MR. JOEL E VAN NOORD (Orcid ID : 0000-0001-5028-9664)

Received Date : 01-Aug-2016
Revised Date : 26-Jan-2017
Accepted Date : 12-Feb-2017
Article type : Regular Paper

Corresponding author mail id:- joel.van.noord@gmail.com

Oceanographic influences on the distribution and relative abundance of market squid paralarvae (*Doryteuthis opalescens*) for the southern and central California coast

Joel E. Van Noord[1] & Emmanis Dorval[2]

1 California Wetfish Producers Association, San Diego, CA, USA
2 Ocean Associates Inc. under contract to Southwest Fisheries Science Center, La Jolla, CA, USA

Abstract

Market squid (*Doryteuthis opalescens*) are ecologically and economically important to the California Current Ecosystem, but populations undergo dramatic fluctuations that greatly affect food web dynamics and fishing communities. These population fluctuations are broadly attributed to 5-7 year trends that can affect the oceanography across 1,000 km areas; however, monthly patterns over kilometer scales remain elusive. To investigate the population dynamics of market squid, we analyzed the density and distribution of paralarvae in coastal waters from San Diego to Half Moon Bay, California from 2011-2016. Warming local ocean conditions and a strong El Niño event drove a dramatic decline in relative paralarval abundance during the study period. Paralarval abundance was high during cool and productive La Niña conditions from 2011-2013, and extraordinarily low during warm and euptrophic El Niño conditions from 2015-2016 over the traditional spawning grounds in southern and central California. Market squid spawned earlier in the season and shifted northward during the transition from cool to warm ocean conditions. We used a general additive model to assess the variability in paralarval density and found that sea surface temperature (SST), zooplankton displacement volume (ZPDV), the log of surface chlorophyll-*a* (SCHL), and spatial and temporal predictor variables explained greater than 40% of the deviance (adjusted r^2 of 0.29). Greatest paralarval densities were associated with cool SST, moderate zooplankton concentrations, and low chlorophyll-*a* concentrations. In this paper we explore yearly and monthly trends in nearshore spawning for an economically important squid species and identify the major environmental influences that control their population variability.

Introduction

The California market squid (*Doryteuthis opalescens*) is ecologically and economically vital to the California Current ecosystem (CCE) and fishing communities. Squid are key components in marine ecosystems across the globe and play an instrumental role in transfering energy from lower to higher trophic levels (Coll *et al.* 2013). Market squid in the CCE are major predators on crustacea and fish (Karpov & Cailliet 1979) and important prey for marine mammals, seabirds, invertebrates, and fish (Morejohn *et al.* 1979). The fishery for market squid is routinely one of the largest and most valuable in the state of California (Leos 2014). Market squid disperese over the continental shelf as juveniles and form dense nearshore spawning aggregations when mature, depositing eggs into clusters over shallow, sandy substrate (Zeidberg & Hamner 2002; Navarro *et al.* 2016). The commercial fishery generally targets these spawning aggregations during summer in the Monterey Bay region (MBR), and during autumn in the southern California Bight (SCB, Fig. 1) (Zeidberg *et al.* 2006), although spawning has been observed year round in some instances (Fields 1950; Jackson & Domeier 2003; Navarro 2014). Market squid die within days after spawning (Macewicz *et al.* 2004) and the life cycle is complete within one year (Butler *et al.* 1999). Market squid populations fluctuate tremendously (Dorval *et al.* 2013), and warm (El Niño) and cool (La Niña) phases of the El Niño Southern Oscillation (ENSO) are considered to be a major influence (Reiss *et al.* 2004; Koslow & Allen 2011).

ENSO phases affect local conditions in the CCE. El Niño periods are warmer and cause reduced ocean productivity and zooplankton standing stock; La Niña periods are cooler and more productive (Lynn *et al.* 1995; Chavez *et al.* 2002). Squid show extreme life history plasticity and populations are able to expand rapidly during favorable conditions, but also decline in unfavorable environments (Pecl & Jackson 2007). Commercial landings reflect this life-history trait (Zeidberg *et al.* 2006). For example, during the historically strong El Niño of 1997 (McPhaden 1999), yearly landings declined from 80,000 to 3,000 metric tons (MT), before rebounding to 118,000 mt the next year (CDFW 2005). Fishery independent surveys find similar trends. Reiss *et al.* (2004) found a contraction of juvenile and adult distribution due to this El Niño and a rapid expansion as cool ocean conditions returned. Zeidberg & Hamner (2002) found paralaraval abundance increased from 1.5 to 78 individuals 1,000 m^{-3} around the Channel Islands in the SCB during the same El Niño, while pelagic surveys in the CCE find decreased paralarval abundance during prolonged warming events (Leising *et al.* 2014).

Such large-scale population variability has a substantial economic toll on fishing communities. Likewise, these changes in the distribution and abundance of market squid have cascading effects on predators of squid (Shane 1995). Bottom-up, oceanographic drivers control the population dynamics of many squid species (Perez *et al.* 2002), but the specific mechanisms that control this population variability, and the fine-scale distributional and spawning effects, are poorly understood, particularly for market squid in the CCE. To address this gap in knowledge, our study expands on previous research (Zeidberg & Hamner 2002; Koslow & Allen 2011) and provides novel data and insights by targeting nearshore spawning locations in shallow water at traditional spawning locations, over a wide geographic range across the SCB and the MBR. We sampled for six years across all seasons and the full range of ENSO conditions, and conducted repeated surveys within a single spawning season. Our results therefore, are meant to provide a relative index of paralarval abundance at the traditional spawning grounds and not a measure of absolute abundance.

The objectives of this study were to 1) determine the relative abundance of market squid paralarvae in order to establish a baseline of population productivity; and 2) determine the conditions that most greatly influence the variability in paralarval densities. Understanding the dynamics in spawning output and the environmental patterns that drive variability in paralarval density is important to the overall understanding of ecosystem functioning in the CCE and elsewhere, while insight into the fitness of adult spawners under different oceanographic conditions can provide information in assessing the stock of this commercially important species. To address these objectives, we derived the relative paralarval densities of California market squid from oblique bongo net tows at the traditional shallow-water spawning grounds in the SCB and MBR, and used these data to model density as a function of SST, ZPDV, SCHL, and spatial and temporal variables.

Materials and Methods

Survey and data

The study area covered a portion of the southern California Current Ecosystem (CCE) from San Diego to Half Moon Bay, CA (Fig. 1). Twenty-six cruises were conducted during a six-year period from 2011 to 2016 in five geographic areas. These areas included the north and south bight regions of the SCB, and the north and south Channel Islands (Fig. 1B). The north Channel Islands included Santa Rosa, Santa Cruz, Anacapa, and Santa Barbara Islands. The south Channel Islands included Catalina and San Clemente Islands.

Paralarvae were collected during a collaborative research program between the California Wetfish Producers Association (CWPA), the National Oceanic and Atmospheric Administration's (NOAA) Southwest Fisheries Science Center (SWFSC), and the California Department of Fish and Wildlife (CDFW). Sampling occurred aboard three chartered fishing vessels (each approximately 50 ft in length). The study was conducted in two areas, the SCB and the MBR and targeted 45 stations. Within each area, stations were sampled at fixed, nearshore, non-random locations, and were systematically assigned to cover the latitudinal gradient along the islands and coastline (Fig. 1). These sites were predominately located over sandy substrate in shallow water (~20 - 130 m), which is a known spawning substrate of market squid. As a result, distance between sites was irregular. San Clemente Island was sampled during the first two years of the study, but sampling was suspended because of access restrictions by the United States Navy. Thirty stations were targeted in the SCB and 15 from the MBR. A greater number of stations were selected in the SCB compared to the MRB to reflect the disproportional geography of these areas. Additionally, ~70% of commercial landings traditionally come from the SCB, while 30% are from the MBR (CDFG 2005).

