulting in continuous recruitment to initial

107   "seed" beds throughout the duration of a season? Or conversely, will squid inundate these initial

108   areas and reach density-dependence (Challier et al., 2006) that orientates populations elsewhere?

109   It is also possible that spawning locations are dependent on abiotic conditions that dictate squid

110   recruitment to varying beds. Adding a stochastic element to spawning behavior, the presence of

111   predators has been observed to disrupt spawning aggregations and force spawning groups to

112   disassemble, likely displacing these squid elsewhere (Roberts, 1998). These behaviors would

113   result in market squid appearing to colonize new locations throughout a season. Differing

114   spawning strategies, defined as the spatial and temporal patterns of egg deposition, would

115 convey varying methods of risk mitigation against poor recruitment, and would therefore be
116 important in understanding population dynamics.

117   While not ideal (Okutani & McGowan, 1969), many researchers have developed indices
118 to use larval abundance to predict adult biomass (Lo et al., 2010), and use larval and paralarval
119 abundance to gain insight into adult spawning dynamics (Sakurai et al., 2000; Smith & Moser,
120 2003; Zeidberg et al., 2006.) Furthermore, it is extremely difficult to obtain direct, broad-scale
121 spawning and embryo information (see methods by Navarro et al. 2018). Therefore, to gain
122 insight into these spawning patterns the following was specifically asked, 1) Is there a large-scale
123 synchronous peak in paralarvae abundance? Or are paralarvae found in similar abundances
124 throughout the duration of a hatching season over the traditional spawning beds in the SCB? 2) If
125 market squid paralarvae are found in a given area during one month, will they be found in similar
126 concentrations, at the same area, in the subsequent month? And 3) Does oceanography influence
127 paralarval abundance within hatching seasons? To elucidate these questions, monthly net tows
128 were conducted throughout seven consecutive hatching seasons from 2012-2019 within the SCB,
129 including the Channel Islands and the coast, targeting paralarvae as an indicator of spawning
130 activity.

131

132   Methods

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134   Survey and Data

135

136   As part of a collaborative research effort between the California Wetfish Producers
137 Association (CWPA) the National Oceanic and Atmospheric Administration's (NOAA)
138 Southwest Science Fisheries Association (SWFSC) and the California Department of Fish and
139 Wildlife (CDFW), two fishing vessels were chartered for 21 surveys across seven years to
140 sample market squid paralarvae. The study area spanned the southern California Bight from La
141 Jolla to Point Conception and included five of the Channel Islands (Fig. 1). Depending on
142 weather conditions and site accessibility, 27 to 33 fixed, non-random stations were sampled

143   yielding a total of 641 net tows. These stations were in shallow-water (~20-130m), over

144   predominately sandy substrate, and were systematically assigned to cover the latitudinal gradient

145   of the traditional spawning habitat in the SCB, therefore, distance between stations was irregular.

146   These areas were sampled monthly (December, January, and February) during each of the seven

147   paralarval hatching seasons (December of one year, and January and February of the subsequent

148   year).

149   Paralarvae were sampled with a 505-μm nylon mesh bongo net. The mouth diameter was

150   0.6 m and the net system was towed obliquely at an approximate angle of 45° to a depth of 27 or

151   55 m during night or day deployments, respectively, unless the station depth was too shallow or

152   the bathymetry was irregular and posed a threat of bottom contact. Sampling depths were chosen

153   based on previously observed patterns of nightly vertical migration by paralarvae upward in the

154   water column (Zeidberg & Hamner, 2002). If stations were shallower than 27 m, the net was

155   deployed to approximately three-fourths of the station depth. Vessel speed during deployment

156   was typically 2 knots or under, in order to maintain the net at a 45° angle. Samples were

157   preserved in 50% ethanol aboard vessels. Mechanical or digital flowmeters (Ocean Test Model

158   MF 315 or EF 325, respectively) were attached to each net on the frame and the amount of

159   seawater filtered was calculated using methods established by Ohman and Smith (1995).

160   Both sides of the bongo net were sorted and enumerated for market squid. Small

161   zooplankton displacement volume (ZPDV, excluding larger planktonic organisms > 5ml) was

162   calculated using methods by Ohman and Smith (1995). Dorsal mantle length (DML) was

163   measured under a dissecting microscope to a tenth of a millimeter. Effort was made to include

164   paralarvae from all month and hatching-seasons, but samples from February 2013 and December

165   2018 were unavailable due to low n values and degradation of specimens. DML was measured

166   from the anterior most point of the mantle to the posterior apex of the mantle tip. A random

167   selection of ten paralarvae were measured from each sample, unless the sample contained <10, in

168   which case all specimens were measured. Paralarvae were not measured if the mantle was

169   damaged or degraded. Paralarval densities were averaged from both sides of the net by summing

170   the volumes and then dividing by the total count of paralarvae. Due to the aggregating spawning

171   behavior of market squid, standard deviations were high. Density values were square-root

172   transformed to preform statistical analyses on monthly mean abundances. Non-parametric,

173 Mann-Whitney *U* tests were used to compare mean monthly paralarvae abundance during a

174 hatching season. Linear regression models were used to test the correlation of paralarvae found

175 in a given area from month *n* to month *n*+1 during each hatching season and across all seasons.

176 For this analysis, proportional contribution by area was calculated by grouping paralarval

177 densities at a given site into one of ten geographic areas (described below), the summed

178 abundance at that area was then divided by the total paralarval abundance during a given month

179 within each hatching season, then transformed to proportions (Fig. 1). Proportional contribution

180 was used to normalize abundances, which ranged widely between years and months. As this

181 study's focus was observing the consistency of paralarval occurrence at spawning beds over

182 time, an area was only included if market squid were present in that area during an initial month.

