
The fishery for California market squid, *Loligo opalescens* (Cephalopoda: Myopsida), from 1981 – 2003

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ABSTRACT

The California market squid, *Loligo opalescens*, has been harvested since the 1860s and has become the largest fishery in California in terms of tonnage and dollars since 1993. The fishery began in Monterey Bay, then shifted to southern California, where effort has increased steadily since 1983. The California Department of Fish and Game (CDFG) collects information on landings of squid including tonnage, location, and date of capture. We compared landings data gathered by CDFG with sea surface temperature (SST), upwelling index (UI), the southern oscillation index (SOI) and their respective anomalies. We found that the squid fishery in Monterey Bay expends twice the effort of that in southern California. Squid landings decreased substantially following large El Niño events in 1982-1983 and 1997-1998, but not the smaller El Niño events of 1987 and 1992. Spectral analysis revealed autocorrelation at annual and 4.5-year intervals (similar to the time period between El Niño cycles). But this analysis did not reveal any fortnightly or monthly spawning peaks, thus squid spawning did not correlate with tides. A paralarvae density index (PDI) for February correlates well with catch per unit effort (CPUE) for the following November recruitment of adults to the spawning grounds. This stock–recruitment analysis was significant for 2000-2003 ($CPUE = 8.42 + 0.41 * PDI$, adjusted coefficient of determination, $r^2 = 0.978$, $p = 0.0074$). Surveys of squid paralarvae explain 97.8% of the variance for catches of adult squid nine months later. This predictive relationship could be used to manage the fishery adaptively, setting catch limits for adult recruitment based upon paralarvae abundance nine months earlier.

INTRODUCTION

The recent discovery of falsification in Chinese fisheries reporting led to the realization that the

majority of the world's fisheries surpassed sustainability in 1988 (Watson and Pauly 2001). The food chain has been fished down by removal of apex predators, such as swordfish and snapper, beyond sustainability; fisheries have subsequently shifted to prey species, such as sardine and mackerel (Pauly *et al.* 1998). We have reached the point where cephalopods are regularly the largest biomass of all commercial species harvested. Since 1970, groundfish landings of flounders, cods, and haddocks have either decreased or maintained their levels, while landings in cephalopod fisheries have increased (Caddy and Rodhouse 1998). Some of this may be due to increased demand; however, lower levels of predation and competition from finfish, in addition to the shorter lifespan of squid, may have allowed cephalopods to increase in abundance worldwide.

Loligo opalescens is a small squid (130-mm mantle length) that occupies the middle trophic level in California waters, and it may be the state's most important forage species. Market squid are principal forage items for at least 19 species of fishes, 13 species of birds, and six species of mammals (Morejohn *et al.* 1978). The effective management of this fishery is of paramount importance not only to the people involved, but also to the millions of fishes, birds, and mammals that compete for this resource. Because cephalopods eat mostly zooplankton (Loukashkin 1976), if we deplete the squid population, it is not clear how oceanic food chains will respond. If the sub-annual population of *L. opalescens* fails to recruit a large biomass in a given year, the long-lived predators of this species, in the California Current, may encounter severe metabolic stress.

Since the decline of the anchovy fishery, market squid is possibly the largest biomass of any single marketable species in the coastal environment of California (Rogers-Bennett 2000). In the 1999 - 2000 season, fishermen landed 105,005 tons of

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California market squid, with ex-vessel revenue of \$36 million (CDFG landing receipts). These squid deposit egg capsules on sandy substrates at depths of 15 - 50 m in Monterey Bay (Zeidberg *et al.* 2004) and 20 - 90 m in the SCB. The majority of squid landings occur around the California Channel Islands, from Point Dume to the Santa Monica Bay, and in the southern portion of the Monterey Bay. The fishery is comprised chiefly of light-boats with high wattage illumination to attract and aggregate spawning squid to the surface, and seine vessels that net the squid (Vojkovich 1998).

To date, management has followed methods that are not dependent upon an estimate of population abundance because no estimate of squid biomass exists. Since 1983, in addition to limiting the catch and the number of vessels, management of the fishery included weekend closure north of Point Conception; recently, weekend closures have been extended to all of California. This regulation is designed to allow a 48-hour period each week for undisturbed spawning. For Monterey Bay, the weekend closure resulted in highest landings on Mondays, decreasing daily through Friday (Leos 1998). Since 2000, light boat and seine vessel operators have been required to complete logbooks for CDFG, so that CPUE can be estimated from data on the cumulative effort required to land squid.

Because of their short lifespan, many squid populations have been more effectively correlated with local oceanographic conditions than pelagic fish species with life spans of 4 - 8 years. Squid landings from all regions of the world fluctuate in conjunction with the temperatures of the previous season. McInnis and Broenkow (1978) found positive temperature anomalies preceded good *Loligo opalescens* landings by 18 months, and poor squid catches followed periods of anomalous lower temperatures in Monterey Bay. Robin and Denis (1999) found similar results. Warmer waters (mild winters) were followed by increased cohort success for *Loligo forbesi* in the English Channel, but this effect was not constant throughout the year. Conversely, Roberts and Sauer (1994) found *Loligo vulgaris reynaudii* landings in South Africa to increase with upwelling that coincided with La Niña (cold water) conditions in the equatorial Pacific. Rocha *et al.* (1999) also found an increase in squid paralarvae of many species during upwelling conditions on the Galician coast.

Modern techniques of coastal ocean monitoring, including weather buoys and satellites, provide a

vast amount of information on the physical environment of fish and squid populations. A well-established correlation exists between cold, upwelled, nutrient-rich water at the sea surface resulting from Eckmann transport and phytoplankton blooms a few days later (Nezlin and Li 2003). Mesoscale eddies generated by coastal processes and islands also serve to concentrate phytoplankton (Aristegui *et al.* 1997, DiGiacomo and Holt 2001, Falkowski *et al.* 1991). The subsequent effect on zooplankton grazers rapidly follows the cycles of upwelling and relaxation (Graham and Largier 1997, Wing *et al.* 1995, Hernandez-Trujillo 1999).