Sampling occurred seasonally during the first two years of study (winter, spring, summer, and autumn) to mimic sampling patterns conducted in part by the SWFSC's California Cooperative Oceanic Fisheries Investigations (CalCOFI). Based on the findings from the initial two years of the study –that the vast majority of paralarvae were encountered during the winter in the SCB, sampling then shifted to target spawning periods when paralarvae were most abundant, while maintaining an "off-season" collection effort to assess the conditions when squid were not prevalent (Fig. 2). Beginning in July, 2012, one survey (utilizing three chartered vessels) occurred during the summer (July or August) and three surveys occurred during the winter (December, January, and February). MBR sampling began in July, 2014 and sampling occurred during July or August, and January.

Paralarvae were sampled with a pair of 505-μm nylon mesh bongo nets with mouth diameters of 0.6 m attached to a frame. The net system was towed obliquely at an approximate angle of 45° to a depth of 27 or 55 m during night or day deployments, respectively, unless the station depth was too shallow. Depths were chosen based on previously observed patterns of paralarval nightly vertical migration upward in the water column (Zeidberg & Hamner 2002). If stations were shallower than 27 m, the net was deployed to approximately three-fourths of the station depth to avoid contact with the seafloor. Average ship speed during deployment was 1.75 knots. Samples were preserved in 50% ethanol aboard vessels. Mechanical or digital flowmeters (Ocean Test Model MF 315 or EF 325, respectively) were attached to each net on the frame and the amount of seawater filtered was calculated using methods established by Ohman & Smith (1995).

Small zooplankton displacement volume (ZPDV) was measured in the laboratory. This measurement excluded large gelatinous animals, fish, crabs, and organisms generally greater than 5 mm in length or greater than 5 mL in volume (Smith & Richardson 1977). Cephalopod paralarvae were sorted from both port and starboard sides of the net. California market squid paralarvae were identified and enumerated under a dissecting microscope. Densities were estimated as numbers of individuals 1,000 m^{-3} of seawater sieved by the net tow (Smith & Richardson 1977).

Paralarval densities were averaged from both sides of the bongo net by summing the volumes and then dividing by the total count of paralarvae. Values were square-root transformed for statistical analyses. Non-parametric, Mann-Whitney U tests were used to compare means of relative abundance. Monthly landings data were obtained from CDFW (https://www.dfg.ca.gov/marine/cpshms/landings.asp) and used to investigate temporal and spatial changes in landings and distribution across major spawning areas. Landings data are reported monthly for northern and southern California, corresponding to the MBR and the SCB for paralarval trawl data, respectively.

Model development

A generalized additive model (GAM) was chosen to model paralarval density using a set of environmental, biological, spatial and temporal predictors. A GAM proved useful in our study because the response variable (paralarval density) did not conform to a normal distribution, and the relationships between the response variables and the predictors was non-linear. GAM's have been used to model lolignid abundances (Bellido *et al.* 2001; Denis *et al.* 2002; Stewart *et al.* 2014), and larval fish abundance in the CCE (Weber & McClatchie 2010). We used the 'gam' function in the 'mgcv' package (Wood 2006) in the program R, version 3.1.1 (R Development Core Team 2014). We used the following equation to model paralarval density,

$$g(Y) = f_1(SST) + f_2(ZPDV) + f_3(SCHL) + f_4(fyear, mon) + f_5(group, sta)$$

where Y was the expected value of the response variable, estimated as the density of market squid paralarvae and $g(\cdot)$ was the link function defining the non-linear relationship between the density of paralarvae and the selected predictors. Our data displayed a negative binomial distribution, therefore we used a log link transformation as the link function, $g(\cdot)$. Finally, $f_k(\cdot)$ was the unique smoothing function assigned to each predictor. We used six predictors to model the abundance of market squid paralarvae, including sea-surface temperature (SST, °C), ZPDV (mL 1000 m^{-3}), log of surface chlorophyll-*a* (SCHL) (Table 1), month and fishing year interaction effect, and station and region interaction effect. SST was included as a station-specific measurement of the physiological suitability of the habitat. ZPDV and SCHL were used as separate predictors of habitat quality and food availability. Fishing year was included because squid spawning and paralarval abundance vary by year according to oceanographic conditions, ENSO state, adult spawning biomass, and other factors. Month was included to reflect the different spawning seasons between the SCB and MBR. Landings data were not included because the fishery routinely reached or neared the maximum catch limit before the end of most fishing years during the study period (sometimes closing voluntarily, as in 2014) which would have resulted in the negation of substantial paralarval information.

SST and SCHL values were obtained from NOAA satellite observations (coastwatch.noaa.gov). SST values were obtained using night and day measurements by the Advanced Very High Resolution Radiometer (AVHRR) instrument aboard the Polar Operation Environmental Satellite (POES) at a resolution of 1.4 km and 8-day composites. SST observations within 5 km of sampling stations the day of sampling were averaged to obtain a SST value for each station. Depending on satellite coverage and location, anywhere from 15-40 observations were used to yield a daily SST value.

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

Spawning peaks, inferred from monthly commercial landings data provided by CDFW, typically occur during autumn in the SCB, and spring in the MBR, with paralarvae hatching during the winter in the SCB and summer in the MBR. The fishery for market squid opens on April 1st and closes March 31st of the subsequent year, or when the maximum catch limit of 107,000 MT is reached. A value between 1 and 12 was given to the sampling month and included in the model. Five regions were also included: Monterey, north and south Channel Islands, and north and south southern California Bight (SCB) (Fig. 1). These regions are not independent, but were included to account for geographic patterns in the data. While market squid can freely migrate across broad north and south gradients off the California coast, these regions were selected as they adequately separated stations into north /south areas in the SCB, as well as between islands and the coast along a general north-west to south-east gradient that semelparous, spawning adults were unlikely to migrate between (Macewicz *et al.* 2004; Perretti 2014). These regions can provide insight into geographic site utilization by adults. SST, ZPDV, and SCHL values were included as main effects in the model, while temporal and geographic factors were allowed as interactions. Station was allowed to interact with region, and month was allowed to interact with fishing year, as the former variables were dependent on the latter.

Several constraints were included in the model to prevent overfitting, while allowing the model to be flexible enough to predict squid response. We limited the number of knots in the smooth splines to four. Secondly, we set the 'gamma' value in the gam formula to 1.4 in order to increase the penalty per degree of freedom fit and to minimize overfitting (Wood 2006). We performed model selection by using the shrinkage feature in the "gam" function instead of a forward/backward stepwise approach using the REML error criterion. This option allowed coefficients with little or no predictive ability to be shrunk to zero, effectively dropping these variables from the model.

Results

Relative paralarval abundance

We conducted 649 net tows in the SCB and MBR from January, 2011 through January, 2016, sampling > 62,000 market squid paralarvae. A total of 247 (38%) of these tows were absent market squid paralarvae, mostly from spring and summer efforts in the SCB (Fig. 2) and during strong El Niño years (2014-15 and 2015-16). For example, during peak El Niño conditions in January, 2016, 84% of net tows conducted in the SCB and the MBR were devoid of paralarvae. During the moderate La Niña of 2012, when paralarval abundance was highest, only 13% of net tows were absent market squid paralarvae. Densities varied widely both spatially and temporally. The mean abundance across all effort was 60.8 paralarvae 1,000 m^{-3} (± 14.1 SE). Paralarval densities were greatest during winter months in the SCB, particularly in January (Fig. 3, Fig. 4). Maximum paralarval density encountered at a single station was 5,691 paralarvae 1,000 m^{-3}, which occurred in January, 2013 in the north SCB. The greatest monthly mean relative abundance in the SCB was 377 (± 1005 SE) paralarvae 1,000 m^{-3} and occurred during January,

2012. The lowest mean relative abundance was 0.08 (± 0.04) paralarvae 1,000 m^{-3} and occurred during January, 2016 (Fig 3).

