THE INFLUENCE OF THE OCEAN ENVIRONMENT ON THE ABUNDANCE OF MARKET SQUID, *DORYTEUTHIS (LOLIGO) OPALESCENS*, PARALARVAE IN THE SOUTHERN CALIFORNIA BIGHT

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ABSTRACT

Using data from January–May CalCOFI surveys from 1981 to 2008, we investigated how the abundance of market squid paralarvae in the southern California Current varied in relation to local and large-scale environmental variables. Market squid paralarval abundance was significantly correlated with both near-surface temperature, nutrient and chlorophyll concentrations; and the El Niño–Southern Oscillation (ENSO) index. Stepwise regression analysis indicated a significant relationship primarily with ENSO and secondarily with the Pacific Decadal Oscillation, with local variables not entering significantly due to their high collinearity with ENSO. Paralarval abundance provides a fishery-independent index of stock biomass, and these statistical relationships suggest that the ENSO and PDO indices can be used for adaptive management of the market squid fishery. CPUE seems to have deficiencies as an index of stock biomass because the fishery is carried out on spawning aggregations.

INTRODUCTION

Doryteuthis (Loligo) opalescens (market squid) have been fished in California since the mid-1800s, when Chinese fishermen used small rowboats and torches to catch adult squid (Fields 1950; Porzio and Brady 2007; Vojkovich 1998). The fishery was of relatively limited value and importance, with landings generally on the order of 10,000 t or less, until the mid-1980s. The fishery then shifted from brail and lampara nets to purse seines (and later, drum seines), and landings increased markedly. In the mid-1990s, market squid became the largest California fishery in terms of both landings and revenue. In 2009, squid fishermen landed over 92,000 metric tons of squid, with an ex-vessel value of about $56.5 million (Sweetnam 2010).

Despite the regional importance of the fishery, the fishery is "monitored," without a formal stock assessment to guide management. The squid fishery is regulated with restrictions on gear, weekend closure dates, a seasonal 118,000 ton catch limit, and permit limits (California Department of Fish and Game 2005). The catch limit is based on the approximate maximum landings obtained in three seasons since 1998–2000, but landings over the past decade have been mostly about half the total allowable catch. Catch per unit effort (CPUE) has been relatively steady, but CPUE is generally unreliable as a proxy for stock biomass, particularly for a fishery with evolving gear technology and that targets spawning aggregations (Hilborn and Walters 2001).

The market squid lives to only 6–9 months (Butler et al. 1999), and the population fluctuates markedly from year to year, largely in apparent response to environmental factors. During El Niño events, the fishery has declined precipitously by an order of magnitude and more. However, it recovers typically within a few years, particularly in response to La Niña events (Zeidberg et al. 2006). The preponderance of evidence indicates that these dramatic fluctuations are more likely due to changes in abundance than mere shifts in availability to the fishery (Reiss et al. 2004). However, the impact of the fishery on the population is not understood, and there are concerns about overexploitation during the periodic downturns of the population (Zeidberg et al. 2006). Improved proxies for stock biomass, as well as a better understanding of the species' response to environmental conditions may contribute to the sustainable management of the fishery.

The role of squid in the food web of the California Current has not been quantified. However, as juveniles they feed predominantly on pelagic crustaceans, such as copepods and euphausiids, shifting to larger prey, such as fish, as they mature (Fields 1965; Karpov and Caillet 1978). They are consumed in turn by a variety of predatory fishes, seabirds, and marine mammals (Fields 1965; Morejohn et al. 1978). In view of their apparently high abundance and rapid turnover, they presumably play a key role in the transfer of production from the plankton to higher trophic levels within the California Current.

To examine changes over time in market squid abundance, we used data from California Cooperative Oceanic Fisheries Investigations (CalCOFI) research cruises. These cruises, carried out quarterly since 1984,
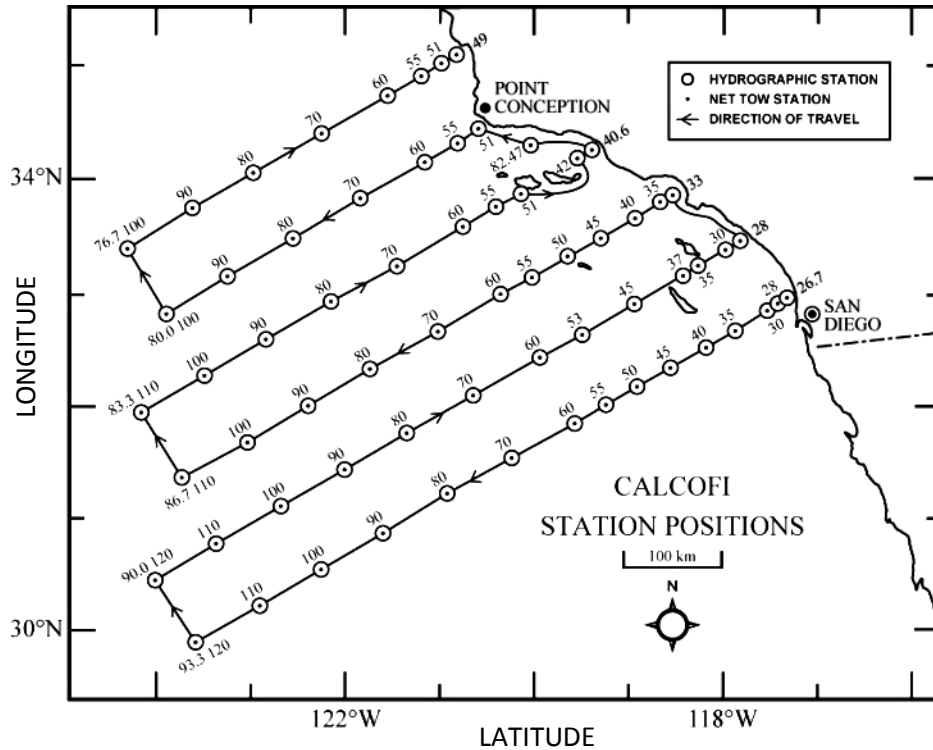
Figure 1.   CalCOFI station map showing the core CalCOFI transects and stations. Market squid paralarvae were examined from station lines 76.7 to 93.3 and station numbers 26.7 to 70.