Waluda *et al.* (1999) found that the CPUE for the *Illex argentinus* fishery was not related to monthly local SST, but CPUE was inversely related to SST on the hatching grounds for the previous July, when hatchlings were in their exponential growth phase (Yang *et al.* 1986, Grist and des Clers 1998). The largest catches followed cold water. Waluda *et al.* (2001) observed a high CPUE when the Brazilian Current dominated and frontal waters diminished in the location where squid hatching occurs. Agnew *et al.* (2000, 2002) found that CPUE for *Loligo gahi* was inversely correlated with SST for hatching areas six months earlier. Sakurai *et al.* (2000) found that *Todarodes pacificus* CPUE was highest following periods when there were large regions of hatchling-favorable habitat (17°C to 23°C waters). They found a positive correlation between the density of paralarvae and the CPUE of adults in the same year ($r^2 = 0.91$). They observed a similar correlation in the CPUE of the following year ($r^2 = 0.77$).

The CDFG has an extensive database from 1981 to present for market squid. Because there is no record of effort prior to 2000 and because the market is driven by demand, it is difficult to use landings and vessel-day data to calculate CPUE and estimate biomass. Fishermen report that even if squid are available they may not be harvested when processors are not accepting squid (D. Brockman 2003, personal communication). However, there is no other database as large and widespread temporally and spatially as the fishery data. Even though there are no data recorded when boats attempt to catch squid and fail, we still use landings and VD to create a CPUE. Thus, although this CPUE is not a methodically collected estimate of biomass, it is still a robust enough estimate of abundance to draw preliminary conclusions as we wait for logbook data to accumulate.

It is important to determine the effects of the

environment on the California market squid fishery so that we can predict future landings from present conditions. Our investigation uses *Loligo opalescens* fishery landings for 1981 - 2003 to examine correlations of landings and CPUE in terms of physical oceanography. We compare landings data (time, location, vessel-days, and pounds) to SST, UI, SOI, NINO3, and their respective anomalies. We also compare CPUE to a PDI based upon distributions determined in the SCB (Zeidberg and Hamner 2002).

METHODS

The CDFG database for commercial California market squid landings from 1981 to present includes weight, date, location (based on CDFG 10 nm x 10 nm blocks), and gear type. Based upon general physical oceanographic properties (Harms and Winant 1998, Brink *et al.* 2000, Bray *et al.* 1999, Hickey *et al.* 2003) and following our previous studies (Nezlin *et al.* 2002), we organized the landings data into six regions to examine subtle differences between them: Northern Coastal (MB; because the majority of the landings in this region occur in southern Monterey Bay), Central Coastal (CC), Santa Barbara Channel (SB), Southern California Bight (SCB), Santa Monica (SM), and San Diego (SD). Also we group the fishery into two larger regions April (APR; comprised of MB) and October (OCT; a combination of the other five regions) based upon the month of greatest recruitment (Figure 1). For the purpose of this paper, recruitment is the aggregation of reproductive adults on the spawning grounds. When CDFG reports squid data they make the distinction at Point Conception, thus we grouped the MB and CC regions as “North” and the SB, SCB, SM, and SD regions as “South”. For this fishery, we defined CPUE as the tons landed recorded per day divided by the number of seine vessels that landed these squid. For days in which there were no landings, we assigned a value of zero. This CPUE is important because, although it does not represent a truly quantifying effort, it provides a proxy for estimating the abundance of squid by providing some basis for the amount of time taken to make a landing. Lampara, brail, and light boat data were not included because of the increased variability in landings/efforts and because data from these vessels have dwindled from ten to zero percent since 1981.

The landings and boat data for each region were summed for each block, each day. For example, assume that on a particular day fishermen caught

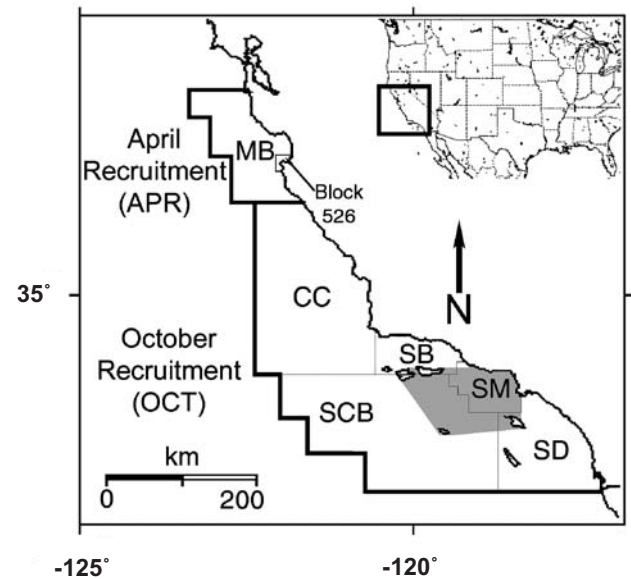


Figure 1. *Loligo opalescens* fishery regions of the California coast. Regions based upon physical oceanography: Northern Coast (MB), Central Coast (CC), Santa Barbara Channel (SB), Southern California Bight (SCB), Santa Monica Bay (SM), and San Diego (SD). Regions based upon fishery recruitment month: April recruiting (APR: MB) and October recruiting (OCT: CC, SB, SCB, SM, and SD combined). Block 526 indicates the area within MB in which the majority of landings occur for that region. Shaded area indicates the location of the paired-net surveys used to generate the paralarvae density index (PDI).

10000 tons, using 4 boats in SM; 18000 tons, using 3 boats in SCB; and 12000 tons, using 3 boats in SB. We would calculate a CPUE of 2500 tons/vessel-day (VD) in SM, 6000 tons/VD in SCB, and 4000 tons/VD in SB. Thus, we were able to determine a CPUE value for each region, for each landing date. Prior to 2002, there had never been a January landing in Monterey; in January 2002, one vessel captured 75 tons. This type of data can produce misleadingly high CPUEs; consequently, all months with less than 7 VDs for the entire period between 1981 and 2002 were removed from the analysis.

