

INVESTIGATING ENVIRONMENTAL EFFECTS ON POPULATION DYNAMICS OF *LOLIGO OPALESCENS* IN THE SOUTHERN CALIFORNIA BIGHT

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ABSTRACT

Using fishery-dependent and fishery-independent data on the distribution of paralarvae, juveniles, and adults, we assess the effects of the transition from the 1997–98 El Niño to the 1999 La Niña on the abundance, distribution, and production of market squid *Loligo opalescens* in southern California. Percentage occurrence of paralarvae within the CalCOFI survey of the Southern California Bight declined during El Niño, indicating that little production occurred during El Niño winters, and abundance from trawl surveys was low during the summer following the 1997–98 El Niño along the coast from Point Conception to Vancouver on the shelf and slope. Mean growth rates of *L. opalescens* declined with increasing temperature in the month of hatch, and hatch month temperature explained 67% of the variability in mean growth during the transition from El Niño to La Niña conditions (1998 and 1999). Using the observed temperature-dependent growth rates, we developed the first age-based, temperature-dependent population model for *L. opalescens*. Population dynamics were dramatically influenced by cumulative mortality, and the results predict that a bimodal recruitment period should be found with periods of 5 and 7 months and that the second peak should be narrower than the first peak.

INTRODUCTION

The market squid *Loligo opalescens* supports one of the most valuable commercial fisheries in central and southern California with a value of more than \$41 million a year (CDFG 2001). The total annual catch has increased exponentially since the 1970s (fig. 1; CDFG 2001). Most of the increased catch (80%) has occurred in the Southern California Bight (SCB), and there is uncertainty whether the increase is related to increasing abundance (Vojtkovich 1998). Rapid declines in squid catch occur during El Niño years, and it has been suggested that the environment may be partially responsible by influencing the availability, population size, and recruitment success of this animal (McInnis and Broenkow 1978).

More remarkable than the near collapse of the fishery during El Niño periods is the rapid recovery of the catch to pre-El Niño levels within a year or two following (fig. 1; Maxwell et al., 2004). This is especially

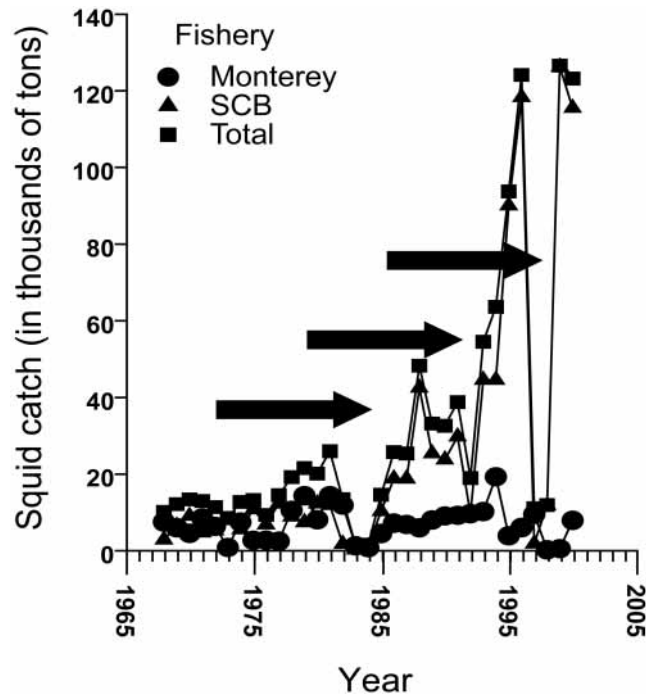


Figure 1. Plot of annual squid catch between 1965 and 2001 for Monterey (circles), Southern California Bight (triangles), and the total of both (squares). Arrows indicate fishery decline during El Niño periods followed by rapid recovery.

noteworthy given that *L. opalescens* is short lived (~ 6 months; Jackson 1994; Butler et al. 1999; although Spratt (1979) hypothesized that *L. opalescens* lived more than 18 months) and evidently semelparous (Knipe and Beeman 1978; Macewicz et al. 2004). The rapid changes in apparent abundance in the fishery have led to considerable speculation regarding the strategy of squid to ride out the presumably harsh El Niño conditions. Given the rapid recovery of squid, some investigators have argued that the population is displaced to the north or offshore during El Niño (CDFG 2001). If so, abundance of squid might increase with latitude during El Niño, or abundance or presence might increase offshore. Alternatively, during El Niño conditions squid may move to deeper waters where the environmental conditions necessary for proper development of eggs may be found, making the squid unavailable to the fishery and to those marine mammals that forage near shore (Lowry and

Carretta 1999; Roberts and Sauier 1994). Both hypotheses suggest that squid become unavailable to the fishery, thus allowing the population to rebound rapidly after an El Niño. They also suggest that harsh El Niño conditions are overcome by redistributing the population to more favorable refuge habitats, potentially maintaining production.

The observed patterns of fishing success during and following the El Niño may also reflect demographic processes occurring in the planktonic or juvenile stages, where the environment may change vital rates. Of the many environmental variables that may affect survival and recruitment of squid, temperature is thought to be one of the dominant mechanisms, because it can reflect different oceanographic regimes (Lynn et al. 1982; Waluda et al. 2001) and because temperature is related to physiological processes (Forsythe 1993). For example, growth rates are strongly influenced by temperature in many squid species including *Loligo* spp. (Hatfield et al. 2001; Forsythe 1993). Using laboratory data, Forsythe (1993) showed that under conditions of *ad libitum* food, growth rates of squid increased with increasing temperatures. Jackson et al. (1997) used field data to show that growth rates increased in warmer conditions for a loliginid common to neritic waters of the northwest Gulf of Mexico. In contrast, Jackson and Domeier (2003) showed that age and size of *L. opalescens* declined with increasing water temperatures and increased with upwelling (an index of secondary production) in the SCB. Based on these data, Jackson and Domeier (2003) suggested that the size difference of squid observed in the diets of sea lions could be explained by variability in the temperature-dependent growth differences in the Southern California Bight. They did not examine the effects on population size and recovery.

Growth rate variability can potentially affect the synchrony of cohorts. Mixing of different cohorts on the spawning grounds may occur as a result of the strong temperature dependencies that cause fast growing cohorts to catch up to slow growing cohorts (Grist and de Clers 1998, 1999), and bimodality in recruitment pulses may result. Thus, the question remains whether the apparent rapid repopulation of *L. opalescens* is a function of environmental variability operating directly on the biological and physiological processes of the population or whether it is simply reflecting changes in availability.