collect data on the physical, chemical and biological oceanography of the southern California Current, including plankton samples from a regular grid of stations (fig. 1). Larval squid, known as paralarvae, are regularly sampled and enumerated from the plankton tows. Although formal stock assessments based on egg and larval data make use of ancillary data on fecundity and other factors (Lasker 1985), ichthyoplankton abundance alone has been shown to be significantly correlated with more formal stock assessments for a variety of taxa (Moser and Watson 1990; Moser et al. 2000, 2001; Koslow et al. in press). Most of the ichthyoplankton obtained on CalCOFI cruises are at very early (preflexion) stages of development, due to net avoidance by better developed larval and juvenile fish. The ichthyoplankton data therefore primarily reflect spawning effort, a function of adult spawning biomass, rather than subsequent recruitment. Market squid largely spawn nearshore, so the paralarval distribution is only partially sampled by CalCOFI (Zeidberg and Hamner 2002). However, CalCOFI presumably samples a reasonably constant proportion of the market squid population during its early life history. Given the length of the CalCOFI data set, its consistency and broad spatial coverage, we believe it may provide insight into the factors affecting market squid population dynamics if examined in relation to environmental variables.

MATERIALS AND METHODS

Several plankton net tows are carried out at each station on CalCOFI cruises: double oblique tows with a bongo net, neuston tows with a manta net, and vertical tows. However, market squid paralarvae were only obtained in sufficient quantities for time-series analysis in the manta tows, which sample 8 cm below the air-sea interface for 15 minutes at about 1.5 knots. Previous studies have also observed a low abundance and low incidence of *Doryteuthis opalescens* from oblique plankton tows (Okutani and McGowan 1969; Recksiek and Kashiwada 1979). The manta data for market squid paralarvae begin in January 1981 and continue through January 2008 and can be found in the NOAA/Scripps Institution of Oceanography Ichthyoplankton Database (IchthyoDB: http://oceaninformatics.ucsd.edu/ichthyoplankton). More detailed descriptions of tow protocol can be found on www.calcofi.org/cruises/stationwork.html. Because the paralarvae are predominantly found in coastal waters (fig. 2) (Zeidberg and Hamner 2002), we used CalCOFI's standard 66 station grid and examined station lines 76.7 to 93.3 and station numbers 26.7 to 70 (fig. 1). Our index of paralarvae abundance in the study area was based on data from January through May, when they were most abundant (see Results). This period corresponds, with appropri-
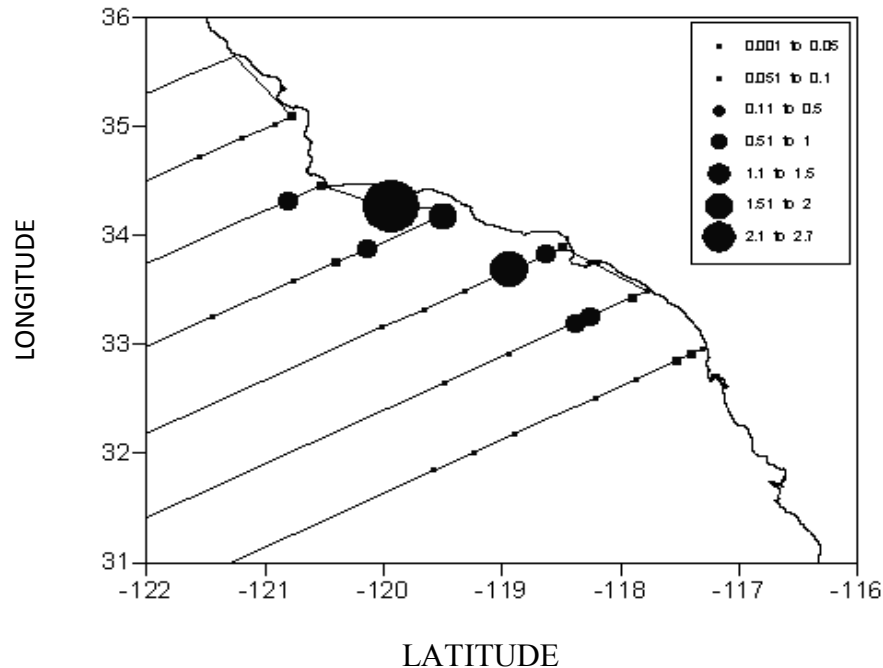
Figure 2.   The average abundance (numbers/m³) of market squid paralarvae at CalCOFI stations, showing their predominantly coastal distribution.