Physical oceanographic data were gathered from the Internet for SST, UI, SOI, and NINO3. The UI is defined as an Ekman offshore water transport ($m^3 s^{-1}$ per 100 m of coastline) estimated from fields of atmospheric pressure (Bakun 1973); SOI is defined as the difference between the standardized measurements of the sea level atmospheric pressure in Tahiti and Darwin; and the NINO3 is determined by averaging the SST anomalies over the eastern tropical Pacific ($5^{\circ}S-5^{\circ}N$; $150^{\circ}W-90^{\circ}W$). The buoys used

for this study were the Monterey buoy (46042, 36°N 122°W) for the MB region, the east Santa Barbara buoy (46053, 34.24°N 119.85°W) for the SB region, and the Santa Monica buoy (46025, 33°N 119°W) for the remaining regions. The SST time-series was obtained from infrared satellite measurements by Advanced Very High Resolution Radiometers (AVHRR) on National Oceanic and Atmospheric Administration (NOAA) meteorological satellites. The data were produced at the University of Miami's Rosenstiel School of Marine and Atmospheric Science (RSMAS) and the NOAA National Oceanographic Data Center (NODC) within the scope of Pathfinder Project (version 4.1) and are available from Jet Propulsion Laboratory (JPL) Physical Oceanography Distributed Active Archive Center (PO DAAC).

We performed a spectral analysis of the entire time-series to look for significant periodicities in the daily data for the entire 1981 - 2002 data set. The CPUE values were natural logs transformed and smoothed with a Parzen window (Ravier and Fromentin 2001). We used a time-series analysis method of cross correlation to determine lag period, in months, between CPUE and the physical features of SST, SOI, NINO3, and UI and their anomalies from averaged seasonal cycles. Using this lag period, we calculated linear regression of the CPUE from SST.

We performed a stock-recruitment analysis from a PDI. Paralarvae were collected with paired nets (505 µm mesh), without bridles and deployed like Bongo-nets, towed in a double oblique mode to 100 m depth. Samples were taken in February from 1999 to 2003, every 7.5 km on transects in regions SCB and SM (Zeidberg and Hamner, 2002). Flow meters were used to standardize the number of paralarvae per 1000 m³ of water. The PDI is the average number of paralarvae/1000 m³ from all tows. We used linear regression to compare the February PDI with the CPUE for the large November adult recruitment event in the SCB and SM regions of the same year.

Statistics were performed with Statview 3.0 (Abacus Concepts, Berkeley, CA) or Statistica 6.0 (Statsoft, Tulsa, OK). Interpretations of t-test, regression, analysis of variance (ANOVA), spectral analysis, and cross-correlation time-series were made in accordance with Zar (1984).

RESULTS

Decadal-regional analysis

The 1981-2002 fishery data for *Loligo*

opalescens were divided into two periods, 1981-1989 and 1990-2003 (Table 1), due to a southward shift in the fishery at that time. For the first period (1981-1989), 87% of the effort and 66% of the landings were predominantly focused in the APR region, specifically the southern portion of Monterey Bay. The amount of squid captured in 1981 and 1982 was not matched again in Monterey Bay until 2002. The MB region was the most focused, with 62% of the total catch and 83% of the CPUE coming from a very small area (block 526, Figure 1), just off Monterey harbor. CPUE in this region and time period was low, 5.54 tons/VD (Table 1). SM had 4.43% of the landings and 2.2% of the vessels yielding a CPUE of 14.85 tons/VD. Data for the SB, SCB, and SD regions were similar to those of the 1980s, with landings approximately 9%, vessels at 3%, and CPUEs varying from 18.5-20.5 tons/VD. The CC region had the smallest percentage of landings (2.5%) and vessels (0.7%), but the highest CPUE 27.4%, most likely due to squid being hauled as a secondary target species in this region. Few fishermen choose to harvest squid in the CC region due to rough seas and rocky, gear-fouling bottoms.

The focus of the California market squid fishery shifted to Southern California in the 1980s and landings surpassed those of MB in 1990 (Figure 2;

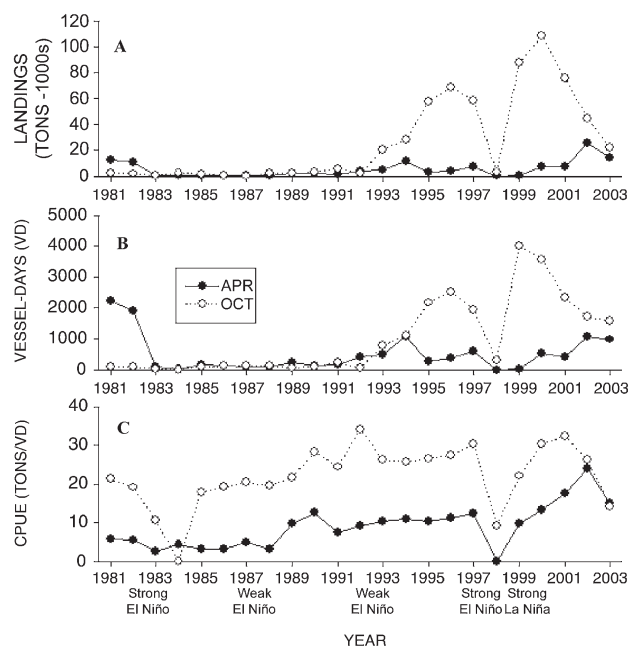


Figure 2. *Loligo opalescens* fishery data summed by year for 1981 - 2003. A) landings, B) vessel days, and C) catch per unit effort (CPUE) by year for Monterey Bay (APR - black circles) and southern California (OCT - unfilled circles). Scale of Y-axis changes between A, B, and C.

Table 1. Fisheries comparison of six physical oceanography regions for Monterey Bay 1981 - 1989 and southern California 1990 - 2003, grouped by the month of greatest recruitment of spawning adults to the fishery.