In this study, we examine the hypotheses regarding the changes in abundance associated with El Niño conditions in an effort to determine whether squid “ride out” El Niño conditions by changing spatial distribution, or whether changes in demographic rates could be responsible for the observed changes and abundance in the fishery. To do this, we use (1) juvenile abundance and distribution data from the Northwest Fishery Science

Center triennial summer trawl survey conducted between Point Conception, California, and Vancouver Island, Canada, to examine changes in distribution; (2) para-larval abundance data from winter and spring CalCOFI surveys conducted in the Southern California Bight to examine changes in productivity; and (3) growth rate data determined from mature adult squid collected from the SCB commercial fishery to examine the environmental control on recruitment to the fishery. After evaluating these hypotheses, we present an age-based temperature-dependent (TDGR) model of squid growth and develop a simple population dynamics model using TDGR to drive the population growth rates. We compare predictions derived from this model to the overall patterns of occurrence of squid in southern California as a starting point for directed studies on *L. opalescens*.

METHODS

Fishery Data

Loligo opalescens were sampled at biweekly intervals from the commercial catch landed at ports within the SCB between 15 November 1998 and 01 July 2000. On each date, mantle length (ML, in millimeters), gonad weight (GW, in grams), maturity stage (immature or mature), and sex (male or female) were obtained from a subsample of the catch. A further subsample of 15–60 animals each month provided statoliths for age and growth analysis. All samples from the SCB were pooled and given equal weight in all analyses.

Several studies have validated the daily deposition of rings in laboratory reared *L. opalescens* (Jackson 1994a; Butler et al. 1999). In the laboratory, statoliths were processed following Butler et al. (1999). Briefly, statoliths were mounted on microscope slides, ground on 400 μ m paper until the primordium was visible. Under magnification (x100–400) daily rings were counted using transmitted light to determine the age of each squid. Hatch date was determined by subtracting the age at capture from the date of capture.

Preliminary analysis showed that most of the animals collected as part of this study were mature adults (98%; Maxwell et al. 2004), so we defined growth rate (GR) of mature animals in the fishery as

$$\text{GR} = \text{mantle length (mm)} / \text{age (d)} \quad (1)$$

Thus, growth rate as estimated here was the average value over the entire life of the animal.

Many growth functions and growth models exist for squid (Jackson et al. 1997; Yang et al. 1986). We feel that the simple relationship we propose is adequate for this exploration for two reasons: (1) We are not predicting the size at any age during the paralarval or juvenile period when a more appropriate growth function

would be necessary; and (2) under any contemporary model, faster (slower) growth rates would result in younger (older) animals recruiting to the fishery. We then correlated the mean growth rate of monthly cohorts, assigned using retrospective hatch-date distributions to examine the relationship between growth rate of survivors caught in the fishery and environmental variables, as indexed by hatch month sea surface temperature (SST) at Scripps Pier, La Jolla, California.

Fishery-independent Data

The relative occurrence and distribution of *L. opalescens* along the west coast of the United States was determined from summer (July–August) triennial groundfish trawl data collected by the Northwest Fisheries Science Center. Briefly, we used data from the 1995, 1998, and 2001 surveys from 512, 528, and 506 stations, respectively. The bottom trawl sampled at depths of between 50 and 300 m, corresponding roughly to 2–50 nmi offshore. The survey uses a high-opening Nor'eastern trawl, with 27.2 m headrope and a 37.4 m footrope. The survey is used to determine the abundance and distribution of principle groundfish species found on the shelf and slope. Given the pelagic and neritic nature of *L. opalescens*, the trawl is likely to be inefficient at capturing them. However, the survey should be consistent enough to provide an index of the spatial distribution and the relative occurrence during these different years, but it is not intended to provide an unbiased estimate of true abundance.

As part of the California Cooperative Fisheries Investigations (CalCOFI) plankton tows are made at each of 66 fixed stations in the SCB (Schwing et al. 2002) using a 1 m by 2 m surface Manta net equipped with 0.947 mm mesh and a General Oceanics, Inc. model 2030 flow meter to estimate the volume of water filtered. The Manta net is neustonic and samples the upper 0.5 m depth. The number of stations positive for paralarvae was counted for each winter (January–February) and spring (April–May) cruise and the average was used to estimate an annual index of productivity (percentage occurrence) for the period 1989 to 2003. Okutani and McGowan (1969) have shown that paralarvae are most abundant at depths of about 50 m, suggesting that the Manta nets may undersample paralarvae compared with bongo tows, which sample the water column. For data that overlap (1997–2003), bongo and manta tows were positively correlated ($r = 0.54$, $n = 7$, $p < 0.05$) and, more important, exhibited declines during the El Niño of 1997–98, suggesting that we can use manta tow data for describing the temporal pattern of production.

Physical Oceanographic Data

Sea Surface Temperature. Daily SST at Scripps Pier was extracted from the coastal temperature database at

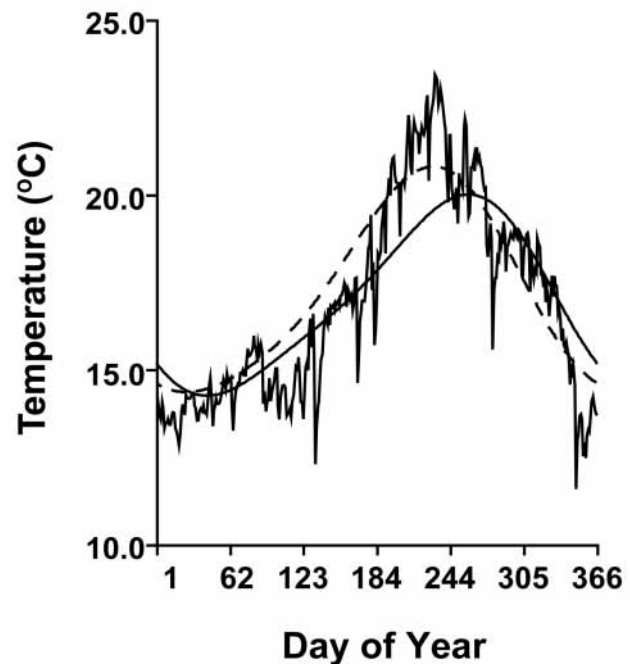


Figure 2. Seasonal daily temperature at Scripps Pier in 1999, as well as seasonal average daily temperature at Scripps Pier between 1977 and 2001 (dashed curve) and seasonal average temperature derived from harmonic constituents (Lynn et al. 1982) for station 90.30 in the Southern California Bight (solid curve).

the University of California San Diego for the period January 1977 to July 2001 and averaged to derive a seasonal cycle (fig. 2). Missing values from this data set were replaced with climatological daily values of the missing days, using a nonlinear regression of the first two harmonics (annual and biannual) for all daily values (see Lynn et al. 1982). Monthly values were derived by averaging daily values, and these monthly values were used to examine temperature dependencies with growth rate.