ate lag for the 1–2 month incubation period for the squid eggs (Zeidberg et al. 2011), with the December–April period of peak fishing on spawning aggregations of market squid in southern California waters. Only data from the night tows were used in the time-series analysis because of their far greater abundance at night (see Results). "Night" was defined as an hour after sunset to an hour before sunrise, based on the average sunrise and sunset times for each month sampled. The paralarval data were quantified as numbers per 1000 m³. To obtain the annual mean abundance index, market squid paralarval abundance from all night manta tows within the grid of interest from January to May were averaged. One anomalous data point was removed from our paralarval data set: station 83.3, 51 on the April 1992 cruise, at which 1,563 paralarvae were obtained, the highest value by a factor of about five for any station in the time series. For the remainder of the cruise, only 6 market squid were caught at a single other station. The anomalous station was likely the result of sampling recently hatched paralarvae above an egg mass.

We examined the relationship between annual mean paralarval abundance and environmental variables sampled on the CalCOFI cruise and indices for several large-scale environmental features: the El Niño–Southern Oscillation (ENSO) (National Oceanic and Atmospheric Administration (NOAA) Climate Prediction Center: http://www.cpc.noaa.gov/data/indices); the Pacific Decadal Oscillation (PDO) (University of Washington: http://jisao.washington.edu/pdo/PDO); the North Pacific Gyre Oscillation (NPGO) (Di Lorenzo: http://www.o3d.org/npgo/data/NPGO.txt); and upwelling based on offshore Ekman transport at 33°N and 119°W (Pacific Fisheries Environmental Laboratory: http://las.pfeg.noaa.gov/las6_5/servlets/dataset). All environmental variable values were averaged between January and May based on monthly mean data.

Physical and biological data were obtained from the same CalCOFI cruises as the paralarvae for temperature (°C), salinity, oxygen (O_2), phosphate (PO_4), silicate (SiO_3), nitrate (NO_3), and chlorophyll a (chl a) from a depth of 10 m, and zooplankton displacement volume (DV) integrated over the water column (0–200 m) from double oblique bongo tows, from which zooplankton > 5 mL DV (i.e., large gelatinous plankton, such as medusae, salps, and doliolids) were removed. These local oceanographic variables were averaged between January and May to obtain annual means corresponding to conditions over the spawning period and early life history. These data were obtained from the CalCOFI database: http://oceaninformatics.ucsd.edu/datazoo/data/calcofi-sio/datasets?action=summary&id=78.

Market squid catch and effort data were obtained from California Department of Fish and Game for the southern California sector of the fishery, the area covered by the CalCOFI grid (D. Sweetnam and B. Brady, California Department of Fish and Game, pers. commn.). We estimated catch per unit effort (CPUE) as average catch per landing for the peak months of the southern California fishery from December through April: the
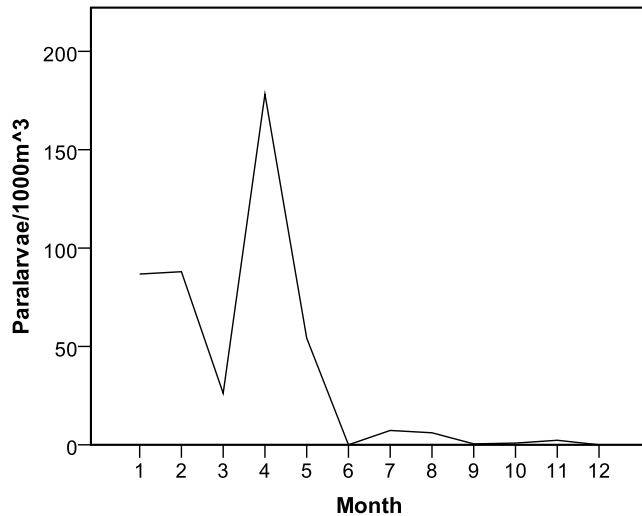
Figure 3.   The mean monthly abundance of *Doryteuthis opalescens* paralarvae (1981–2008) (#/1000 m³) at the core CalCOFI stations.
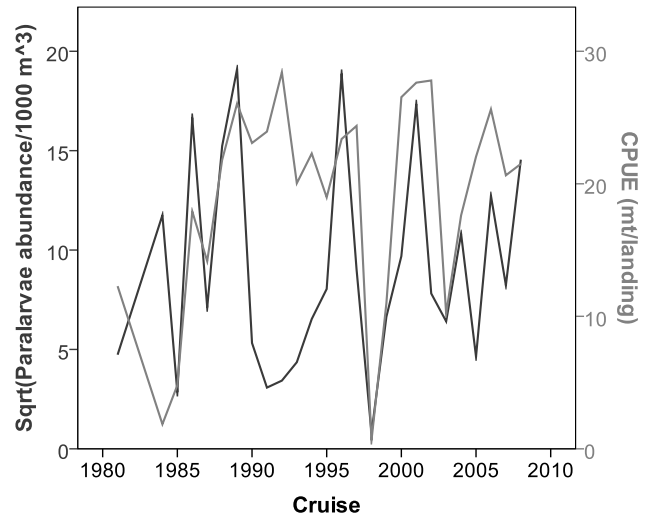

Figure 4.   Time series of *Doryteuthis opalescens* paralarval abundance ((#/1000 m³)½) and CPUE for the southern California commercial fishery (mt/landing).

total squid catch for those months divided by the number of vessel landings.

