

Abstract—The California market squid (*Loligo opalescens*) has been harvested since the 1860s and it has become the largest fishery in California in terms of tonnage and dollars since 1993. The fishery began in Monterey Bay and 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 1982–83 and 1997–98, but not following 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 correlated well with catch per unit of effort (CPUE) for the following November recruitment of adults to the spawning grounds. This stock–recruitment analysis was significant for 2000–03 ($CPUE = 8.42 + 0.41PDI$, adjusted coefficient of determination, $r^2 = 0.978$, $P = 0.0074$). Surveys of squid paralarvae explained 97.8% of the variance for catches of adult squid nine months later. The regression of CPUE on PDI could be used to manage the fishery. Catch limits for the fishery could be set on the basis of paralarvae abundance surveyed nine months earlier.

Manuscript submitted 7 May 2004
to the Scientific Editor's Office.

Manuscript approved for publication
20 June 2005 by the Scientific Editor.
Fish. Bull. 104:46–59 (2006).

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

Louis D. Zeidberg

Monterey Bay Aquarium Research Institute
7700 Sandholdt Rd.
Moss Landing, California 95039-9644
E-mail address: zelo@mbari.org

William M. Hamner

Dept. of Ecology and Evolutionary Biology
Univ. California, Los Angeles
621 Charles E. Young Drive South
Box 951606
Los Angeles, California 90095-1606

Nikolay P. Nezlin

Southern California Coastal Water Research Project
7171 Fenwick Lane
Westminster, California 92683-5218

Annette Henry

California Department of Fish and Game
Southwest Fisheries Science Center
Marine Region, La Jolla Field Office
8604 La Jolla Shores Drive
La Jolla, California 92037

The recent discovery of falsification in Chinese fisheries reporting has 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 like swordfish and snapper beyond sustainability, and fisheries have subsequently shifted to prey items like 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 the larger cephalopod landings may be due to increased demand, but lower levels of predation and competition from finfish, and 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 a minimum of 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 fishermen 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 also deplete the squid population, it is not clear how oceanic food chains will respond. If the subannual 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 probably constitutes 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 metric tons of California market squid (*Loligo opalescens*) with an exvessel (wholesale) revenue of \$36 million (California Department of Fish and Game [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 Southern California Bight. The majority of squid landings occur around the California Channel Islands, from Pt. Dume to Santa Monica Bay, and in southern Monterey Bay. The fishery comprises chiefly light-boats with high wattage illumination to attract and aggregate spawning squid to the surface, and seine vessels that net the squid (Vojkovich, 1998).

Management to date has followed methods that are not dependent upon an estimate of population abundance because no estimate of squid biomass exists. In addition to limiting the catch and the number of vessels, management of the fishery has included weekend closures north of Point Conception since 1983, and these closures have recently extended to all of California coastal waters. 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 and decreasing daily landings through Friday (Leos, 1998). Since 2000, light boat and seine vessel operators have been required to complete logbooks for CDFG, such 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 have 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 low 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 Galacian-coast.

Modern instruments for monitoring coastal ocean conditions, including weather buoys and satellites, provide a vast amount of information on the physical environment of fish and squid populations. The correlation between cold, upwelled nutrient-rich water at the sea

surface resulting from Eckman transport and phytoplankton blooms a few days later is well established (Nezlin and Li, 2003). Mesoscale eddies generated by coastal processes and islands also serve to concentrate phytoplankton (Falkowski et al., 1991; Aristegui et al., 1997; DiGiacomo and Holt, 2001). The subsequent effect upon zooplankton grazers rapidly follows the cycles of upwelling and relaxation (Wing et al., 1995; Graham and Largier, 1997; Hernandez-Trujillo, 1999).

Waluda et al. (1999) found that the CPUE for the *Illex argentinus* fishery was not related to monthly local sea surface temperature (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) found a large 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 (17–23°C waters). They found a positive correlation between the density of paralarvae and the catch per unit of effort (CPUE) of adults in the same year ($r^2=0.91$) and also in the CPUE of the following year ($r^2=0.77$).

The CDFG has an extensive database of landings data from 1981 to the 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 a CPUE and therefore estimate biomass. Fishermen report that even if squid are available, they may not be harvested when processors are not accepting squid (Brockman¹). However, there is no other database as large and widespread temporally and spatially as fishery data. Even though there are no data recorded when boats attempt to catch squid and fail, we can still use landings and vessel-days to create a CPUE. This CPUE therefore is not a methodically collected estimate of biomass, but 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 California market squid landings for 1981–2003 to examine correlations of landings and CPUE with physical oceanography. We compare landings data (time, location, vessel-days, and landings [in pounds]) to sea surface temperature (SST), upwelling index (UI), the Southern Oscillation index (SOI), the index of sea surface temperature in the eastern equatorial tropical Pacific NINO3, and their respective anomalies. We also compare CPUE to a paralarvae density index

¹ Brockman, D. 2002. Personal commun. Davies Locker Sportfishing, 400 Main St. Newport Beach, CA 92611.

(PDI) based upon distributions determined in the Southern California Bight (Zeidberg and Hamner, 2002).

Materials and methods

The CDFG database for commercial California market squid landings from 1981 to present includes weight, date, location (based on CDFG 10×10 nm blocks), and gear type. Accounting for general physical oceanographic properties (Harms and Winant, 1998; Bray et al., 1999; Brink et al., 2000; Hickey et al., 2003) and following our previous studies (Nezlin et al., 2005), we organized the landings data into six areas to look at subtle differences between them: MB=northern coastal (because the majority of the landings in this area occur in southern Monterey Bay), CC=central coastal, SB=Santa Barbara Channel, SCB=Southern California Bight, SM=Santa Monica, and SD=San Diego. Also we grouped the fishery into two larger regions April (APR, equal to MB above) and October (OCT, a combination of the other five areas) based upon the month of greatest recruitment (Fig. 1). For the purpose of our study, recruitment is the aggregation of reproductive adults on the spawning grounds. When CDFG reports squid data, they make a distinction at Point Conception, thus our MB and CC areas are grouped as the “north” and our SB, SCB, SM, and SD are named “south.” For this fishery we defined CPUE as the recorded tons landed in a day, divided by the number of seine vessels that landed these squid. Those days in which there were no landings were assigned a value of zero. This CPUE is important because, although not truly a quantifying effort, it does provide a means 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 increased variability in landings and effort and the fact that these vessels have dwindled from ten to zero percent since 1981.

The landings and boat data for each area were summed for each block by day. For example, assume that on a particular day fishermen caught 10,000 metric tons with four boats in the area of SM, 18,000 tons from three boats in SCB, and 12,000 tons from three boats in SB. We would calculate a CPUE of 2500 tons/vessel-day in SM, 6000 tons/VD in SCB, and 4000 tons/VD in SB, respectively. Thus for every date for which there was a landing we were able to calculate CPUE value for each area. Until 2002, there had never been a landing in Monterey in January, when one vessel captured 75 tons. Data such as this produce misleadingly high CPUEs; therefore all months with less than seven vessel-days for the entire 22-year period were removed from the analysis.

