LONG-TERM CHANGES IN BIOLOGICAL CHARACTERISTICS AND FISHERY OF *LOLIGO OPALESCENS*

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ABSTRACT

LONG-TERM CHANGES IN BIOLOGICAL CHARACTERISTICS AND FISHERY OF *LOLIGO OPALESCENS*

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Opalescent squid, *Loligo opalescens*, captured from central and southern California fisheries were examined for long-term changes in size, sex ratio, and fecundity. Samples were collected in Monterey from 1948 to 2006 and in the Channel Islands and Catalina Island from 1999 to 2007. A significant (P<0.0001) decline in opalescent squid size and fecundity occurred in Monterey. The trend in monthly mean sizes was similar among locations. Monthly mean sizes were negatively correlated with fishing pressure; when fishing pressure was strong, smaller individuals were captured the following fishing season. Body size was also negatively correlated with hatch-month sea surface temperature (SST). Negative correlations between anomalies for monthly mean SST and sizes were found – individuals grew larger if a winter was anomalously cooler. In addition, monthly mean upwelling and body sizes were positively correlated during the juvenile stage. The ratio of males to females captured in the fishery fluctuated in all areas.

DEDICATION

I would like to dedicate my master's thesis to David VenTresca. David was my first mentor in studying California's marine ecosystems. He always gave aspiring marine biologists first-hand opportunities to study the ocean. David passed away in November. He enjoyed life to the fullest, and will always be in my memories and prayers.

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TABLE OF CONTENTS

List of Tables viii

List of Figures x

Introduction 1

  Opalescent Squid Fishery 5

  Biology of the Opalescent Squid Fishery 7

  Environmental Variables 13

  Changes in Biological Aspects of Opalescent Squid 15

Methods 16

  Biological Datasets and Analyses 17

  Fishing and Environmental Datasets and Analyses 23

Results 26

  Biological Data 26

  Fishery and Environmental Data 41

Discussion 59

Summary 74

References 76

LIST OF TABLES

Table 1 Origin of datasets, years for which data were available, location where data were collected, and variables reported

Table 2 Number of opalescent squid sampled and minimum and maximum sizes for each study period in Monterey

Table 3 Results for a one-way ANOVA in RS for mean DML and mass for the month of June in Monterey, 1948 to 2006

Table 4 Chi-square results for comparing opalescent squid sex ratios to 1:1 for Monterey, 1948 to 2006

Table 5 Pearson correlation coefficients of mean DML and mass by month between regions from 2000-01 to 2006-07

Table 6a-c Chi-square results for opalescent squid sex ratios compared to 1:1 for 3 regions

Table 7a-b Pearson correlation coefficients for mean DML versus fishery and environmental variables by month for Monterey from 1948-49 to 2006-07

Table 8a-b Pearson correlation coefficients for mean DML versus fishery variables by month for Monterey from 2000-01 to 2006-07 and two southern California sites from 1999-00 to 2006-07

Table 9a-b Pearson correlation coefficients for mean DML versus SST by month for Monterey from 2000-01 to 2006-07 and two southern California sites from 1999-00 to 2006-07

Table 10a-b Pearson correlation coefficients for mean DML versus upwelling by month for Monterey from 2000-01 to 2006-07 and two southern California sites from 1999-00 to 2006-07

Table 11a-b Pearson correlation coefficients for mean mass versus SST by month for Monterey from 2000-01 to 2006-07 and two southern California sites from 1999-00 to 2006-07

Table 12a-b Pearson correlation coefficients for mean mass versus upwelling by month for Monterey from 2000-01 to 2006-07 and two southern California sites from 1999-00 to 2006-07

Table 13 Pearson correlation coefficients for a measure of fecundity (standing stock of oocytes) versus total catch for Catalina Island from 1999-00 to 2002-03

LIST OF FIGURES

Figure 1 Statewide opalescent squid landings and strong El Niño events north and south of Point Conception for fishing seasons from 1927-28 to 2006-07 (data source *CDFG landing receipts*)

Figure 2 Opalescent squid landings for Monterey area ports for purse and lampara nets for fishing seasons 1969-70 to 2006-07 (data source *CDFG landing receipts*)

Figure 3 Location of 7 commercial fishing ports for sample collection

Figure 4a DML, climate, sex ratio, and sample size for Monterey, 1948 to 2006
Figure 4b Opalescent squid mass from Monterey, 1948 to 2006 (data source *See Table 1*)

Figure 5a-d Mean DML and mass with corresponding 95% CI pooled by month for each study period in Monterey, 1948 to 2006 (data source *See Table 1*)

Figure 6a-d Mean DML and mass with corresponding 95% CI for June for Monterey, 1948 to 2006 (data source *See Table 1*)

Figure 7a DML maximum for each sample month for Monterey, 1948 to 2006
Figure 7b Mass maximum for each sample month for Monterey, 1948 to 2006 (data source *See Table 1*)

Figure 8a-b Mean proportion of maturity, DML, and mass with corresponding 95% CI by month with total catch (mt) for Monterey, 1989 to 1994 (data source *See Table 1*)

Figure 9a-b The number of sample days and number of opalescent squid sampled per month for 3 regions from 1999-00 to 2006-07 (data source *See Table 1*)

Figure 10a-d Mean DML and mass with corresponding 95% CI for 3 regions from 1999-00 to 2006-07 (data source *See Table 1*)

Figure 11a-c Mean proportion of males with corresponding 95% CI by month for 3 regions from 1999-00 to 2006-07. The upper and lower solid lines depict the 95% CI for the entire period, and the middle solid line depicts the mean. The upper and lower dashed lines show the 95% CI for a daily sample size of 30 squid, and the middle dashed line signifies a sex ratio of 1:1. (data source *See Table 1*)

Figure 12 Fraction of potential female fecundity released with corresponding 95% CI for 3 regions from 1999-00 to 2003-04 (data source *See Table 1*)

Figure 13a-c Monterey area fishery data from 1950-51 to 2006-07 (data source, *See Table 1)*

Figure 14a-c Regional fishery data from 1998-99 to 2006-07 (data source, *See Table 1)*

Figure 15a-d Total catch summed for each month throughout each time period and overall mean DML by month (data source *See Table 1*)

Figure 16a-l Monterey SST anomalies from the long-term annual mean from 1945 to 2006 (data source *see Table 1*)

Figure 17a-l Monterey upwelling anomaly from 1945 to 2006 (data source *see Table 1*)

Figure 18a-c Mean SST with corresponding 95% CI, SST anomaly, and upwelling by month for 3 regions from 1998-99 to 2006-07 (data source *See Table 1*)

Figure 19a-d Pearson correlation for monthly mean DML and mass versus environmental variables for Monterey, 1948 to 2006; $^*P<0.05$

INTRODUCTION

Approximately 120 fishing vessels have participated in California's commercial opalescent (market) squid (*Loligo opalescens*) fishery during the past decade; and landings have averaged 70,000 metric tons (mt), making the fishery one of the state's most important by quantity and value (CDFG 2005). The Market Squid Fishery Management Plan (MSFMP) indicates the harvest of this species is sustainable, although opalescent squid abundance appears to fluctuate greatly as evidenced by fishery landing receipts recorded in the California Department of Fish and Game's (CDFG) Commercial Fisheries Information System (Figure 1). Many aspects of the life history and population biology of opalescent squid are greatly influenced by changes in sea surface temperature (SST) from year to year (Starr et al. 1997, 2002; CDFG 2005; Keiper et al. 2005). In occurrence with strong El Niño events, which create a warm-water, low-nutrient environment, fishery landings may decline by greater than 90%, and will usually rebound the following season (McInnis and Broenkow 1978; Ish et al. 2004; Reiss et al. 2004). Fishery-dependent data from the Monterey area from 1989 to 1994 indicated that body size and sex ratios differed from samples collected from the 1940s to the 1970s (Leos 1998). Variables that may be associated with the observed differences in the biological characteristics of opalescent squid include changes in fishing gear, regulations, fishing pressure, and environmental conditions.

Determining possible causes for changes in the life history characteristics of opalescent squid is essential for successful fishery management. For this study, potential factors influencing fluctuations in biological aspects of the opalescent squid fishery were

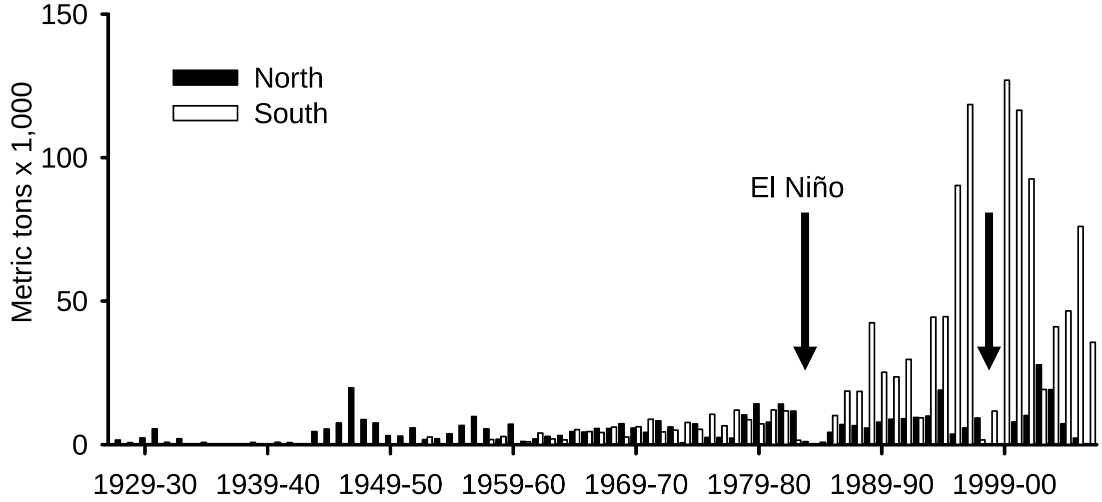

Figure 1 Statewide opalescent squid landings and strong El Niño events north and south of Point Conception for fishing seasons from 1927-28 to 2006-07 (data source *CDFG landing receipts*)

examined through: 1) the analysis of long-term (1948 to 2006) changes in dorsal mantle length (DML), mass, sex ratios, and fecundity using original data collected in Monterey from Fields (1965), Evans (1976), Spratt (1979), Leos (1998), and CDFG's most recent sampling program (1999 to 2006); 2) the assessment of recent (1999 to 2007) changes in DML, mass, sex ratios, and fecundity from CDFG sample data for central (Monterey) and southern California (northern Channel Islands and Catalina Island); and, 3) the correlation of long- and short-term biological fluctuations with patterns in fishery and environmental variables.