Model Development. For use in the model, the annual climatic temperature cycle within the SCB was developed using published harmonics (Lynn et al. 1982) at CalCOFI station 90.30, located at 33.45°N and 117.43°W for the period 1977–99 (fig. 2).

Using TDGR we developed a first-order, age-based model of the population dynamics of *L. opalescens* to investigate the ability of this animal to respond to seasonal environmental forcing (fig. 3). In the first generation (the first year of the model), 53 weekly cohorts were released and hatched with a temperature-dependent growth rate that was determined by the climatic water temperature at hatching and subject to a uniformly distributed random error proportional to 1°C.

An appropriate mortality rate for the planktonic and juvenile period must be specified but is difficult to parameterize. Estimates of adult mortality range from 0.3 month⁻¹, suggesting a mortality rate of 0.01 d⁻¹; yet that mortality rate would mean that over a 200-day

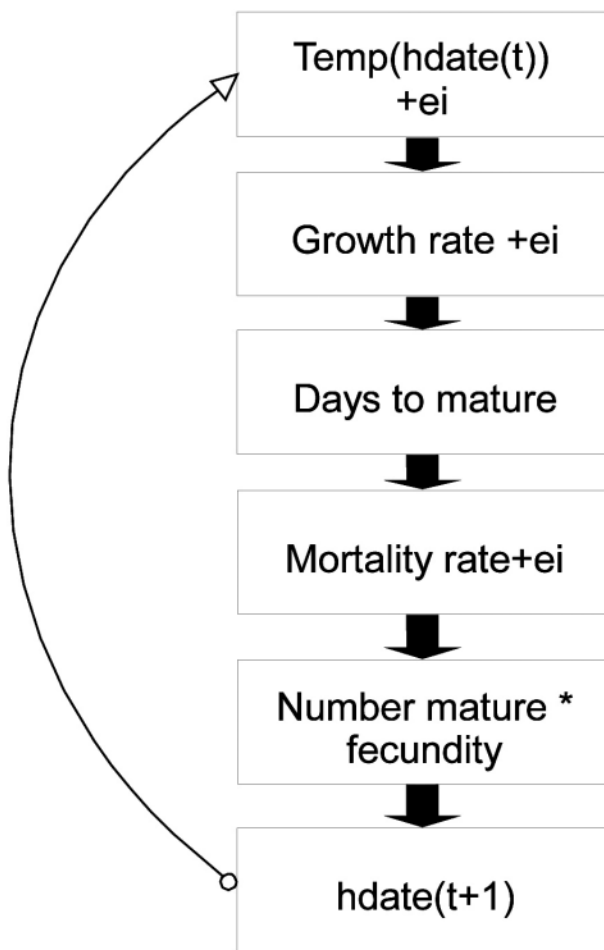


Figure 3. Diagram of temperature-dependent population model for *Loligo opalescens* in the Southern California Bight.

larval-juvenile period (Butler et al. 1999) 13% of eggs spawned would mature, suggesting that a higher planktonic mortality rate is necessary. A mortality rate of 0.035 means that over a 100- to 200-day larval-juvenile period, 3% to 0.01%, respectively, of the eggs would mature. Thus, we prescribed the mortality rate as fixed at 0.035 d^{-1} with a small amount of error (up to 0.005 d^{-1}) assigned using a uniformly distributed proportional error term. In the first generation, survivors from each of the 53 weekly cohorts produces 10^8 offspring to generate an initial population to spin up the model. In subsequent generations, we used the length-based total fecundity relationship described by Macewicz et al. (2004) where potential fecundity (F) was linearly related to mantle length (ML) as:

$$F = 29.8 * ML \quad (2)$$

Macewicz et al. (2004) estimated that the average escapement prior to capture in the fishery is 36%, and

the mean lifetime of animals on the spawning grounds is 1.67 days.

While there is some discussion in the literature regarding the effect of growth rate on size at maturity (Lipinski and Underhill 1995), we did not vary size at maturity. Instead, our model tracked the number of days required to reach a specified size at maturity (129 mm ML) and assumed that all animals that reached that size would spawn and would then be removed from the population through natural mortality or fishing. The hatch date of their offspring was calculated from the date of maturation of their parents and by adding 30 days to account for egg development time. No egg mortality was prescribed because there are no published data to provide a reference point. We calculated the monthly population size and the monthly number of weekly cohorts contributing to the population in each month of each year. The model was run for 25 years, roughly equivalent to 50 generations, in order to examine the long-term dynamics within the population.

RESULTS

Temperature

Sea surface temperature in the SCB showed a distinctive but skewed seasonal pattern with a minimum between January and April and a gradual heating between April and October before reaching a maximum and then a rapid decline (fig. 2). Little difference existed between the seasonal daily average temperature at Scripps pier and at station 90.30 in the SCB. The differences were principally related to the time of the mean maximum temperature that was shifted by about 30 days from the coast to the central SCB and exhibited a difference of about 2°C in mean maximum temperature.

Abundance and Distribution

Coastwide distributions of squid exhibited distinct patterns associated with the presence of El Niño conditions (fig. 4). Expanding-symbols plots of the numbers of *L. opalescens* collected in trawl surveys showed distinct spatiotemporal differences in the distribution of catch. Prior to the El Niño of 1997–98, squid were found all along the coast from Point Conception to Vancouver, British Columbia. During the summer 1998 El Niño squid abundance in trawl samples was very low with a considerable fraction of the stations containing no squid at all. No evidence for a shift in the abundance of squid to the more northern areas was observed, nor was there any apparent shift to slope waters from shelf waters. In 2001, squid were again abundant all along the west coast. The overall pattern of distribution strongly suggests that the decline of squid during El Niño is consistent along the coast, and its return is also a coastwide phenomenon.