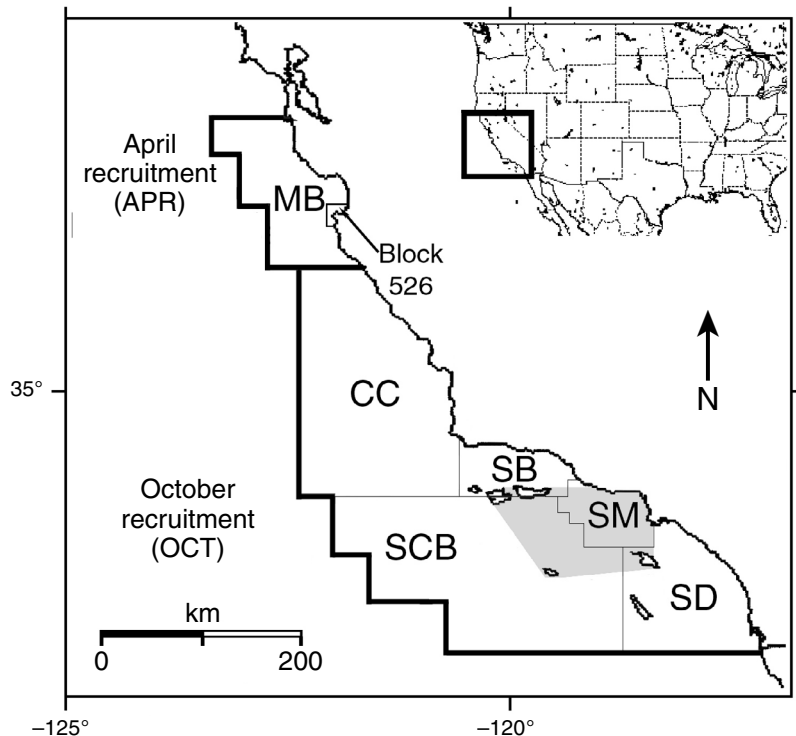


Figure 1

The California coast with the fishery areas for the California market squid (*Loligo opalescens*) identified. Areas were classified according to physical oceanographic features: Northern Coast (MB), Central Coast (CC), Santa Barbara Channel (SB), Southern California Bight (SCB), Santa Monica Bay (SM), and San Diego (SD). Regions were also classified by fishery recruitment month: April recruiting (APR: same as MB area) and October recruiting (OCT: CC, SB, SCB, SM, and SD areas combined). Block 526 (indicated with a slender arrow) is where the majority of the MB-APR landings occur. Shaded area indicates the location of the paired-net surveys used to generate the paralarvae density index (PDI).

Physical oceanography data were gathered from the Internet for sea surface temperature (SST),² upwelling index (UI),³ southern oscillation index (SOI),⁴ and NINO3.⁵ Upwelling index (UI) is an Ekman offshore water transport (m^3/s per 100 m of the coastline) estimated from fields of atmospheric pressure (Bakun, 1973). Southern Oscillation index (SOI) is the difference between the standardized measurements of the sea level atmospheric

² NOAA (National Oceanic and Atmospheric Administration). National Data Buoy Center. 2000. Website: <http://facstaff.scripps.edu/surf/buoys.html> [Accessed on 24 April 2003.]

³ NOAA Pacific Fisheries Environmental Laboratory. 2003. Website: <http://www.pfeg.noaa.gov/products/las.html> [Accessed on 20 March 2003.]

⁴ Australian Government Bureau of Meteorology. 2005. Website: <http://www.bom.gov.au/climate/current/soihtml1.shtml> [Accessed on 29 March 2003.]

⁵ IRI (International Research Institute for Climate Prediction). 2005. Website: <http://ingrid.ldeo.columbia.edu/SOURCES/Indices/.nino/.EXTENDED/.NINO3/> [Accessed on 20 April 2004.]

Table 1

Totals of vessel-days, landings (metric tons), and CPUE (tons/vessel-day) for two time periods of the California market squid (*Loligo opalescens*) fishery (1981–2003). The majority of the fishery occurred in Monterey Bay, 1981–89, and in southern California, 1990–2003. The six small areas represent physical oceanographic features and the larger regions (APR and OCT) are grouped by the month of greatest recruitment of spawning adults to the fishery (see bolder border in Fig. 1). MB and APR are synonymous terms. MB=northern coastal area, predominantly southern Monterey Bay; CC=central coast; SB=Santa Barbara; SCB=Southern California Bight; SM=Santa Monica; and SD=San Diego. VD=vessel days.

Years	Region and area	Vessel-days (VD)	Percent VD	Landing (tons)	Percent landings (tons)	CPUE (tons/VD)
1981–89	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

pressure in Tahiti and Darwin. NINO3 is determined by averaging the SST anomalies over the eastern tropical Pacific (5°S–5°N; 150°W–90°W). The buoys used 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.

We performed a spectral analysis of the entire time series to look for significant periodicities in the daily data for the entire 22-year data set. CPUE values were natural log-transformed and smoothed with a Parzen window (Ravner and Fromentin, 2001). We used a time series analysis method of cross correlation to determine the 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.

Sea surface temperature (SST) time series was obtained from infrared satellite measurements with advanced very high resolution radiometers (AVHRRs) on National Oceanic and Atmospheric Administration (NOAA) meteorological satellites. The data were processed 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, available from the Jet Propulsion Laboratory Physical Oceanography Distributed Active Archive Center [JPL PO DAAC]).⁶

We performed a stock-recruitment analysis from a paralarvae density index (PDI). Paralarvae were collected with paired nets (505- μ m mesh) without bridles, deployed like bongo-nets, and 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, ANOVA,

⁶ <http://podaac.jpl.nasa.gov/> [Accessed on 15 March 2003.]

spectral analysis, and cross correlation time series were made in accordance with Zar (1984).

Results

Decadal-regional analysis

The 22-year fishery data for *Loligo opalescens* were divided into two periods: 1981–89 and 1990–2003 (Table 1) due to a southward shift in the fishery after 1989. For the first period (1981–89), 87% of the effort and 66% of the landings were predominantly focused in the MB or APR region, specifically in 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 region; 62% of the total catch and 83% of the CPUE came from a very small area (block 526, Fig. 1)—just off Monterey harbor. CPUE in this region and time period was low, 5.54 tons/vessel-day (Table 1). SM had 4.43% of the landings and 2.2% of the vessels, yielding

a CPUE of 14.85 tons/vessel-day. The SB, SCB, and SD areas were similar in the 1980s with landings around 9%, vessels at 3%, and CPUEs varying from 18.5 to 20.5 tons/vessel-days. The CC area 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 central California area because of rough seas and rocky, gear-fouling ocean bottoms.

The focus of the market squid fishery shifted to southern California in the 1980s and landings surpassed those of Monterey Bay in 1990 (Fig. 2, Table 1). Whereas vessel-days per year decreased by 17.6% in the MB area, vessel-days increased 20-fold in the other areas. For the period 1990–2003, SM and SB ranked third and fourth for landings and vessel-days because of hauls made on the northern coasts of the Channel Islands and off the Malibu and Redondo Canyons, respectively. CC is the area least targeted, with only 5% of landings and vessels. CPUE for this period was 26 tons/vessel for all areas except MB, where it was little more than half that at 14 tons/vessel. CPUE in APR/MB has nearly tripled since 1981–82. CPUE in the OCT region has increased more modestly, except in SM.