183 Areas were considered geographically distinct, insomuch as paralarvae were unlikely to be

184 dispersed between, based on residence time over spawning beds (Zeidberg & Hamner, 2002),

185 typical current velocity, and ageing work by Van Noord and Dorval (unpublished). From north to

186 south in the SCB, these areas included the North Bight, Santa Rosa, Santa Cruz and Anacapa

187 Islands, Oxnard, Malibu, Central Bight, Santa Barbara and Catalina Islands, and South Bight

188 (Fig. 1). Due to the differences in geographic sizes of the islands, the number of stations per area

189 ranged from two to five. Areas were further grouped into regions for additional statistical

190 analysis. Four regions were identified, North Bight, North Islands, South Bight, and South

191 Islands. These regions were separated between the coast and islands and from a transect out from

192 Santa Monica Bay, separating Catalina Island to the south and Santa Barbara Island to the north

193 (Fig. 1). The data that support the findings of this study are available from the corresponding

194 author upon reasonable request.

195   General Additive Models (GAMs) were used to elucidate the importance of

196 environmental and geographic explanatory variables on paralarval density by hatching season.

197 GAMs were used because the response variable did not conform to a normal distribution, and the

198 relationships between the response variable and the predictors was often non-linear. The "gam"

199 function in the "mgcv" package in the statistical program R (Wood, 2006) was used. The

200 following equation was used to model paralarval density by hatching season,

201
$$g(Y) = f_1(\text{SST}) + f_2(\text{ZPDV}) + f_3(\text{SCHL}) + area(s)$$

202   where Y is the expected value of the response variable, estimated as paralarval density and $g(\cdot)$ is

203   the link function defining the non-linear relationship between paralarval density and the selected

204   predictors. Paralarval density was square root transformed and displayed a negative binomial

205   distribution; therefore, a log link transformation was used as the link function. Finally, $f_k(\cdot)$ was

206   the unique smoothing function assigned to each predictor. Four predictor variables were used to

207   model paralarval density: SST (°C), ZPDV (ml/1,000 m^3), surface chlorophyll-*a* (SCHL,

208   mg/m^3), and area. SST was included as a station-specific measurement of the physiological

209   suitability of the habitat. ZPDV and SCHL were used as separate predictors of habitat quality

210   and food availability. Areas were considered geographically distinct, where paralarval dispersal

211   between was considered to be of a low likelihood. This assumption was based on typical

212   residence times over spawning beds (Zeidberg & Hamner, 2002), typical current velocity, and

213   ageing work by Van Noord and Dorval (unpublished). Area was included to infer whether site

214   fidelity influenced paralarval density during a given hatching season.

215   Several steps were taken to obtain parsimonious models and to prevent over-fitting. First,

216   the number of knots in the smooth spline was limited to 4. The "gamma" value in the gam

217   formula was set at 1.4 in order to increase the penalty per degree of freedom fit and to minimize

218   overfitting (Wood, 2006). Lastly, a backward stepwise approach was used to select the best

219   model for each hatching season. All predictor variables were included upon the initial model run

220   and the variable with the lowest p-value was removed. The model was then re-run with the

221   remaining variables and the process was continued until all remaining variables had p-values $\leq$

222   0.1. Intra-season model goodness-of-fits and residual degrees of freedom were compared using

223   analysis of variance tests (ANOVA) to help select the best model. All statistical analysis was

224   done in the statistical package R, version 3.4.3 (R Development Core Team, 2017).

225   Sea surface temperature and SCHL values were obtained from NOAA satellite

226   observations (coastwatch.noaa.gov). Sea Surface Temperature values were obtained using night

227   and day measurements by the Advanced Very High Resolution Radiometer instrument aboard

228   the Polar Operation Environmental Satellite at a resolution of 1.4 km and 8-day composites. Sea

229   Surface Temperature observations within 5 km of sampling stations the day of sampling were

230   averaged to obtain a SST value for each station. Depending on satellite coverage and location,

231   anywhere from 15 to 40 observations were used to yield a daily SST value.

232   The Moderate Resolution Imaging Spectroradiometer instrument aboard the Aqua
233   satellite was used to obtain surface chlorophyll-*a* values at a resolution of 2.5 km and 14-day
234   composites. Data points within 5 km of a given station were averaged for the day of paralarval
235   sampling and the preceding day. Depending on satellite coverage and station location, anywhere
236   from five to 15 chlorophyll-*a* values were averaged to yield one value for that station.

237

238

239   Results

240   DML's of 944 individuals were measured to ensure paralarvae were not part of the same
241   spawning cohort and being measured over time. Mean DML was 2.61 (± 0.63) across all effort.
242   Mean DML for all December effort was 2.54 (± 0.34), mean January DML was 2.61 (± 0.42),
243   and mean February DML was 2.68 (± 0.61). Mean lengths by month for each hatching season
244   suggests paralarvae of a similar post-hatching state were captured by the net tow methods (Table
245   1). Preliminary ageing work suggests these paralarvae are ~1-5 days in age (Van Noord &
246   Dorval, unpublished). Table 1 displays the mean DML by month for each hatching season, along
247   with standard deviations, n values, and maximum and minimum sizes for each sampling period.

248   High variability was observed in paralarval abundance, timing of peak hatching within a
249   season, fidelity to spawning areas, and in the importance of oceanographic parameters in
250   predicting paralarval density across hatching seasons (Table 2, Fig. 2). Furthermore, no
251   predominant spawning patterns were evident across all years of data, suggesting that market
252   squid spawning patterns are adaptable on a seasonal basis.

253   Measurements of productivity, both ZPDV and SCHL, declined with the onset of the El
254   Niño, which peaked in 2016. Despite the changing ENSO state, ZPDV continued to decline
255   throughout the study period. Levels of SCHL rebounded during the 2016-17 season. Local SST
256   peaked above 17° C during the 2015-16 season and subsequently cooled (Fig. 3). Overall mean
257   paralarval abundance by area did not reflect overall proportional contribution of paralarvae at a
258   given area (Table 2). The greatest overall mean abundance occurred in the Malibu area (177
259   paralarvae 1,000m^{-3} ± 748 SD), but the proportional contribution of that area over the study

260 period was only 0.16. Conversely, the mean paralarval abundance at the Santa Rosa Island area

261 was 13.4 1,000m^{-3} ($\pm$ 31.5) but the proportional contribution was almost 0.20 (Table 2).