Years	Region	Vessel-days (VD)	Percent (VD)	Landings (tons)	Percent landings (tons)	CPUE (tons/VD)
1981-1989	APR					
	MB	4918	87.4	27242	66.5	5.5
	OCT					
	CC	38	0.7	1040	2.5	27.4
	SB	186	3.3	3811	9.3	20.5
	SCB	169	3.0	3475	8.5	20.6
	SM	122	2.2	1811	4.4	14.8
	SD	194	3.4	3597	8.8	18.5
Subtotal		709	12.6	13735	33.5	19.4
Total		5627		40977		7.3
1990-2003	APR					
	MB	6508	22.5	92323	13.6	14.2
	OCT					
	CC	1283	4.4	33964	5.0	26.5
	SB	3822	13.2	104172	15.3	27.3
	SCB	8037	27.7	212986	31.3	26.5
	SM	4408	15.2	113569	16.7	25.8
	SD	4918	17.0	124147	18.2	25.2
Subtotal		22468	77.5	588838	86.4	26.2
Total		28976		681161		23.5

Table 1). While VD per year decreased by 17.6% in the MB region, VD increased 20-fold in the other regions. For the period 1990 - 2003, SM and SB ranked third and fourth respectively for landings and VD due to hauls made on the northern coasts of the Channel Islands and off the Malibu and Redondo Canyons, respectively; CC was the region least targeted, with only 5% of landings and vessels. CPUE for this period was 26 tons/vessel for all regions except MB, where it was 14 tons/vessel. CPUE in APR/MB nearly tripled since 1981. CPUE in the OCT regions increased more modestly except in the SM region.

Since 1999, annual landings have decreased in OCT, from 91,229 tons to 22,180 tons; and increased in APR, from 289 to 14,521 tons, with 22,770 tons reported in 2002 (Figure 2A). Effort has increased as well in the last 23 years (Figure 2B). With the exception of MB 1981-1982, all regions have seen the number of VD/month increase until the 1997-1998 season. Since 1999, the number of VD has decreased in OCT, from 4011 to 1573, and increased in APR, from 20 to 978. The average number of days between landings for individual boats in APR (2.3) and OCT (2.1) was not significantly different (t -test_{t_{0.05(2)}}, $df = 977$, t -value 0.87, $p = 0.39$).

There have been increases in CPUE concomitant with gains in experience, and advances in technology have enhanced abilities to locate squid. There has been a “ratcheting up,” both in terms of vessel size and the use of dual sonar (50 to 200 kHz), as the fishermen compete with each other. However, CPUE decreased substantially in all regions in 1984 and 1998, the second years of the two biggest El Niño events recorded. Milder El Niño events in 1987 and 1992 preceded dips in CPUE values in 1988 and 1993 (Figure 2C). Average CPUE was calculated for the APR and OCT regions by splitting the data according to frequencies determined from spectral analysis. These splits resulted in three separate means for CPUE in APR (7.5-year frequency) and five means for the OCT region (4.5-year frequencies). Anomalies of CPUE from these means were compared to the climatic indices, with significant linear regressions in NINO3, SOI and UI anomalies, but explained less than 5% of the variance (data not shown).

1981 - 2003 squid fishery data

When comparing landings (Figure 3A) by month, the six regions fell into two categories, grouped as APR and OCT. Effort in VD and CPUE

show similar trends. The *Loligo opalescens* fishery generally occurs from April through November in APR. The largest landings occur in May for the APR region and in November for the OCT region, when SST is 11.7°C and 16.1°C, respectively. Although landings peak in May, the number of active vessels also peaks in this month such that CPUE dwindles to one-half of April values (Figure 3B and 3C). Notably, a second landings pulse occurs in August.

In the five regions that comprise the OCT grouping, landings typically begin in October, build to a peak in January, and diminish to lows in August (Figure 3A). A large unimodal pulse of squid landings occurred in November for all regions except SCB. The SCB had a bimodal recruitment pulse, the two largest recruitment events in all of California: one in November and a larger one in January. In SD, like SCB, landings peaked in January, but there was no strong November signal in this region.

CPUE by month for APR was typically half that of OCT. The APR CPUE varied between 8 and 20 tons/VD, for months with more than seven VD, whereas the southern California OCT regions ranged from 17 to 36 tons/VD (Figure 3C).

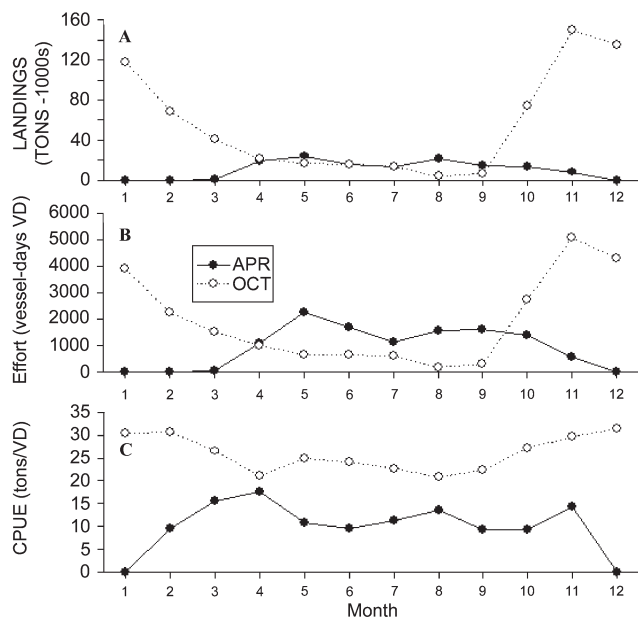


Figure 3. *Loligo opalescens* fishery data summed by month for 1981-2003. Landings (tons; A), effort in vessel-days (VD; B), and catch per unit effort (tons/VD; C) in Monterey Bay (APR - black circles) and southern California (OCT - unfilled circles). Scale of Y-axis changes between A, B, and C.

Time-series analysis

We used spectral analysis to deconstruct the CPUE time-series data into a series of sums of sine and cosine functions. The periods of the 10 highest peaks of the variance spectrum were determined for all 6 regions (Table 2). The largest peaks from the spectral analysis occurred at periods of 372 and 356 days, or roughly 1 year for all regions. There was a 7.5-year peak in the MB and CC regions. There was a 4.5-year peak for all regions except MB, similar to

Table 2. Top 10 periods of greatest spectral variance for the daily CPUE data of the squid fishery for 1981 - 2003, significance: $p < 0.01$. Numbers in bold are repeated in more than one region. Harmonics of factors of 2: 2, 4,...4096 (blank spaces) have been omitted as they are inherent in spectral analysis and not relevant to this species.