Significant deviations from normality were assessed based on visual inspection of the probability distributions combined with the Kolmogorov-Smirnov test. The paralarval abundance and zooplankton data departed significantly from normality and were square-root transformed, which better achieved normality than log-transformation.

We initially carried out an exploratory analysis in which we examined for the presence of significant correlations among the time series. Where there were nominally significant correlations, we examined first for the presence of significant trends among the time series, which can be a source of spurious correlations. Where present, trends were removed by replacing the original time series with the residuals from the regression of the original time series with YEAR. Correlation analysis was rerun on the residual time series, and where the correlation remained significant based on the nominal degrees of freedom, we examined the time series correlograms for autocorrelation of the time series at successive lags. Autocorrelation reduces the effective number of independent data points (or degrees of freedom), leading to inflated estimates of significance, if uncorrected (Pyper and Peterman 1998). Autocorrelation was not detected as a significant source of bias in our analysis.

Because many local environmental variables were intercorrelated, we applied a principal component analysis (PCA) to reduce the dimensionality of the variable set (Legendre and Legendre 1983). The PCA was based on the correlation matrix for the following variables: upwelling, temperature, salinity, O_2, NO_3, chl *a*, and zooplankton DV. Several nutrient variables were

removed from the PCA due to their high collinearity with NO_3 (see Results). Stepwise regression analysis was used to assess the contribution of environmental variables and indices to explaining the variability of the paralarval data set.

RESULTS

Doryteuthis opalescens paralarvae were 26-fold more abundant from January to May than during the latter part of the year (fig. 3). During this period of peak abundance, the larvae were 520 times more abundant in the night than the daytime manta tows, indicating a strong tendency to migrate into near-surface waters at night. There was no significant difference in the size composition of *D. opalescens* paralarvae from the manta and oblique bongo tows (William Watson, pers. commn., SWFSC), indicating that diel vertical migrations are carried out through the paralarval period of the life history.

The paralarvae were most abundant around the coastal islands and inshore regions of the Southern California Bight (fig. 2). They were infrequently present in deeper waters out to station 70, less than 300 km from shore, but were rarely observed farther out to sea. This is consistent with other studies of their distribution based on other sampling methods, such as with oblique bongo tows (Okutani and McGowan 1969; Zeidberg and Hamner 2002).

Paralarval Abundance as an Index of Spawning Stock Biomass

We examined the market squid paralarval abundance in relation to the catch per unit effort (CPUE) data for the commercial fishery to assess their suitability as indices of *D. opalescens* spawning stock biomass (fig. 4). The
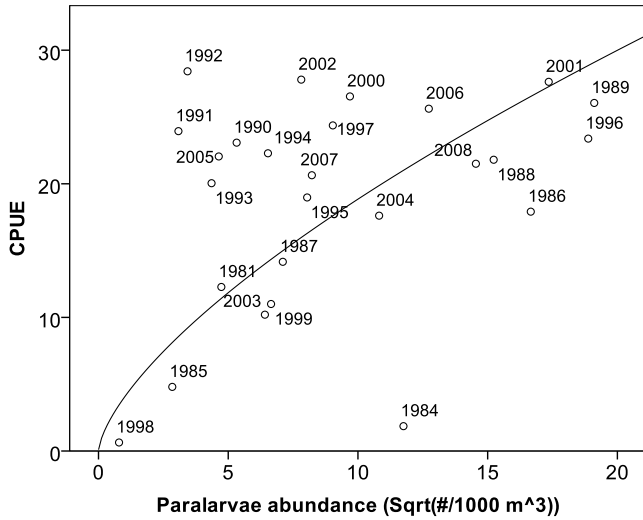
Figure 5. Scatterplot of market squid CPUE from the southern California fishery (mt/landing) and paralarvae abundance ((#/1000 m³)⁰·⁵). The fit of a power function is shown: $y = 4.03 \, x^{0.67}$, $R^2 = 0.30$, $p < 0.01$.

CPUE data, but not the paralarval data, exhibited significant trend, increasing with time ($p < 0.05$). The linear correlation between the time series was marginal ($r = 0.35$, $p = 0.08$). However, the initial sharp increase in CPUE appears to have led to a significant nonlinear relationship between the two time series (fig. 5). Both time series record the precipitous drop in squid spawn-

ing stock during the major El Niño events of 1998 and lesser decline during the moderate El Niño of 2003. However, during several periods of moderate El Niño conditions, notably the early 1990s and around 2005, paralarval abundance was reduced but the fishery and CPUE remained high. There was no significant relationship between paralarval abundance and CPUE in the following year, indicating that paralarval abundance is not significantly related to subsequent recruitment.