Opalescent Squid Life History

The scientific name for opalescent squid in past research was *Loligo opalescens*, although recent work based on morphology and molecular data suggests the name should be changed to *Doryteuthis (Amerigo) opalescens* (Anderson 2000; Vecchione et al. 2005). Opalescent squid inhabit the coastal, pelagic zone from southeast Alaska to Baja California (Recksiek and Frey 1978). Hatching at a DML of less than 3 mm, they remain within 1 km of the shore for approximately 1 month and then are widely distributed by ocean currents (Zeidberg and Hamner 2002). There is a limited understanding of opalescent squid distribution between birth and spawning (Cailliet and Vaughan 1983); however, some observations of opalescent squid indicate they are common within the upper 400 m of the water column (Hunt et al. 2000). Opalescent squid live to an age of 10 months (Butler et al. 2001), grow to an average DML of 152 mm (CDFG 2005), and reproduce at the end of their lifespan (Macewicz et al. 2004) when they congregate to spawn in nearshore areas. Prior to more recent work (Jackson 1994; Butler et al. 1999), age estimates were as great as 4 years with an estimated average of 2 years (Fields 1965; Spratt 1979).

Primary spawning grounds occur in shallow, sandy habitats in central and southern California in less than 180 m, but eggs have been reported as far north as British Columbia and as deep as 792 m (CDFG 2005). Multiple cohorts recruit to the spawning grounds within a season and individuals die soon after spawning (semelparous). Near the end of their lifespan, as reproduction takes place and eggs and spermatophores are released, the mantle condition of females and males deteriorates, and their body mass decreases. Females lose more mass than males, because as much as 50% of female body mass can be attributed to gonad size (Fields 1965). A female of 134 mm in DML has the potential to lay 4000 eggs (potential fecundity). Females may lay 20 egg cases and each egg case, which is attached to the substrate or other egg masses, can contain up to 300 eggs. On average, females lay less than 40% of their potential fecundity or the number of eggs present within the ovary and oviduct (Macewicz et al. 2004). Female opalescent squid do have the ability, however, to release 78% of their potential fecundity. As egg cases accumulate, up to 100 m^2 of seafloor are covered by egg case clusters (Dickerson and Leos 1992).

Eggs hatch in about 4 to 5 weeks at a surrounding water temperature of 12 °C (Isaac et al. 2001). The SST and productivity during hatch-month affects growth rates and the DML at which opalescent squid mature and recruit to the fishery (Jackson and Domeier 2003; Reiss et al. 2004). According to Jackson and Domeier's (2003) study, female (r=0.72, P=0.002, n=15) and male (r=0.61, P=0.013, n=16) DMLs were negatively correlated with the SST of the hatch-month. They also found that female (r=0.65, P=0.008, n=15) and male (r=0.81, P<0.001, n=16) DMLs were positively correlated with the hatch-month upwelling index (Jackson and Domeier 2003). The DMLs of male opalescent squid aged during the 1997-98 El Niño and 1998-99 La Niña events were not dependent on age, whereas female DMLs were found to be partially correlated with age – so females were larger because of being older, not solely from having faster growth rates.

At an age of about 1 month, juveniles enter the water column where they feed on macrozooplankton and remain until they reach maturity. As adults, they prey upon crustaceans, other squid, and coastal pelagic finfish such as sardines (*Sardinops sagax carulea*), anchovies (*Engraulis mordax*), and mackerel (*Scomber japonicus*) (Fields

1965; Karpov and Cailliet 1979). They are prey items for marine mammals, seabirds, coastal pelagic finfish, and other squid (Morejohn et al. 1978; Lowry and Carretta 1999; Keiper et al. 2005).

Opalescent Squid Fishery

The commercial opalescent squid fishery began in 1863 in Monterey and expanded to southern California where a substantial increase in landings occurred during the 1960s (Vojkovich 1998). In both areas, fishing may occur year round; however, the fishery usually spans from April through October in Monterey and from October through March in southern California. Although the fishery may extend from San Francisco to the Big Sur coast, the Monterey fishery is concentrated mainly off the Monterey Peninsula. In southern California, fishing activity may be strong along the coast from Pt. Conception to San Diego and out to the Channel Islands. Since the inception of the fishery, opalescent squid have been used as food and bait abroad and within the U.S.

When the commercial fishery began in the mid 1860s, fishing occurred during the night, and fishermen used a handheld torch to attract and aggregate opalescent squid at the surface. The opalescent squid were then captured with a handheld net that was deployed by two other boats (Fields 1965). A similar system is in use today; however, fishing also may occur during the day. Current fishing practices use a light boat with up to 30,000 watts and a purse or drum seine and tender vessel that wrap the opalescent squid with a large net. The corralled opalescent squid are brought onboard with an automated pumping system. Within the last decade, the average mesh size was 1 inch (2.5 cm) (CDFG 2005). Another form of gear used in the current fishery is the hydraulic brail (scoop) net, which is used onboard vessels that are usually smaller than purse seiners. Because brail vessels are compact and more maneuverable, they are used in shallower depths that are closer to shore and in areas where seiners are prohibited (e.g., Santa Monica Bay and the mainland side of Catalina Island).

In Monterey during the early 1900s, when the lampara net was first used to capture opalescent squid, the average reported mesh size was 1.25 inches (3.2 cm) (Fields 1965). Average opalescent squid landings in the early 1900s in Monterey were about 100 mt a year and sometimes reached 5,500 mt (Scofield 1924). By the 1970s, about 6,000 mt were landed a year in Monterey. In the late 1980s, the lampara net was replaced by the purse seine net in Monterey (Figure 2). From 1999 to 2007, the average catch was 8,000 mt in Monterey.

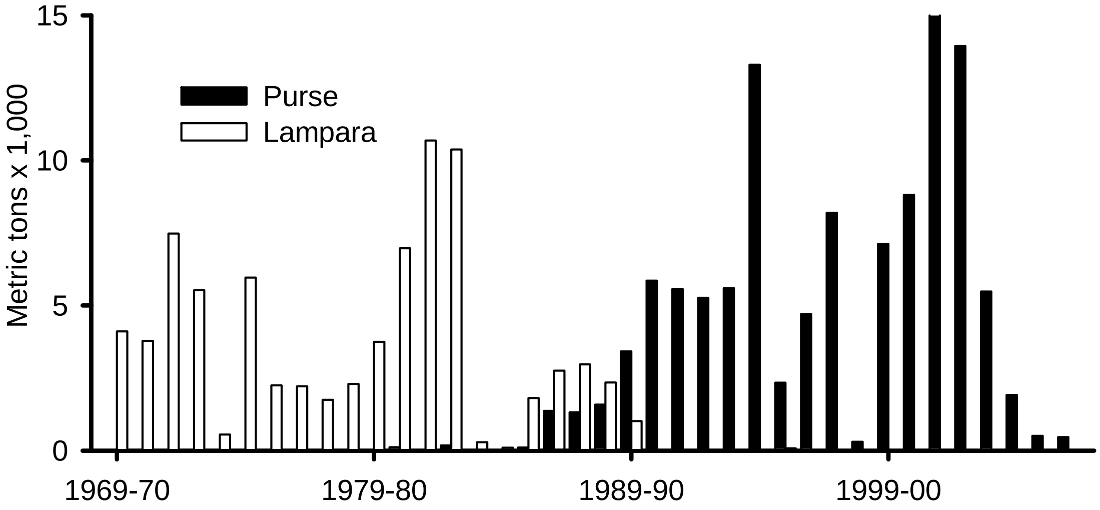

Figure 2 Opalescent squid landings for Monterey area ports for purse and lampara nets for fishing seasons 1969-70 to 2006-07 (data source *CDFG landing receipts*)

In southern California, where brail nets were primarily used until the 1970s, annual landings were sometimes as high as 6,000 mt. Once purse seine nets replaced the majority of brail nets, landings in southern California typically surpassed those in Monterey. Since 1999, landings in southern California have averaged 66,000 mt.

Opalescent squid fishing regulations have been minimal throughout the duration of the fishery with most pertaining to area and time closures, gear restrictions, catch amounts, and permits. Until 1959 in Monterey, the opalescent squid fishery was permitted to use lights to attract opalescent squid to the surface. Using lights as an attractant was restricted to prevent the harvest of opalescent squid directly from Monterey fishing docks and to reduce the disruption of lights on spawning opalescent squid (Dickerson and Leos 1992). The ban on lights was lifted in the Monterey area in the late 1980s, just as Leos (1998) began sampling opalescent squid. In 1984, to allow periods of uninterrupted spawning, a weekend closure went into effect for the Monterey area, and the closure was extended to southern California in 2000. Also, in 2000 light wattage was restricted to 30,000 per vessel to reduce detrimental effects on nesting marine birds. A harvest guideline (HG) of 113,398 mt (125,000 short tons (st)) was set in 2001 to avoid overfishing. The HG was reduced to 107,048 mt (118,000 st) in 2005. To attain a capacity goal in fleet size, the California Fish and Game Commission adopted a restricted access permit program in 2005.