262

263   Synchronous and protracted spawning

264   Monthly peak paralarval abundance shifted temporally during hatching seasons in the

265 SCB (Fig. 2). Across all effort from 2012-2019, mean paralarval abundance was 51.3 paralarvae

266 1,000m^{-3} filtered sea water ($\pm$ 342 SD). Monthly abundance ranged from a low of 0.08 ($\pm$ 0.21)

267 in January, 2016 to 308 paralarvae 1,000m^{-3} ($\pm$ 1004) in January, 2012. Across the seven years of

268 effort, peak monthly paralarval abundances varied widely. January was the month with the

269 greatest in-season abundance during three of the seven seasons, while December and February

270 each claimed two seasons for greatest peak monthly abundance. January had the lowest

271 abundance during two seasons. Unimodal, bimodal, and both left and right skewed distributions

272 were observed during the hatching seasons. Significant between-month differences in paralarval

273 abundance were observed during the first two sampling seasons (2012-13 and 2013-14), as well

274 as the 2015-16 season and 2018-19 season (Fig. 2).

275

276   Spawning philopatry and explanatory variables

277   Paralarvae were not preferentially found at any given spawning area across all effort.

278 This pattern was mixed between hatching seasons. During the 2013-14 (p-value $<$ 0.01) and

279 2014-15 (p-value $<$ 0.05) hatching seasons, paralarvae were found at the same areas in the same

280 proportions from one month to the next, indicating spawners were likely recruiting to the same

281 spawning beds across time (Fig. 4). This fidelity occurred during the transition from high to low

282 paralarval abundance and from cool and productive oceanographic conditions (La Niña) to warm

283 and unproductive oceanographic conditions (El Niño). No correlation was found during the other

284 five seasons when paralarval abundance was markedly low.

285   The importance of predictor variables in explaining the observed deviance in paralarval

286 densities ranged greatly by year, as different variables potentially became limiting factors. SST

287 and SCHL were the most consistent predicator variables over time, both were significant and

288　included in four of the seven models (Table 3). ZPV was statistically significant and included in

289　two models. The Northern Islands region was the most consistent geographic area, and was

290　included in two of the seasonal models. The amount of variance explained in the models ranged

291　from 24.8 to 44.5% (Table 3).

292

293

294　　　Discussion

295

296　　　Many neritic squids, and the California market squid in particular, are known for their

297　"boom and bust" life history patterns that are characterized by periodic phases of rapid

298　population expansion and subsequent contraction, these phases are largely attributed to bottom-

299　up forcing (Rodhouse, 2001; Denis et al., 2002; Rodhouse et al. 2014). For market squid, these

300　fluctuations are largely related to warm and cool phases of the ENSO cycle, which likely drive

301　prey availability for squids (Reiss et al., 2004; Zeidberg et al., 2006; Koslow & Allen, 2011).

302　Warm ocean temperature has been shown to accelerate metabolic rate in squids and hasten

303　maturation (Forsythe, 2004; Boavida-Portugal et al., 2010). Paralarvae are highly susceptible to

304　starvation and this increased metabolic demand often occurs simultaneously as reduced ocean

305　productivity limits foraging opportunities, which would decrease survivorship. This study period

306　captured an ENSO cycle, from a subsiding La Niña, through an historically warm El Niño, and

307　back to a mild La Niña and neutral conditions; paralarval abundance dropped precipitously post

308　La Niña, low densities were evident through the development of the El Niño, and have yet to

309　recover with the onset of mild La Niña and neutral conditions. This trend may indicate market

310　squid need sustained periods of favorable oceanographic conditions for populations to rebound to

311　what was observed during strong La Niña periods (Zeidberg, 2013), or may highlight a

312　disconnect between basin wide metrics focused on equatorial regions, and that of local

313　conditions. This study area was limited to southern California, and it is possible population

314　reserves are evident outside the sampling frame. Squid spawning strategies, as inferred from

315　paralarval abundance and density distributions over time, were dynamic. Paralarvae abundance

316　peaked during different months in different hatching seasons; paralarvae also displayed both

317 protracted spawning as well as synchronous spawning during various hatching seasons.
318 Additionally, evidence of site-fidelity was observed during some hatching seasons, while in
319 others, paralarvae densities shifted spatially over time and correlated more strongly to
320 environmental variables. Additively, these results suggest squid spawning strategies are plastic
321 and squid may exhibit different patterns in paralarval density and distribution across hatching
322 seasons as a response to oceanographic changes. Squids are notable for their life-history
323 plasticity (Pecl et al., 2004; Moltschaniwskyj & Pecl, 2007). This adaptable spawning strategy
324 may explain their reproductive success, ability to capitalize on favorable ocean conditions, and
325 their ability to rapidly rebuild their abundance after periodic "busts" in the population.