Rank	MB			CC		
	Days	Years	Month	Days	Years	Month
1	372.4	1	12.2			
2	356.2	1	11.7	372.4	1	12.2
3				1638.4	4.5	53.7
4	7	0	0.2	2730.7	7.5	89.5
5	315.1	0.9	10.3	455.1	1.2	14.9
6	2730.7	7.5	89.5	481.9	1.3	15.8
7	341.3	0.9	11.2	356.2	1	11.7
8	455.1	1.2	14.9	390.1	1.1	12.8
9	3.5	0	0.1			
10	1365.3	3.7	44.8			

Rank	SB			SCB		
	Days	Years	Month	Days	Years	Month
1	372.4	1	12.2	372.4	1	12.2
2	356.2	1	11.7	1638.4	4.5	53.7
3	390.1	1.1	12.8	356.2	1	11.7
4	1365.3	3.7	44.8	1365.3	3.7	44.8
5	1638.4	4.5	53.7	390.1	1.1	12.8
6	910.2	2.5	29.8			
7						
8	264.3	0.7	8.7			
9				819.2	2.2	26.9
10	182	0.5	6	682.7	1.9	22.4

Rank	SM			SD		
	Days	Years	Month	Days	Years	Month
1	372.4	1	12.2	356.2	1	11.7
2	1638.4	4.5	53.7			
3	182	0.5	6	372.4	1	12.2
4				182	0.5	6
5				1638.4	4.5	53.7
6	356.2	1	11.7	682.7	1.9	22.4
7	390.1	1.1	12.8	341.3	0.9	11.2
8	315.1	0.9	10.3	1365.3	3.7	44.8
9	204.8	0.6	6.7	390.1	1.1	12.8
10	7	0	0.2	178.1	0.5	5.8

the period of the four El Niño events that occurred in this region from 1981-2002. There was a 3.7-year peak for all regions except CC and SM. The seven-day cycle is most likely a stochastic factor of fishermen working within weekend closures as data before 1998 did not have this periodicity. There was no 28- or 14-day cycle in any of the regions, strongly suggesting that spawning squid do not respond to tidal currents or lunar light.

The most significant cross-correlations of time lag analysis for CPUE to SST are listed in Table 3. In this table, significant correlation coefficients occurred when CPUE lagged behind SST from buoys and AVHRR by 4 to 10 months for all regions except CC. Negative correlation coefficients demonstrate that high CPUE corresponds to low temperatures in the lagged month from column two; positive values suggest a direct relationship. In all cases of biological significance, CPUE lagged SST by 4, 5, or 10 months. For the MB, CPUE was highest in May when SST was low four months earlier (January); hence, a negative correlation was observed. In all other regions, the four or five month correlation was positive, with CPUE high in November when SSTs were high four months earlier (July). For the southern California regions there was a negative correlation to the SSTs 10 months prior (January). Consequently, cold winters and warm summers correlate to larger landings. Recruitment of spawning adults to the fishery occurs during the productive

Table 3. Time-series analysis of SST and CPUE by region.

CPUE region	Lagged (months)	SST source	Correlation coefficient
MB	4	MB Buoy	-0.48
	5	AVHRR	-0.36
SCB	4	SM Buoy	0.21
	10	SM Buoy	-0.34
	9	AVHRR	-0.34
SD	4	SM Buoy	0.22
	10	SM Buoy	-0.40
	10	AVHRR	-0.39
SM	5	SM Buoy	0.18
	10	SM Buoy	-0.34
	10	AVHRR	-0.33
SB	4	ESB Buoy	0.39
	4	SM Buoy	0.42
	9	AVHRR	-0.37

seasons in both APR and OCT. Productivity in APR co-occurs with the spring-summer upwelling season, and in OCT productivity correlates with winter storms that lead to a deeper mixed layer. There were significant cross-correlations to SOI, NINO3, and UI, but not to the anomalies of SOI and UI. Figure 4 illustrates these relationships as follows: SOI – atmospheric pressure differences between Tahiti and Darwin (A and B) and NINO3 – SST anomaly in eastern equatorial Pacific (C and D) in regions OCT (A and C) and APR (B and D). The correlation between CPUE and NINO3 is greater than SOI in both regions. CPUE lags NINO3 by 9 to 11 months in APR and 4 months in OCT; thus, the effects of an El Niño event cause declines in CPUE for *Loligo opalescens* in southern California 4 months later and in Monterey Bay 9 to 11 months later (long arrows, Figure 4). High correlation coefficients at a 10-month lag in southern California (OCT) may be due to a second generation responding to changes in SST (shorter arrow, Figure 4). Interestingly, this figure shows that correlations for NINO3 were greater than SOI, suggesting that the CPUE of *Loligo opalescens* is more closely related to oceanic teleconnection than to atmospheric teleconnection.

Assuming a 6 to 9 month lifespan of *L. opalescens*, we used linear regression to compare SST from buoy data 6 to 10 months prior. We performed 10-month comparisons because squid eggs take 30 days to hatch at 12°C, which is typical for egg beds in winter in Southern California and in spring-summer in Monterey Bay. For the SM region, November is the month of highest recruitment. Notably, the only significant regression observed occurred in this region, between January and November (CPUE = 131.19 - 7.24 x SST;

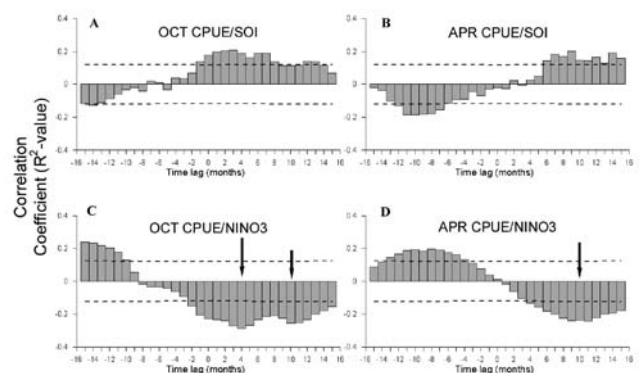


Figure 4. Time-series analysis: cross-correlation between CPUE and the global climatic indices.