Environmental Relationships

About half of the environmental variables were significantly correlated with market squid paralarval abundance: temperature, nitrate, phosphate, and silicate, and chlorophyll a at 10 m and the ENSO index (table 1). However, the PDO and NPGO indices, as well as upwelling, salinity, oxygen, and zooplankton biomass, were not significantly correlated with the *D. opalescens* time series. None of these variables were significantly autocorrelated.

Most of the local variables significantly correlated with *D. opalescens* paralarval abundance were also significantly correlated with ENSO and with each other (table 2). This is not surprising: upwelling intensity, near-surface ocean temperature, salinity, nutrient and oxygen concentrations, and phytoplankton and zooplankton abundance are interrelated ocean properties influenced by the ENSO cycle. We therefore carried out a princi-

TABLE 1

Pearson correlations of market squid (*Doryteuthis opalescens*) paralarval abundance, square-root transformed with local environmental variables measured at 10 m depth: temperature (T), salinity (S), oxygen (O$_2$), nitrate (NO$_3$), phosphate (PO$_4$), silicate (SiO$_3$),chlorophyll a (chl), and square-root transformed zooplankton displacement volume (Zoo); also, upwelling at 33°N, 119°W, and the ENSO, PDO, and NPGO environmental indices. The temperature, nitrate, and zooplankton time series were detrended. *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$ (two-tailed significance). N = 26.

	T	S	O$_2$	NO$_3$	PO$_4$	SiO$_3$	Chl	Zoo	Upwell	ENSO	PDO	NPGO
Doryteuthis opalescens paralarvae	0.47★	0.06	0.33	0.49★	0.49★	0.53★★	0.51★★	0.29	0.17	0.71★★★	0.09	0.25

TABLE 2

Pearson correlations for mean values (January–May) of the ENSO index, upwelling at 33°N, 119°W and local environmental variables measured at 10 m depth: temperature (T), salinity (S), oxygen (O$_2$), nitrate (NO$_3$), phosphate (PO$_4$), silicate (SiO$_3$), chlorophyll a (chl), and square-root transformed zooplankton displacement volume (Zoo). The local variables are averaged over all CalCOFI stations shown in Figure 1. The temperature, nitrate, and zooplankton time series were detrended. The correlation coefficients are shown in the right upper part of the table and the significance levels in the lower left (n = 27–28). *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$ (two-tailed significance).

	ENSO	T	S	O$_2$	NO$_3$	PO$_4$	SiO$_3$	Chl	Zoo	Upwell
ENSO		.79	.20	.55	.67	.55	.58	.48	.49	.49
T	★★★		−.32	−.60	−.79	−.56	−.70	-.47	−.53	−.60
S				.16	.36	.20	.29	.02	.26	.49
O$_2$	★★	★★			.43	.45	.07	.21	.55	.32
NO$_3$	★★★	★★★		★		.86	.82	.61	.28	.43
PO$_4$	★★	★★		★	★★★		.30	.52	.17	.18
SiO$_3$	★★	★★★			★★★			.52	.09	.43
Chl	★	★			★★	★★	★★		.20	.01
Zoo	★★	★★		★★						.47
Upwell	★★	★★	★★		★		★		★	

TABLE 3

Variable loadings on principal component 1 (PC1). The variables were transformed and detrended as in Table 2.

Variable	PC1
Temperature (C)	−0.92
Salinity (PSU)	0.50
O_2 (ml/L)	0.71
NO_3 (uM/L)	0.81
Chl *a* (mg/m^3)	0.49
Zooplankton Biomass	0.68
Upwelling	0.71
Variance Explained	49.6%

pal component (PC) analysis of the local oceanographic variables, including upwelling intensity, to reduce the dimensionality of the data set prior to further analysis. We also considered it unlikely that any single variable, except possibly zooplankton availability or temperature, influenced squid abundance in isolation. Because the nutrient variables were closely intercorrelated (r = 0.82–0.86 for the correlation of NO_3 with PO_4 and SiO_3), only NO_3 was entered into the PCA to avoid biasing the analysis toward the nutrients.

The first PC explained 49.6% of the variance of the seven environmental variables entered into the analysis (eigenvalue (λ) = 3.5), more than twice the explanatory power (18.7%) of PC2 (λ = 1.3). All seven variables had factor loadings on PC1, equal to the correlation of the PC1 time series with the time series of the individual variables, of 0.49 or greater (table 3). Temperature and nitrate concentration at 10 m depth were most closely linked to PC1 (loadings = −0.92 and 0.81, respectively), followed by upwelling and oxygen concentration at 10 m (loadings = 0.71). PC1 was significantly correlated with the abundance of market squid paralarvae (r = 0.43, n = 26, p < 0.05), as well as with ENSO, the PDO, and NPGO, but not with the squid fishery CPUE (table 4). The strongest correlation was with ENSO (r = 0.77, p < 0.001). The strong relationship between ENSO and the market squid paralarval abundance is seen in Figure 6. The apparent outliers to the relationship (1985, 1999, 2000) followed the strong El Niño events of 1983 and 1998. It is apparent that although the fishery recovered within a year of these El Niño events (fig. 4), paralarval abundance (and by implication, the squid stock biomass) required more than two years to recover.