326

327   Synchronous and protracted spawning

328   Market squid displayed both temporally dynamic, synchronous spawning and protracted
329 spawning across hatching seasons. Such plasticity has been shown to be an advantageous trait in
330 fishes and similar squids, such as *Loligo vulgaris*, in regions of variable productivity (Cushing,
331 1990; Boavida-Portugal et al., 2010). Market squid may display large-scale, synchronous
332 spawning under favorable oceanographic conditions, and protracted spawning when temperature
333 and productivity are constraining factors. Synchronous spawning was observed in the first two
334 hatching seasons, coincident with very high paralarval abundance and cool and productive, but
335 weakening, La Niña conditions. Conversely, protracted spawning was observed during the latter
336 hatching seasons. Additionally, peak synchronous spawning was temporally dynamic, in that the
337 month of peak paralarval hatching shifted from January, during 2013-14, to December, the
338 following hatching season. This temporal shift is likely explained by gradually warming ocean
339 temperatures in the CCE, which causes squids, including the California market squid, to mature
340 faster, spawn, and hatch earlier in the season (Forsythe, 2004; Van Noord & Dorval, 2017).
341 Jackson and Domeier (2003) observed this phenomena in the CCE, where mean age-at-
342 recruitment ranged from ~4.5 to 8 months and was dependent on ocean temperature. Agnew et
343 al. (2000) observed similar results around the Falkland Islands with *Loligo gahi*, finding higher
344 temperatures led to faster embryonic and paralarval development, causing earlier recruitment.
345 Additionally, warm and oligotrophic conditions in the Gulf of California led *Dosidicus gigas* to

346 adopt a small size-at-maturity phenotype, leading to the collapse of that fishery (Frawley et al., *in*
347 *press*).

348   Large-scale synchronous spawning occurs in systems with seasons of high productivity,
349 where spawners "match" their recruits to peaks in food abundance (Cushing 1990). Market squid
350 are highly energetic animals with elevated metabolic rates that require substantial foraging
351 opportunity (O'Dor & Webber, 1986; Wells & Clarke, 1996; Vidal et al., 2002). The CCE is a
352 productive upwelling current, where upwelling is typically greatest during spring (although the
353 strength of this upwelling is highly variable), leading to large euphausiid blooms, which are
354 important prey for juvenile and adult market squid (Karpov & Cailliet, 1979; Lynn et al., 2003;
355 Santora et al., 2012). Cushing's theory is a parsimonious explanation for market squid during
356 highly productive oceanographic conditions. During oligotrophic conditions however, when
357 market squid densities are low, protracted spawning is observed (Van Noord & Dorval, 2017).
358 Highly variable and unpredictable ocean temperature and food availability can lead to extreme
359 life-history plasticity in squids, and market squid may display different spawning strategies
360 depending on their abundance and environmental cues (Moltschaniwskyj & Pecl, 2007).
361 Protracted spawning during periods of physiologically challenging ocean conditions with low
362 food availability would serve to spread recruits temporally, where the probability of some
363 paralarval encountering favorable rearing conditions would increase, these recruits would also
364 face less competition for limited resources (Johannes, 1978; Vila-Gispert et al., 2002; Ganias et
365 al., 2007). Squid display just such adaptive spawning behavior and diverse reproductive
366 strategies across many systems (Rocha et al., 2001). Boavida-Portugal et al. (2010) showed that
367 reproductive strategies changed with ocean temperature and season in *Loligo vulgaris*, finding
368 that warm water resulted in higher fecund females that matured younger at a smaller size. In cold
369 water, conversely, animals were larger, older, and had a lower fecundity, but the survival rate of
370 those individuals was higher, due to increased egg fitness and larger oocytes observed (Boavida-
371 Portugal, et al. 2010). This shows squids are capable of adaptable spawning strategies that could
372 aid them in enduring sustained periods of low productivity.

373   Low densities of spawning adults could also make it more difficult for small schools of
374 squid to encounter larger spawning aggregations, which could have resulted in more temporal
375 patchiness if individuals had to significantly increase search effort. The presence of eggs or

376   spawning adults may also trigger aggregation and spawning behavior in the individual (Arnold,

377   1962; Hurley, 1977), so low densities may delay egg deposition.

378

379   Spawning philopatry and environmental influence

380   For an aggregation of spawning squid to amass and initiate spawning, a suite of abiotic

381   and biotic attributes must be realized. For example, the habitat must be in relatively shallow-

382   water, over predominately sandy substrate, within certain temperature, nutrient, and chemical

383   thresholds (Zeidberg et al., 2011; 2012; Navarro et al., 2018). Once those criteria are met, the

384   exact location of spawning aggregations may be somewhat random and resultant on an initial

385   seed population that colonizes a given area. Recruiting market squid are then visually attracted

386   by the presence of egg clusters, spawning adults, and possibly through pheromone cues (Hurley,

387   1977; Foote et al., 2006; Cummins et al., 2011). This behavior would result in an accumulating

388   effect of recruits to established egg beds that lasts until either spawning is complete for the

389   population, or until some density-dependent effect, or outside influence, such as predation or

390   storms, drives the aggregation apart (Fields, 1950; McGowan, 1954; Susswein & Nagle, 2004).

391   While large-scale synchronous spawning can be advantageous when recruits match with

392   abundant food sources and favorable environmental conditions (Cushing, 1990), adverse density-

393   dependence could occur when embryo densities reach critical densities, either diminishing the

394   fitness or survival of embryos or paralarvae (Minto et al., 2008; Villanueva et al., 2011; Zeidberg

395   et al. 2012), or causing adults to emigrate. Very high spawning stock biomass has been

396   correlated to reduced recruitment by *Loligo gahi* in the southwest Atlantic (Agnew et al., 2002);

397   similarly in the northeast Atlantic, higher spawning stock biomass was associated with slower

398   growth and lower survival in *Loligo forbesi* (Challier et al., 2006). Market squid in this study

399   displayed no overall site fidelity considering this studies sampling effort in the SCB, meaning no

400   area was preferentially selected by squids and spawning concentrations were likely dependent on

401   local oceanographic conditions or random settlement from pioneering squids. However, it should

402   be reiterated that all sampling locations in this study are fixed at known squid aggregation

403   locations and squid likely express fidelity to these known aggregation locations because of their

404   bathymetric characteristics. On a seasonal basis, site fidelity was observed during two hatching

405   seasons, 2013-14 and 2015-16, which coincided with the period of transition from weak La Niña

406 to neutral and warm El Niño conditions, and high to low paralarval abundance. Density-
407 dependent effects were possibly observed during the 2012-13 season –when paralarval
408 abundance was greatest and high proportions of paralarvae in a given location, during an initial
409 month, was consistently followed by low paralarval proportions the next month, at the same area.
410 Meaning squid seemed prone to spawn in a given area and establish new areas the subsequent
411 month. Detrimental effects on growth, hatching, and survival can occur when eggs are too dense
412 (Steer & Moltschaniwskyj, 2007). Density-dependent effects could be particularly acute for
413 market squid as they lay dense egg clusters that are resident on the sea-floor for up to 12 weeks
414 (Zeidberg et al., 2012). Without adequate flow to maintain tolerance thresholds in water
415 characteristics, the embryos can suffer effects from siltation, low oxygen, high pH, and so on
416 (Zeidberg et al., 2012; Kaplan et al., 2013; Navarro et al. 2018).