Since 1999, annual landings have decreased in OCT (91,229 tons to 22,180 tons) and increased in APR (289 to 14,521 tons—with 22,770 tons in 2002, Fig. 2A). Effort has increased as well in the last 23 years (Fig. 2B). With the exception of MB 1981–82, all areas saw the number of vessel-days/month increase until the 1997–98 season. The number of vessel-days has decreased since 1999—in OCT (4011 to 1573)—and has increased in APR (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_{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 the ability of fishermen to locate squid. There has been a “ratcheting up,” both in terms of size of vessel and in the amount of sonar (from single to dual frequency [50 to 200 kHz]) used in the competition among fishermen. 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 (Fig. 2C). Average CPUE was calculated for the APR and OCT regions by splitting the data

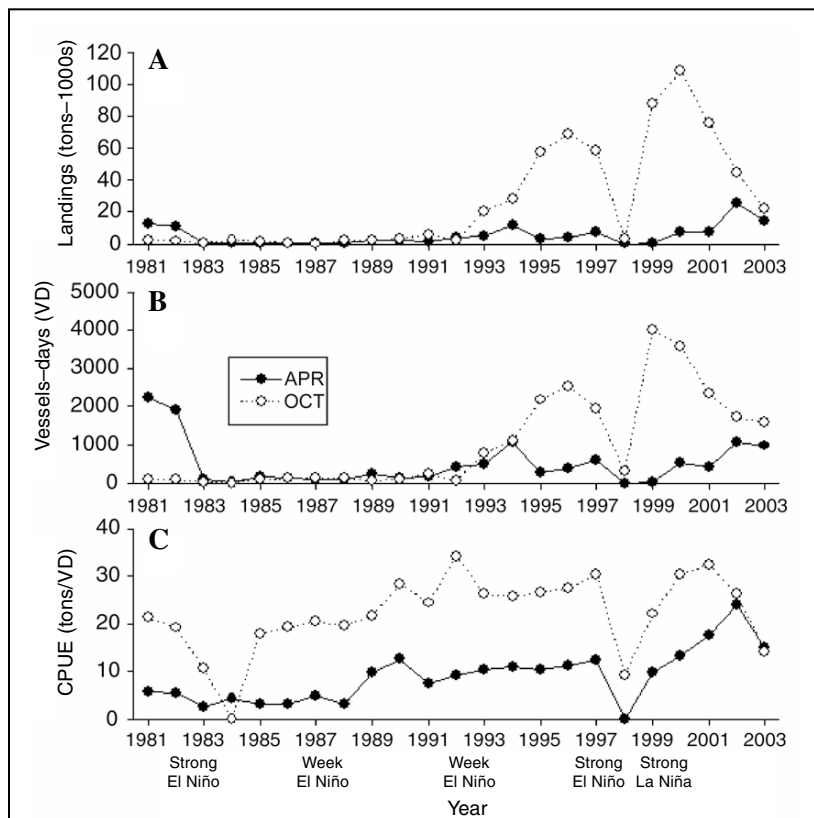


Figure 2

Fishery data for *Loligo opalescens*, summed by year for 1981–2003. (A) landings, (B) vessel days, and (C) catch per unit of effort (CPUE) by year for Monterey Bay (April [APR]—black circles) and southern California (October [OCT]—unfilled circles) regions. Scale of y-axis changes between A, B, and C. Note the lack of landings in OCT in 1984 and APR in 1998, following strong El Niño events.

by the frequencies determined from the 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, and had significant linear regressions to NINO3, SOI, and UI anomalies, but explained less than 5% of the variance (data not shown).

1981–2003 squid fishery data

In comparisons of landings (Fig. 3A) by month, the six areas fell into two categories: APR and OCT. Effort in vessel-days and CPUE showed similar trends. The *Loligo opalescens* squid fishery generally occurs from April through November in APR. Although landings peak in May, by then there are so many vessels in operation that CPUE has dwindled to half that of April (Fig. 3, B and C). There is a second landings pulse in August.

In the five areas of the OCT grouping, landings typically begin in October, build to a peak in January, and diminish to lows in August (Fig. 3A). A large unimodal pulse of squid landings occurred in November for all areas 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/vessel-day, for months with more than seven vessel-days, whereas CPUE for the southern California (OCT) areas ranged from 17–36 tons/vessel-day (Fig. 3C).

Time-series analysis

The periods of the ten highest peaks of the variance spectrum were determined for all six areas (Table 2). The largest peaks from the spectral analysis occurred at periods of 372 and 356 days, or roughly 1 year for all areas. There was a 7.5-year peak in the MB and CC areas. There was a 4.5-year peak (for all areas except MB) that was similar to the period of the four El Niño events that occurred in this area during the 22-year period. There was a 3.7-year peak for all areas except CC and SM. The seven-day cycle is most likely a stochastic factor of fishermen working within weekend closures because data before 1998 did not have this periodicity. There was no 28- or 14-day cycle in any of the areas; this finding likely indicates that spawning squid do not respond to tidal currents or lunar light.

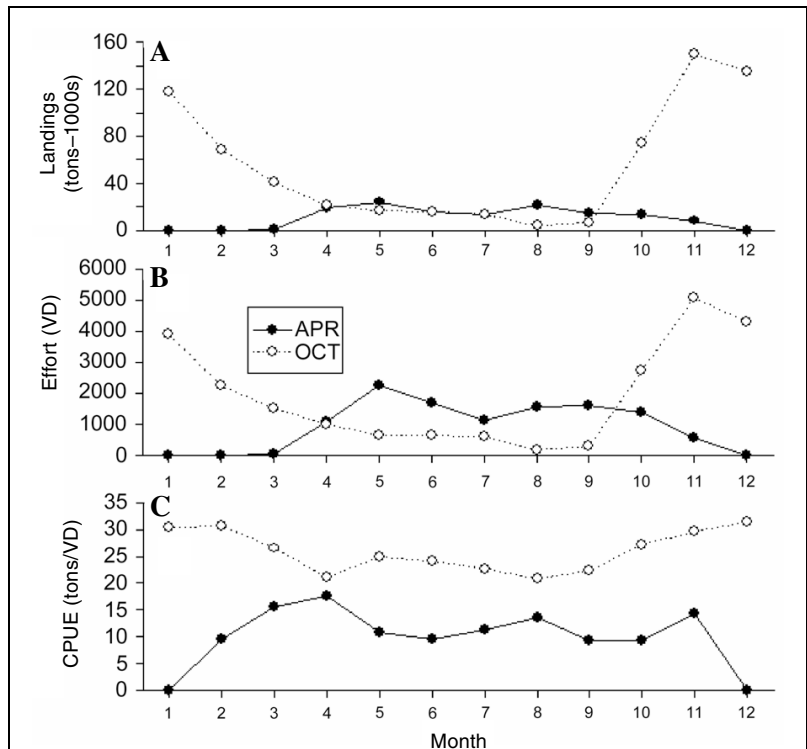


Figure 3

Fishery data for *Loligo opalescens*, summed by month for 1981–2003. (A) Landings (metric tons). (B) Effort in vessel-days (VD). (C) Catch per unit of effort (tons/VD). Monterey Bay (April [APR]—black circles) and southern California (October [OCT]—unfilled circles). Scale of y-axis changes between A, B, and C. Largest landings occurred one month later in May in the APR region and in November in the OCT region when SST was 11.7°C and 16.1°C, respectively.