Stepwise regression was used to examine the explanatory power of PC1 and the ENSO, PDO, and NPGO
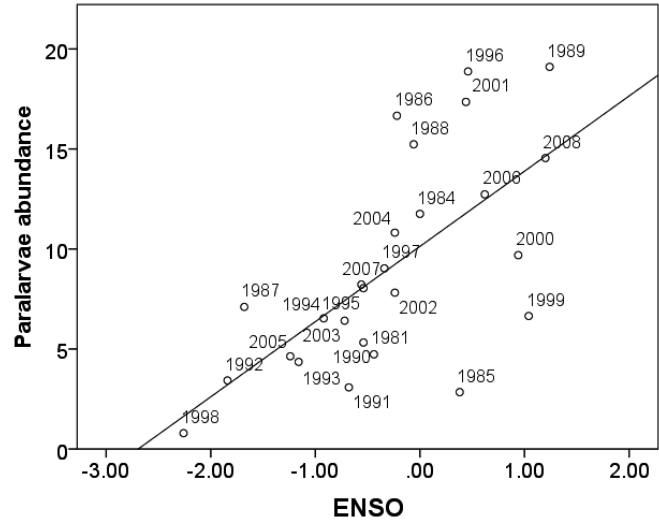

Figure 6. Scatterplot of the ENSO index and market squid paralarval abundance per 1000m³, square-root transformed. El Niños correspond with periods when the index is negative, La Niñas with when it is positive. The three years that appear to be outliers to the linear relationship (1985, 1999, 2000) followed the strong El Niño events of 1983 and 1998. (1982, 1983 not shown because CalCOFI did not sample those years.) The linear relationship is shown: $y = 10.13 + 3.76*ENSO$, $R^2 = 0.43$, $p < 0.001$.

TABLE 5

Results of stepwise regression analysis with market squid paralarvae abundance as dependent variable and PC1, ENSO, PDO, and NPGO as independent variables. ENSO and PDO entered significantly into the regression in that order. *: p < 0.05; **: p < 0.01; ***: p < 0.001 (two–tailed significance).

Regression Components	Unstandardized Coefficients		Standardized Coefficients	
	R^2	B	β	t
Constant		9.15		10.52***
ENSO	0.43	4.94	0.87	5.20***
PDO	0.54	2.46	0.39	2.35*

indices in explaining the variance in market squid paralarval abundance. ENSO was most highly correlated with paralarval variance and entered the regression first. Once ENSO entered the regression, only the PDO contributed significantly to explaining the remaining variance in paralarval abundance (table 5). ENSO explained 43% of the variance in the paralarval data; adding the PDO explained a further 11% of the variance, for a total of 54%. The standardized regression coefficients (β) indicate that ENSO explained more than twice the variance in paralarval abundance than the PDO (table 5). Time

TABLE 4

Correlations of PC1 with market squid paralarval abundance (Paralarvae), ENSO, PDO, NPGO and the detrended CPUE for the squid fishery. *: p < 0.05; **: p < 0.01; ***: p < 0.001 (two–tailed significance).

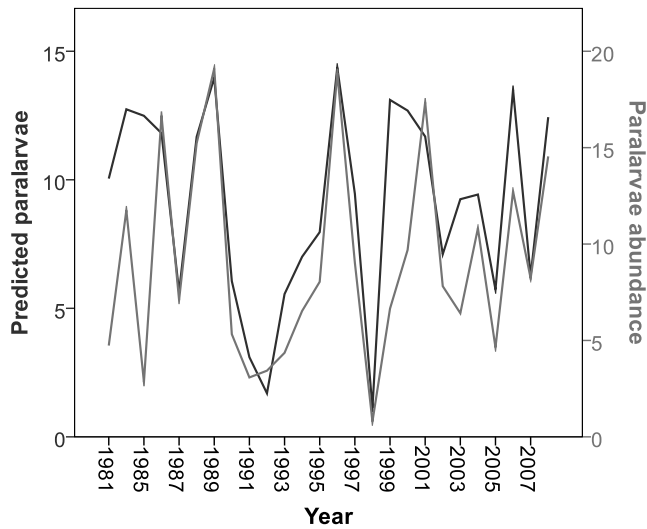| Variables	Paralarvae	ENSO	PDO	NPGO	CPUE
PC1	0.43*	0.77***	0.45*	0.43*	0.10

Figure 7. Market squid paralarval abundance and its abundance predicted based on a stepwise regression with ENSO and PDO.

series of the observed paralarval abundance and that predicted by this regression indicate a strong relationship, with most high-frequency variability (rapid shifts in abundance) explained (fig. 7).

DISCUSSION

Several studies have examined the vertical distribution of *D. opalescens* paralarvae, based on plankton tows at discrete depths from 5 or 10 m to several hundred meters depth (Okutani and McGowan 1969; Zeidberg and Hamner 2002). However, previous studies did not sample the neuston. The exceptionally high relative concentration of the paralarvae in the night manta tows (>500-fold more abundant in the manta tows at night than in the day) indicates that a substantial fraction of the paralarvae migrate into the neuston at night. This was critical to our study, since their density from the CalCOFI integrated water-column sampling appeared too low and patchy to allow successful analysis. The nighttime manta tow data provide a readily accessible fishery-independent time series for this key species in the California Current.