417   When the potential spawning habitat is compressed due to environmental constraints,
418 market squid may be restricted to limited areas throughout their potential range for the duration
419 of a spawning season (Navarro et al., 2018). This habitat compression can be substantial. During
420 the strong 1998 El Niño, Zeidberg (2013) estimated a 90% loss of potential market squid
421 spawning habitat. Large fluctuations in potential spawning habitat have also been seen in the
422 squid, *Todarodes pacificus* off Japan (Sakurai et al., 2000). This habitat compression may have
423 happened during the onset of El Niño conditions, when squid largely avoided spawning along the
424 coast, particularly the South Bight. During the oceanographic transition from cool to warm,
425 spawning squid, as inferred from paralarval densities, were largely restricted to areas off Santa
426 Cruz island, the windward side of Catalina Island, and Santa Barbara Island, where the
427 proportion of hatching paralarvae was consistent from month to month. These island locations
428 generally benefit from more upwelling and zooplankton abundance than coastal locations, and
429 may provide some rationale as to why spawning may have focused on these areas (Fiedler et al.,
430 1998). Sea surface temperature, surface chlorophyll, zooplankton displacement volume and
431 geography played important roles in explaining inferred spawning fidelity during the high
432 productive hatching seasons of 2012-13 and 2013-14, indicating a cumulative effect of a suite of
433 variables that promote suitable spawning habitats. During the subsequent seasons, only one or
434 two variables were significant each season, likely indicating that these ocean environments were
435 limiting. The temporal stability of environmental conditions and whether or not those conditions
436 stay within the tolerance threshold throughout a season also dictates their relative importance.

437 For example, during the 2017-18 season, ZPDV and SST remained relatively static from
438 December to February and did not contribute significantly to the model. Conversely, during the
439 2018-19 season, mean SST dropped ~6° C from January to February, while ZPDV increased
440 roughly three times, this cooler, zooplankton-rich period coincided with a significant increase in
441 paralarval abundance.

442

443   Conclusion

444   This study marks the first attempt to sample and understand the fine-scale spawning
445 patterns in market squid by conducting multiple surveys within a single hatching season.
446 Although market squid spawn at low levels throughout the year (Zeidberg et al., 2012; Navarro
447 et al., 2018), the vast majority of paralarvae are observed during the winter hatching season in
448 the SCB (Van Noord & Dorval, 2017); this study provides insight into those spawning patterns.
449 While not perfect, many authors have highlighted the benefits of using larval abundance as an
450 index of spawning dynamics (Smith & Richardson, 1977; Hilborn & Walters, 1992), but future
451 studies would benefit from exploring how variable survivorship is during the embryonic phase
452 and how determinant geography and environmental constraints are to survival. Additional work
453 would also benefit from combining fine-scale and *in situ* abiotic parameters, such as pH,
454 dissolved oxygen, and micro-chemistry data into the explanatory framework (Navarro et al.,
455 2016). This work has implications for future climate change scenarios. As oceans continue to
456 absorb heat and acidify, and anomalously warm events become more intense and unpredictable
457 (Ashok & Yamagata, 2009), the life-history plasticity shown by market squid could help them
458 cope with these changes. Additionally, developing paralarvae are encased in embryos that may
459 be able to ameliorate exposure to harmful conditions. Under climate change forecasts, the
460 assumption is that animals will move north as waters warm, but the direct effects of chronic
461 warming and low pH environments are unknown (Navarro et al., 2014). It is unknown how
462 suitable northern habitats would be or how permanent California Market Squid would become in
463 those ecosystems; the implications of this migration would have cascading ecological and
464 economic impacts.

465   Seasonal paralarval abundance varied tremendously, and low abundances may mask
466 trends in spawning patterns that may otherwise be evident. Regardless, this study shows that

467   market squid display different spawning strategies based on oceanographic conditions and
468   population size, and this adaptable behavior helps to explain their ability to capitalize on
469   favorable oceanographic conditions in order to expand their range and abundance. On the other
470   hand, protracted spawning behavior and flexible spawning fidelity may allow market squid to
471   sustain a baseline population level during oligotrophic conditions when the animals are most
472   susceptible. This study also demonstrates the advantage of multiple in-season surveys, as times
473   of peak larval hatching can vary, missing the peak abundance of a target species would introduce
474   error into stock assessments that rely on spawning output.

475

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662

663

664 **Table 1.** Dorsal mantle length (DML) information from 944 individual paralarvae measured
665 across seven hatching seasons. Standard deviations (SD) are shown in parentheses. Hatching
666 seasons refer to December, and January, February of the subsequent month. Specimens were
667 collected in southern California.