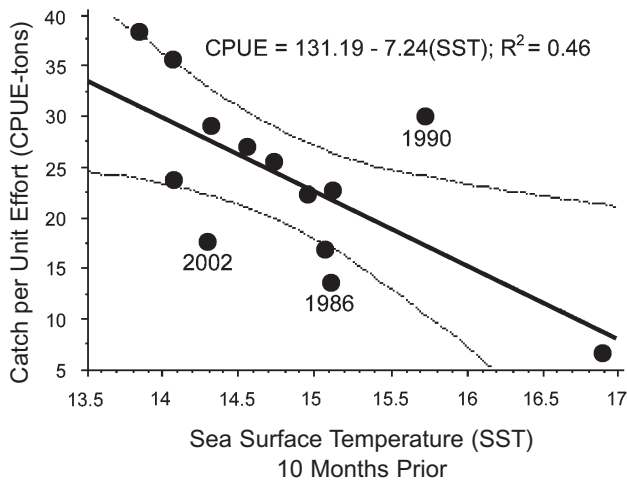


Figure 5. Linear regression and 95% confidence intervals for November CPUE with respect to SSTs (January to November) in the SM region.

$r^2 = 0.46$, $p = 0.0033$; Figure 5). We compared satellite-derived (AVHRR) estimates of SST for 1985 - 2002, for areas with high densities of paralarvae and juveniles (within 8 km of shore), to CPUE, using cross-correlation time-series analysis. While there were significant correlations, linear regression yielded no significant predictions of landings or CPUE from SST.

Stock recruitment analysis

We compared PDI to CPUE for the SCB and SM regions (Figure 6, shaded area of Figure 1). Collections of paralarvae were made in February. After the initial 1999 surveys, methods developed in Zeidberg and Hamner (2002) resulted in 34 - 50 stations of oblique bongo tows to collect paralarvae in the SCB and SM regions. Paralarvae/1000 m³ from all stations were averaged to create the February PDI (Figure 6, lower right), and then compared to the November recruitment of spawning adults (CPUE) to the fishery for the same year. Linear regression was not significant for 1999 - 2003 ($r^2 = 0.522$, $p = 0.1683$). However, if 1999 was treated as an outlier because it lacked nearshore sampling sites where 76% of the paralarvae were captured subsequently, the regression explains 97.8% of the variance, and the F-value of the ANOVA ratio test for this regression is significant ($p = 0.007$; Figure 7). From 1992 to 2002 the SCB (36.2%) and SM (16.2%) regions represented nearly half of the landings for California, suggesting that this technique could apply throughout the state.

DISCUSSION

We report landings, effort, and CPUE for *Loligo opalescens* in California for 1981 - 2003. It is important to reiterate that CPUE is an approximation of abundance in the fishery and fails to estimate biomass of squid in California waters. Vessels that attempt to capture squid and fail cannot be tracked with this method; squid that are not harvested commercially are not accounted for in this report. *L. opalescens* reproduces by aggregating from small, foraging groups of hundreds of individuals into groups of millions of individuals. As such, it is possible that a large decrease in biomass can be masked by a larger percentage of the population aggregating in seemingly similarly-sized spawning masses. Such species are vulnerable to highly mobile fisheries (Oostenbrugge *et al.* 2002).

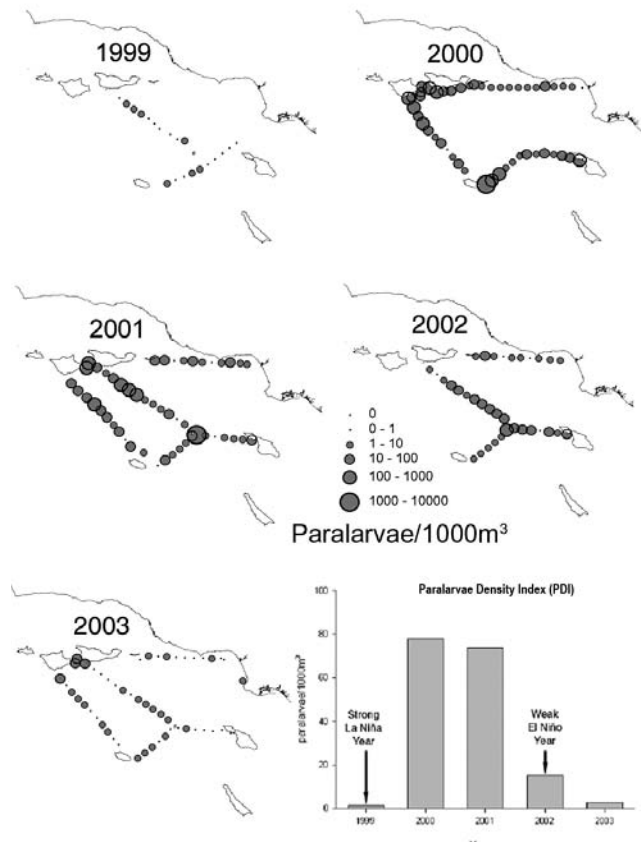


Figure 6. Density profiles (exponential bubble plot) for *Loligo opalescens* paralarvae surveys in the SCB, February 1999-2003. Size of circle corresponds to number of paralarvae/1000 m³ seawater sampled. Data for 1999-2001 reprinted with permission from Springer-Verlag, originally in Zeidberg and Hamner (2002). Data from all tows are averaged to obtain a PDI for each year (lower right). The 1999 La Niña (cold) and 2002 El Niño (warm) events are labeled above bars in PDI.

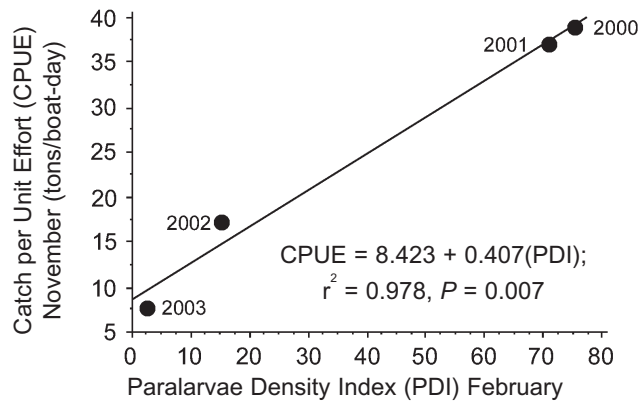


Figure 7. Stock-recruitment model: linear regression of CPUE of spawning adults in November from February PDI in the SM and SCB regions for 2000-2003.