Biology of the Opalescent Squid Fishery

Due to the value of the opalescent squid resource, several fishery-dependent studies have focused on collecting biological data from landings. Fields (1965) worked with CDFG to collect fishery-dependent data concerning size, sex, and age information from 1946 to 1962. CDFG continued to sponsor work in the 1970s when Moss Landing Marine Laboratories (MLML), Spratt (CDFG, 1979), and Evans (MLML, 1976) analyzed size, sex, and age data from fishery catches from 1972 to 1975 in Monterey using methods similar to Fields (1965). Leos (1998) completed a similar sampling project from 1989 to 1994 for the same area in Monterey. In 1998, CDFG, with input from the National Marine Fisheries Service (NFMS), established an ongoing sampling program targeting the fishing ports near Monterey, Santa Barbara, and Los Angeles (Figure 3).

Fields (1965) documented aspects of the life history characteristics of opalescent squid collected from the Monterey fishery from 1946 to 1962. During the course of Fields' (1965) sampling efforts, approximately 7,660 opalescent squid were collected from random samples from fishing vessels and processing pumps. Fields (1965) found that sex ratios were nearly equal, and females had a narrower size range than males at spawning. Opalescent squid were estimated to live to 4 years, but this was based on an analysis of size groups only and was never validated. The average DML of opalescent squid collected during Fields' (1965) study was 140 mm for females and 150 mm for males with their respective average masses being 50 g and 70 g. Size of opalescent squid during his study varied, however, from 1948 to 1962 (Figure 4a-b). Fields made the point that the decline in size was not the effect of more animals of a certain size group but an absence of larger opalescent squid. For instance, in 1948, 15% of males had DMLs greater than 172 mm, whereas in 1950 less than 1% of DMLs of males were larger than 172 mm.