668

	December			January			February		
	Mean mm (± SD)	n	min-max	Mean mm (± SD)	n	min-max	Mean mm (± SD)	n	min-max
2012-13	2.52 (± 0.38)	86	1.9 - 4.0	2.67 (± 0.53)	71	1.9 - 4.4			
2013-14	2.51 (± 0.27)	127	1.9 - 3.7	2.53 (± 0.34)	33	1.9 - 4.3	2.56 (± 0.48)	60	1.8 - 4.5
2014-15	2.55 (± 0.22)	30	1.8 - 2.9	2.46 (± 0.37)	121	2.0 - 4.1	3.08 (± 0.59)	11	2.4 - 4.6
2015-16	2.43 (± 0.17)	13	2.2 - 2.7	2.36 (± 0.58)	62	1.8 - 3.4	2.69 (± 0.93)	19	2.0 -5.9
2016-17	2.73 (± 0.55)	12	2.1 - 4.0	2.64 (± 0.41)	9	2.1 - 4.6	2.71 (± 0.86)	35	1.5 - 6.2
2017-18	2.62 (± 0.38)	69	1.7 - 3.7	2.73 (± 0.21)	31	2.3 - 3.0	2.64 (± 0.22)	62	1.9 - 3.1
2018-19				2.60 (± 0.40)	57	2.2 - 3.3	2.82 (± 0.74)	36	2.1 - 6.4
Total	337			384			223		

669

670

671 **Table 2.** Overall market squid mean paralarval abundance and overall mean proportional
672 contribution, plus or minus standard deviation, by area in the Southern California Bight, 2012-
673 2019. The number of sampling stations per area is included in parenthesis. Areas are ranked by
674 overall mean paralarval abundance and decimal numbers are aligned to display the magnitude of
675 values. Standard deviations are high due to the aggregation behavior of spawning market squid.

Area	Overall mean abundance (ind. 1,000m^{-3})	Overall mean proportional contribution
Malibu (3)	177 (± 748)	0.157 (± 0.267)
Santa Barbara Is (2)	135 (± 697)	0.086 (± 0.193)
Santa Cruz Is (5)	112 (± 442)	0.232 (± 0.268)
Anacapa Is (2)	35.2 (± 81.9)	0.050 (± 0.079)
Central bight (3)	17.5 (± 86.9)	0.029 (± 0.086)
Catalina Is (5)	17.2 (± 85.5)	0.179 (± 0.203)
North Bight (5)	13.6 (± 64.4)	0.033 (± 0.068)
Santa Rosa Is (3)	13.4 (± 31.5)	0.194 (± 0.251)
South Bight (3)	12.9 (± 65.0)	0.029 (± 0.115)
Oxnard (2)	11.0 (± 32.4)	0.017 (± 0.033)

676

677

678 **Table 3.** Mean seasonal paralarval abundance and select environmental variables by hatching
679 season as well as deviance explained and Adjusted R-Squared from the Generalized Additive
680 Model (GAM) output. Hatching season is December and January, February of the subsequent
681 calendar year. Sea surface temperature (SST), Zooplankton displacement volume (ZPDV), and
682 log of surface chlorophyll (SCHL) values are displayed. Geographic variables used in the GAM
683 model include northern islands (NI), north bight (NB), southern islands (SI), and south bight
684 (SI). A (.) indicates an important, but not significant variable ($p<0.01$), (*) indicates $p<0.05$, (**)
685 indicates $p<0.001$, and (***) indicates $p<0.0001$.

686

Hatching Season	Seasonal paralarval abundance, ind. 1,000m^{-3} (± SD)	Important Variables	Deviance Explained (%)	Adjusted R-squared	Mean (± S.D.)
2012-13	132 (± 607)	ZPDV***, SST**, NI**, SI**, NB.	39.9	-0.119	SST: 14.02 (± 1.58) ZPDV: 88.2 (± 90.3) SCHL: 5.82 (± 10.7)

2013-14	70.4 (± 174)	NI***, NB***, SST**, SCHL*, ZPDV., SI.	24.8	-0.253	SST: 15.59 (± 0.92) ZPDV: 53.0 (± 35.3) SCHL: 2.21 (± 4.16)
2014-15	2.75 (± 16.3)	SCHL***, SST., NI.	44.5	0.13	SST: 17.3 (± 0.90) ZPDV: 34.7 (± 42.8) SCHL: 2.04 (± 2.99)
2015-16	0.63 (± 2.42)	SST**, NI**	33.9	0.18	SST: 16.3 (± 1.33) ZPDV: 31.7 (± 36.7) SCHL: 1.56 (± 1.35)
2016-17	1.34 (± 5.53)	SCHL**, SST*	34.8	0.17	SST: 14.7 (± 1.21) ZPDV: 31.6 (± 26.7) SCHL: 4.79 (± 8.36)
2017-18	7.43 (± 46.9)	SB***, SCHL*	25.8	-0.002	SST: 16.0 (± 1.05) ZPDV: 22.2 (± 21.8) SCHL: 5.25 (±7.68)
2018-19	3.17 (± 19.2)	ZPDV***, SST.	37.1	-0.008	SST: 15.3 (± 1.24) ZPDV: 19.2 (± 19.5) SCHL: 3.94 (± 5.33)

687

688

689 **Figure 1** Map of the Southern California Bight displaying the sampling locations and the
690 delineations samples were pooled together into areas for analysis.

691

692 **Figure 2** Mean paralarval abundance by hatching season from 2012-13 on the top, to 2018-19 on
693 bottom, including the months of December and, January and February of the subsequent year,
694 from left to right in each panel. Data are from the Southern California Bight. In order to display
695 the in-season trends clearly, scale of the vertical axis varies for each hatching season.