The most significant cross correlations of time lag analysis for CPUE to SST are listed in Table 3. In all cases of biological significance, CPUE lagged SST by 4, 5, or 10 months. MB CPUEs were highest (in May) when SST was low four months earlier (Jan), and hence gave a negative correlation. In all other regions, the four or five month correlation was positive, with CPUE high (Nov) when SSTs were high four months earlier (Jul). For the southern California areas there was a negative correlation with SSTs 10 months earlier (Jan). Therefore, cold winters and warm summers correlate with larger landings. Recruitment of spawning adults to the fishery occurs during the productive seasons in both APR, MB, and OCT. Productivity in APR and MB 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 with SOI, NINO3, and UI, but not with the anomalies of SOI and UI. Interestingly correlations for NINO3 were greater than those for SOI (Fig. 4), indicating that the CPUE of *Loligo opalescens* is more closely related to the “oceanic teleconnection” than to “atmospheric teleconnection.”

Table 2

Periods of greatest spectral variance in the daily CPUE data of the market squid (*Loligo opalescens*) fishery for 1981–2003. Significance: $P < 0.01$. Numbers in bold are repeated in more than one area. Harmonics of factors of 2: 2, 4, ... 4096 (blank spaces) are omitted because they are inherent in spectral analysis and not relevant to this species. MB=northern coastal area, predominantly southern Monterey Bay; CC=central coast; SB=Santa Barbara; SCB=Southern California Bight; SM=Santa Monica; and SD=San Diego.

Top ten periods of spectral variance						
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

Table 3

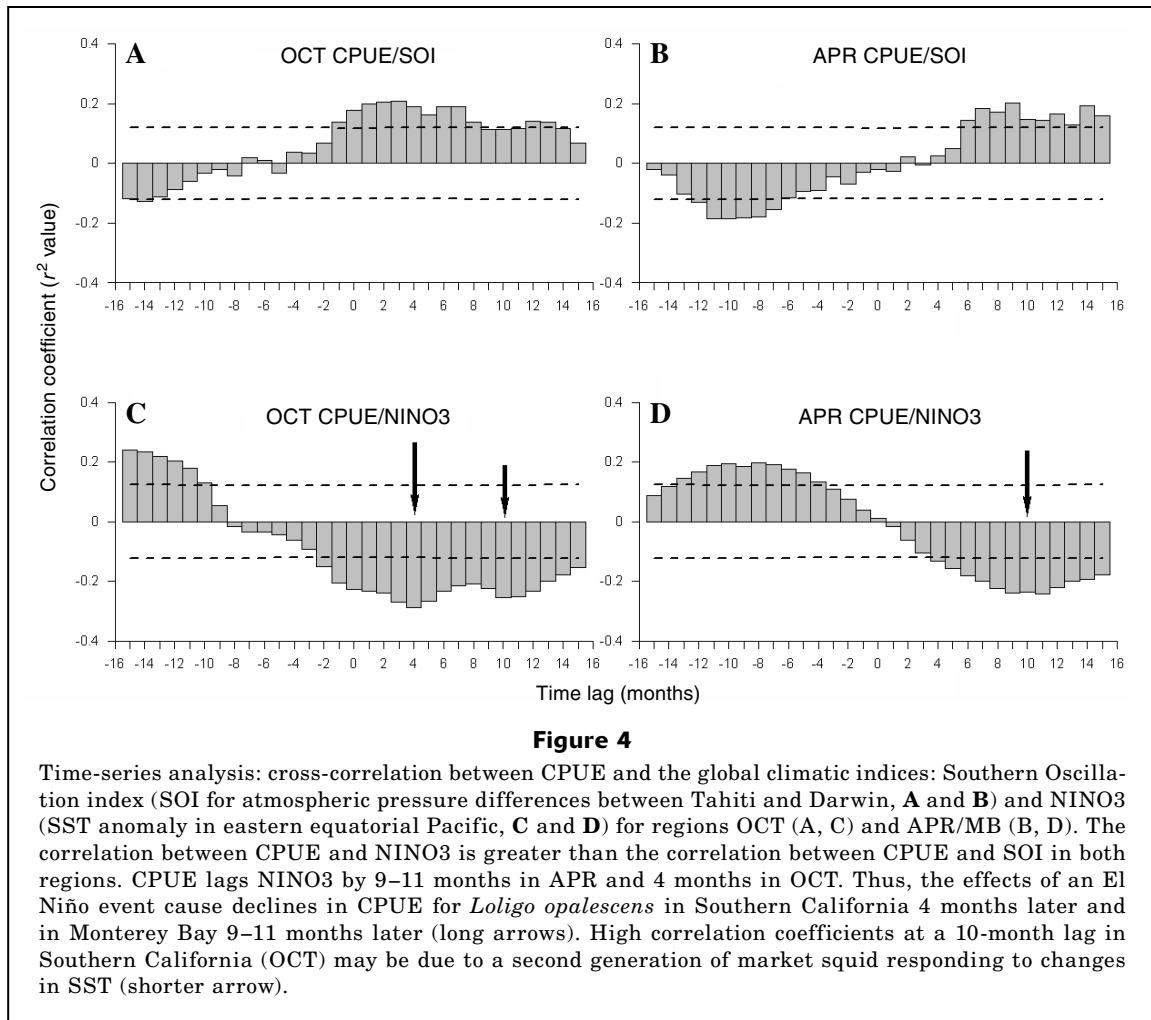
Results of the time series analysis. Significant correlation coefficients occurred when CPUE lagged behind sea surface temperature (SST) from buoys and advanced very high resolution radiometers (AVHRRs) by 4–10 months for all areas, except CC. Negative correlation coefficients demonstrate that high CPUE corresponds with low water temperatures in the lagged month from column two; positive values may indicate a direct relationship. MB=northern coastal area, predominantly southern Monterey Bay; CC=central coast; SB=Santa Barbara; SCB=Southern California Bight; SM=Santa Monica; and SD=San Diego.

CPUE region	Lagged (months)	SST source	Correlation coefficient
MB	4	MB buoy	−0.481
	5	AVHRR	−0.358
SCB	4	SM buoy	0.206
	10	SM buoy	−0.344
SD	9	AVHRR	−0.340
	4	SM buoy	0.220
	10	SM buoy	−0.398
SM	10	AVHRR	−0.387
	5	SM buoy	0.176
	10	SM buoy	−0.340
SB	10	AVHRR	−0.334
	4	ESB buoy	0.387
	4	SM buoy	0.415
	9	AVHRR	−0.372

Assuming a 6–9 month lifespan for *L. opalescens*, we used linear regression to compare SST from buoy data for the previous 6–10 months. We performed comparisons up to 10 months because squid eggs take 30 days to hatch at 12°C, which is a typical time period for eggs to hatch in winter in Southern California and spring–summer in Monterey Bay. The only significant regression occurred in the SM region with SSTs 10-months earlier ($r^2=0.46$, $P=0.0033$, Fig. 5). We compared satellite-derived (AVHRR) estimates of SST for 1985–2002 from areas with high densities of paralarvae and juveniles (within 8 km of shore) with CPUE by using cross correlation time series analysis. Although there were significant correlations, linear regression yielded no significant predictions for landings or CPUE from SST.