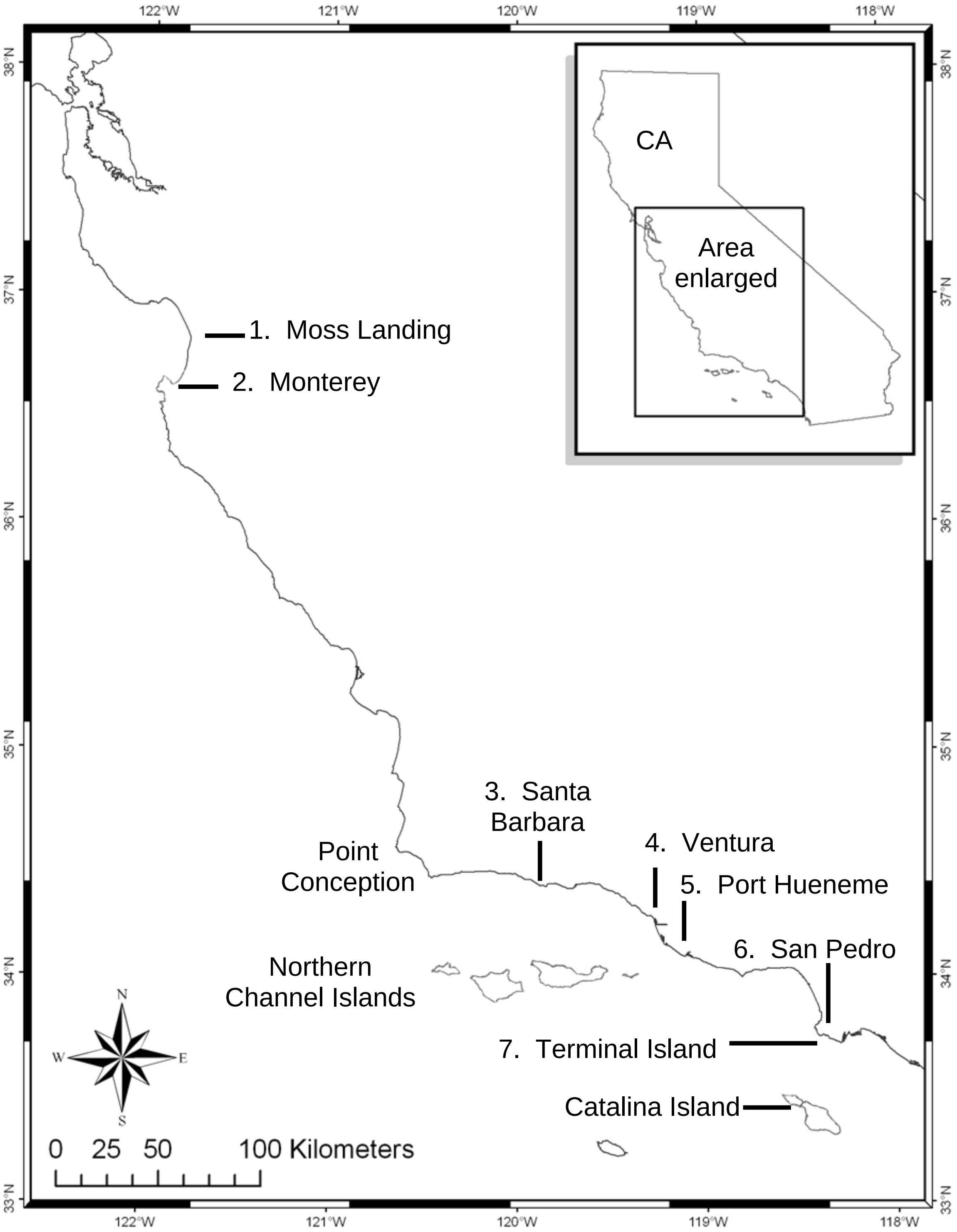

Figure 3 Location of 7 commercial fishing ports for sample collection

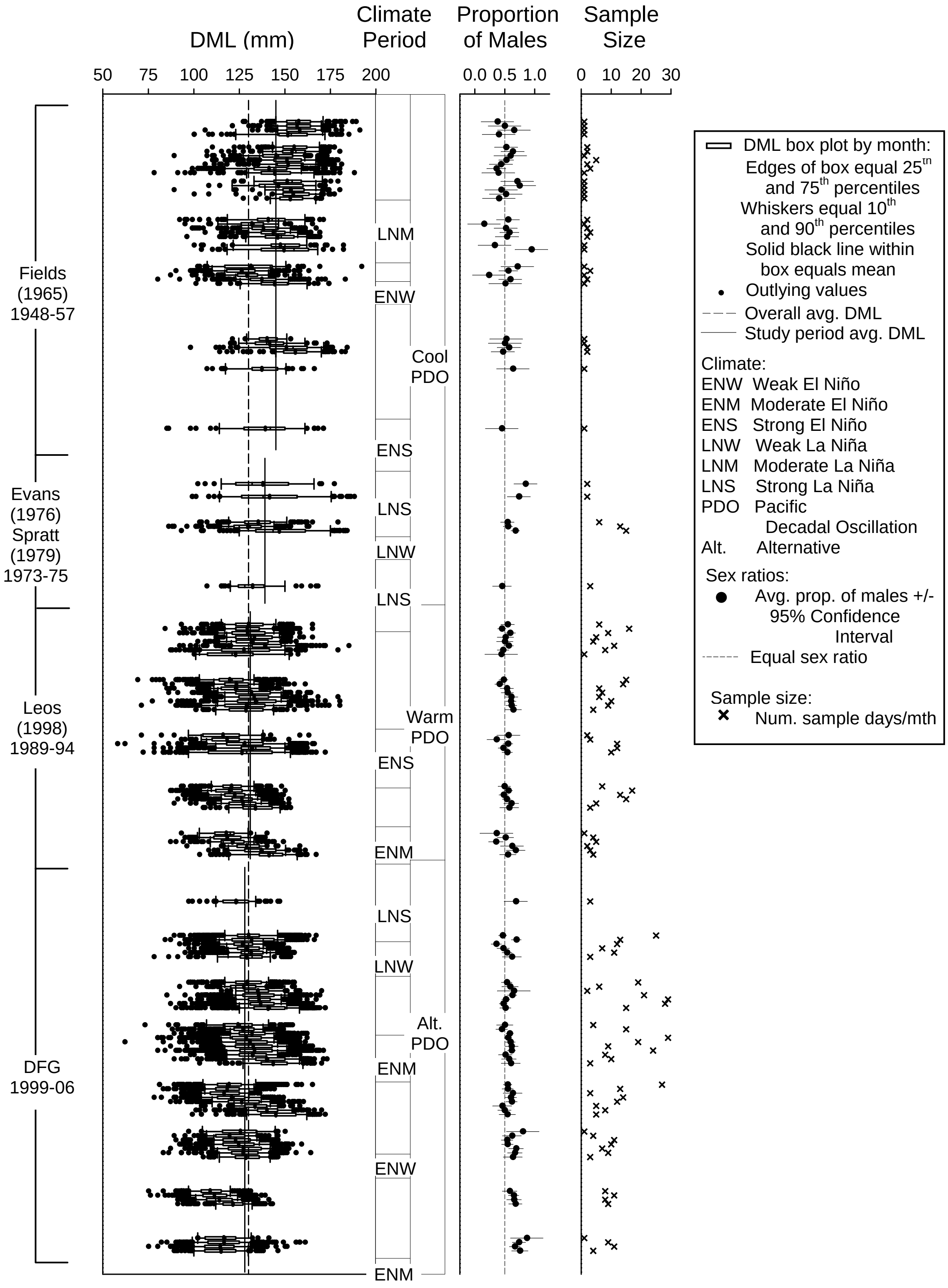

Figure 4a DML, climate, sex ratio, and sample size for Monterey, 1948 to 2006

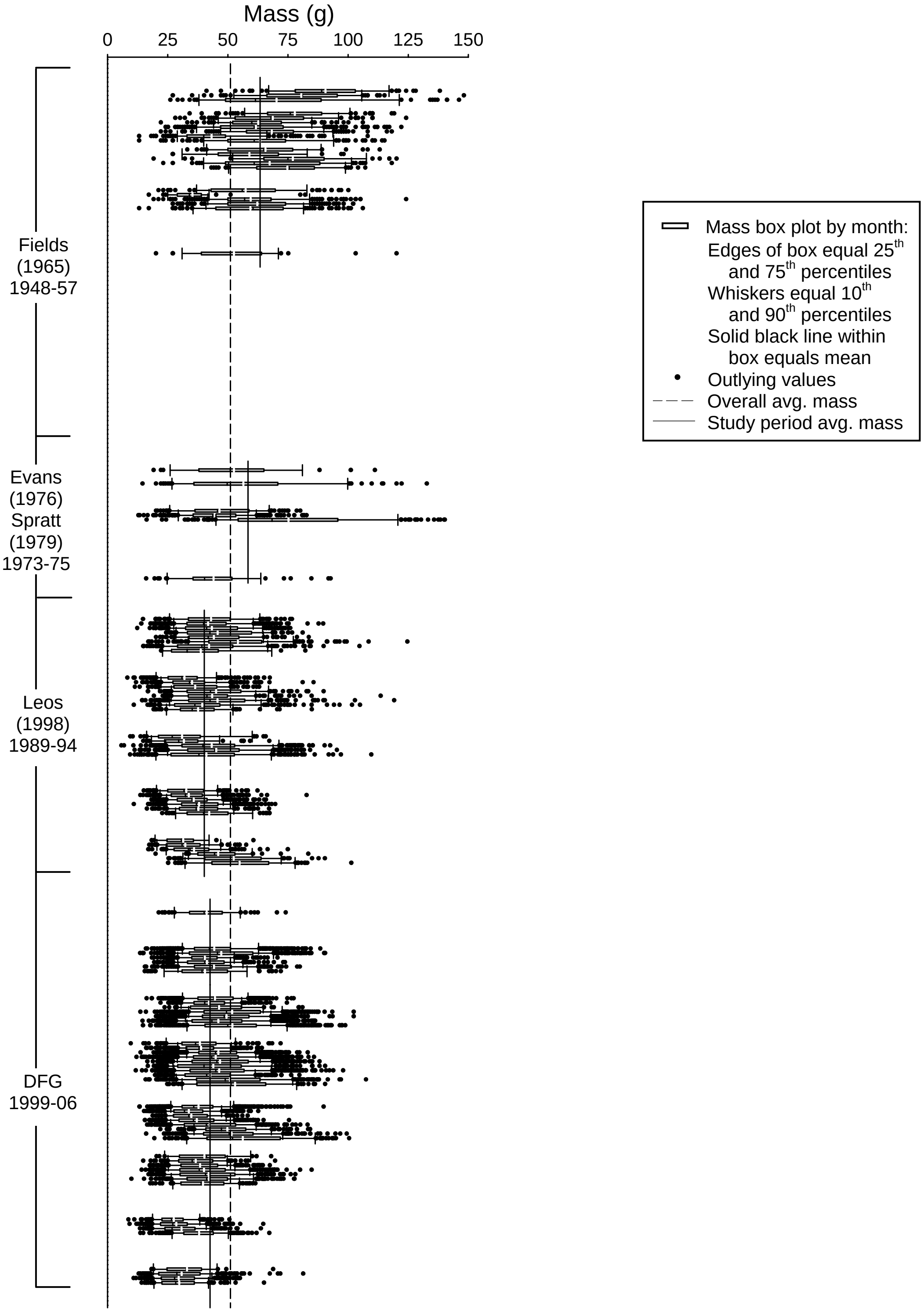

Figure 4b Opalescent squid mass from Monterey, 1948 to 2006

(data source *See Table 1*)

In the 1970s, Spratt (1979) counted statolith growth rings and found opalescent squid lived up to 4 years, but this too was not validated. In his publication, mean DMLs were not referred to – although some of the raw DML, mass, and sex ratio data were available from his analysis (Spratt 1979). Evans (1976), however, did publish results for mean opalescent squid size, but the results were for samples collected in only 1974. Evans (1976) assessed opalescent squid samples from the Monterey and southern California commercial fishery catches. For Monterey, DML and mass of commercially caught opalescent squid were of comparable size to some of the values reported by Fields (1965). Sex ratios were dominated by males in both geographic regions, whereas Fields (1965) had reported equal sex ratios for Monterey. Opalescent squid in southern California were longer in DML; however, Monterey opalescent squid had greater body mass at length. Evans (1976) found there were greater numbers of immature opalescent squid in southern California and opalescent squid matured at a smaller size in Monterey. As Fields (1965) had discovered, female opalescent squid were less variable in size than males.

Leos (1998) collected opalescent squid samples from the commercial fishery in Monterey Bay in the late 1980s and early 1990s just after a regulatory measure for a weekend closure was adopted. A greater proportion of spawned opalescent squid were found in the catch on Mondays, the day following the weekend closure. The results from Leos' (1998) study indicated that the weekend closure gave opalescent squid the opportunity to spawn without interruption, thereby allowing more eggs to be released by females. Opalescent squid were not aged during the 1998 study. The results from a

Students T-Test indicated DML and mass were significantly ($P < 0.001$) smaller than the sizes reported by Fields (1965). Sex ratios were equal in Monterey fishery landings. The distribution of size for females was narrower than males. Leos (1998) also detected that mean DMLs of opalescent squid were larger during the first month of the fishing season, which typically coincided with the onset of upwelling – DMLs immediately decreased, and then increased as the fishing season progressed. The majority (93.5%) of the sampled opalescent squid were sexually mature.

In 1998, the beginning of the latest CDFG-sponsored sampling program, a group of about 200 opalescent squid were collected for ageing purposes. These opalescent squid were aged by counting statolith increments and were determined to be an average of 6 months old, with some as old as 10 months (Butler et al. 1999, 2001). Since then, daily growth increments were validated by growing opalescent squid from hatching to 52 days in a laboratory setting (Vidal et al. 2002), and have shown that opalescent squid DML at capture can be linked to the regional SST of the hatch-month (i.e., 4 to 10 months prior to capture) (Jackson and Domeier 2003; Reiss et al. 2004). Additional information collected in the CDFG sample program included gonad weight and mantle condition, which can be used to calculate the standing stock of oocytes or fecundity within a female opalescent squid at time of capture.

Environmental Variables

Opalescent squid spawning activity is associated with local and seasonal influxes of nutrients from upwelling or winter mixing events (Zeidberg et al. 2006). In Monterey, the upwelling season and the spawning activity of opalescent squid usually begin between February and April. During these months, when winds from the northwest become more common, nutrient-rich water from the ocean-bottom near the upwelling-center off Point Año Nuevo is driven to the surface, and provides an abundant food source for the zooplankton communities upon which newly hatched opalescent squid prey. In southern California, opalescent squid spawning coincides with winter mixing of surface waters and deeper-water upwelling, which usually happens from October to March.

SST, nutrients, and surface water circulation in central and southern California undergo long- and short-term cycles. Climatic regime shifts and El Niño Southern Oscillation (ENSO) events are described by indices that reflect such oceanographic changes over long- and short-time periods, respectively. The Pacific Decadal Oscillation (PDO), an example of a regime shift, fluctuates between anomalously warm and cool SST every 20 to 30 years (Hare and Mantua 2000; Mantua and Hare 2002). During cool water phases, primary productivity increases and causes a bloom in phytoplankton that is reflected through trophic cascades up the food chain from zooplankton to small coastal pelagic finfish and invertebrates and onto larger organisms (Francis et al. 1998). The ENSO is similar to the PDO but occurs on a much shorter time scale lasting from 6 to 18 months, and is called El Niño during warm water, low-nutrient phases and La Niña during periods of cool water and high-nutrients (Parrish and Tegner 2001; Marinovic et al. 2002). Warm water PDO or ENSO periods cause food availability for opalescent squid to diminish greatly.

Changes in Biological Aspects of Opalescent Squid

Populations of many harvested marine organisms exhibit fluctuations in biological aspects through time. Distinguishing the proportion of those variations caused by direct impacts due to fishery exploitation, environmental factors, or biotic factors (e.g., competition, predation) remains a challenge. Many researchers have focused on changes in the abundance of fished species caused by oscillations in the environment and fishing pressure (MacCall 1996; Hofmann and Powell 1998; Klyashtorin 1998; Beamish et al. 1999; Moser et al. 2000, 2001; Steneck and Wilson 2001; Chavez et al. 2003; Mason 2004). Others have correlated changes in life history traits of fished species, such as body size, age, and reproductive potential, with oceanographic or fishery variables (Trippel 1995; VenTresca et al. 1995; Law 2000).

Although the opalescent squid fishery often collapses during episodic El Niño events, a fishable population has persisted throughout the duration of the warm water, low-nutrient PDO cycle that began in 1977 (Jackson and Domeier 2003; Reiss et al. 2004). Recent El Niño and La Niña cycles are correlated with short-term changes in opalescent squid abundance (Ish et al. 2004; Zeidberg et al. 2006), age, growth, timing of maturity (Jackson and Domeier 2003; Reiss et al. 2004), and paralarval densities (Zeidberg and Hamner 2002). Results of previous studies on opalescent squid indicate age and growth are dependent on SST and food availability (Forsythe 2004), and body size increases as SST decreases (Jackson and Domeier 2003; Reiss et al. 2004). Fluctuations in SST and nutrient availability are not as extreme in different phases of regime shifts compared with ENSO; however, past research has shown long-term changes in the size and sex ratios of opalescent squid from the earlier phases of the fishery (i.e., 1940s), through regime shifts and many ENSO events, to the present (Fields 1965; Evans 1976; Leos 1998).