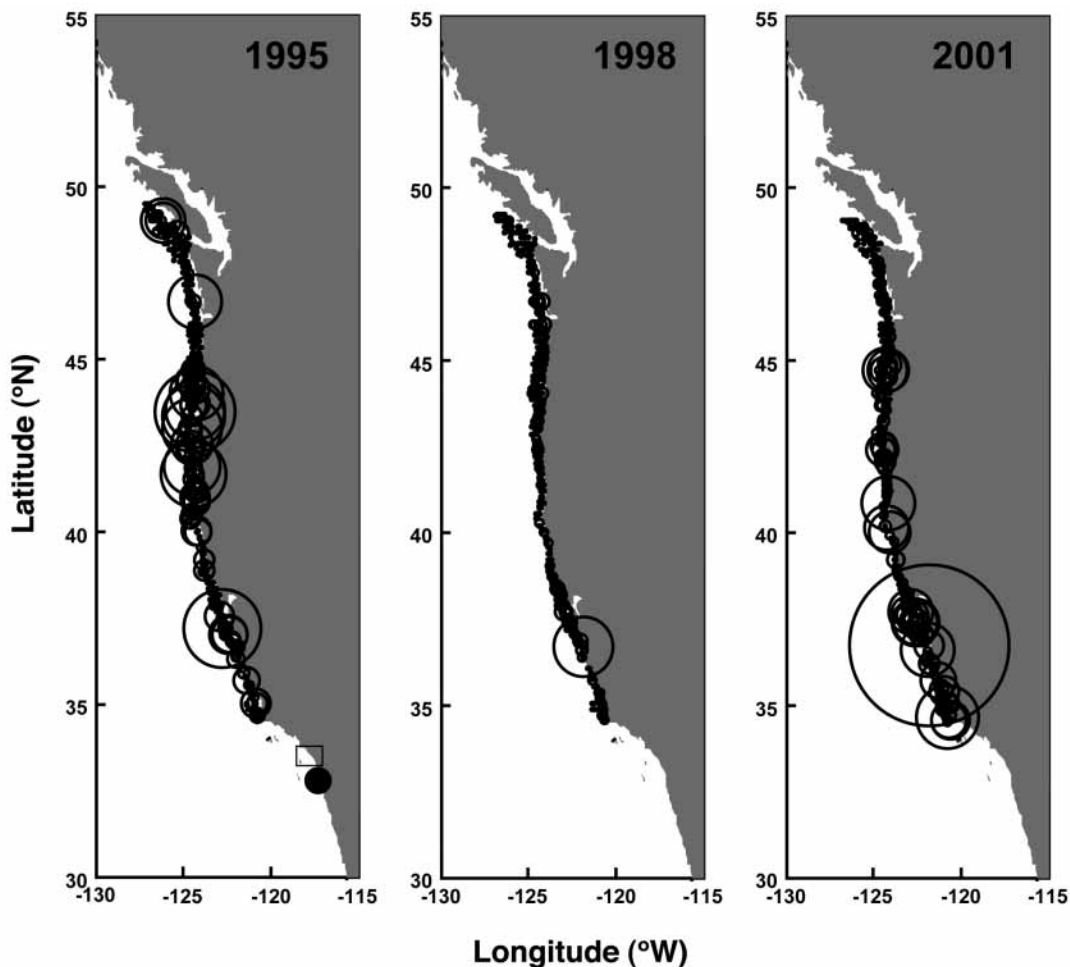


Figure 4. Expanding-symbol plots of *L. opalescens* collected as part of the by-catch in the summer triennial groundfish survey conducted by the NWFSC, between Vancouver Island, Canada, and Point Conception, California. Sample sizes were 512, 528, and 506 stations in 1995, 1998, and 2001, respectively. In the panel for 1995, the location of Scripps Pier is indicated by the filled circle, and the location of station 90.30 is indicated by the small rectangle.

Larval Production

Paralarval production (percentage occurrence) within the SCB also follows the pattern observed for juveniles and adults collected along the west coast as part of the trawl survey (fig. 5). Mean occurrence of paralarvae at CalCOFI stations between 1989 and 2002 was 14%. During El Niño years of 1992–93 and 1997–98, paralarval occurrence declined to less than 3% of stations. Immediately following the El Niño, mean percentage of occurrence increased from less than 3% to between 15% and 25% in a single year.

Size and Age

Market squid exhibit inter- and intra-annual variability in age and size at capture (fig. 6). A variety of patterns in size and age are evident when squid are plotted against hatch month (fig. 6). For example, after hatching during January and February of 1999, squid

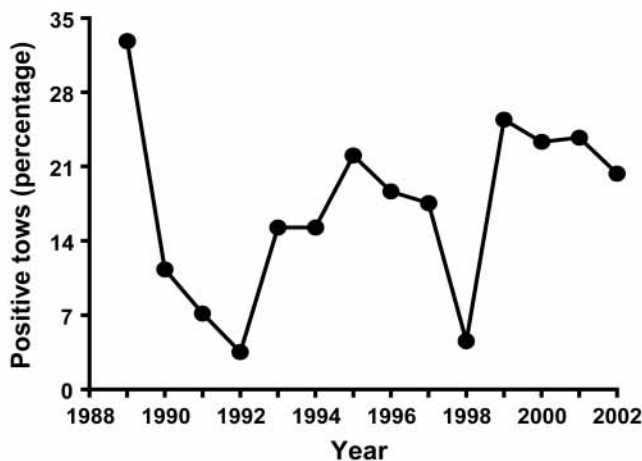


Figure 5. Percentage occurrence of *L. opalescens* paralarvae collected from manta tows conducted as part of the winter (January–February) and spring (March–April) CalCOFI surveys in the Southern California Bight between 1989 and 2003. The number of stations occupied in each cruise year ranged from 120 to 133.

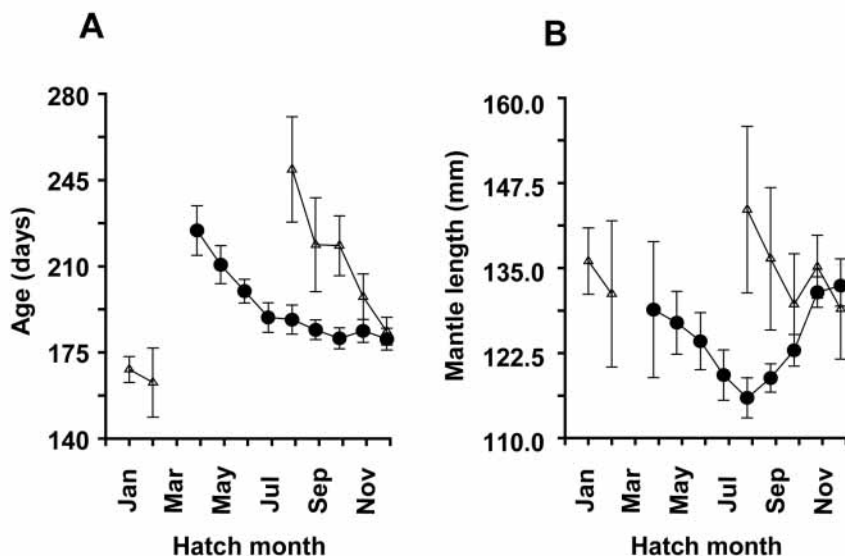


Figure 6. Age and mantle length of mature *L. opalescens* sampled from the Southern California Bight fishery in 1998 (circles) and 1999 (triangles) plotted by month of hatch.