Stock recruitment analysis

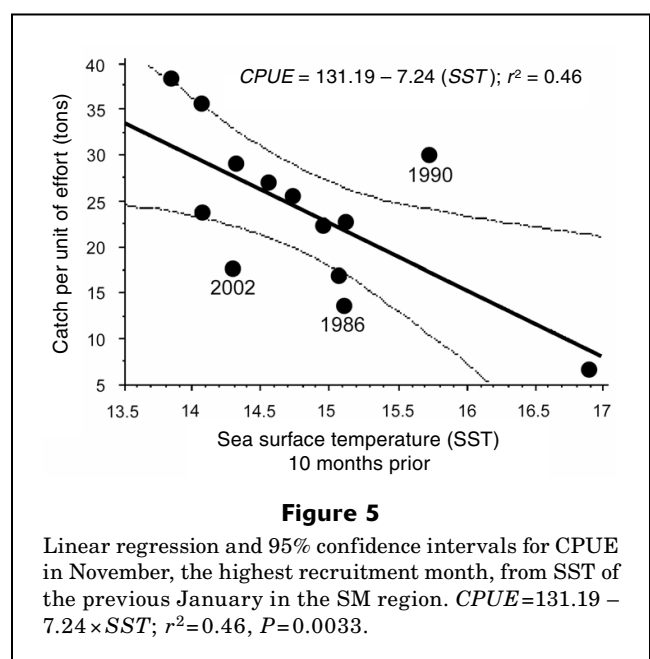
We compared a paralarvae density index (PDI) with CPUE for the SCB and SM regions (Fig. 6, shaded area of Fig. 1). Collections of paralarvae were made in February (Fig. 6). After the initial surveys of 1999, methods developed in Zeidberg and Hamner (2002) resulted in 34–50 stations for oblique bongo tows to collect paralarvae in SCB and SM regions. Paralarvae/1000 m³ from

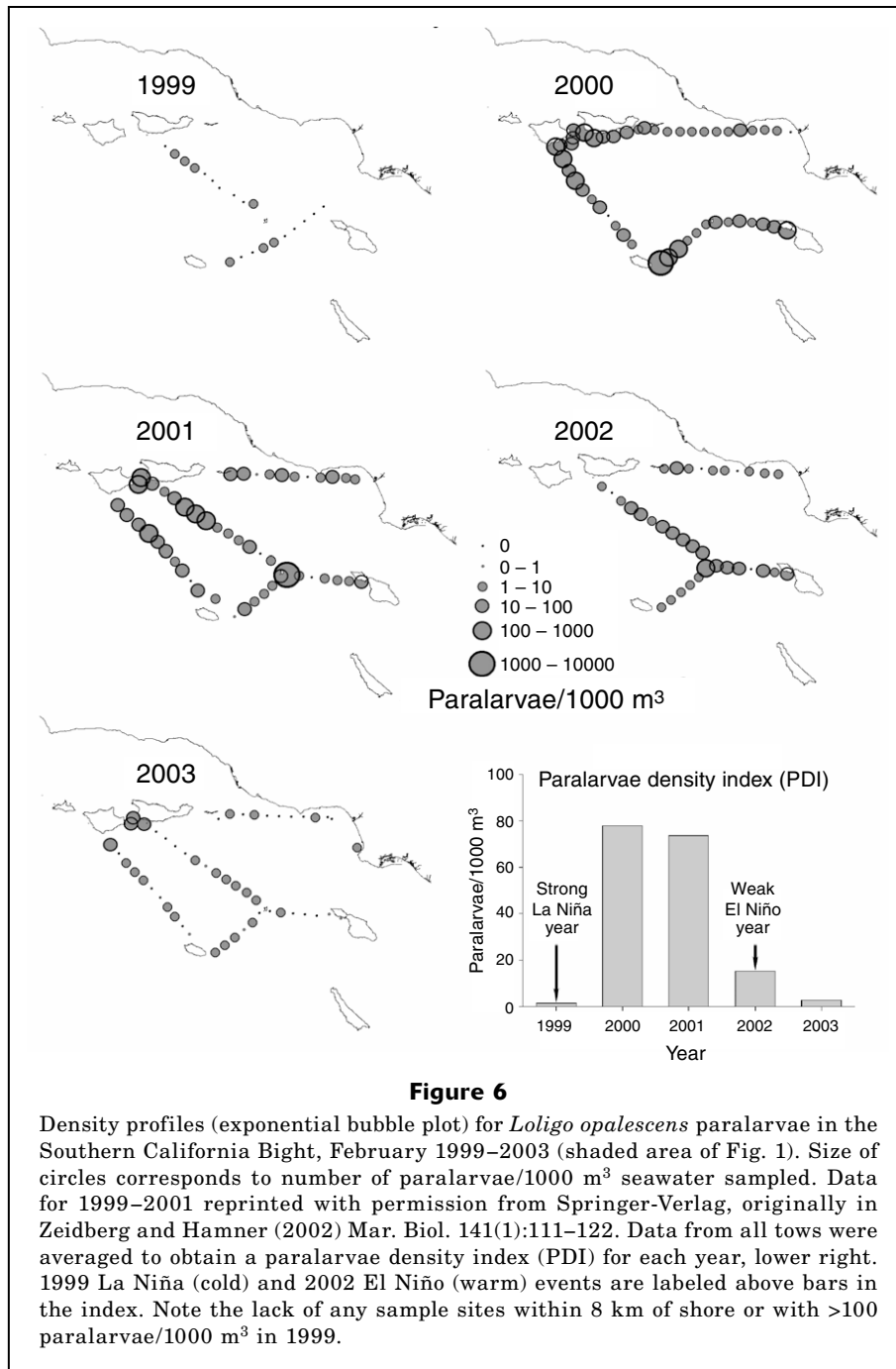


all stations were averaged to create the February PDI (Fig. 6 lower right), and this PDI was then compared to the November recruitment of spawning adults (CPUE) to the fishery for the same year. Linear regression was not significant for 1999–2003 ($r^2=0.522$, $P=0.1683$). However, if 1999 was treated 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, $P=0.007$ (Fig. 7). From 1992 through 2002, SCB (36.2%) and SM (16.2%) represented nearly half of the landings for the state, and therefore this technique (regression of CPUE on PDI) could apply throughout the state.

Discussion

We report landings, effort, and catch per unit of effort 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 cap-

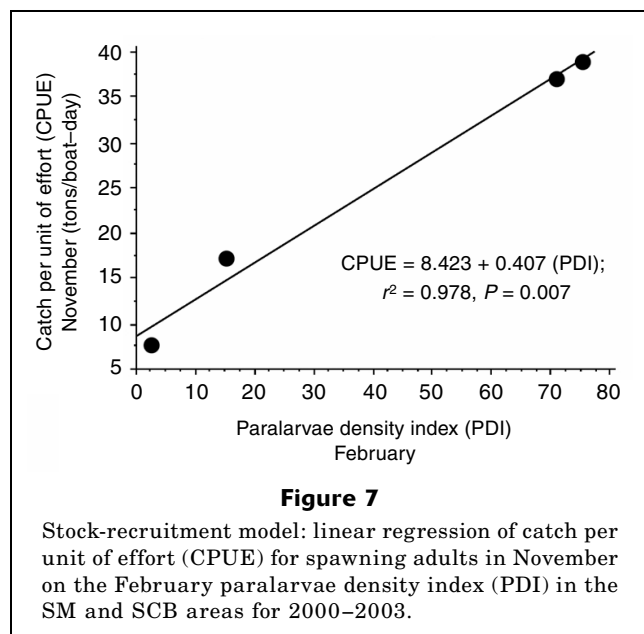




ture squid and fail cannot be tracked with this method, and squid that are not harvested commercially are not accounted for in this report. *Loligo opalescens* reproduces by aggregating from small, foraging groups of hundreds of individuals to groups of millions of individuals. It is possible, therefore, that a large decrease in biomass can be masked by a larger percentage of the population aggregating in seemingly similar-size spawning masses. Such species are vulnerable to highly mobile fisheries (Oostenbrugge et al., 2002).