These studies indicated that changes in the life history of opalescent squid may be related to fishing pressure and environmental variables; however, the strength of a relationship among these variables has yet to be determined. For this study, the following hypotheses were addressed to evaluate changes in biological characteristics of opalescent squid and to attempt to separate environmental effects from fishery induced. The results of this study will provide information that is necessary for successful management of the fishery. The hypotheses include:

1) DML, body mass, the proportion of females, and fecundity have declined in the opalescent squid fishery through time, and these biological aspects were similar among geographic locations; and

2) Observed biological changes, as identified in hypothesis 1, correspond to patterns in fishery or environmental data: a) Size was negatively correlated with fishing pressure from the previous fishing season; b) Size was negatively correlated with hatch-month SST; and c) Size was positively correlated with hatch-month upwelling.

METHODS

Eight different, historic data sources (biological, fishery, and environmental information) were used in the analyses (Table1). Data were presented temporally by year, fishing season (from April 1 to March 31 of the following year), and month. For

Monterey, data were available from 1948 to 2006 and were compared by: 1) consecutive months (i.e., January through December); and 2) by the same month for each fishing season (e.g., June for each year). Data from 1999 to 2007 were compared on a monthly basis for the Monterey area (only to 2006), the northern Channel Islands (Anacapa, Santa Cruz, Santa Rosa, and San Miguel Islands), and Catalina Island. These 3 areas were chosen because spawning in Monterey occurs during the opposite season of the southern California sites, and spawning activity will sometimes occur only in the northern Channel Islands or Catalina Island – although in some years spawning occurs at all locations simultaneously.

Biological Datasets and Analyses

Fields (1965), Evans (1976), Spratt (1979), and Leos (1998) provided only summarized biological information in their publications. The original data collected in Monterey for each study period were found in various sources. A reference for Fields' (1965) data was located online at the University of Victoria's library web site. DML, mass, and sex data were obtained from X, Y plots created by Fields (1965) – only data for 1948 to 1957 were available. DML, mass, and sex data collected by Spratt (1979) and Evans (1976) from 1972 to 1975 were found in archived CDFG files. Data from 1989 to 1994 were available from the original CDFG data sheets and contained DML, mass, sex, and maturity records (Leos 1998). The most recent CDFG sampling project spanned from 1998 to 2007 for 3 port complexes: 1) Monterey and Moss Landing; 2) Santa Barbara, Ventura, and Port Hueneme; and 3) San Pedro and Terminal Island (see Figure 3). Data from 1999 to 2007 were used in the analysis because data collected in

1998 were not comprehensive. In addition to size and sex information, this dataset also contained fecundity estimates. Because reliable age data were not available for any of the studies, the effect of age on opalescent squid size could not be evaluated.

Table 1 Origin of datasets, years for which data were available, location where data were collected, and variables reported

Dataset source	Time period	Location	Variables
Fields (1965)	1948 to 1957	Monterey	DML, mass, sex
Evans (1976) Spratt (1979)	1974 1973 to 1975	Monterey	DML, mass, sex
Leos (1998)	1989 to 1992, 1994	Monterey	DML, mass, sex, maturity
CDFG samples	1999 to 2006 1999 to 2007	Monterey, N. Channel Islands, Catalina Island	DML, mass, sex, gonad weight, mantle condition
CDFG landing receipts	1950 to 1953, 1969 to 2007	Monterey, N. Channel Islands, Catalina Island	Fishing location, catch amount, gear used
Hopkins Marine Station	1947 to 2006	Monterey	SST
National Oceanic Atmospheric Administration	1998 to 2007	Buoy 46053 - N. Channel Islands, Buoy 46025 – Catalina	SST
	1950 to 2006	Pacific Ocean	ENSO and PDO events
Pacific Fishery Environmental Laboratory	1947 to 2007	Monterey (36° N, 122° W), S. California (33° N, 119° W)	Upwelling

Biological data from the various time periods were collected with similar methods. Samplers visited commercial fishing docks throughout the fishing season and collected a sample of opalescent squid from fishing vessel holds, the processing pump, or transportation bins. In the lab, opalescent squid were drained of excess fluid, weighed to the nearest 0.1 g, measured along the dorsal side of the mantle to the nearest mm, and the sex was determined. In some of the earlier samples, opalescent squid were either measured immediately or after being frozen; whereas all samples taken in the 1980s or later were measured on the same day of collection.

Fields (1965) collected random numbers of opalescent squid at the docks throughout the unloading process. Spratt (1979) and Evans (1976) collected a random sample of approximately 1,000 g and then measured different numbers of opalescent squid each time. Leos (1998) measured 25 randomly selected opalescent squid from 2,000 g samples. Handfuls of opalescent squid were collected throughout the entire offloading process until a 2,000 g sample filled a bucket. In the most recent sampling regimen, approximately 40 opalescent squid were randomly taken from the processing pumps – samplers watched the majority of the offloading process and took 5 or 6 individuals with a handheld net as the opalescent squid were pumped into shipping bins (Kong et al. 2004). Thirty opalescent squid were then measured. In addition to recording DML, mass, and sex information for the 1999 to 2007 samples, fecundity and age data were collected. Gonads, mantle punches, and statoliths were taken for the first 5 females of every sample and a mantle punch and statoliths were removed for the first male of every sample. Statoliths were not aged or validated, and were not available for use in this analysis, although they may be used later for additional verification purposes.

The number of opalescent squid and days sampled each month varied for all the collection periods in Monterey. The sample unit that was used for analyses was a day. Means and 95 % confidence intervals (CI) for DML, body mass, sex ratio, maturity, and fecundity were calculated for each day a sample was taken and were used in subsequent analyses. Samples were not collected in every month. Because opalescent squid size differs in relation to the month of capture, samples could not be combined within a year to determine if the biological aspects of opalescent squid changed through time. DML and body mass were graphed by month in box plots, which show the minimum, maximum, mean, and the 10th, 25th, 75th, and 90th percentiles of the size distribution. Corresponding sex ratios and samples sizes were graphed adjacent to monthly DMLs to reveal temporal patterns. A Chi-square test was used to compare the monthly sex ratios. In this instance, the numbers of female and male opalescent squid were summed by month and not by sample day, and the proportion of males was used in comparisons. The Chi-square statistic was 3.84 with 1 degree of freedom (i.e., 2 sexes, 2-1=1).

A one-way ANOVA was used to determine if DML and mass changed significantly through time in Monterey. The month of June was sampled the most from 1948 to 2006 – 18 years for DML and 15 years for mass. Because some months of June had only 1 sample day, variances could not be compared with a Cochran’s Test. Due to variances for the month of June being unequal and sample sizes being largely different, Resampling Statistics (RS) for Excel was used to run a one-way ANOVA to compare

DML and mass for females and males (RS 2006). The RS ANOVA was executed with 10,000 iterations and with replacement (bootstrap).

The proportion of immature, mature, and spent individuals captured by the fishery from 1989 to 1994 in Monterey was calculated for each month. Mean DML and mass also were depicted with the maturity data to illustrate how the monthly index of maturity changed with size through time. To determine if patterns in the maturity index related to fishery landings, total catch also was graphed by month.

Biological data were compared by month for 3 geographic regions for fishing seasons from 1999-00 to 2006-07. Mean DMLs and masses were graphed by month for each region. Pairwise comparisons for monthly sizes for each region were made with a Pearson product-moment correlation. The mean proportion of males captured in the fishery from each region was calculated for each month. Since past studies found sex ratios to be 1:1, this ratio was included in the graphs. The 95% CI from 1999 to 2007 was computed for each region. Similar to the analysis computed for sex ratios in Monterey from 1948 to 2006, a Chi-square test was used to compare the monthly sex ratios to 1:1 for each region. RS for Excel was used to compute the 95% CI for a proportion of 0.50 for a daily sample size of 30 opalescent squid.

For the 3 geographic regions, gonad weight and mantle condition were available from 1999 to 2004 (only 2002 measurements were available for Monterey). The fraction of released potential fecundity for individual females was calculated from the following (Macewicz et al. 2004):

$$E_p = 29.8L, \ [r^2 = 0.34]$$

where E_p = potential fecundity, L= female DML in mm,

and

$E_{YD} = 378.28e^{(2.33C + 0.2447G - 0.24CG)}$,

where E_{YD} = standing stock of oocytes and ova in a mature female opalescent squid, C = mantle condition index; and G = gonad (ovary and oviduct) mass,

and,

$1\text{-}(E_{YD}/ E_p)$ = fraction of potential fecundity released

The mean fraction of released potential fecundity was then calculated for each sample day. The potential fecundity (E_p) equation, however, was based originally on the number of eggs present in the ovaries of only 13 preovulatory mature females (Macewicz et al. 2004). Those females ranged in size from approximately 107 to 133 mm, which did not include the full size range of mature opalescent squid captured in the fishery and collected in samples used for this analysis. There was the possibility the number of eggs associated with the DML of a female changed over time, although fecundity calculations for the current analysis were made with the assumption that potential fecundity, based on DML for females, has not changed. Due to uncertainties involved with using the potential fecundity equation, the standing stock of oocytes also was used as a proxy for fecundity. This was based on the assumption that the standing stock of oocytes of opalescent squid sampled from spawning grounds could be used as a proxy for opalescent squid not captured by the fishery but were instead left to spawn until they died from natural mortality. If the fishery always captured opalescent squid at the same time within their life history, the standing stock of eggs in opalescent squid should signify a relative amount of eggs that non-captured opalescent squid were capable of releasing.