Environmental conditions

A transition from cool to warm ocean conditions occurred during the course of our study. The study period began during a moderate La Niña in 2011. Conditions gradually warmed, and an El Niño was issued by NOAA during early spring, 2015 and peaked as a strong El Niño in December, 2015 (cpc.ncep.noaa.gov, Table 1). Pacific Decadal Oscillation (PDO) values steadily increased throughout the study period, from approximately -2 in September, 2010 to > 2 in March, 2015, indicating that the eastern north Pacific became anomalously warmer during the investigation (Fig. 3). Local SST values were low during the initial three years of the study, and were higher during the final three years. Surface chlorophyll-*a* and ZPDV were considerably higher during the initial three years compared to the final three (Table 1, Fig. 4). These variables indicate that local waters were cooler and more productive during the La Niña phase, and warmer and less productive during the El Niño phase.

Density trends

Spawning shifted spatially and temporally during the transition from cool to warm ENSO conditions. Relative squid paralarval abundance in the SCB was high during the initial three years of the study, and steadily declined to very low levels during the final three years (Fig. 3). Sampling in the MBR began in the summer of 2014. Moderate levels of paralarval abundance were observed in the summers of 2014 and 2015 in the MBR. Greater paralarval abundance was observed in the MBR than the SCB during both the 2014-2015 and 2015-2016 fishing year (commercial fishing year extends from April 1st – March 31st). Paralarval abundance was greatest during the summer in the MBR (Fig. 3). The number of net tows absent market squid paralarvae increased during the study period as ocean conditions warmed. Only 9 out of the 92 (9.78%) January net tows conducted in the SCB during the first three years of cool ocean conditions were absent market squid paralarvae. In contrast, 49 out of 86 (57.7%) net tows conducted in the SCB during January from the last three years were absent market squid paralarvae, indicating a contraction of suitable spawning habitat during warmer periods in the SCB.

Relative paralarval abundance during January in the SCB was high (291.8 paralarvae 1000 m^{-3} ± 898.9 SE) during the cool La Niña period from 2011-2012, moderate during the winter of 2013-2014 (65.0 ± 125.0), and quite low (0.08 ± 0.04) during the strong El Niño of January, 2016 (Fig. 4). Relative January paralarval abundances in the SCB during both the cool (2011-2013) and neutral phase (2014) of the study were significantly greater ($p < 0.001$) than relative January paralarval abundance during the warm El Niño phase (2015-2016) of the study.

Spatial and temporal trends in density

Squid shifted northward from the SCB to the MBR, and spawning occurred earlier in the season during the ENSO transition, as evidenced by both paralarval densities and landings data from the fishery (Fig. 3). Commercial squid landings were very high in southern California during the La Niña, and gradually declined through the study period beginning in the fall of 2012. As landings declined in the SCB, they increased in the MBR, until the summer of 2015, when statewide landings dropped (Fig. 3). Approximately 88% of market squid landings occurred in southern California (SC) during the 2011-2012 fishing season, while 22% came from northern California (NC). Conversely, SC landings dropped to 52% (48% from NC) during the 2014-2015 fishing season. Relative paralarval abundances at the traditional spawning grounds showed a similar south to north shift. Paralarval densities in both the SCB and the MBR were lower statewide during the 2014-2015 fishing season, relative paralarval abundance was greater in the MBR than the SCB during July, 2014, August, 2015 ($p < 0.01$) and January, 2016 survey efforts.

The portion of the market squid population analyzed in this study appeared to spawn earlier in the year during the 2013-2014 commercial fishing-year. This temporal shift occurred during the ENSO-driven transition from cool to warm ocean conditions. During this cool to warm ocean transition, peak commercial landings shifted to the summer months in SC. Autumn months (particularly October and November) are typically the peak fishing times in SC. Relative paralarval densities exhibited a similar trend. Greater paralarval densities in the SCB occurred during summer surveys (Fig 3) and relative SCB paralarval abundance (37.3 ± 124.3 SE) in 2013 was greater than all other summer survey estimates, and significantly greater ($p < 0.05$) than paralarval abundance in the summer of 2011.

Model output

Strong relationships between paralarval density and SST, ZPDV, SCHL, and geographic and temporal variables were evident (Fig. 5). Greater densities were associated with cooler temperatures (< ~16.5 °C). Paralarval density increased with increasing ZPDV until approximately 200 ml 1,000m^{-3}. After this zooplankton concentration, the paralarval density decreased, but the associated model error increased considerably, indicating that zooplankton concentration is less important after ~200 ml 1,000m^{-3}, perhaps because food was no longer a limiting factor. Greater paralarval densities were associated with low SCHL values, and declined with increased SCHL values (Fig. 5). The model explained 40.6 % of the deviance associated with predicting paralarval density, and had an adjusted r^2 value of 0.31. Sea surface temperature, ZPDV, the interaction pairs of temporal and spatial variables ($p < 0.001$), and SCHL all contributed significantly to the model ($p < 0.05$) and are biologically important in determining market squid paralarval abundance at the traditional spawning locations in the SCB and the MBR.

Discussion

High market squid paralarval densities over the traditional spawning grounds in the SCB and MBR were associated with cool and productive La Niña conditions. Densities declined as the ocean moved to a warm and unproductive El Niño state. Gradually warming ocean conditions were related to earlier market squid spawning and northward shift in distribution toward cooler water. Subsequent years of anomalously warm temperatures then caused dramatic declines in relative paralarval densities and landings to the fishery.

Ecological and physiological effects of warm water on squid

Ocean temperature, squid metabolism, and prey availability are coupled, and these variables synoptically drive the variability observed in paralarval densities through ecological and physiological mechanisms. Ocean temperature influences the survival and growth of squids in many ecosystems (Bellido *et al.* 2001; Denis *et al.* 2002; Staaf *et al.* 2013). Cool ocean temperatures often indicate upwelled waters, elevated primary productivity, greater nutrient and oxygen availability, and consequently, greater zooplankton standing stock, which benefit the fitness and survival of market squid (Lynn *et al.* 1995; Mackas *et al.* 2006; Checkley & Barth 2009).

Warm ocean temperatures pose physiological restraints on market squid at each life-history stage. During the embryonic phase, lab studies demonstrated a hatching preference between 9-14 °C and a greatly reduced hatching rate at warmer temperatures (Zeidberg *et al.* 2011). We found high paralarval density associated with cooler surface temperatures (< ~16.5 °C), similar to the ambient temperatures found in the Zeidberg *et al*. (2011) study, and very few paralarvae at higher SST, indicating poor survivorship at the embryonic stage. Waters warmer than that eventually yield malformations in squid (Rosa *et al.* 2012). Additional variables beyond temperature can affect the process of embryogenesis and market squid development, however. Navarro (2014) found oxygen availability, important for the growth and survival of embryonic squid, increased over the shelf environment during El Niño.

At the paralarval stage, lab experiments indicate warm waters cause earlier hatching at a smaller size, produce individuals with reduced egg yolk, and cause these individuals to utilize their egg yolk faster (Vidal *et al.* 2002; Oosthuizen *et al.* 2002). This would indicate paralarvae would need to feed earlier and with a greater success rate compared to paralarvae hatched during cooler conditions. Conversely, field work by Perretti & Sedarat (2016) found larger length-at-age paralarvae during El Niño compared to La Niña, which they attribute to larger paralarval hatch sizes during El Niño, these contradictory results indicate more research is needed to resolve this issue. Market squid paralarvae consume anywhere from 35 to 80% of their body weight daily (Hurley 1976; Yang *et al.* 1986) and can starve after four days without food (Vidal *et al.* 2006), which underlies the importance of egg yolk quality, size, and reliable feeding opportunities. In our study, we found a strong relationship between high paralarval density and moderate zooplankton concentration in the water column. Spawning adults may have evolved to prefer areas of moderate zooplankton density as a way to ensure feeding opportunity for hatchlings and to increase their survivability. Paralarval density was then found to dramatically decrease at the highest zooplankton concentrations encountered. Several ideas could explain this trend. Some of these plankton-dense samples were dominated by a single organism type, which may not reflect an environment with a rich, stable, and diverse food source. High paralarval abundance would then not be expected in these examples. A zooplankton-rich environment dominated by a single species could also indicate a spawning event from a competitor species they may either outcompete squid paralarvae, or prey directly on paralarvae. Furthermore, zooplankton-rich waters could reduce oxygen availability to either the embryos or hatchlings and reduce survivability.