We were not surprised that ENSO and the PDO, rather than the local environmental variables synthesized in PC1, entered the regression to explain paralarval abundance. There was high collinearity between PC1 and the ENSO index (a correlation of 0.71), so the two indices explained a highly overlapping component of the variability. Once ENSO had entered the regression, PC1 no longer explained a significant portion of the variability. However, the PDO, which was not significantly correlated with paralarval abundance on its own, explained a significant portion of the remaining variability after ENSO entered the regression. The mecha-

nism underlying this relationship is uncertain but may be related to loss of suitable spawning habitat during El Niño events. Zeidberg et al. (2011) have shown that *D. opalescens* exhibits a narrow temperature range for its preferred spawning habitat (optimum ~12°C, range+ 9–14°C), which is generally found at 20–70 m depth. Depression of isotherms during strong El Niño events deepens the squid's spawning habitat to depths where diminished currents may affect oxygen availability on the dense spawning beds.

Several authors have previously noted the dramatic impact of strong El Niño events on the southern California market squid fishery (Reiss et al. 2004; Zeidberg et al. 2006). This may result from enhanced mortality or deepening of squid spawning beyond the range of the fishery's purse seine gear. Decreased incidence of market squid in the diet of sea lions, a major squid predator, during El Niño events also indicates a major decline of the squid population at those times (Lowry and Carretta 1997). However, more remarkable than the dramatic decline of the squid fishery during an El Niño event has been its recovery, often within a year (fig. 4) (Reiss et al. 2004). Without a fishery-independent time series or other means to assess stock size, it has not been possible to assess whether the stock had in fact recovered to the extent that the improved fishery indicated. The fishery is conducted on nearshore spawning aggregations (Vojkovich 1998). As a result, landings and CPUE likely provide only crude indices of stock abundance, revealing only extreme fluctuations (or possibly changes in availability), such as during major El Niño events. The fishery-independent paralarval time series suggests that the *D. opalescens* spawning stock may recover more slowly than the fishery, consistent with focused spawning ground paralarval surveys following the 1997–98 El Niño event (Zeidberg and Hamner 2002).

Although the CalCOFI surveys were designed to sample the extensive spawning habitat of the Pacific sardine within the southern California Current, rather than the nearshore spawning habitat of the market squid, the sampling grid is extensive, with transects extending to the 20 m isobaths, and consistent over almost 30 years of manta-tow sampling. This provides a fishery-independent paralarval-based index of *D. opalescens* spawning stock size that may be used for research purposes and management of the fishery.

Our data indicate that the squid fishery CPUE is not significantly linearly correlated with the time series of paralarval abundance. In part this is due to apparently a rapid enhancement in the fishery's CPUE as the fishery adopted more efficient gear in the 1980s, switching to purse and drum seines from brail nets (Vojkovich 1998). However, our data based on paralarval abundance also suggest that the population requires several years to recover

from major El Niño events, such as 1983 and 1998 (fig. 6), and is depressed during moderate El Niños, such as prevailed during the early 1990s and around 2005. These fluctuations are not reflected in the fishery CPUE, suggesting that CPUE may not provide a valid index of squid spawning stock (fig. 4, 5). Bias in CPUE-based indices of stock biomass is commonly observed, particularly for aggregating species (Hilborn and Walters 2001).

Paralarval abundance may also be biased as an index of stock biomass, if paralarval mortality is enhanced or squid fecundity is diminished during El Niño events. Field studies indicate a marked decrease in mantle length of *D. opalescens* during El Niño events, apparently due to the interaction of higher temperatures and decreased zooplankton prey on growth and maturity (Lowry and Carretta 1997; Zeidberg and Hamner 2002; Jackson and Domeier 2003). This could influence fecundity, although the weight-specific relationship for fecundity in *D. opalescens* has not been determined. Laboratory experiments indicate that the increased water temperatures and decreased food availability during El Niño events could also lead to increased mortality during the early life history (Vidal et al. 2002), but this needs to be confirmed in the field.

Further research on the reproductive biology and early life history of the squid is required to develop egg production estimates of market squid spawning stock biomass. However, until such research is carried out, the incidence of relatively high CPUE during the early 1990s and 2005–2007 (fig. 4) indicate that it may provide a positively (i.e., optimistically) biased indicator of spawning stock. Paralarval abundance is fishery-independent and may provide a more parsimonious and precautionary representation of stock biomass than CPUE.

Our results suggest that the squid fishery could be more actively managed based on the relationship of ENSO and the PDO with paralarval abundance. The ENSO and PDO indices are known in the months leading up to the fishing season and can therefore be used to modulate catch quotas. Furthermore, given the extended squid spawning season, paralarval abundance estimates from CalCOFI or targeted surveys in the first part of the spawning season could be used to manage fishing activity in the latter part of the season.

ACKNOWLEDGMENTS

LITERATURE CITED

California Department of Fish and Game. 2005. Market Squid Fishery Management Plan. California Department of Fish and Game, Marine Region. Available from: www.dfg.ca.gov/mrd/marketsquid/index.html.

Butler, J. L., D. Fuller, and M. Yaremko. 1999. Age and growth of market squid (*Loligo opalescens*) off California during 1998. Calif. Coop. Oceanic Fish. Invest. Rep. 40: 191–195.