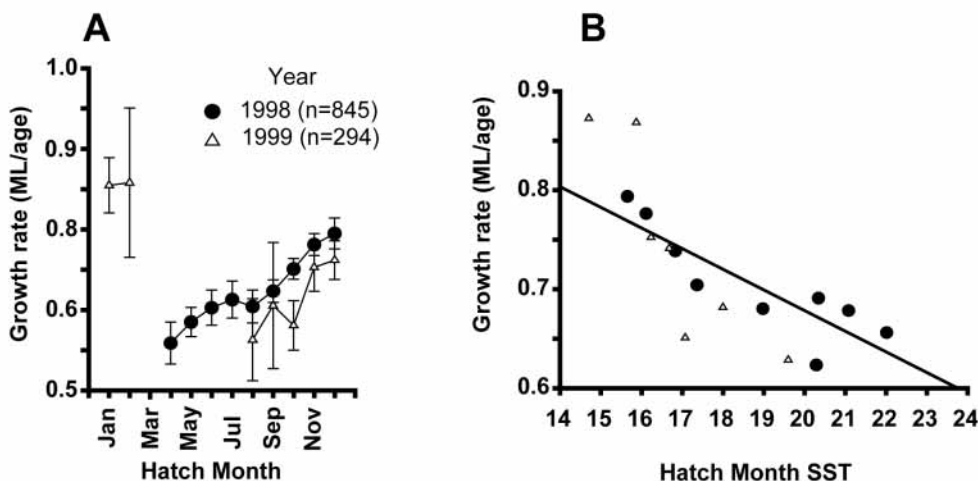


Figure 7. Mean growth rate (± 1 SE) of mature *L. opalescens* from the Southern California Bight commercial fishery in 1998 and 1999 plotted by month of hatch (A), and means of growth rates in relation to hatch-month SST as calculated from the monthly mean temperature recorded at Scripps Pier (B).

grew large (130–135 mm) but were young (140–160 d) at capture. At other times, smaller (115 mm), older (~190 d) squid were captured. There were also large differences between years. For example, squid hatched in July 1999 were older (~240 d) and larger (140 mm) than squid hatched in July 1998. Furthermore, the change in mean age at capture for animals hatched from July to November in each year declined at different rates, while size increased in 1998, and declined over the same months in 1999. This interannual variability limits the usefulness of age or size data used independently in developing seasonal growth models.

Growth Rates and Temperature

Mean growth rates plotted as a function of the month of hatch show that growth rates of animals are more similar over seasons and between years than would be expected simply on the basis of age or size (fig. 7A). Growth rates were highest in January and February of 1999 (during La Niña), and were low during spring in both years, increasing from May to December. For periods where the data overlap (July to December of 1998 and 1999), mean growth rates were not significantly different ($p > 0.3$) between years in a two-way fixed factor ANOVA with year and hatch month as factors. Hatch-month

growth rates did vary, with growth rates in July and August significantly different from those in October to December ($p < 0.01$). The slopes seem to be similar, yet the paucity of data (only 7 months) precludes formal testing. There is also a fair amount of variability in the first half of the year, but we have little data with which to examine that relationship further.

When growth rate is plotted against the mean temperature of the hatch month at Scripps Pier, growth rates for squid spawned during the two-year period decline with increasing temperature (fig. 7). Owing to the incomplete nature of our sampling, there were no animals sampled for age determination in mid- and late 1999 from which to estimate growth rates in March and April, yet the fishery operated successfully during that period. Overall, however, the mean growth rates for each year are the same, suggesting a similar temperature dependency for each year where the data overlap. A linear regression, fit to the combined data of growth rates versus mean monthly temperature during the hatch month and derived from monthly composite satellite data for the SCB, yielded a strong negative relationship between temperature and growth rate:

$$GR = 1.18 - 0.0395 * T$$

$$(R^2 = 0.67, df = 14, p < 0.0001) \quad (3)$$

These results indicate that the timing of the seasonal warming and cooling cycles, which are different during El Niño and La Niña periods, can explain the variability in size and age differences when plotted against hatch month.

Model Runs

To shed light on the influence of the seasonal asymmetry in temperature on growth rates and recruitment, a baseline run of the model was made using the seasonal temperature-dependent growth rates and an initial (first year only) weekly egg production of 10^8 individuals, with a fixed (0.035 d^{-1}) mortality rate, and no stochastic variability. The resulting stable model showed that the seasonal temperature cycle produces an asymmetric recruitment pattern, with the first mode occurring in March and the second in August. In both recruitment peaks, most of the animals recruiting consisted of fast-growing animals, and recruitment occurred during early spring and summer.

The results of the stochastic model (variability in mortality rate and temperature dependent growth function) produced a variety of interesting patterns that reflected the balance between slight increases and decreases in mortality rate and growth variability. Figure 8 shows the results of one model run to illustrate the types of patterns produced by this simple model. The initial production of 10^8 individuals produced weekly during the

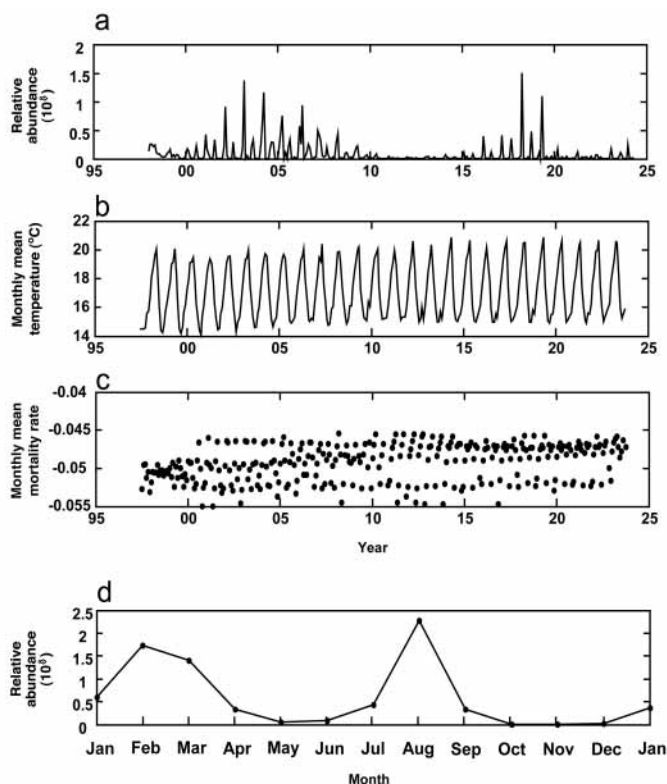


Figure 8. Twenty-five year population simulations of *L. opalescens* using an age-based temperature-dependent growth model. Time series of monthly population abundance (a), monthly average temperature (b), monthly mortality rates (c), and seasonal pattern of recruitment (d).

first year is replaced by the fixed but length-specific fecundity beginning with the second generation. The population rapidly becomes bimodal after just a few generations (fig. 8a,b,c). In fact, in all model runs this bimodal pattern occurs and is a product of the ~6-month life cycle of this animal. Moreover, in all iterations this bimodal recruitment pattern was dominated by a broader peak in the spring and a narrower peak in the mid- to late summer period (fig. 8d). In model runs where the population remained fairly stationary the late winter recruitment was usually more than twice the summer recruitment. In some iterations and the one shown in Figure 8a, the population exhibited runs of successful recruitment and growth for periods of 10 to 15 years. In many instances, these periods of high abundance were followed by periods of rather low recruitment. During periods of rapid growth, the population was capable of increasing orders of magnitude in just a few generations, suggesting that the rapid increases observed in the fishery following an El Niño are well within the biological capacity of this species. Monthly mean temperature and mortality rates show that small differences in either factor create conditions sufficient to rapidly affect the population size.