Mean surface chlorophyll-*a* concentrations across the SCB surveys co-varied with paralarval abundance across the time series, indicating that squid abundance is higher during productive oceanographic regimes. From a station to station perspective, however, we found an inverse relationship between paralarval density and surface chlorophyll-*a* concentration, with fewer paralarvae associated with higher chlorophyll-*a* levels. This would indicate that, while the overall productivity of the ecosystem is likely important, there is no direct causation between chlorophyll-*a* levels and paralarval abundance.

During the adult stage, gradually warming ocean conditions cause squid to mature faster (Forsythe 2004) and recruit to the spawning beds months earlier than anticipated (Sims *et al.* 2001). Warm temperatures increase the metabolic rate of squid, which not only results in early maturation, but also exerts additional energetic demands precisely when food is limited (O'Dor 1982). Accelerated maturation could affect the phenology of squid (the timing of biological events to environmental conditions), and cause a "match-mismatch" scenario that regulates recruitment variation (Cushing 1969). Market squid spawn in November, hatch in January, and reach the juvenile stage in spring during normal conditions in the SCB (Zeidberg *et al.* 2012). Spring corresponds to the period of greatest wind-driven upwelling in the CCE, which yields the greatest ocean productivity and highest euphausiid concentrations (Marinovic *et al.* 2002). Euphausiids are an integral prey resource for market squid (Karpov & Cailliet 1979, Van Noord unpubl.). If warming oceans cause squid to spawn early, juvenile stages could miss this reliable feeding event at a critical period of growth, affecting the timing of maturation and recruitment to the fishery. Additionally, El Niño events adversely affect the duration and intensity of upwelling in the CCE (Kahru & Mitchell 2000).

ENSO effects on the relative abundance, distribution, and behavior of squid

Warm oceanic conditions pose ecological and physiological challenges to market squid at multiple life history stages (Zeidberg & Hamner 2002; Reiss *et al.* 2004). These deleterious effects are evidenced by declines and distributional shifts in commercial fishery landings and relative paralarval abundances at the traditional spawning grounds in the SCB and MBR. As a result of the strong El Niño event of 1997, paralarval abundance and suitable habitat contracted in the CCE (Zeidberg & Hamner 2002; Reiss *et al.* 2004). Likewise, landings declined from 80,000 to 3,000 MT from one year to the next. Conversely, the population recovery during favorable ENSO conditions was equally dramatic. Paralarval abundance around the Channel Islands increased 98% one year after El Niño conditions abated (Zeidberg *et al.* 2006), while landings rebounded to 118,000 MT (CDFG 2005). Similar trends were observed in this study, relative paralarval abundance declined more than 99% from the moderate La Niña in 2012, to the to the strong El Niño of 2016, considering our January SCB survey effort. The fishery voluntarily closed during the 2014-2015 season, just shy of reaching the maximum catch limit of 107,000 MT. During the 2015-2016 season, the total catch was much lower, at 37,000 MT, with a majority of that catch coming from northern California as squid populations likely contracted and moved north, seeking cooler ocean conditions.

While well-documented, these dramatic boom and bust cycles are enigmatic (Butler *et al.* 1999; Reiss *et al.* 2004; Perretti 2014). Questions remain as to whether the population truly contracts in ways that reflect the paucity and glut of landings and paralarval density. Alternative hypotheses suggest that squid seek non-traditional spawning habitats in deeper, offshore waters or habitats farther north than what is currently sampled or commercially fished (Navarro 2014). Regardless of where adult squid may be spawning, there is likely a substantial overall reduction of paralarvae in the ecosystem. Surveys targeting the pelagic environment of the CCE (Leising *et al.* 2014) found a dearth of market squid paralarvae after prolonged El Niño events. If landings reflect the population biomass, then the intrinsic growth rate of the population and the survivorship of paralarvae following strong El Niño events would have to be remarkably high for the fishery to recover as rapidly as it does (CDFW 2005).

Alternatively, fishermen report changes in squid behavior that reduces catchability during El Niño periods of low abundance and density. Squid observed on the seafloor during strong El Niño conditions are unresponsive to the high-powered lights normally used to attract them to the surface where they are harvested by purse-seine nets, (N. Guglielmo, pers. comm.); given this avoidance behavior, a commercial fishery is not possible and commercial landings would therefore not reflect the true population. Under this scenario, squid could be spawning at harvestable densities but at deeper depths where the water is colder, and they are not attracted to the surface by traditional lighting methods. Paralarval would then be spread out over a wider surface area, and densities would be reduced, explaining the drop in paralarvae abundances observed in this study and elsewhere (Zeidberg & Hamner 2002; Navarro 2014).

Navarro (2014) has found evidence that spawning habitat during some El Niño scenarios may expand to include deeper shelf-waters. This deeper, shelf expansion would decrease the observable density through net tows and by commercial operations, but would not necessarily indicate a reduction in the abundance if the population is spread out across a greater area (Erisman *et al.* 2011). Reports have indicated that squid egg capsules have been observed in waters hundreds of meters deep (Butler *et al.* 1999; Zeidberg *et al.* 2012), which further suggests squid retreat to colder and deeper waters during warm ocean conditions, although pH and oxygen availability also influence habitat selection by market squid (Navarro *et al.* 2016).

The response by market squid to changes in temperature has implications for climate change. Warmer waters can shift fisheries north or into deeper offshore waters where they are not harvestable. The inshore environment in the CCE is also expected to suffer from lower pH and oxygen availability, further stressing market squid populations (Navarro *et al.* 2016). Ecosystem alternations due to climate change can affect the timing of the fishery and industry operations and reduce the standing stock, potentially costing millions in lost revenue. Chronically warm ocean temperatures can have cascading effects on food webs, as squid may disappear from southern locations in the CCE as a reliable food source for top-predators, while outcompeting and potentially replacing some fishes in northern ecosystems due to their high food demands, rapid growth, and high turnover rate (Pecl & Jackson 2007). Understanding the resiliency of squid and the effects from warming oceans can help predict climate change impacts to the CCE and the fishery.

This study represents the most comprehensive, on-going effort to directly assess the relative abundance of market squid paralarvae in nearshore waters and the conditions that influence the variability in the stock, density, and distribution. Warm temperatures pose ecological and physiological limitations on squid through feeding constraints and metabolic stress that alter the timing and location of spawning. We found that the densities and distribution of market squid paralarvae show a strong relationship to local sea surface temperatures and ocean productivity, where colder temperatures and moderate zooplankton displacement volumes promote greater paralarval densities, while warmer temperatures cause the population to spawn earlier, shift north, and contract. These findings indicate that squid density at the traditional spawning grounds in the SCB and MBR, distribution, and timing of spawning are largely driven by environmental forcing, while the effect from the fishing pressure is likely much less.

Acknowledgments Funding for this project was possible through the California Wetfish Producers Association and a cooperative grant from NOAA’s SWFSC. We would like to thank the CDFW for their cooperation, the captains and crews of charter vessels Sea Jay, Stardust, Donna Kathleen, and the many squid fishermen who provided observations and local knowledge. Thanks to L. Zeidberg and scientists at the NOAA SWFSC who assisted in establishing the survey protocol. Thanks to D. Hanan, the FV Outer Banks, and fishermen who participated in pilot surveys. Thanks to M. Sedarat, R. Taylor, L. Olsen, S. Martinez, and P. Carrey for laboratory assistance. Thanks to J. Zwolinski and B. Taylor for edits to improve this manuscript.