696

697   **Figure 3** Values by hatching season (December and, January and February of the subsequent
698   year) from 2012-2019 for market squid paralarval abundance, zooplankton displacement volume,
699   surface chlorophyll, sea surface temperature, and the Oceanic Niño Index (from left to right).
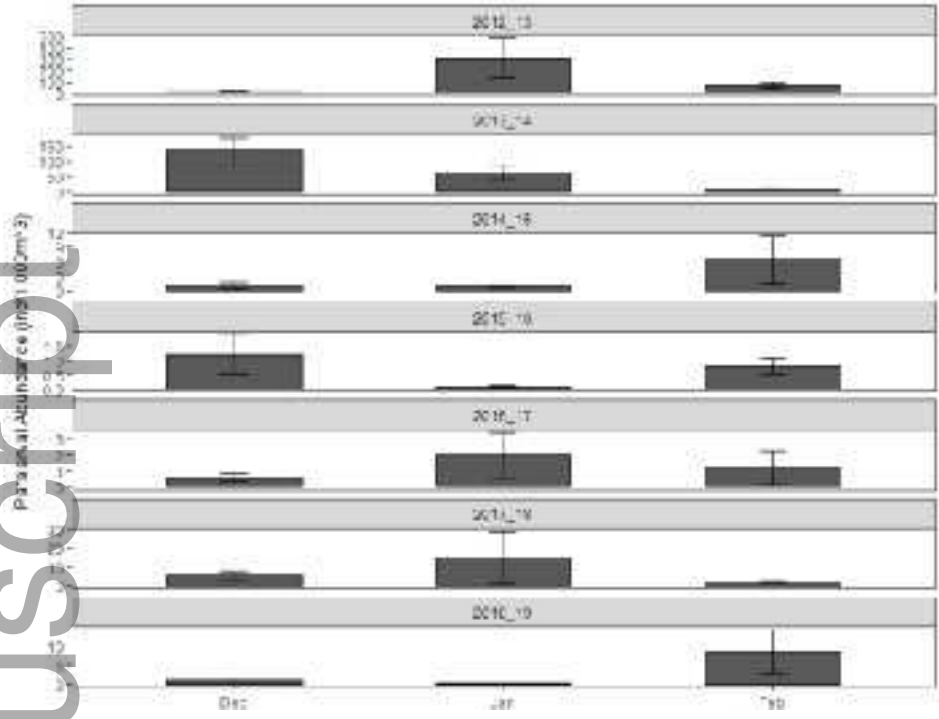700   Shaded areas indicate a 95% confidence interval.

701

702   **Figure 4.** Linear relationships in the monthly proportional contribution of paralarvae at a given
703   area over the total abundance during that time, and the proportional contribution of paralarvae in
704   the same area during the subsequent month across the seven hatching seasons are displayed.
705   Pooled areas are identified in Figure 1. Shapes indicate larger regions. Lines show the linear
706   model.
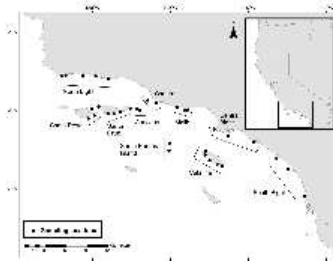
maec_12598_f1.jpg