DISCUSSION

The paucity of data regarding the life history of market squid complicates our ability to understand how this animal will respond to changing environmental conditions and fishing pressure. The lack of a reliable biomass time series obviates correlating environmental variables with catch. Instead, the exploration that we have pursued here should serve as a model to focus research questions in the near term, in order to elucidate the role of environmental forcing in the population dynamics of this species.

The results of this study indicate that, more likely than not, the collapse of the squid fishery in California is a result of a decline in the production of offspring during El Niño rather than a shift in habitat that lowers the availability of squid to the fishery. Our results also show that growth rate is negatively related to temperature and is generally predictable from the hatch month SST. This predictability provides a mechanism to model growth rate variability in years as environmentally diverse as the transition from El Niño (warmer-than-normal) and La Niña (cooler-than-normal) conditions.

The decline of the squid catch during El Niño periods has been attributed to a variety of behavioral responses to the environment that affect squid availability in the nearshore fishery because the increase in catch following an El Niño suggests a population growth rate that seems unnaturally high (CDFG 2001). Several studies have indirectly examined the availability hypothesis. For example, evidence from monitoring the scat of sea lions that eat squid suggests that the squid population collapses during El Niño years (Lowry and Carretta 1999). However, because the marine mammals studied forage nearshore, there is no way to quantify whether dietary changes result from changes in squid behavior or from population collapse (Lowry and Carretta 1999; but see Preti et al., this volume). Our data from fishery-independent surveys of juvenile and adult squid along the coast, coupled with data showing large declines in the occurrence of paralarvae in the SCB during El Niño, provide stronger evidence that the population declines to nonfishable levels all along the coast and that production resumes when conditions improve immediately following the El Niño. If squid simply moved offshore, or to depth to spawn, we would still expect to capture squid paralarvae in the CalCOFI surveys that extend much further offshore than the fishery. Likewise, offshore movement or northward migration of juveniles and adults would result in higher catches of squid in the trawl survey along the slope or in northern waters. Assuming that the bottom trawl surveys capture squid in sufficient quantity, their decline along the coast and throughout the survey area makes the possibility of their capture less likely.

Many researchers have fit length-based growth functions to squid (e.g., Mohamed and Rao 1997); however, it has become clear that plasticity in the growth function (generally attributed to temperature) and the short life span of most squids requires an age-based approach (Jackson 1994b). For example, Dawe and Beck (1992) showed that growth rates of *Illex* in the northwest Atlantic were substantially underestimated when length-based methods were used. Moreover, they showed that growth varied among individuals and with hatch date. These and other studies suggest that great care is needed to properly describe growth in all squids. Recent work (Butler et al. 1999; Jackson 1994a; Jackson and Domeier 2003) has validated the daily deposition of rings in *L. opalescens* and provided a solid foundation from which to assess growth variability. Our data provide another reason for using age to describe growth: it better quantifies environmental effects than either length or other measures of size alone do.

Generally, mantle length is either linearly or exponentially related to age (Bettencourt et al. 1996; Jackson and Domeier 2003), although logistic (Arkipkin 1995; Brunetti et al. 1998) and two-stage (Yang et al. 1986) models have been used. No age-based growth model has, to our knowledge, explicitly incorporated temperature (but see Hatfield et al. 2001). Instead, most generate seasonally specific growth functions and acknowledge the effect of temperature (Collins et al. 1995; Jackson et al. 1996). In this study, we assumed that size and age at maturity could be combined to provide an index of the mean growth rate over the lifetime. Yet, even if growth rates are exponential—or two-stage, as has been suggested—our model has considerable utility because fast (slow) growth would result in younger (older) animals arriving on the spawning grounds in a manner predictable from the hatch-month temperature. Furthermore, this simple relationship will hold as long as we do not try to model intermediate sizes at age, when a better growth model would be needed. However, if the appropriate growth model for squid is more aptly described by a von Bertalanffy with a long asymptotic growth period, the use of our simple function would be less useful.

Given that a high level of variability in mean lifetime growth rate was explained by hatch-month temperature within and between years, we feel confident that hatch-month temperature is a proxy for the environmental conditions that may control growth of *L. opalescens* in the SCB. The exact function describing growth may well change when more data are included, so the exact parameter estimates here should be considered preliminary and subject to change. Moreover, there may be better measures of life-long temperature exposure prior to maturity (degree days or integral heat exposure) that would require a better growth model. However, to be

useful, any other measure of environmental exposure during the larval and juvenile stages must have better predictive capacity, not only in terms of variability explained but also in predictions derived. Notwithstanding these considerations, given any hatch-date temperature and the mean lifetime growth function, it should be possible to predict the average arrival date on the spawning grounds.

Forsythe (1993) showed that under *ad libitum* conditions squid exhibit increased growth rates with increasing temperature. Jackson et al. (1997) were the first to show this response in the field for a Gulf of Mexico loliginid. In contrast to the predictions based on the temperature-growth model of Forsythe (1993), we found that growth rates in the SCB declined with increasing temperature. A negative relationship between age and temperature was also found by Jackson and Domeier (2003) for *L. opalescens*; and since they found a positive relationship between upwelling and size and age of squid in the SCB, they suggested that the negative relationship was a tradeoff between temperature and food. Such a possibility further emphasizes the preliminary nature of our relationships, and the importance of understanding the role of the environment on demographic characteristics of this species. Furthermore, the inconsistency between laboratory predictions and our observations suggests that generalizations from other congeners are unlikely to be supported unless the ecosystem (upwelling, boundary current, coastal temperature, and so on) is included.

We have developed the first age-based, temperature-dependent population model for any squid species. It differs in several ways from the two-stage, length-based and temperature-dependent growth model of Grist and des Clers (1998, 1999). In their model, they used temperature to modify seasonal growth, which allowed faster growing animals spawned later in the season to catch up with slower growing members hatched earlier. In this manner, they were able to develop a bimodal recruitment pattern of *Loligo* spp. based on the probability of reaching a given size. Our model explicitly assigns a growth rate based on an empirical relationship and tracks the time required to reach a prescribed size at maturity. By including a mortality term, the seasonality in our recruitment patterns is driven by differential levels of cumulative mortality in fast-growing and slow-growing cohorts rather than by differential growth producing synchronous recruitment through growth variability. It should be possible to test the predictions from either model by examining growth histories of mature animals collected in the commercial fishery.