References

Bellido J.M., Pierce G.J., Wang J. (2001) Modelling intra-annual variation in abundance of squid *Loligo forbesi* in Scottish waters using generalised additive models. *Fisheries Research,* **52**, 23–39.

Butler J., Fuller D., Yaremko M. (1999) Age and growth of market squid (*Loligo opalescens*) off California during 1998. *California Cooperative Oceanic Fisheries Investigations Reports,*

40, 191–195.

Chavez F.P., Pennington J.T., Castro C.G., Ryan J.P., Michisaki R.P. (2002) Biological and chemical consequences of the 1997 – 1998 El Niño in central California waters. *Progress in Oceanography*, **54**, 205–232.

Checkley D.M., Barth J. A. (2009) Patterns and processes in the California Current System. *Progress in Oceanography,* **83**, 49–64.

Coll M., Navarro J., Olson R.J., Christensen V. (2013) Assessing the trophic position and ecological role of squids in marine ecosystems by means of food-web models. *Deep Sea Research Part II: Topical Studies in Oceanography*, **95**, 21–36.

Cushing D. (1969) The regularity of the spawning season of some fishes. *ICES Journal of Marine Science*, **33**, 81–92.

Denis V., Lejeune L., Robin J.P. (2002) Spatio-temporal analysis of commercial trawler data using General Additive models: patterns of Loliginid abundance in the north-east Atlantic. *ICES Journal of Marine Science*, **59**, 633–648.

Dorval E., Crone P.R., McDaniel J.D. (2013) Variability of egg escapement, fishing mortality and spawning population in the market squid fishery in the California Current Ecosystem. *Marine and Freshwater Research*, **64**, 80–90.

Erisman B.E., Allen L.G., Claisse J.T., Pondella D.J., Miller E.F., Murray J.H., Walters C. (2011) The illusion of plenty: hyperstability masks collapses in two recreational fisheries that target fish spawning aggregations. *Canadian Journal of Fisheries and Aquatic Sciences*, **68**, 1705–1716.

Fields (1950) A preliminary report on the fishery and on the biology of the squid, *Loligo opalescens*. *Calififornia Department of Fish and Game Fishery Bulletin*, **36**, 366–377.

Forsythe J.W. (2004) Accounting for the effect of temperature on squid growth in nature: from hypothesis to practice. *Marine and Freshwater Research*, **55**, 331.

Hurley A.C. (1976) Feeding behavior, food consumption, growth, and respiration of the squid *Loligo opalescens* raised in the laboratory. *Fishery Bulletin*, **74**, 176–182.

Jackson G.D., Domeier M.L. (2003) The effects of an extraordinary El Niño / La Niña event on the size and growth of the squid *Loligo opalescens* off Southern California. *Marine Biology,* **142**, 925–935.

Kahru M., Mitchell B.G. (2000) Influence of the 1997-98 El Niño on the surface chlorophyll in the California Current. *Geophysical Research Letters,* **27**, 2937–2940.

Karpov K.A., Cailliet G.M. (1979) Prey composition of the Market Squid, *Loligo opalescens* Berry, in relation to depth and location of capture, size of squid, and sex of spawning squid. *CalCOFI Rep* **20**, 51–57.

Koslow, J. A., and Allen, C. (2011). The influence of the ocean environment on the abundance of market squid , Doryteuthis (Loligo) opalescens , paralarvae in the Southern California Bight. *California Cooperative Oceanic Fisheries Investigations Reports,***52**, 205–213.

Leising A.W., Schroeder I.D., Bograd S.J., Bjorkstedt E.P., Field J.G., Sakuma K.M., Abell J., Robertson R.R., Tyburczy J., Peterson W.T., Brodeur R.D., Barcelo C., Auth T.D., Daly E.A., Campbell G.S., Hildebrand J.A., Suryan R.M., Gladics A.J., Horton C.A., Kahru M., Manzano-Sarabia M., Mcclatchie S., Weber E.D., Watson W., Santora J.A., Sydeman W.J., Melin S.R., DeLong R.L., Largier J., Kim S.Y., Chavez F.P., Golightly R.T., Schneider S.R., Warzybok P., Bradley R.W., Jahncke J., Fisher J., Peterson J. (2014) State of the California Current 2013 – 14 : El Niño Looming. *California Cooperative Oceanic Fisheries Investigations Reports,***55**, 51–87.

Leos R.R. (2014) California marine fish landings for 1987-1999. *Department of Fish and Game, Fishery Bulletin,* **181**, 1–53.

Lynn R.J., Schwing F., Hayward T.L. (1995) The effect of the 1991-1993 ENSO on the California Current system. *California Cooperative Oceanic Fisheries Investigations Reports,* **36**, 57–71.

Macewicz B.J., Hunter J.R., Lo N., LaCasella E. (2004) Fecundity, egg deposition, and mortality of market squid (*Loligo opalescens*). *Fishery Bulletin,* **102**, 306–327.

Mackas D.L., Peterson W.T., Ohman M.D., Lavaniegos B.E. (2006) Zooplankton anomalies in the California Current system before and during the warm ocean conditions of 2005.

Geophysical Research Letters, **33**, L22S07.

Marinovic B.B., Croll D.A., Gong N., Benson S.R., Chavez F.P. (2002) Effects of the 1997-1999 El Niño and La Niña events on zooplankton abundance and euphausiid community composition within the Monterey Bay coastal upwelling system. *Progress in Oceanography,* **54**, 265–277.

McPhaden M.J. (1999) Genesis and evolution of the 1997-98 El Niño. *Science,* **283**, 950–954.

Morejohn G.V., Harvey J.T., Krashnow L.T. (1979) The importance of *Loligo opalescens* in the food web of marine vertebrates in Monterey Bay, California. *California Department of Fish and Game Fishery Bulletin,* **169**, 67–98.

Navarro M.O. (2014) Consequences of environmental variability for spawning and embryo development of inshore market squid *Doryteuthis opalescens*. University of California, San Diego.

Navarro M.O., Kwan G.T., Batalov O., Choi C.Y., Pierce N.T., Levin L.A. (2016) Development of Embryonic Market Squid, *Doryteuthis opalescens*, under Chronic Exposure to Low Environmental pH and [O2]. *Plos One,* **11**, e0167461.

O'Dor R.K. (1982) Respiratory metabolism and swimming performacne of the squid, *Loligo opalescens*. *Canadian Journal of Fisheries and Aquatic Sciences,* **39**, 580–587.

Ohman M.D., Smith P.E. (1995) A comparison of zooplankton sampling methods in the CalCoFI time series. *California Cooperative Oceanic Fisheries Investigations Report,* **36**, 153–158.

Oosthuizen A., Roberts M.J., Sauer W.H.H. (2002) Temperature effects on the embryonic development and hatching success of the squid *Loligo vulgaris retnaudii*. *Bulletin of Marine Science,* **71**, 619–632.

Pecl G.T., Jackson G.D. (2007) The potential impacts of climate change on inshore squid: biology, ecology and fisheries. *Reviews in Fish Biology and Fisheries,* **18**, 373–385.

Perez J.A.A., de Aguiar D.C., Oliveira U. C. (2002) Biology and population dynamics of the long-finned squid *Loligo plei* (Cephalopoda: Loliginidae) in southern Brazilian waters. *Fisheries Research,* **58**, 267–279.

Perretti C. T. (2014) The boom and bust dynamics of California market squid (*Doryteuthis opalescens*). University of California, San Diego.

Perretti C.T., Sedarat, M. (2016) The influence of the El Niño Southern Oscillation on paralarval market squid (*Doryteuthis opalescens*). *Fisheries Oceanography*, 1–9.

R Development Core Team (2014) 'R: a language and environment for statistical computing'. (R Foundation for Statistical Computing: Vienna.)

Reiss C.S., Maxwell M.R., Hunter J.R., Henry A. (2004) Investigating environmental effects on population dynamics of Loligo opalescens in the southern California Bight. *California Cooperative Oceanic Fisheries Investigations Reports,***45**, 87–97.