Trends in the fishery

The fishery for California market squid has increased in all parts of the study area since 1983 due to an internationally increasing demand for calamari and the collapse of other fisheries, both within and outside of California waters. The majority of fishing activity shifted from MB to the SCB region in the 1980s. Fishing activity in the SCB experienced a second increase in the 1990s, reflecting an increase in participants from Alaska, Washington, and Oregon. The most economically harmful trend is that landings decreased substantially during the second year of strong El Niño events, but decreased only slightly during weak El Niño events.

The initial impetus of performing the spectral analysis was to determine if the squid were migrating to the spawning grounds in relation to a lunar or tidal signal. It is important to note that the spectral analysis using CPUE and landings (not shown) did not show that squid recruit to spawning sites in a fortnightly fashion. There was no 14-day period in any region. Spectral analysis demonstrated periodicities of *Loligo opalescens* CPUE on scales ranging from days to years. The most common periods for all regions were annual. Varying from 315 to 390 days, annual cycles made up more than half of the top 10 signals in the analysis. The 4.5-year cycle corresponds well with the El Niño events of 1982-1983, 1987, 1992, and 1997-1998 (Hayward *et al.* 1999). In each of these cases, the CPUE anomalies were negative (Zeidberg 2003). The longest period was 7.5 years in the MB and CC regions. There were evident leaps in the mean

CPUE based on mean CPUE +/- five months in MB at mid-1988 and the end of 1995, when out-of-state fishermen began to harvest squid in California (Zeidberg 2003). While these may correspond to changes in the biomass of the squid, it is more likely due to enhancements in the capacity of the fishery as acoustic and communication technology has improved. The 3.7-year period is probably a statistical harmonic of the 7.5-year period.

PDI can predict CPUE

Zeidberg and Hamner (2002) sampled the SCB and SM regions for *Loligo opalescens* paralarvae since 1999, and we used that data to create a PDI. The CPUE appears to be a better indicator of stock abundance than landings data for squid (Sakurai *et al.* 2000). Adults recruiting to the fishery in November, measured in CPUE, can be predicted by linear regression from the PDI of February. A regression of the CPUE data from the PDI data for 1999 - 2003 is not significant; however, if 1999 is treated as an outlier, the remaining four points (2000 - 2003) create a regression that explains 97.8% of the variance. Our 1999 paralarvae sampling may not be indicative of the fishery, because this was the first sample year and the sampling sites were located more offshore than sampling sites for 2000 - 2003. In 1999, there were no sites within 7.4 km of shore, where 76% of the paralarvae were captured in the subsequent four years of sampling. Despite these caveats, this method could provide the first opportunity to manage the California market squid fishery based upon scientifically gathered biological indicators with very few of the inherent assumptions needed for many other types of forecasting (Mangel *et al.* 2002). As the years of logbook data accumulate, estimates of CPUE will be more closely related to the actual biomass of the species. By the end of February, we could have a prediction for the CPUE for the following year's adult recruitment. Paralarvae may be the best stage of the life cycle for fishery prediction, as juveniles can escape trawls, fewer assumptions need to be made than with estimates from spawning females (Macewicz *et al.* 2004), and there is sufficient time (6 to 9 months) to develop predictions. These predictions could assist managers in setting catch limits and aid fishermen in deciding how to invest in gear for the following season.

In addition to our paralarvae sampling, CalCOFI has sampled the waters of California for

zooplankton in a manner similar to ours since 1949. *Loligo opalescens* paralarval distributions have been described from these data (Okutani and McGowan, 1969). The greatest difference between the two sampling efforts is the number of stations that are in close proximity to land. The majority of the paralarvae (76%) captured by Zeidberg and Hamner (2002) were at stations less than 8 km from shore, but there is only one CalCOFI station with this proximity to land. Based upon their surveys and models of larval dispersal (Botsford *et al.* 2001, Franks 1992, Siegel 2003), we predict that a PDI calculated from CalCOFI samples will be substantially lower than ours. However, given the long time period of the CalCOFI sampling program, any significant correlations could be more powerful statistically than ours. Furthermore, fishermen could be employed to perform bongo tows for paralarvae, in proximity to shore, to complement CalCOFI data. If the CalCOFI bongo net data were sorted for *Loligo opalescens* paralarvae, and if fishermen collected paralarvae nearshore, Monterey Bay and Southern California CPUE could be predicted months in advance. Separate management of the two regions would be necessary, given the time lag of recruitment (APR and OCT).

Comparison of fishery data to physical data

We found a correlation between CPUE of the largest recruitment month with SST buoy data from 10 months prior in the SM region only. There may be physical features specific to this region that increase the correlation between spawning recruitment and SST. For example SM is a small region; it is close to the buoy; most of the area is sandy bottom; and it contains the Redondo Canyon. Thus, if further attempts to match physical oceanography to the biology of a pelagic species were to occur, the Santa Monica Bay could be the most ideal location. Alternately, this may be a seasonal effect, as the regression is significant for SST only and not SST anomaly. Furthermore, we caution that the significance of the correlation between CPUE and SST in the SM region may be a type I error, because it was the only significant test, of the 30 tests run, using an alpha level of 0.05. The size of the recruitment event was not strongly related to small deviations from average monthly SST; thus, the timing of squid recruitment to spawning grounds in APR and OCT may be tied to annual fluctuations of prey availability,

and correlations with temperature may be coincidental. The 10-month lag corresponds to the egg laying date of 9-month old squid. The lack of a greater number of correlations may be due to the small spatial resolution of the buoy data and the enormous variability of SST due to mesoscale oceanographic features in the large fishery regions. In some regions the nearest buoy was quite distant from the fishery zone.