Fishing and Environmental Datasets and Analyses

Fishery information from landing receipts was used to determine how fishing gear and catch amounts changed through time and differed among geographic regions. The CDFG had landing receipts in digital format from 1969 to 2007. Historic landing receipts were available via microfiche from 1950 to 1968. Receipts from 1950 to 1953, which overlapped with the biological data, were searched for opalescent squid information and then added to the landing receipt database to increase the time coverage for opalescent squid catch. Summaries of landings data were available from CDFG Fishery Bulletins from 1929 to the present; however, these summaries did not include the number of landings made, so a catch-per-trip (or catch-per-unit-effort (CPUE)) estimate could not be calculated. Therefore, the data from the landing receipt microfiche were used even though total metric tons landed did not match those reported in CDFG Fishery Bulletins. Only fishery data reflecting accurate information about the geographic distribution of opalescent squid were used in the analysis – any information pertaining to an area outside of the normal depth distribution of opalescent squid was not included. Total catch amounts and CPUE were calculated for each period and area.

To determine if the observed change in mean opalescent squid size was valid or if it was instead an artifact of sampling (i.e., fishing gear), a comparison of opalescent squid DML in relation to gear type was made with data from Leos (1998). During the late 1980s, opalescent squid were caught with lampara, purse, or drum seine nets. An RS bootstrapped ANOVA with 10,000 iterations was used to compare the mean size of opalescent squid caught with lampara nets or purse and drum seine nets.

SST and upwelling data were available for locations proximal to opalescent squid fishing grounds in central and southern California. For Monterey, SSTs collected at Hopkins Marine Station were available from 1945 to 2006. In southern California, SST data were available from National Oceanic and Atmospheric Administration buoys near the northern Channel Islands (buoy #46053) and Catalina Island (buoy #46025) from 1998 to 2007. Fluctuations in mean SSTs were calculated from 1945 to 2006 for Monterey, and for 1998 to 2007 for Monterey, the northern Channel Islands, and Catalina Island. SST was used as a proxy for food availability for opalescent squid (Roemmich and McGowan 1995; Jackson and Domeier 2003; Ish et al. 2004). SST anomalies were computed in Matlab (version 12.0). Mean monthly SSTs were assigned a consecutive number from 1 to 12. The average SST for each single month of the year for the entire time series was calculated (e.g., all January months, all February months) and then subtracted from the corresponding month within each year to compute the anomaly for that month. Upwelling index and anomaly values were available from the Pacific Fisheries Environmental Laboratory web site for Monterey and southern California.

The relationship between opalescent squid size and fecundity and fishing or environmental variables was tested with Pearson product-moment correlations. To determine which fishing related and oceanographic factors had the greatest influence on opalescent squid size, SST, upwelling, and fishery landings (i.e., number of fishing days, total catch, and CPUE) were correlated with opalescent squid DML and mass. The size to which an individual opalescent squid may grow to and be captured by the fishery may be determined more so during certain stages of their life history. Because certain stages of an opalescent squid's life history may be more susceptible to environmental factors or fishing pressure, correlations were performed for 1-month lags for up to 1 year prior to the individual being captured. A Sequential Bonferroni Test was used to correct for multiple correlation tests with the following steps: 1) P-values for 13 months of correlations (month 0 was equal to the time of capture) were sorted from least to greatest; 2) the alpha-value (0.05) was divided sequentially by the number of lags (i.e., 13, 12, 11…1); and 3) if the P-value was less than the newly calculated alpha-value, then it was considered to be significant. To determine if any correlations between opalescent squid body size and environmental factors were affected by relatively weaker or stronger values, anomalies for DML and mass were calculated. The statistical software SAS (version 9.1) was used to compute the anomalies for DML and mass because there were months without values, and the code used in Matlab was not written to accept missing values.

The longest time series for the fecundity data was from Catalina Island. The fraction of potential fecundity released and standing stock of oocytes data from Catalina Island were correlated with fishery landings between 1 to 12 months following the month samples were collected to determine if a proxy for fecundity was related to the amount of opalescent squid captured at a later time. All correlations were calculated in JMP (version 7.0) with a Pearson product-moment correlation.

RESULTS

Biological Data

Of the original data collected from each time period in the Monterey area, 27,680 records for individual opalescent squid were analyzed. As previously documented (Leos 1998), mean DMLs and masses of opalescent squid decreased for both sexes from 1948 to 1994 – this decline continued into the 2000s. The minimum and maximum values for DML and mass of opalescent squid caught by the fishery decreased through time for each study period (Table 2 and see Figure 4a-b).

In Monterey, there was a general trend in mean DML and mass in which size was relatively small near the beginning of the season and then increased into the fall months (Figure 5a-d). Opalescent squid sampled from the 1940s to the 1950s were consistently greater in mean DML and mass each month than opalescent squid sampled in the studies from the 1980s to the 2000s (see Figure 5a-d). In comparing the average DMLs and masses between the two periods of the 1940 to the 1950s to the 1990 to the 2000s, there was an approximate decrease of 20 mm. Comparisons of mean DML sampled by lamapara or purse seine gear were not significantly ($P > 0.05$) different for data from 1989. Although sampling activity did not occur every month during the 1970s and the 1980s to the 1990s, sampling did apparently occur every month in the 1940s to the 1950s. Sample days were scheduled for every month during the 1990s to the 2000s, but landings may not have occurred during randomly chosen sample days.

Table 2 Number of opalescent squid sampled and minimum and maximum sizes for each study period in Monterey

Study period	Squid	Minimum	Maximum
		DML (mm)	
All squid			
1948-1957	4,533	78.0	192.0
1973-1975	831	86.0	188.0
1989-1994	6,200	58.0	185.0
1999-2006	16,116	62.0	173.0
Female squid			
1948-1957	2,272	86.0	179.0
1973-1975	331	96.0	167.0
1989-1994	2,970	58.0	159.0
1999-2006	7,022	83.0	158.0
Male squid			
1948-1957	2,261	78.0	192.0
1973-1975	500	86.0	188.0
1989-1994	3,230	62.0	185.0
1999-2006	9,094	62.0	173.0
		Mass (g)	
All squid			
1948-1957	2,761	13.0	148.0
1973-1975	831	12.7	140.1
1989-1994	6,200	5.6	124.5
1999-2006	16,116	8.5	107.3
Female squid			
1948-1957	1,429	13.0	112.0
1973-1975	331	15.9	108.7
1989-1994	2,970	5.6	84.3
1999-2006	7,022	8.5	76.9
Male squid			
1948-1957	1,332	13.0	148.0
1973-1975	500	12.7	140.1
1989-1994	3,230	6.7	124.5
1999-2006	9,094	9.0	107.3

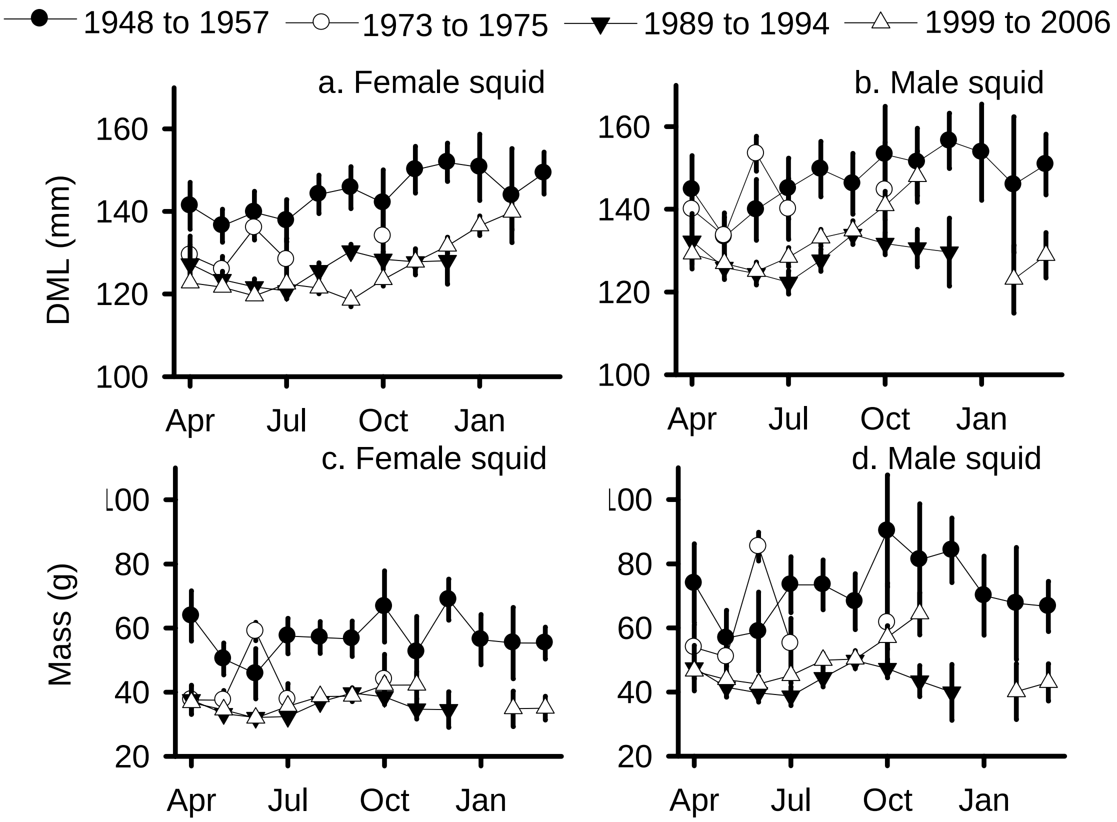

Figure 5a-d Mean DML and mass with corresponding 95% CI pooled by month for each study period in Monterey, 1948 to 2006 (data source *See Table 1*)

Mean DMLs and masses of females and males were significantly different in June from 1948 to 2006 (Table 3). June was sampled the most among all sampling years due to the relatively greater fishery landings during this month, and was chosen to depict the overall pattern of decline in size (Figure 6a-d). In some years, opalescent squid DML or mass did overlap in size, which signifies the variability of opalescent squid body size. However, in only 1 month (May 2000) following the 1970s did the maximum sizes reach those of the earlier samples (Figure 7a-b).