Rosa R., Pimentel M.S., Boavida-Portugal J., Teixeira T., Trübenbach K., Diniz M. (2012) Ocean warming enhances malformations, premature hatching, metabolic suppression and oxidative stress in the early life stages of a keystone squid. *PloS one,* **7**, e38282.

Shane S.H. (1995). Relationship between pilot whales and Risso's dolphins at Santa Catalina Island, Califrnia, USA. *Marine Ecology Progress Series*, **123**, 5–12.

Sims D.W., Genner M.J., Southward A.J., Hawkins S.J. (2001) Timing of squid migration reflects North Atlantic climate variability. *Proceedings of the Royal Society of London B: Biological sciences*, **268**, 2607–2611.

Smith P., Richardson S. (1977) Standard techniques for pelagic fish egg nad larva surveys. *FAO Fishery Technical Paper*, **175**, 1–100.

Staaf D.J., Redfern J.V., Gilly W.F., Watson W., Ballance L.T. (2013) Distribution of ommastrephid paralarvae in the eastern Tropical Pacific. *Fishery Bulletin*, **111**, 78–89.

Stewart J.S., Hazen E.L., Bograd S.J., Byrnes J.E.K., Foley D.G., Gilly W.F., Robison B.H., Field J.C. (2014) Combined climate- and prey-mediated range expansion of Humboldt squid (*Dosidicus gigas*), a large marine predator in the California Current System. *Global Change Biology*, **20**, 1832–1843.

Vidal É.A.G., DiMarco F.P., Wormuth J.H., Lee P.G. (2002) Influence of temperature and food availability on survival, growth and yolk utilization in hatchling squid. *Bulletin of Marine Science*, **71**, 915–931.

Vidal, É.A.G., DiMarco F.P., Lee P.G. (2006) Effects of starvation and recovery on the survival, growth and RNA/DNA ratio in loliginid squid paralarvae. *Aquaculture,* **260**, 94–105.

Weber E., McClatchie S. (2010) Predictive models of northern anchovy *Engraulis mordax* and Pacific sardine *Sardinops sagax* spawning habitat in the California Current. *Marine Ecology Progress Series,* **406**, 251–263.

Wood S. (2006) ‘Generalized additive models: an introduction with R’. (Chapman & Hall/CRC: Boca Raton, FL.)

Yang W.T., Hixon R.F., Turk P.E., Krejci M.E., Hulet W.H., Hanlon, R.T. (1986) Growth, behavior, and sexual maturation of the market squid, *Loligo opalescens*, cultured through the life cycle. *Fishery Bulletin,* **84**, 771–798.

Zeidberg L.D., Butler J.L., Ramon D., Cossio A., Stierhoff K.L., Henry A. (2012) Estimation of spawning habitats of market squid (*Doryteuthis opalescens*) from field surveys of eggs off Central and Southern California. *Marine Ecology,* **33**, 326–336.

Zeidberg L.D., Hamner W.M., Nezlin N., Henry A. (2006) The fishery for California market squid (*Loligo opalescens*) (Cephalopoda: Myopsid), from 1981 through 2003. *Fishery Bulletin,* **104**, 46–59.

Zeidberg L.D., Isaac G., Widmer C.L., Neumeister H., Gilly W.F. (2011) Egg capsule hatch rate and incubation duration of the California market squid, *Doryteuthis* (=*Loligo*) *opalescens*: insights from laboratory manipulations. *Marine Ecology,* **32**, 468–479.

Zeidberg L.D., Hamner W.M. (2002) Distribution of squid paralarvae, *Loligo opalescens* (Cephalopoda: Myopsida), in the Southern California Bight in the three years following the 1997-1998 El Niño. *Marine Biology,* **141**, 111–122.

Table 1 Mean values of environmental and biological variables (± standard deviation) estimated using the January sampling effort within the southern California bight (SCB) from the winter of 2010 – 2016. Fishing season runs from April 1st to March 31st of the subsequent year. Ocean state is a qualitative description and refers to the general ocean condition during the squid fishing season and considers local sea surface temperature (SST), Multivariate ENSO index (MEI), and Pacific Decadal Oscillation (PDO) values. SCHL refers to surface chlorophyll-*a* values. SST and SCHL were aggregated from NOAA satellite data (see Methods). ZPDV refers to small zooplankton displacement volume.

Table and Figures

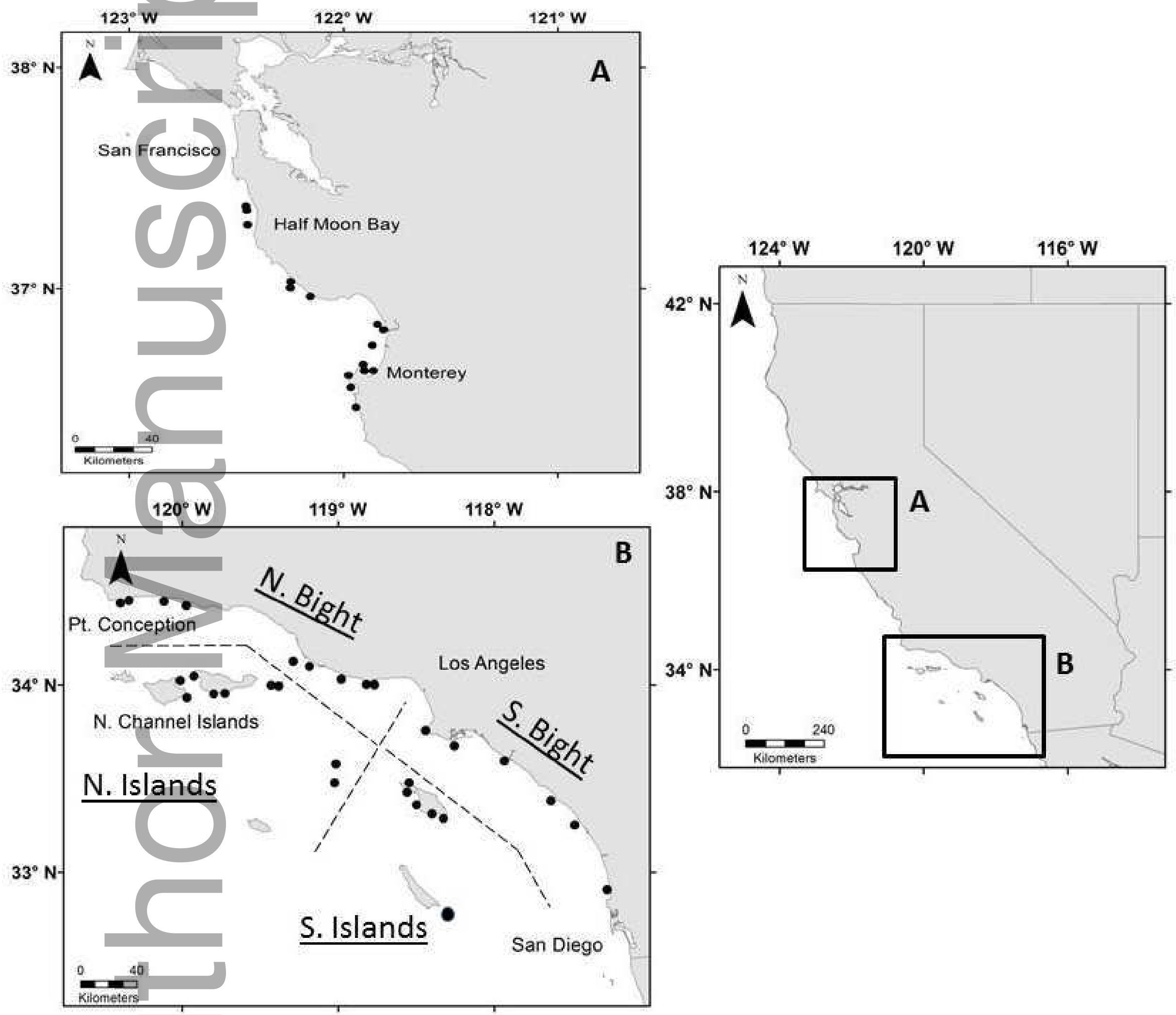

Figure 1 Sampling areas off California (right figure) are shown as black circles in the Monterey Bay Region (MBR), panel A, and in the Southern California Bight (SCB), panel B. Five regions are identified across the sampling effort and include Monterey, panel A; and, the north Bight and south Bight of the SCB, and north and south Channel Islands, panel B. Sampling occurred from 2011 – 2016 and occurred four times each year.