Our simulations of the population dynamics of squid show that bimodal recruitment patterns can be generated from small changes in cumulative mortality arising from slightly lower or higher growth rates; they

can produce the kinds of abundance fluctuations generally seen in the SCB fishery and are a consequence of squid's approximately 6-month life span. The model produced periods of relatively high abundance followed by periods of relatively low abundance, despite a climatic, seasonal temperature field. The model also produced periods where the population increased rapidly over a few generations, similar in magnitude to that observed in the SCB fishery following an El Niño. The model uses climatic seasonal temperatures and does not incorporate El Niño or La Niña conditions. The variability in population size over longer time periods is a consequence of the variability in the mortality rate and in the temperature-derived growth rate. Our model is not suitable for predicting recruitment trends since neither food nor density-dependent processes are included and the exact environmentally derived growth function is almost sure to change. For example, including food in this model through either upwelling indexes or some other measure will affect the dynamics of this population model by changing the empirically derived growth relationship. Specifically, it should shift the period of maximal growth rate from winter to late spring, when temperature is low and food is plentiful. And this should affect the size and persistence of annual recruitment peaks. Likewise density-dependent processes, although unknown, may effect recruitment by decreasing survival during the egg stage or by increasing cannibalism during the juvenile stage at high spawning biomass (O'Dor 1998). Several sources of mortality were not included in the model and should be considered when data are available. One important component is mortality during the egg stage, which in this model can be adjusted simply by decreasing fecundity. Yet, we have not varied it because it would also be a function of temperature given the temperature-dependent egg-development time. Field and laboratory studies on egg mortality are clearly needed. Moreover, because mortality rate is the only variable that can drive the population variability in this model, it is a truism that the population will be driven by mortality. On balance, however, this model provides a way forward that should be useful in defining effective research strategies.

We are encouraged by the present model because it provides hypotheses regarding the dynamics of the population that can be modeled or tested in the field. We anticipate that this model and its derivatives will begin to address such fishery questions as: Can fishing mortality over the last several days of life affect production more than a small change in the mortality or growth rates? To ensure future recruitment, is it necessary to protect the summer or winter recruitment pulse? Likewise, how different are the magnitudes of the abun-

dance and duration of the summer and winter recruitment pulses? Yet it is clear that the preliminary nature of the model, and the fact that there are significant differences between seasonal catch patterns, means that this model cannot be used in any predictive sense.

The development of appropriate long-term management strategies for this species will likely require considerable modeling to understand the sensitivity and population dynamics of market squid to changes in fishing and the environment. Modeling will, in turn, require a large amount of high-quality demographic and biomass data. Future studies must investigate the effects of temperature and food on the growth rate of *Loligo*. Regionally, we know little about how growth rates in the Monterey fishery compared to those in the SCB. Are they similar, can they explain the shorter seasonal pattern in the fishery in Monterey Bay? Addressing these questions is crucial because recent data show that the fishery is beginning to be prosecuted during daytime and throughout the year in the SCB, potentially capturing mature squid prior to and during spawning (Forsythe et al. 2004). More generally, the role of the environment is critical in assessing the long-term productivity and persistence of this species. We see declines occurring during warm El Niño periods, yet the fishery has increased its catch during a warm phase of ocean temperature associated with general basin-scale ocean conditions (Hollowed et al. 2001). How different are populations likely to be during cooler periods? Was the population historically larger than it is now? Moreover, we know little about the relationship of growth rate and size at maturity of *L. opalescens*. Such details are critical to understanding energetic tradeoffs to future reproduction. The efficacy of retrospective growth determination using the statolith needs to be addressed by collecting multiple samples of cohorts during their pelagic period, an expensive but necessary task given the ecological role of squid in the California Current. The questions above suggest directions for future research that will provide the data necessary to support, modify, or refute the strawman we have built to understand the population dynamics of and environmental influences on squid.