Table 3 Results for a one-way ANOVA in RS for mean DML and mass for the month of June in Monterey, 1948 to 2006

	Female	Male
DML	$P < 0.0001$	$P = 0.01$
Mass	$P = 0.04$	$P = 0.05$

Sex ratios fluctuated in Monterey from 1948 to 2006. The majority of monthly sex ratios of females and males captured in the fishery were significantly different from 1:1 (Table 4, see Figure 4a). From 1989 to 2006, there was a general trend in which the mean proportion of males increased throughout the fishing season.

The monthly maturity index for females and males exhibited different patterns for each fishing season from 1989 to 1994 in Monterey (Figure 8a-b). Opalescent squid recruiting to the fishery in 1989 and 1990 were mature from April to August and then an increase in the proportion of spent individuals occurred. In 1991, the proportion of immature females increased at the end of the fishing season rather than the proportion of spent individuals. Also in 1991, the proportion of spent males captured in the fishery was greatest in July. During the 1992 fishing season, individuals were identified as mature throughout the fishing season with no notable increase in the proportion of immature or spent individuals. In 1994, the proportion of mature female opalescent squid remained consistent throughout the season, whereas males were spent in most months. Total catch decreased at the end of the fishing season as more spent opalescent squid recruited to the fishing grounds. Trends in mean DML and mass did not correspond to the monthly patterns exhibited in the maturity index.

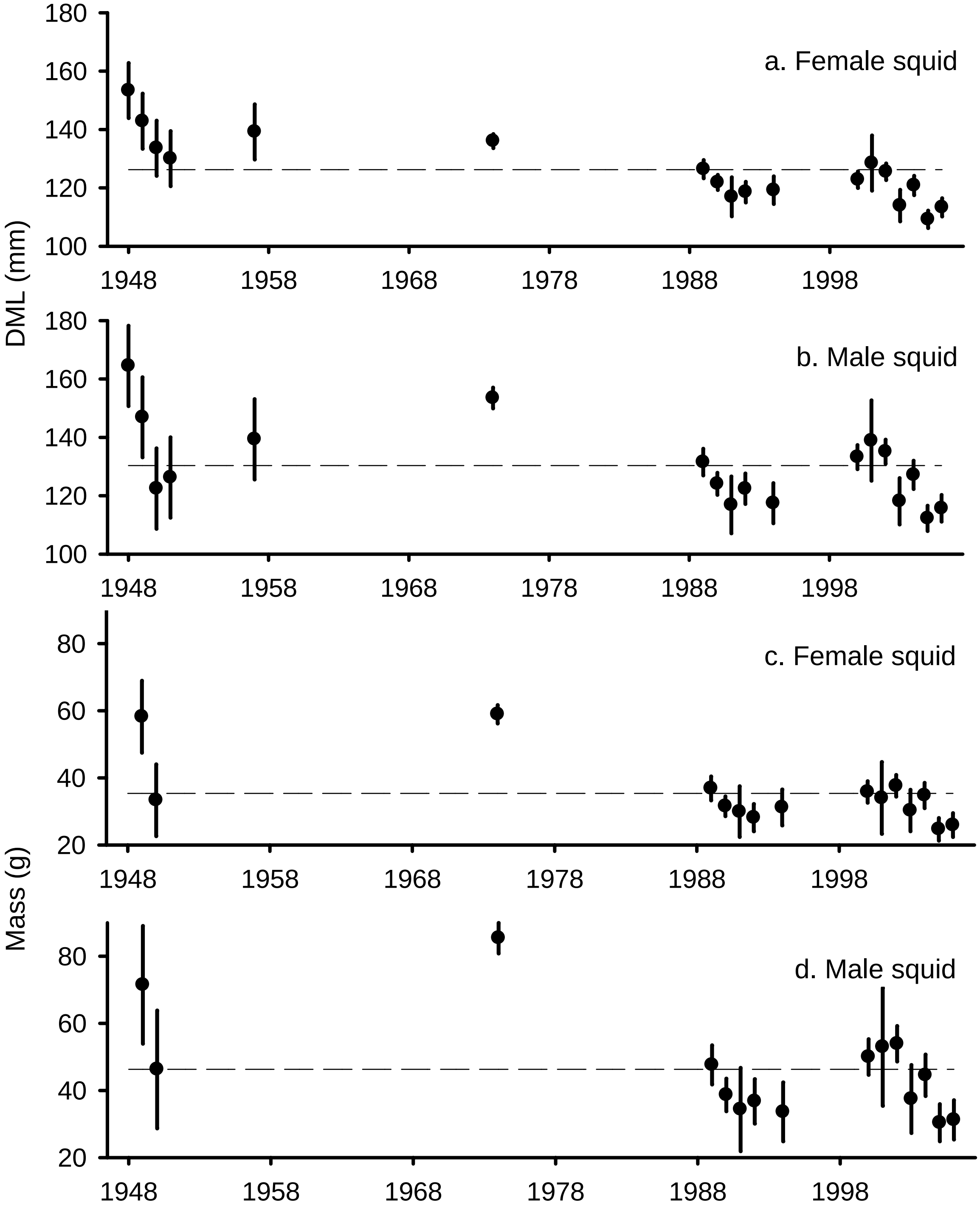

Figure 6a-d Mean DML and mass with corresponding 95% CI for June for Monterey, 1948 to 2006 (data source *See Table 1*)

Table 4 Chi-square results for comparing opalescent squid sex ratios to 1:1 for Monterey, 1948 to 2006

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1948						**8.4***	0.0	**8.5***	**4.1***			0.4
1949	**8.7***	**4.4***	2.7	3.4	**20.4***	**8.5***		**8.7***		0.9	0.1	2.4
1950					1.2	**22.3***	1.4	**5.1***	1.1	**9.3***	**9.9***	**43.7***
1951			**10.9***		**5.6***	**57.7***	**8.5***	0.0				
1952									0.1	0.0	0.7	0.4
1953				**4.6***								
1957						0.7						
1973							**18.7***			**23.0***		
1974				0.3	3.3	**20.7***						
1975							0.7					
1989				1.3	**4.0***	**6.8***	0.0	0.0	**4.5***	0.7	0.4	
1990					0.6	**9.6***	0.7	1.3	**6.8***	**10.0***	**10.7***	**7.8***
1991						0.7	**5.9***	1.9	0.9	1.6		
1992						0.1	**5.6***	0.5	1.4	**5.8***	1.6	
1994					2.0	0.0	**11.0***	2.9	**9.7***	1.0		
1999									**5.4***			
2000					**4.3***	**64.4***	**26.8***	0.6	1.6	**5.0***		
2001				3.3	1.8	**5.4***	**33.8***	0.8	1.2	0.6		
2002		0.0	7.0	**19.9***	**15.7***	**18.3***	**13.3***	**30.4***	0.2	**5.6***	3.6	
2003				**8.9***	1.9	**6.1***	**5.0***	**22.5***	2.7	0.6	1.0	
2004			**10.8***	**8.5***	**7.0***	2.6	**26.1***	**30.0***	**6.4***			
2005					**6.0***	**28.6***	**17.1***	**30.8***				
2006					**75.6***	**49.3***	**30.0***					