To address the spatial distance of spawning grounds from buoys, we compared SSTs derived from satellite AVHRR images to CPUE. AVHRR data were collected only from the shelves and slopes of the six fishery regions because these are the most important areas for the growth of hatchlings and juveniles. Cross-correlation time-series analyses were significant at 5 to 10 month lags (Table 3), but this did not translate into any predictive capabilities with linear regression.

Similarly, cross-correlations of CPUE to SOI and NINO3 were significant at a 10-month lag in the MB region and a 4-month lag in the SCB. Thus, the Monterey fishery (10% of landings) is offset by six months (roughly one short cohort) from the SCB fishery. The correlation coefficients for NINO3 were greater than those of SOI, corroborating the idea that the direct influence of the coastal waves (oceanic teleconnection) is the main source of the changes in the hydrographic and ecological features of the California Current system (Huyer and Smith 1985, Rienecker and Mooers 1986, Lynn *et al.* 1995, Chavez 1996, Ramp *et al.* 1997) rather than the ENSO related changes of atmospheric circulation (atmospheric teleconnection; Simpson 1983, Simpson 1984a, Simpson 1984b, Mysak 1986, Breaker and Lewis 1988, Breaker *et al.* 2001, Schwing *et al.* 2002).

Loliginid life cycles and future squid fisheries management

A correlation between SST and CPUE in the following season could have resulted from the unique development pattern of teuthids. The use of CPUE as an index of abundance of the population (Sakurai *et al.* 2000), in combination with studies of squid growth in relation to SST (Jackson and Domeier 2003), could explain large fluctuations in landings data from year to year. In terms of bottom-up forcing, individual squid health and the resulting population size result from a combination of prey availability and metabolic rates. Squids

grow exponentially in the first two months of life, then logarithmically until senescence. In rearing tanks, given a constant food supply, Loliginids also grow faster in warmer temperatures (Yang *et al.* 1986, Forsythe *et al.* 2001), as their metabolic rates increase (O'Dor 1982). Grist and des Clers (1998) predict that annual fluctuations in SST that cause differential growth of squids can lead to younger cohorts hatched in warm temperatures, surpassing in size older cohorts born in colder seasons. Thus in October, a large 6-month squid that hatched in April and developed in warm water may spawn with a smaller 9-month squid that hatched in the cold waters of January.

However, in California, and possibly other upwelling systems, the situation is more complex than in rearing tanks. For example, Jackson and Domeier (2003) demonstrated that due to the influences of El Niño/La Niña cycles and upwelling, the mean mantle length of *Loligo opalescens* is shortest when hatched in the warmest temperatures and longest when hatched in cold waters. Mantle length is also positively correlated with the upwelling index. In the ocean, squid do not have a constant food supply. The high productivity and cold temperatures caused by upwelling and La Niña combine to create a period of rich food resources and lower metabolic rates for squid, probably enhancing the recovery of the fishery in 1999. During the El Niño event, squids were small and less abundant, because they had a high metabolic rate due to increased temperatures and lower levels of prey availability due to decreased ocean productivity. Seasonal maxima of phytoplankton in the MB region occur in summer; in the southern part of the SCB productivity peaks in winter (Nezlin *et al.* 2002). These differences may be an indicator of the reason that the fishery occurs in the MB region from April to November, coinciding with the upwelling season, and in the SCB from November to May, coinciding with less stratification and more mixing due to winter storms and colder air temperatures.

Lowry and Carretta (1999) corroborate the temperature induced mantle length (ML) plasticity from beaks of squid in California sea lion (*Zalophus californianus*) scats and spewings. MLs of squid prey were half the size during El Niño years on San Clemente and Santa Barbara Islands. However, at San Nicholas Island during El Niño events, there were both small and regular sized squid prey, suggesting that the squid stock may have moved off-

shore to find productive waters. Alternatively, San Nicholas sea lions could be feeding upon squids from Baja California. Zeidberg and Hamner (2002) suggested the possibility of a northern shift in the squid population in El Niño years, as found for most zooplankton (Colebrook 1977).

However, the growth plasticity and fluctuating reproductive success for *Loligo opalescens* should not be underestimated. The possibility remains that the entire California market squid biomass may undergo huge fluctuations in response to strong El Niño and La Niña years, rather than due to population migrations away from traditionally fished spawning grounds. Triennial groundfish surveys demonstrate that California market squid experienced a coast-wide population decrease, not a poleward migration, during the 1997-1998 El Niño.

With the exception of El Niño years, the fishery increased its landings each year until 2000. However, it remains unknown if the capacity of the fishery is close to reaching the total biomass of squid in California. The California sardine (*Sardinops sagax*) fishery collapsed in the 1960s, and a twenty-year moratorium was required before there was recovery to a fraction of prior spawning biomass (Wolf 1992). Whether over-fishing or large-scale, multi-decadal climatic regime shifts caused this collapse is matter of debate (Chavez *et al.* 2003), but without an effective management plan, squid will continue to be fished based on market demand. Markets are driven by economic forces and traditionally do not control themselves in a biologically sustainable manner. A full recovery of the fishery for California market squid occurred between 1998 and 2000, thus spanning four generations of squid, given a 6- to 9-month lifecycle. For the California sardine, with a 6- to 8-year lifecycle, a proportionally similar recovery period would be 24 to 32 years (Richard Parrish, personal communication).

From 1998 to 1999, the *Loligo opalescens* fishery decreased to low levels during the El Niño event, then recovered to record levels in the following years. This is most likely due to the plasticity of development in relation to water temperature, upwelling, and short life span. One should not assume that the ability of this species to recover from environmental stress like El Niño applies also to the recent anthropogenic stresses associated with increasing fishery capacity. It remains to be seen if the large decline, from 119,780 to 24,449 tons/year, in southern California landings over the last five

years is due to the small El Niño of 2002-2003, the climate-regime shift in 1998, overfishing, or other factors, such as increased stratification due to global warming. While the short-lived squid may be able to recover from overexploitation in short order, the huge number of long-lived birds, fish, and marine mammals (Morejohn *et al.* 1978, Lowry and Carretta 1999) that depend on squid as a key forage species may not recover as rapidly from lack of management foresight. The recent establishment of the marine reserve system in the Channel Islands eliminates 13% of key squid fishing grounds. This ecosystem based management approach may assist in protecting not only the squid but also their predators.

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