Trends in the fishery

The fishery for market squid (*Loligo opalescens*) has increased in all parts of the study area since 1983 because of an increase in demand for calamari internationally and because of the collapse of other fisheries both within and outside California waters. The majority of fishing activity has shifted from Monterey Bay to the Southern California Bight since the 1980s. Fishing activity in the bight experienced a second increase in



the 1990s, reflecting fishery participants from Alaska, Washington, and Oregon. The most economically harmful trend has been the substantial decrease in landings during the second year of strong El Niño events, and the slight decrease in landings after weak ones.

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 with CPUE and landings data (not shown) did not show that squid recruit to spawning sites in a fortnightly cycle. There was no 14-day period in any area. Spectral analysis demonstrated periodicities for CPUE of *Loligo opalescens* on scales ranging from days to years. The most common periods for all areas were annual. Varying from 315 to 390 days, annual cycles made up more than half of the top ten signals in the analysis. The 4.5-year cycle corresponds well with the El Niño events of 1982–83, 1987, 1992, and 1997–98 (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 areas. There were evident leaps in the mean CPUE based on mean CPUE ± 5 months in MB at mid-1988 and the end of 1995, when out-of-state fishermen began to harvest squid in California (Zeidberg, 2003). Although these leaps may correspond to changes in the biomass of the squid, they are more likely due to enhancements in the capacity of the fishery to capture squid as acoustic and communication technology has improved. The 3.7-year period is probably a statistical harmonic of the 7.5-year period.

Paralarvae density index (PDI) can predict CPUE

Zeidberg and Hamner (2002) have sampled the SCB and SM areas for *Loligo opalescens* paralarvae since

1999 and we used that data to create a paralarvae density index (PDI). 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, but if 1999 is treated as an outlier the remaining four points (2000–03) create a regression that explains 97.8% of the variance. Our 1999 sampling of paralarvae may not be representative of the fishery because it was the first sampling year and the sampling sites were located farther offshore than those sampled in 2000–03. In 1999 there were no sites within 7.4 km of shore, where 76% of the paralarvae were captured in the following four years of sampling. Despite these caveats, this method could provide the first opportunity to manage California's market squid fishery according to scientifically gathered biological indicators and 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 can have a prediction for the CPUE for the following year's adult recruitment. Paralarvae may be the best stage of the life cycle for a fishery prediction because 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 (6–9 months) to develop predictions. These predictions could help managers set 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. Paralarval distributions for *Loligo opalescens* 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 at this proximity to land. After reviewing their surveys and models of larval dispersal (Franks, 1992; Botsford et al., 2001; Siegel, 2003), we predict that a PDI calculated from CalCOFI samples will be substantially lower than ours, but 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 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 with physical data

We found a correlation between CPUE of the largest recruitment month with SST buoy data from 10 months earlier in the SM area only. There may be physical features specific to this area that increase the correlation between spawning recruitment and SST. For example, SM is a small area, 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. But this correlation between CPUE of the largest recruitment month with SST in the SM area may be a seasonal effect because the regression is significant for SST only and not an SST anomaly. Furthermore, we caution that the significance of the correlation between CPUE and SST in SM may be a type-I error because it was the only significant test of the 30 tests run with 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 data due to meso-scale oceanographic features in the large fishery areas. In some areas 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 with CPUE. AVHRR data were collected from just the shelves and slopes of the six fishery areas because these are the most important areas for the growth of hatchlings and juveniles. Cross-correlation time series analyses were significant at 5–10 month lags (Table 3), but this significance did not translate into any predictive capabilities with linear regression.

Similarly, cross-correlations of CPUE with SOI and NINO3 were significant at a 10-month lag in Monterey Bay and a 4-month lag in the Southern California Bight. 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 Moers, 1986; Lynn et al., 1995; Chavez, 1996; Ramp et al., 1997) rather than the ENSO (El Niño Southern Oscillation)-related changes of atmospheric circulation ("atmospheric teleconnection") (Simpson, 1983; Simpson, 1984a, 1984b; Mysak, 1986; Breaker and Lewis, 1988; Breaker et al., 2001; Schwing et al., 2002).

Loliginid life cycles and future management of squid fisheries

The correlation between SST and CPUE in the following season may 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 and then logarithmically until senescence. In rearing tanks and 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) predicted that annual fluctuations in SST that cause differential growth in squids can lead to younger cohorts hatched in warm temperatures and surpassing in size older cohorts born in colder seasons. Thus in October, a large 6-month-old squid that hatched in April and developed in warm water may spawn with a smaller 9-month-old squid that hatched in the cold waters of January.

However, in the California system and possibly in 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 and La Niña cycles and upwelling, the mean mantle length of *Loligo opalescens* is shortest when larvae are 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 combined 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 the squids were small and less abundant because they had a high metabolic rate due to increased temperatures and were exposed to lower levels of available prey due to decreased ocean productivity. Seasonal maxima of phytoplankton in Monterey Bay occur in summer; but in the southern part of the Southern California Bight productivity peaks in winter (Nezlin et al., 2002). These differences may be an indicator of why the fishery operates in Monterey Bay from April to November, coinciding with the upwelling season, and in the Southern California Bight from November to May, coinciding with less stratification of the water column and more mixing due to winter storms and colder air temperatures.

Lowry and Carretta (1999) corroborated the temperature-induced plasticity of mantle length (ML) 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-

size squid prey; this finding may indicate that the squid stock moved offshore to find productive waters. Alternatively, San Nicholas sea lions may have been feeding on squids from Baja California. Zeidberg and Hamner (2002) suggested the possibility of a northern shift of the squid population in El Niño years, as has been 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 huge fluctuations in squid landings during strong ENSO events is due to the entire biomass of market squid waning and waxing rather than to population migrations away from traditionally fished spawning grounds. Triennial groundfish surveys demonstrate that market squid experienced a coast-wide population decrease, not a poleward migration during the 1997–98 El Niño.⁶

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, multidecadal 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 because of market demand. Markets are driven by economic forces and traditionally do not control themselves in a biologically sustainable manner. A full recovery of the squid fishery occurred from 1998 to 2000 and thus spanned four generations of squid given a 6–9 month lifecycle; for the California sardine (with a 6–8 year lifecycle), a proportionally similar recovery period would be 24–32 years (Parrish⁷).

In 1998–99 the fishery for *Loligo opalescens* decreased to low levels during the El Niño event, then recovered to record levels in the following years. This was most likely due to the plasticity of squid development in relation to water temperature and upwelling and the short (4–6 month) life span of squid. 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 in southern California landings in the last five years (119,780–24,449 tons/year) is due to the small El Niño of 2002–03, the climate-regime shift in 1998, overfishing, or some other factor such as increased water stratification due to global warming. Although the short-lived squid may not 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 be able to recover 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.