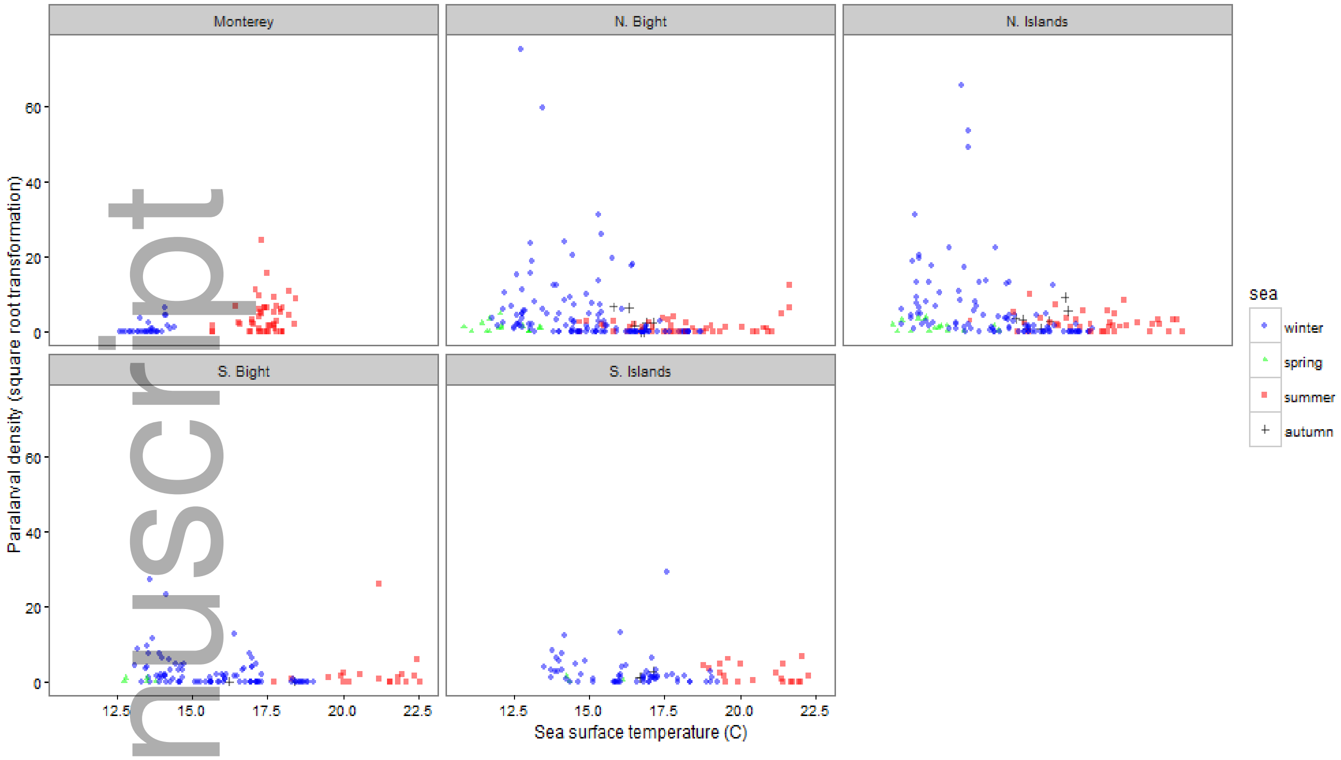

Figure 2 Square-root transformed paralarval abundance and sea surface temperature are shown by region (identified in Fig. 1) and season. Regions are indicated by panels and include Monterey, north and south Bight of the southern California Bight (SCB), and north and south Channel Islands. Seasons (sea) are shown by symbols and color. Transparency of color is related to the intensity of points at that location, with darker shades of color indicating greater points in that area.

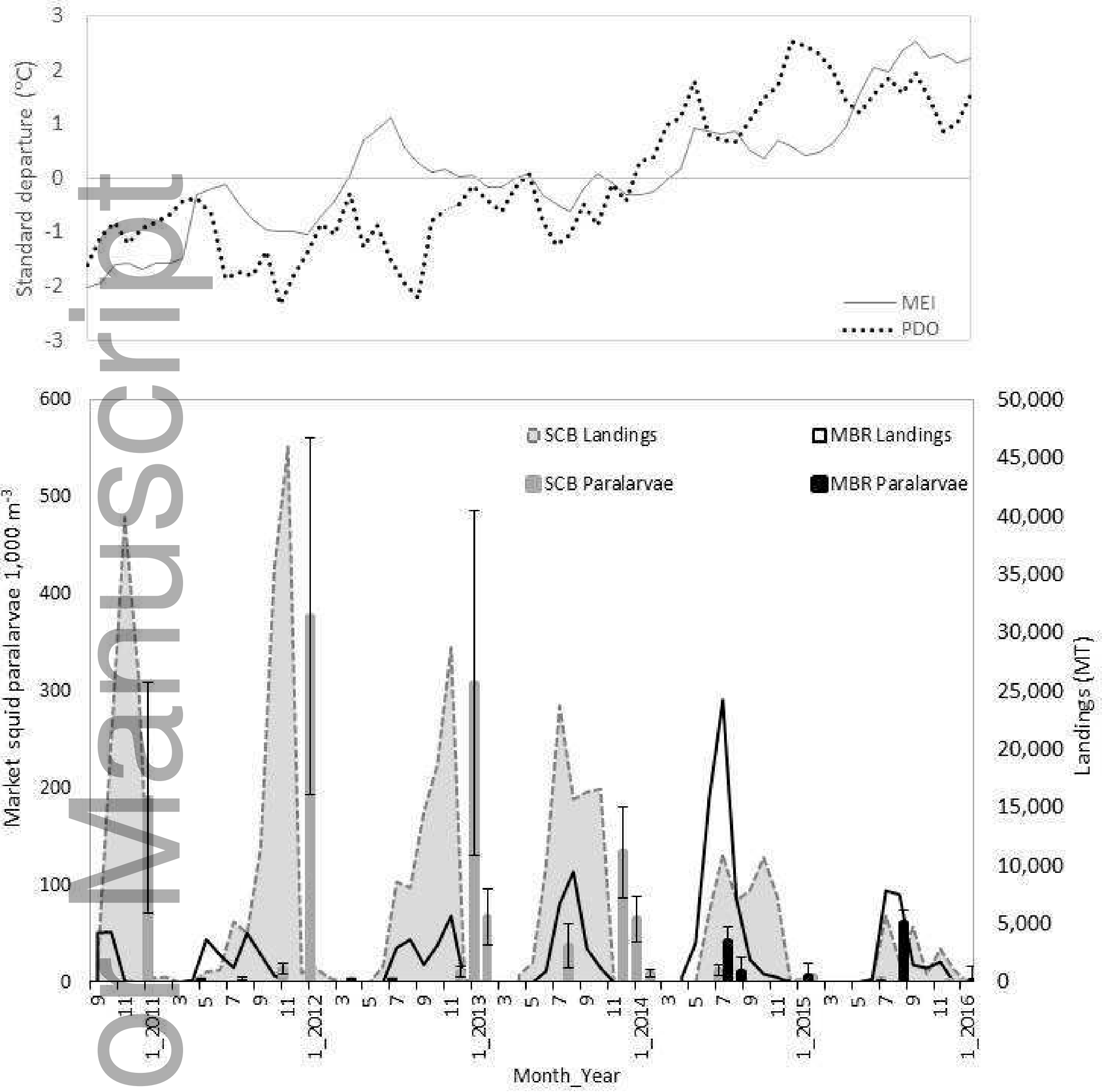
Standard departure (°C)
3
2
1
0
-1
-2
-3
MEI
PDO
Market squid paralarvae 1,000 m^{-3}
600
500
400
300
200
100
0
Landings (MT)
50,000
45,000
40,000
35,000
30,000
25,000
20,000
15,000
10,000
5,000
0
SCB Landings
MBR Landings
SCB Paralarvae
MBR Paralarvae
9
11
1_2011
3
5
7
9
11
1_2012
3
5
7
9
11
1_2013
3
5
7
9
11
1_2014
3
5
7
9
11
1_2015
3
5
7
9
11
1_2016
Month_Year