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LITERATURE CITED

- Arkhipkin, A. 1995. Age, growth, and maturation of the European squid *Loligo vulgaris* (Myopsida, Loliginidae) on the west Saharan shelf. *J. Mar. Biol. Ass. U.K.* 75:593–604.
- Bettencourt, V., L. Coelho, J. P. Andrade, and J. Guerra. 1996. Age and growth of the squid *Loligo vulgaris* off the south coast of Portugal, using statolith analysis. *J. Molluscan Stud.* 62:359–366.
- Butler, J., D. Fuller, and M. Yaremko. 1999. Age and growth of *Loligo opalescens* off California during 1998. *Calif. Coop. Oceanic Fish. Invest. Rep.* 40:191–195.
- Brunetti, N. E., B. Elena, G. R. Rossi, M. L. Ivanovic, A. Aubone, R. Guerrero, and H. Benavides. 1998. Summer distribution, abundance, and population structure of *Illex argentinus* on the Argentine shelf in relation to environmental features. *S. Afr. J. Mar. Sci.* 20:175–186.
- California Department of Fish and Game (CDFG). 2001. Squid stock assessment review: scientific papers for stock assessment review committee, 14–17 May 2001. Fisheries Resources Division, NMFS, La Jolla, Calif.
- Collins, M. A., G. M. Burnell, and P. G. Rodhouse. 1995. Age and growth of the squid *Loligo forbesi* (Cephalopoda: Loliginidae) in Irish waters. *J. Mar. Biol. Ass. U.K.* 75:605–620.
- Dawe, E. G., and P. C. Beck. 1992. Population structure, growth, and sexual maturation of short-finned squid at Newfoundland, Canada, based on statolith analysis. *ICES C. M. Shellfish Committee* 1992, K:33, 23 pp.
- Forsythe, J. W. 1993. A working hypothesis of how seasonal temperature change may impact the field growth of young cephalopods. *In* Recent advances in Fisheries Biology, T. Okutani, T., R. K. O'Dor, and T. Kubodera, eds. Tokyo: Tokai University Press, pp. 133–143.
- Forsythe, J., N. Kangas, and R. T. Hanlon. 2004. Does the California market squid (*Loligo opalescens*) spawn naturally during the day or at night? A note on the successful use of ROVs to obtain basic fisheries biology data. *Fish. Bull.* 102:389–392.
- Grist, E. P. M., and S. des Clers. 1999. Seasonal and genotypic influences on life cycle synchronization: further insights from annual squid. *Ecol. Mod.* 115:149–163.
- . 1998. How Seasonal temperature variations may influence the structure of annual squid populations. *IMA J. Math. Appl. Med. Biol.* 14:1–22.
- Hardwick, J. E., and J. D. Spratt. 1979. Indices of the availability of market squid, *Loligo opalescens*, to the Monterey Bay fishery. *Calif. Coop. Oceanic Fish. Invest. Rep.* 20:35–39.
- Hatfield, E. M. C., R. T. Hanlon, J. W. Forsythe, and E. P. M. Grist. 2001. Laboratory testing of a growth hypothesis for juvenile squid *Loligo pealeii* (Cephalopoda: Loliginidae). *Can. J. Fish. Aquat. Sci.* 58:845–857.
- Hollowed, A. B., S. R. Hare, and W. S. Wooster. 2001. Pacific basin climate variability and patterns of northeast Pacific marine fish populations. *Prog. Oceanogr.* 49:257–282.
- Jackson, G. D. 1994a. Statolith age estimates of the loliginid squid *Loligo opalescens* (Mollusca: Cephalopoda): corroboration with culture data. *Bull. Mar. Sci.* 54:554–557.
- . 1994b. Application and future potential of statolith increment analysis in squids and sepioids. *Can. J. Fish. Aquat. Sci.* 51:2616–2624.
- Jackson, G. D., and M. L. Domeier. 2003. The effects of an extraordinary El Niño/La Niña event on the size and growth of the squid *Loligo opalescens* of southern California. *Mar. Biol.* 142:925–935.
- Jackson, G. D., and N. A. Moltschawskyj. 2001. Temporal variation in growth rates and reproductive parameters in the small near-shore tropical squid *Loliolus noctiluca*: is cooler better? *Mar. Ecol. Prog. Ser.* 218:167–177.
- Jackson, G. D., and G. Pecl. 2003. The dynamics of the summer-spawning population of the loliginid squid (*Sepioteuthis australis*) in Tasmania, Australia: a conveyor of recruits. *ICES J. Mar. Sci.* 60:290–296.
- Jackson, G. D., J. W. Forsythe, Hixon, R. F., and Hanlon, R. T. 1997. Age, growth and maturation of *Loliginucula brevis* (Cephalopoda: Loliginidae) in the northwestern Gulf of Mexico with a comparison of length-frequency versus statolith age analysis. *Can. J. Fish. Aquat. Sci.* 54:2907–2919.
- Knipe, J. H., and R. D. Beeman. 1978. Histological observations on oogenesis in *Loligo opalescens*. *In* Biological, oceanographic, and acoustic aspects of the market squid, *Loligo opalescens* Berry, C. W. Recksiek and H. W. Frey, eds. Calif. Dep. Fish Game, Fish. Bull. 169:23–33.
- Lipinski, M. R., and L. G. Underhill. 1995. Sexual maturation in squid: quantum or continuum? *S. Afr. J. Mar. Sci.* 15:207–223.

- Lowry, M. S., and J. V. Carretta. 1999. Market squid (*Loligo opalescens*) in the diet of California sea lions (*Zalophus californiensis*) in southern California (1981–95). Calif. Coop. Oceanic Fish. Invest. Rep. 40:196–207.
- Lynn, R. J. 1967. Seasonal variations of temperature and salinity at 10 meters in the California Current. Calif. Coop. Oceanic Fish. Invest. Rep. 11:157–174.
- Lynn, R. J., K. A. Bliss, and L. E. Eber. 1982. Vertical and horizontal distributions of seasonal mean temperature, salinity, sigma-t, stability, dynamic height, oxygen, and oxygen saturation in the California Current, 1950–1978, Calif. Coop. Oceanic Fish. Invest. Rep. Atlas 30, 513 pp.
- Macewicz, B., J. R. Hunter, and N. Lo. 2004. Fecundity, egg deposition, and mortality of market squid (*Loligo opalescens*). Fish. Bull. 102:306–327.
- Maxwell, M. R., A. Henry., C. D. Elvidge, J. Safran, V. R. Hobson, I. Nelson, B. T. Tuttle, J. B. Dietz, and J. R. Hunter. 2004. Fishery dynamics of the California market squid (*Loligo opalescens*), as measured by satellite remote sensing. Fish. Bull. 102:661–670.
- McInnis, R., and W. W. Broenkow. 1978. Correlations between squid catches and oceanographic conditions in Monterey Bay, California. Fish Bull. (Calif.) 169:161–170.
- Mohamed, K. N., and G. D. Rao. 1997. Seasonal growth, stock recruitment relationship, and predictive yield of the Indian squid *Loligo duvauceli* (Orbigny) exploited off Karnataka coast. Indian J. Fish. 44:319–329.
- O'Dor, R. K. 1998. Can understanding squid life-history strategies and recruitment improve management? S. Afr. J. Mar. Sci. 20:193–206.
- Okutani, T., and J. A. McGowan. 1969. Systematics, distribution, and abundance of the epipelagic squid (Cephalopoda, Decapoda) larvae of the California Current, April 1954–March 1957. Bull. Scripps Inst. Oceanogr. Univ. Calif. 14:190.
- Roberts, M. J., and W. H. H. Sauer. 1994. Environment: the key to understanding the South African chokka squid (*Loligo vulgaris reynauldii*) life cycle and fishery? Ant. Sci. 6:249–258.
- Schwing, F. B., S. J. Bograd, C. A. Collins, G. Gaxiola-Castro, J. García, R. Goericke, J. Gómez-Valdéz, A. Huyer, K. D. Hyrenbach, P. M. Kosro, B. E. Lavaniegos, R. J. Lynn, A. W. Mantyla, M. D. Ohman, W. T. Peterson, R. L. Smith, W. J. Sydeman, E. Venrick, and P. A. Wheeler. 2002. The state of the California Current 2001–2002: will the California current keep its cool, or is El Niño looming? Calif. Coop. Oceanic Fish. Invest. Rep. 43:31–68.
- Spratt, J. D. 1979. Age and growth of market squid *Loligo opalescens* Berry, from statoliths. Calif. Coop. Oceanic Fish. Invest. Rep. 20:58–64.
- Waluda, C. M., P. G. Rodhouse, P. N. Trathan, and G. J. Pierce. 2001. Remotely sensed mesoscale oceanography and the distribution of *Illex argentinus* in the South Atlantic. Fish. Oceanogr. 10:207–216.
- Vojkovich, M. 1998. The California fishery for market squid (*Loligo opalescens*). Calif. Coop. Oceanic Fish. Invest. Rep. 39:55–60.
- Yang, W. T., R. F. Hixon, P. E. Turk, M. E. Krejci, W. H. Hulet, and R. T. Hanlon. 1986. Growth, behavior, and sexual maturation of market squid, *Loligo opalescens*, cultured through the life cycle. Fish. Bull. 84:771–798.
- Zeidberg, L. D., and W. M. Hammer. 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(1):111–122.