Acknowledgments

This research was funded by a California Fish and Game award (no. FG7334MR) and a Coastal Environmental Quality Initiative Program grant (no. 783828-KH-19900) and was supported in part by the David and Lucile Packard Foundation through the Monterey Bay Aquarium Research Institute. Bruce Robison, Rich Ambrose, Peggy Fong, and Dick Zimmer provided thoughtful reviews. Andrea Steinberger assisted with data management.

Literature cited

- Agnew, D. J., J. R. Beddington, and S. L. Hill.
2002. The potential use of environmental information to manage squid stocks. *Can J. Fish. Aquat. Sci.* 59:1851–1857.
- Agnew, D. J., S. Hill, and J. R. Beddington.
2000. Predicting the recruitment strength of an annual squid stock: *Loligo gahi* around the Falkland Islands. *Can J. Fish. Aquat. Sci.* 57:2479–2487.
- Aristegui, J., P. Tett, A. Hernandez-Guerra, G. Basterretxea, M. F. Montero, K. Wild, P. Sangra, S. Hernandez-Leon, M. Canton, J. A. Garcia-Braun, M. Pacheco, and E. D. Barton.
1997. The influence of island-generated eddies on chlorophyll distribution: a study of mesoscale variation around Gran Canaria. *Deep Sea Res.* 44:7–96.
- Bakun, A.
1973. Coastal upwelling indices, west coast of North America, 1946–1971, 103 p. NOAA Tech. Rep. NMFS SSRF-671.
- Botsford L. W., A. Hastings, and S. D. Gaines.
2001. Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. *Ecol. Lett.* 4(2):144–150.
- Bray N. A., A. Keyes, and W. M. L. Morawitz.
1999. The California Current system in the Southern California Bight and Santa Barbara Channel. *J. Geophys. Res.* 104 C4:7695–7714.
- Breaker, L. C., and P. A. W. Lewis.
1988. A 40–50 day oscillation in sea-surface temperature along the central California coast. *Estuar. Coast. Shelf Sci.* 26:395–408.
- Breaker, L. C., P. C. Liu, and C. Torrence.
2001. Intraseasonal oscillations in sea surface temperature, wind stress, and sea level off the central California coast. *Cont. Shelf Res.* 21(6-7):727–750.
- Brink, K. H., R. C. Beardsley, J. Paduan, R. Limeburner, M. Caruso, and J. G. Sires.
2000. A view of the 1993–1994 California Current based on surface drifters, floats, and remotely sensed data. *J. Geophys. Res. Oceans.* 105(C4):8575–8604.

⁷ CDFG (California Department of Fish and Game). 2005. Final market squid fishery management plan. Website: <http://www.dfg.ca.gov/mrd/msfmp/index.html> [Accessed on 6 June 2005.]

⁷ Parrish, R. 2005. Personal commun. Fisheries and Marine Ecosystems Program, Pacific Fisheries Environmental Laboratory, 1352 Lighthouse Ave. Pacific Grove, CA 93950-2097.

- Caddy, J. F., and P. G. Rodhouse
1998. Cephalopod and groundfish landings: evidence for ecological change in global fisheries? *Rev. Fish Biol. Fish.* 8:431-444.
- Chavez, F. P.
1996. Forcing and biological impact of onset of the 1992 El Niño in central California. *Geophys. Res. Lett.* 23(3):265-268.
- Chavez, F. P., J. Ryan, S. E. Lluch-Cota, and M. Niquen-C.
2003. From anchovies to sardines and back: multidecadal change in the Pacific ocean. *Science* 299:217-221.
- Colebrook, J. M.
1977. Annual fluctuations in biomass of taxonomic groups of zooplankton in the California Current 1955-59. *Fish. Bull.* 75:357-368.
- DiGiacomo, P. M., and B. Holt.
2001. Satellite observations of small coastal ocean eddies in the Southern California Bight. *J. Geophys. Res.* 106 (C10):22,521-22,543.
- Falkowski, P. G., D. Ziemann, Z. Kolber, P. K. Bienfang.
1991. Role of eddy pumping in enhanced primary production on the ocean. *Nature* 352:55-58.
- Forsythe, J. W., L. S. Walsh, P. E. Turk, and P. G. Lee.
2001. Impact of temperature on juvenile growth and age at first egg-laying of the Pacific reef squid *Sepioteuthis lessoniana* reared in captivity. *Mar. Biol.* 138:103-112.
- Franks, P. J. S.
1992. Sink or swim: accumulation of biomass at fronts. *Mar. Ecol. Prog. Ser.* 82:1-12.
- Graham, W. M., and J. L. Largier.
1997. Upwelling shadows as nearshore retention sites: the example of northern Monterey Bay. *Cont. Shelf Res.* 17:509-532.
- Grist, E. P. M., and S. des Clers.
1998. How seasonal temperature variations may influence the structure of annual squid populations. *IMA J. of Math. Appl. Med. Biol.* 15:187-209.
- Harms, S., and C. D. Winant.
1998. Characteristic patterns of the circulation in the Santa Barbara Channel. *J. Geophys. Res.* V103, C2:3041-3065.
- Hayward T. L., T. R. Baumgartner, D. M. Checkley, R. Durazo, G. Gaxiola-Castro, K. D. Hyrenbach, A. W. Mantyla, M. M. Mullin, T. Murphree, F. B. Schwing, P. E. Smith, M. J. Tegner.
1999. The state of the California Current in 1998-1999: Transition to cool-water conditions. *Calif Coop Oceanic Fish Invest Rep* 40:29-62.
- Hernandez-Trujillo, S.
1999. Variability of community structure of Copepod related to El Niño 1982-83 and 1987-88 along the west coast of Baja California Peninsula, Mexico. *Fish. Oceanog.* 8:284-295.
- Hickey B. M., E. L. Dobbins, and S. E. Allen.
2003. Local and remote forcing of currents and temperature in the central Southern California Bight. *J. Geophys. Res. Oceans* 108(C3):3081-3084.
- Huyer, A., and R. L. Smith.
1985. The signature of El Niño off Oregon in 1982-83. *J. Geophys. Res.* 90:7133-7142.
- 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* off Southern California. *Mar. Biol.* 142:925-935.
- Leos, R. R.
1998. The biological characteristics of the Monterey Bay squid catch and the effect of a two-day-per-week fishing closure. *CalCOFI Reports* 39:204-211.
- Loukashkin, A. S.
1976. On biology of market squid, *Loligo opalescens*, a contribution toward the knowledge of its food habits and feeding behavior. *CalCOFI Reports* 18:109-111.
- Lowry, M. S., and J. V. Carretta.
1999. Market squid (*Loligo opalescens*) in the diet of California sea lions (*Zalophus californianus*) in southern California (1981-1995). *CalCOFI Reports* 40:196-207.
- Lynn, R. J., F. B. Schwing, T. L. Hayward.
1995. The effect of the 1991-1993 ENSO on the California Current system. *CalCOFI Reports* 36:57-71.
- Macewicz, B. J., J. R. Hunter, N. C. H. Lo, E. L. LaCasella.
2004. Fecundity, egg deposition, and mortality of market squid (*Loligo opalescens*). *Fish. Bull.* 102:306-327.
- Mangel, M., B. Marinovic, C. Pomeroy, and D. Croll.
2002. Requiem for Ricker: unpacking MSY. *Bull. Mar. Sci.* 70:763-781.
- Morejohn, G. V., J. T. Harvey, and L. T. Krasnow.
1978. The importance of *Loligo opalescens* in the food web of Marine vertebrates in Monterey Bay, Calif. *Fish Game Fish Bull.* 169:67-98.
- McInnis, R. R., and W. M. Broenkow.
1978. Correlations between squid catches and oceanography conditions in Monterey Bay, Calif. *Fish Game Fish Bull.* 169:161-170.
- Mysak, L. A.
1986. El Niño, interannual variability and fisheries in the northeast Pacific Ocean. *Can. J. Fish. Aquat. Sci.* 43:464-497.
- Nezlin, N. P., W. M. Hamner, and L. D. Zeidberg.
2005. Influence of El Niño 1997-1998 on the Pelagic Ecosystem off California: remote sensed analysis. *In* California and the World Ocean '02 (O. T. Magoon, H. Converse, B. Baird, B. Jines, and M. Miller-Henson, eds.), p. 1233-1252.
- Nezlin, N. P., and B. L. Li.
2003. Time series analysis of remote-sensed chlorophyll and environmental factors in the Santa Monica-San Pedro Basin off Southern California. *J. Mar. Syst.* 39:185-202.
- O'Dor, R. K.
1982. Respiratory metabolism and swimming performance of the squid *Loligo opalescens*. *Can J. Fish. Aquat. Sci.* 39:580-587.
- Okutani T., and J. A. McGowan.
1969. Systematics, distribution and abundance of the epiplanktonic squid (Cephalopoda, Decapoda) larvae of the California Current April, 1954-March, 1957. *Bull. Scripps Inst. Oceanog.* 14:1-90.
- Oostenbrugge, J. A. E., J. J. Poos, W. L. T. van Densen, and M. A. M. Machiels.
2002. In search of a better unit of effort in the coastal liftnet fishery with lights for small pelagics in Indonesia. *Fish. Res.* 59:43-56.
- Pauly, D., V. Christensen, J. Dalsgaard, R. Froese, and F. Torres Jr.
1998. Fishing down marine food webs. *Science* 279: 860-863.
- Ramp, S. R., J. L. McClean, C. A. Collins, A. J. Semtner, and K. A. S. Hays.
1997. Observations and modeling of the 1991-1992 El Niño signal off central California. *J. Geophys. Res.* 102(C3):5553-5582.