Figure 3 Top panel displays the trends in the Multivariate ENSO index (MEI), dotted grey line, and the Pacific Decadal Oscillation (PDO), solid black line. Negative values indicate a temperature that is cooler than the long term average from 1981-2010, while positive values indicate the opposite. Bottom panel displays market squid paralarval abundance on the left, and landings on the right y-axis. Southern California Bight (SCB) information is displayed in grey, bars for paralarvae, and shaded areas for landings. Monterey Bay Region (MBR) data are show in black, bars for paralarvae, and lines for landings. Error bars indicate two standard error. All data span September, 2011 through March, 2015. MEI and PDO data are from ersl.noaa.gov and jisao.washington.edu, respectively.

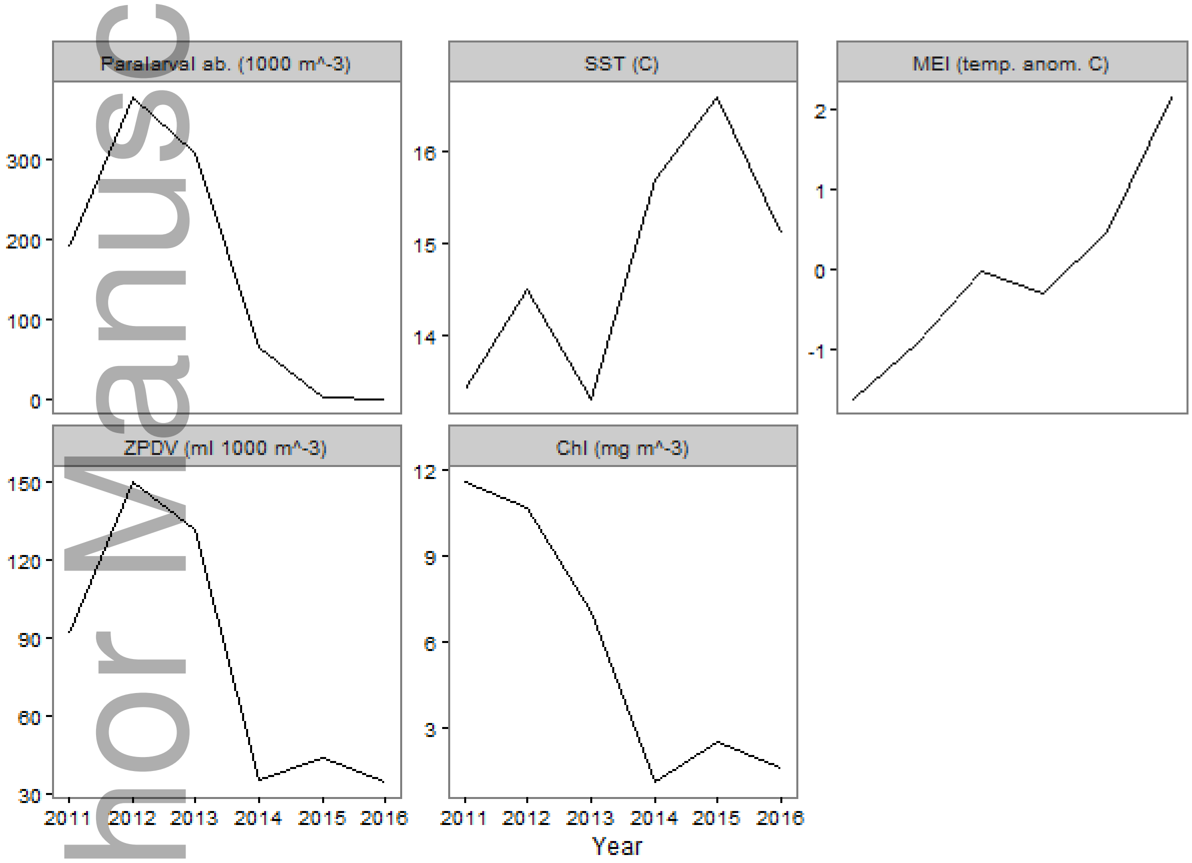

Figure 4.

Values for paralarval density and oceanographic variables sampled during the January survey effort in the southern California Bight for the six years, 2011-2016. SST indicates sea surface temperature, MEI is the multivariate ENSO (El Niño southern oscillation) Index, ZPDV is small zooplankton displacement volume, and Chl is surface chlorophyll-*a*.

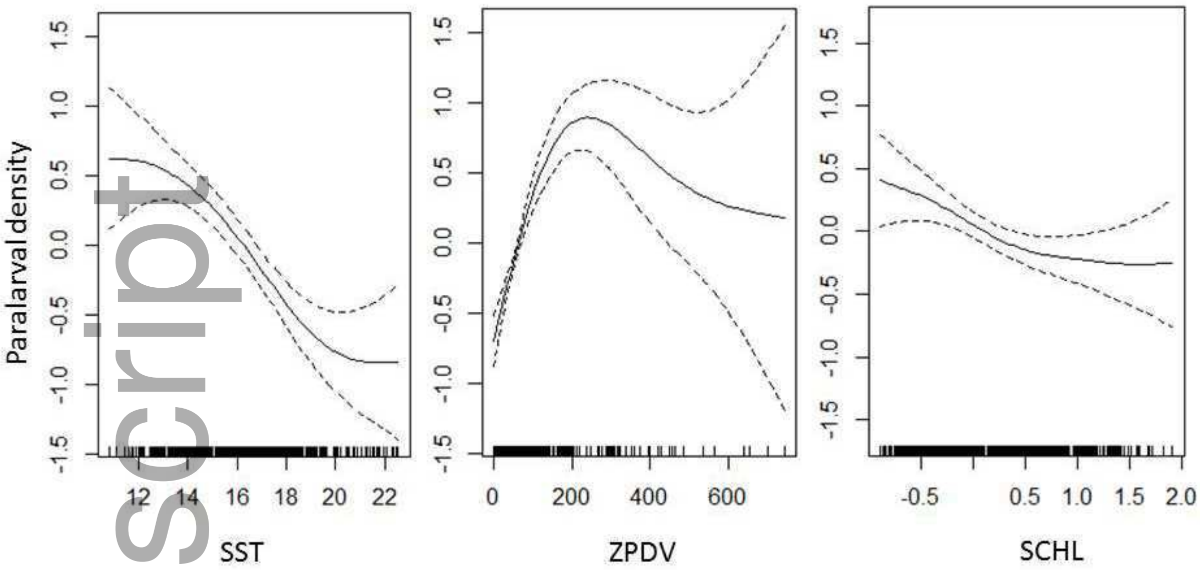

Figure 5 GAM model outputs showing the predicted paralarval density as a function of sea surface temperature (SST °C, left) and zooplankton displacement volume (ZPDV mL 1,000 m^{-3}, center) and the log of surface chlorophyll-*a* (SCHL mg m^{-3}, right). Dotted lines represent 95% confidence intervals. Vertical lines along the x-axis of each figure represent data points collected during the study.