maec_12598_f2.tiff

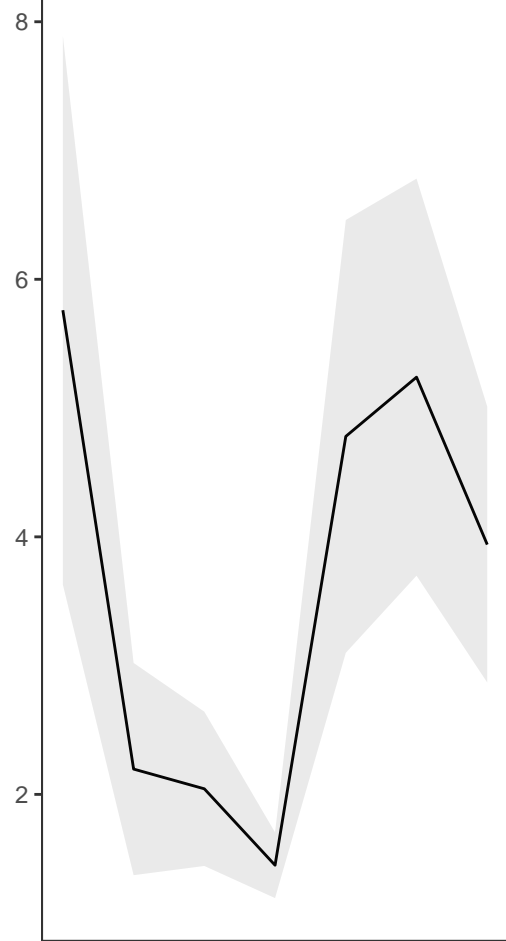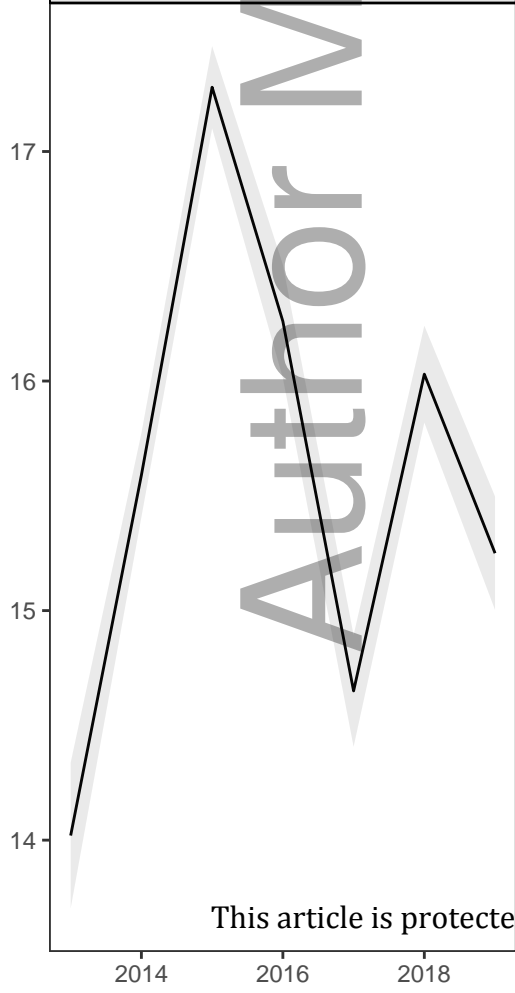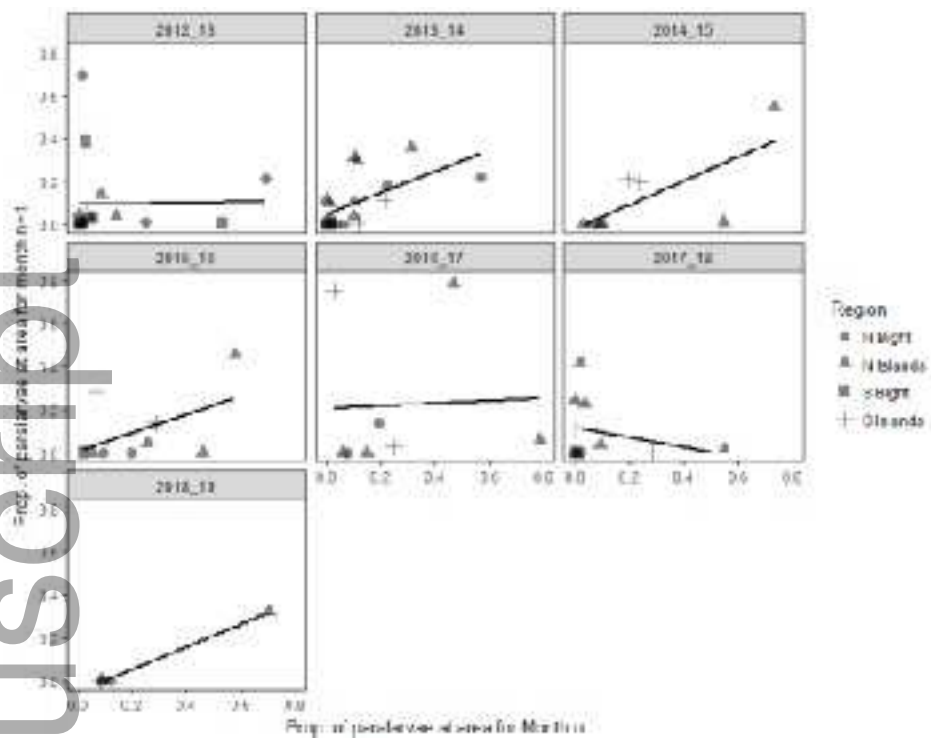Paralarval ab. (1000 m^−3) | ZPD2508_t300dm^−3) maec_12500_f300dm | Chl (mg m^−3)
SST (C) | ONI (temp. anom. C)
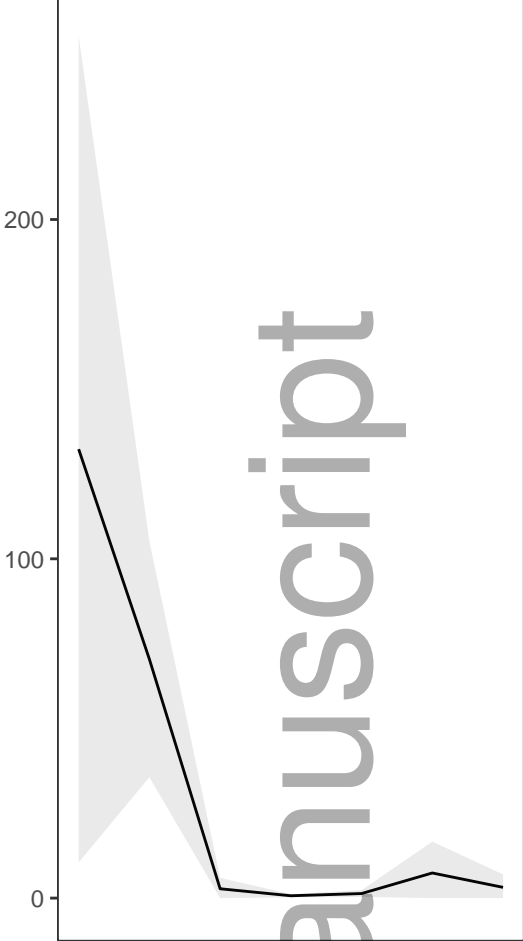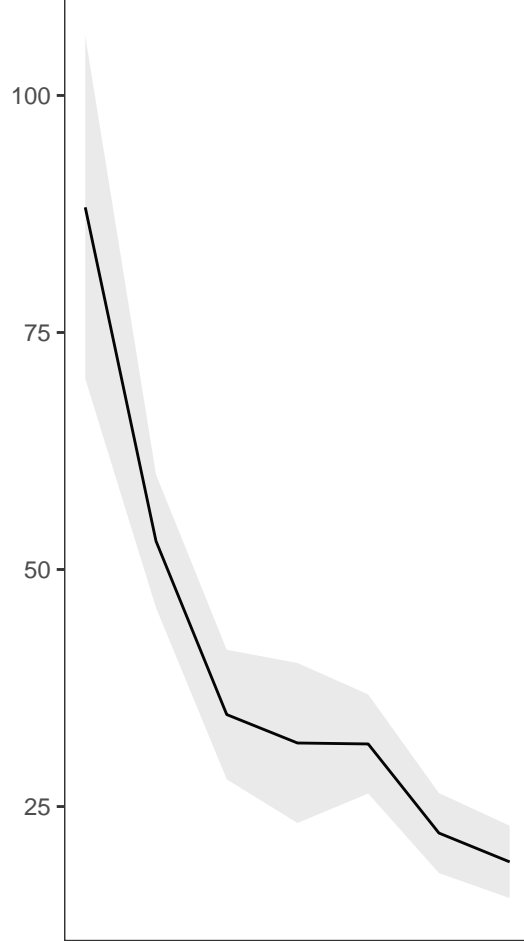
Year

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