- Ravier, C., and J. M. Fromentin.
2001. Long-term fluctuations in the eastern Atlantic and Mediterranean bluefin tuna population. *ICES J. Mar. Sci.* 58:1299–1317.
- Rienecker, M. M., and C. N. K. Mooers.
1986. The 1982–1983 El Niño signal off northern California. *J. Geophys. Res.* 91:6597–6608.
- Roberts, M. J., and W. H. H. Sauer.
1994. Environment: the key to understanding the South African chokka squid (*Loligo vulgaris reynaudii*) life cycle and fishery? *Antarctic Science* 6:249–258.
- Robin, J. P., and V. Denis.
1999. Squid stock fluctuations and water temperature: temporal analysis of English Channel Loliginidae. *J. Appl. Ecol.* 36:101–110.
- Rogers-Bennett, L.
2000. Review of some California fisheries for 1999: market squid, dungeness crab, sea urchin, prawn, abalone, groundfish, swordfish and shark, ocean salmon, nearshore finfish, Pacific sardine, Pacific herring, Pacific mackerel, reduction, white seabass, and recreational. *CalCOFI Rep.* 41:8–26.
- Rocha, F., A. Guerra, R. Prego, U. Piatkowski.
1999. Cephalopod paralarvae and upwelling conditions off Galician waters (NW Spain). *J. Plank. Res.* 21:21–33.
- Sakurai, Y., H. Kiyofuji, S. Saitoh, T. Goto, and Y. Hiyama.
2000. Changes in inferred spawning areas of *Todarodes pacificus* (Cephalopoda: Ommastrephidae) due to changing environmental conditions. *ICES J. Mar. Sci.* 57:24–30.
- Schwing, F. B., T. Murphree, L. deWitt, and P. M. Green.
2002. The evolution of oceanic and atmospheric anomalies in the northeast Pacific during the El Niño and La Niña events of 1995–2001. *Prog. Oceanog.* 54(1–4):459–491.
- Siegel, D. A., B. P. Kinlan, B. Gaylord, and S. D. Gaines.
2003. Lagrangian descriptions of marine larval dispersion. *Mar. Ecol. Prog. Ser.* 260:83–96.
- Simpson, J. J.
1983. Large-scale thermal anomalies in the California Current during the 1982–1983 El Niño. *Geophys. Res. Lett.* 10:937–940.
1984a. El Niño-induced onshore transport in the California current during 1982–1983. *Geophys. Res. Lett.* 11(3):241–242.
1984b. A simple model of the 1982–1983 Californian “El Niño”. *Geophys. Res. Lett.* 11(3):243–246.
- Vojkovich, M.
1998. The California fishery for market squid (*Loligo opalescens*). *CalCOFI Rep.* 39:55–61.
- Waluda, C. M., P. N. Trathan, and P. G. Rodhouse.
1999. Influence of the oceanographic variability on recruitment in the *Illex argentinus* (Cephalopoda: Ommastrephidae) fishery in the South Atlantic. *Mar. Ecol. Prog. Ser.* 183:159–167.
- Waluda, C. M., P. G. Rodhouse, G. P. Podesta, P. N. Trathan, and G. J. Pierce.
2001. Surface oceanography of the inferred hatching grounds of *Illex argentinus* (Cephalopoda: Ommastrephidae) and influences on recruitment variability. *Mar. Biol.* 139:671–679.
- Watson, R., and D. Pauly.
2001. Systematic distortions in world fisheries catch trends. *Nature* 414:534–536.
- Wing, S. R., J. L. Largier, and L. W. Botsford.
1995. Settlement and transport of benthic invertebrates in an intermittent upwelling region. *Limnol. Oceanog.* 40(2):316–329.
- Wolf, P.
1992. Recovery of the Pacific sardine and the California sardine fishery. *CalCOFI Reports* 33:76–86.
- 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 the market squid, *Loligo opalescens*, cultured through the life cycle. *Fish. Bull.* 84:771–798.
- Zar, J. H.
1984. *Biostatistical analysis*, 2nd ed., 718 p. Prentice Hall, Englewood Cliffs, NJ.
- Zeidberg, L. D., and W. M. Hamner.
2002. Distribution of squid paralarvae, *Loligo opalescens* (Cephalopoda: Myopsida), in the Southern California Bight in the three years following the 1997 El Niño. *Mar. Biol.* 141:111–122.
- Zeidberg, L. D.
2003. The early life history and fishery of the California market squid, *Loligo opalescens*. Ph.D. diss., 136 p. Univ. California Los Angeles, Los Angeles, CA.
- Zeidberg, L. D., W. Hamner, K. Moorehead, and E. Kristof.
2004. Egg masses of *Loligo opalescens* (Cephalopoda: Myopsida) in Monterey Bay, California following the El Niño event of 1997–1998. *Bull. Mar. Sci.* 74:129–141.