Fields, W. G. 1950. A preliminary report on the fishery and on the biology of the squid *Loligo opalescens*. Calif Fish Game 36: 366–377.

Fields, W. G. 1965. The structure, development, food relations, reproduction, and life history of the squid *Loligo opalescens* Berry. Calif. Dept. Fish Game Fish. Bull. 131: 1–108.

Hilborn, R. and C. Walters. 2001. Quantitative Fisheries Stock Assessment: Choice, Dynamics, and Uncertainty, Kluwer Academic Publishers, Norwell, MA.

Jackson, G. D. and M. L. Domeier. 2003. The effects of an extraordinary El Niño/La Niña event on the age and growth of the squid *Loligo opalescens* off southern California. Mar. Biol. 142: 925–935

Karpov, K. A. and G. M. Caillet. 1978. Feeding dynamics of *Loligo opalescens*. Calif. Dept. Fish. Game, Fish. Bull. 169: 45–66.

Koslow, J. A., R. Goericke, A. Lara-Lopez & W. Watson. In press. Impact of declining intermediate-water oxygen on deepwater fishes in the California Current. Mar. Ecol. Prog. Ser.

Lasker, R. 1985. An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*. NOAA Tech. Rept. NMFS 36.

Legendre, L. and P. Legendre. 1983. *Numerical Ecology.* New York: Elsevier, pp: 268–288.

Lowry, M. S. and J. V. Carretta. 1999. Market squid (*Loligo opalescens*) in the diet of California sea lions (*Zalophus californianus*) in southern California (1981–1995). Calif. Coop. Oceanic Fish. Invest. Rep. 40: 196–207.

Morejohn, G. V., J. T. Harvey and L. T. Krasnow. 1978. The importance of *Loligo opalescens* in the food web of marine vertebrates in Monterey Bay, California. Calif. Dept. Fish Game Fish. Bull. 169: 67–98.

Moser, H. G., R. L. Charter, W. Watson, D. A. Ambrose, J. L. Butler, S. R. Charter and E. M. Sandknop. 2000. Abundance and distribution of rockfish (*Sebastes*) larvae in the Southern Californbia Bight in relation to environmental conditions and fishery exploitation. Calif. Coop. Oceanic Fish. Invest. Rep. 41: 32–47.

Moser, H. G., R. L. Charter, W. Watson, D. A. Ambrose, K. T. Hill, P. E. Smith, J.L. Butler, E.M. Sandknop and S.R. Charter. 2001. The CalCOFI ichthyoplankton time series: potential contributions to the management of rocky-shore fishes. Calif. Coop. Oceanic Fish. Invest. Rep. 42: 112–128.

Moser, H.G. & W. Watson. 1990. Distribution and abundance of early life history stages of the California halibut, *Paralichthys californicus* and comparisons with the fantail sole, *Xystreurys liolepis*. Calif. Dept. Fish Game Fish. Bull. 174: 31–84.

Okutani, T. and J. A. McGowan. 1969. Systematics, distribution, and abundance of the epiplanktonic squid (Cephalopoda, Decapoda) larvae of the California Current April, 1954–March, 1957. Bull. Scripps Institution of Oceanography 14: 1–90.

Porzio, D. and B. Brady. 2007. Status of the Fisheries Report on Market Squid. Los Alamitos, California: California Department of Fish and Game: http://www.dfg.ca.gov/marine/status/report2006/squid.pdf .

Pyper, B.J. and R.M. Peterman. 1998. Comparison of methods to account for autocorrelation in correlation analyses of fish data. Can. J. Fish. Aquat. Sci. 55: 2127–2140.

Recksiek, C.W. and J. Kashiwada. 1979. Distribution of larval squid, *Loligo opalescens*, in various nearshore locations. Calif. Coop. Oceanic Fish. Invest. Rep. 20: 31–34.

Reiss, S. C., M. R. Maxwell, J. R. Hunter, and A. Henry. 2004. Investigating environmental effects on population dynamics of *Loligo opalescens* in the Southern California Bight. Calif. Coop. Oceanic Fish. Invest. Rep. 45: 87–98.

Sweetnam, D. (ed.). 2010. Review of selected California fisheries for 2009: coastal pelagic finfish, market squid, red abalone, Dungeness crab, Pacific herring, groundfish/nearshore live-fish, highly migratory species, kelp, California halibut, and sandbasses. Calif. Coop. Oceanic Fish. Invest. Rep. 51: 14–38.

Vidal, E.A.G., F.P. DiMarco, J.H. Wormuth and P.G. Lee. 2002. Influence of temperature and food availability on survival, growth and yolk utilization in hatchling squid. Bull. Mar. Sci. 71: 915–931.

Vojkovich, M. 1998. The California fishery for market squid (*Loligo opalesces*). Calif. Coop. Oceanic Fish. Invest. Rep. 39: 55–60.

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

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

Zeidberg, L.D., G. Isaac, C.L. Widmer, H. Neumeister and W.F. Gilly. 2011. Egg capsule hatch rate and incubation duration of the California market squid, Doryteuthis (*Loligo*) *opalescens*: insights from laboratory manipulations. Mar. Ecol. doi:10.1111/j.1439–0485.2011.00445.x.