*****Sex ratios were significantly different from 1:1

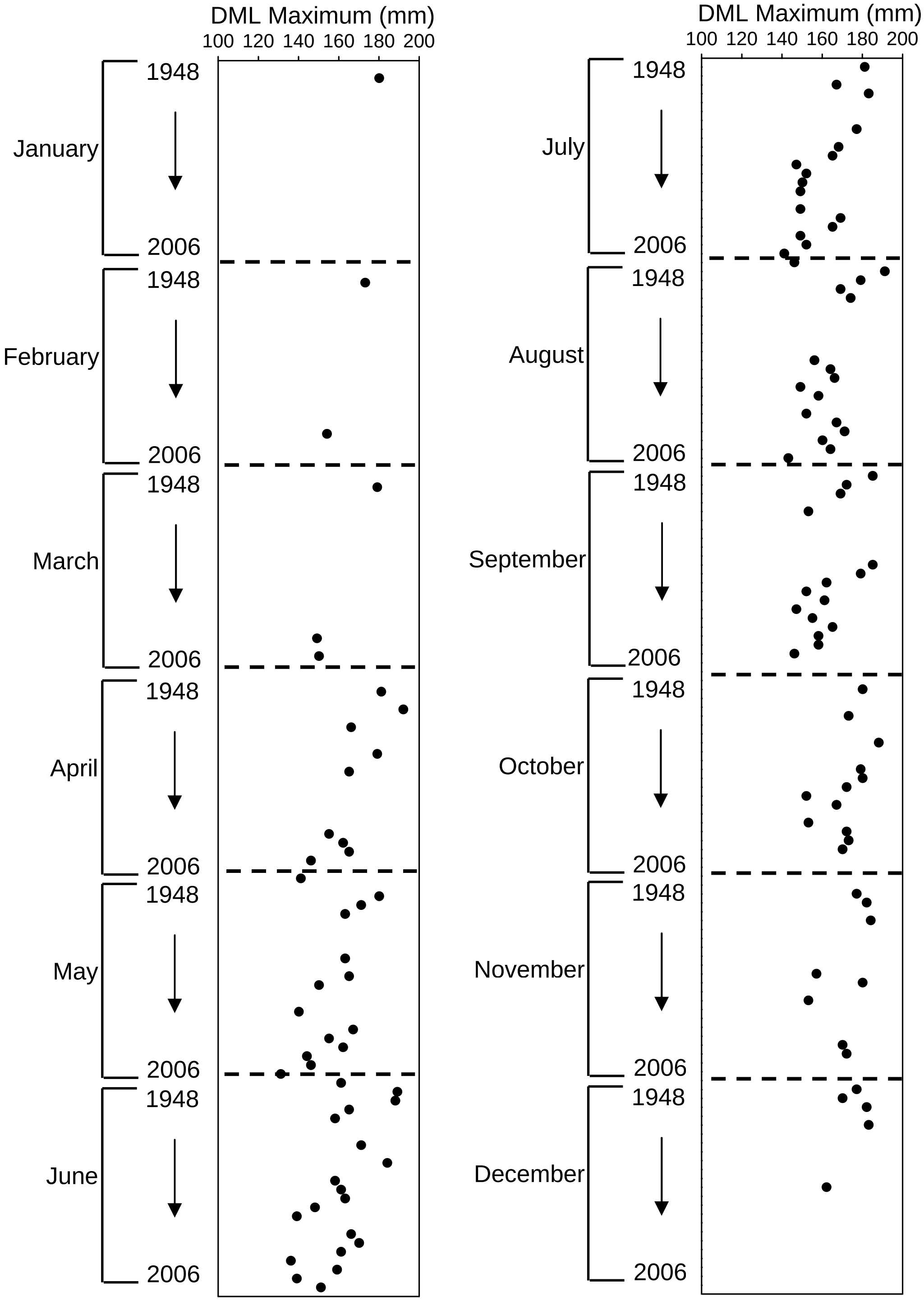

Figure 7a DML maximum for each sample month for

Monterey, 1948 to 2006

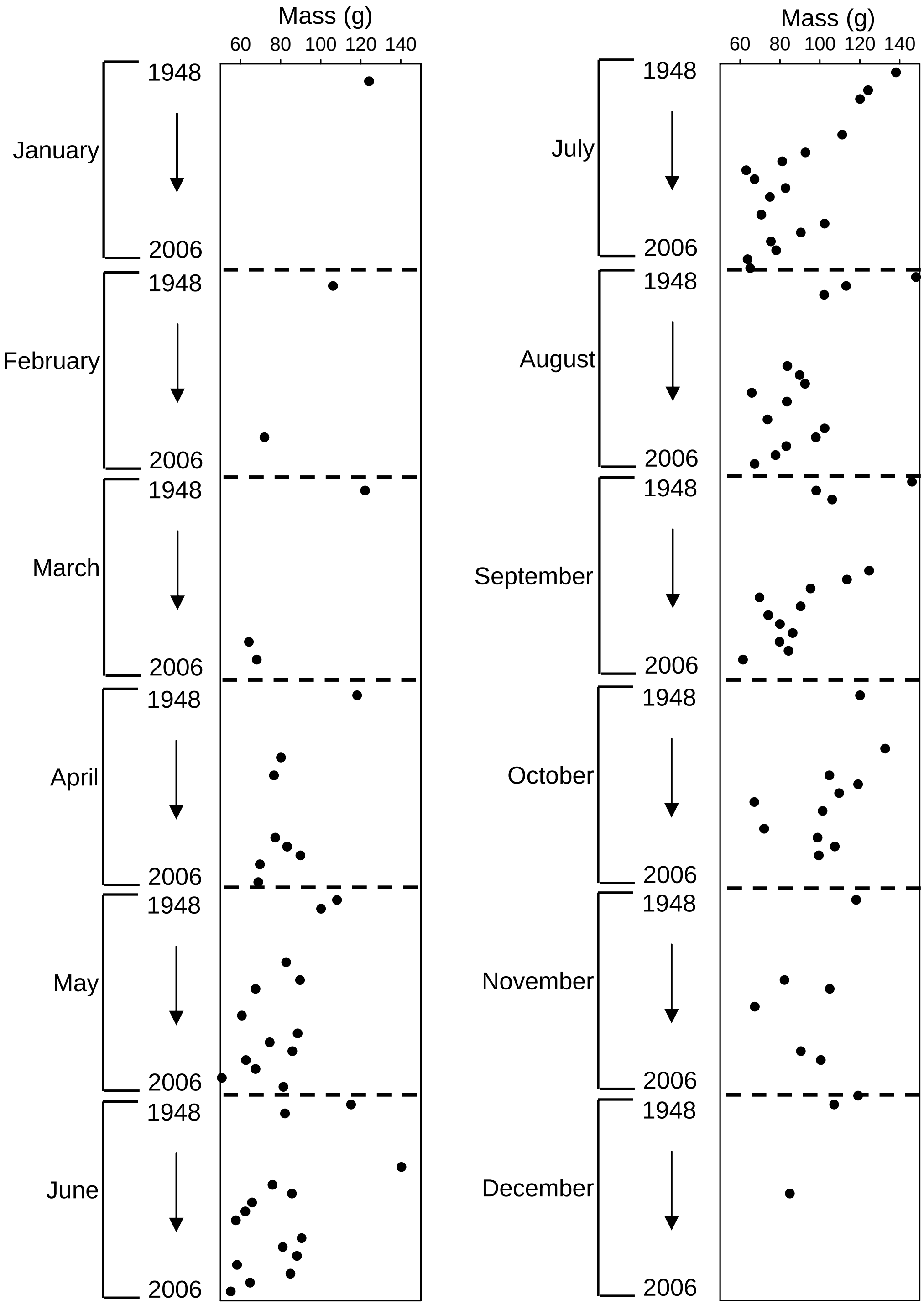

Figure 7b Mass maximum for each sample month for

Monterey, 1948 to 2006 (data source *See Table 1*)

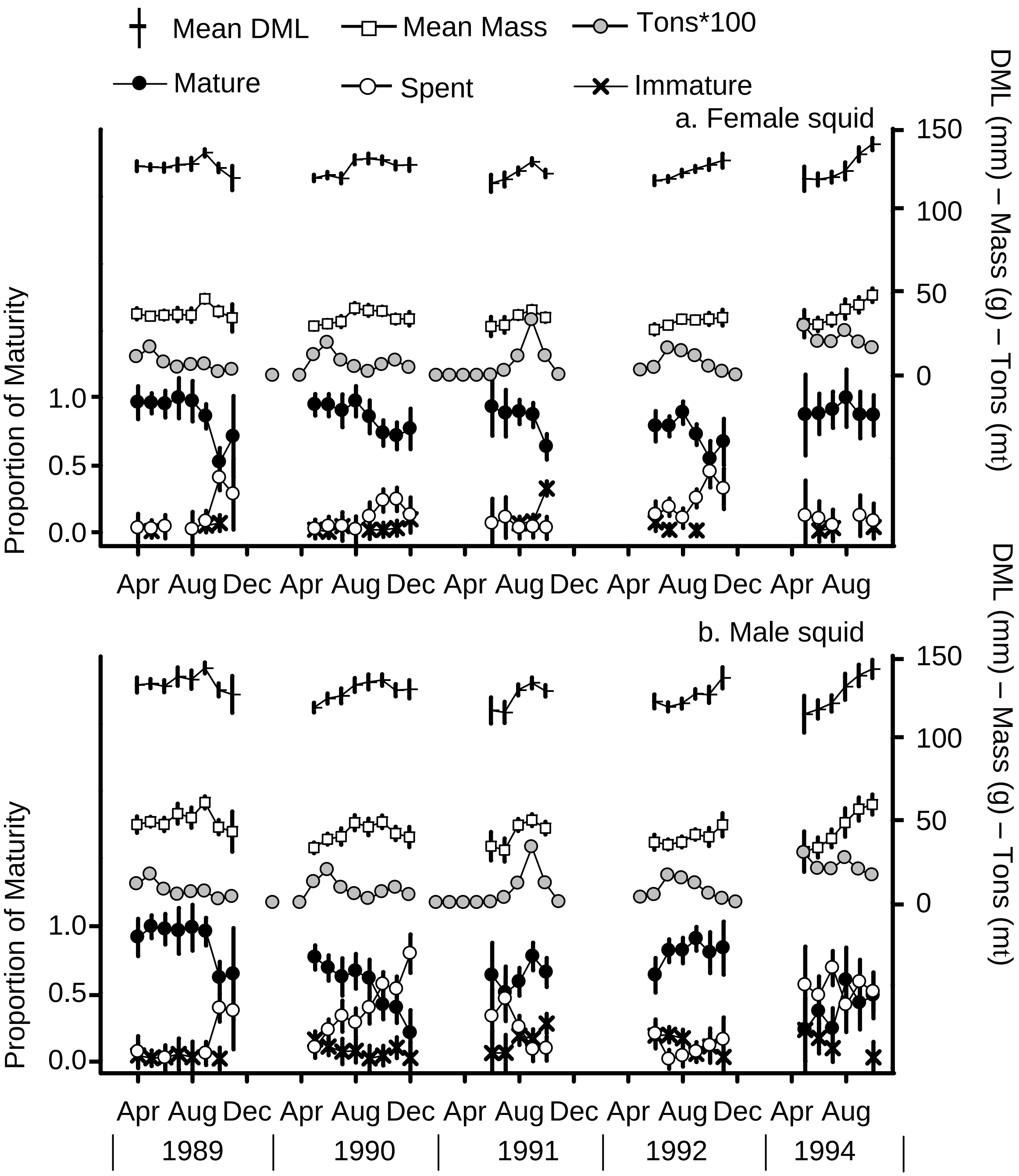

Figure 8a-b Mean proportion of maturity, DML, and mass with corresponding 95% CI by month with total catch (mt) for Monterey, 1989 to 1994 (data source *See Table 1*)

For the geographic comparison of the biological aspects of opalescent squid, 60,022 individuals were sampled from Monterey, the northern Channel Islands, and Catalina Island (Figure 9a-b). From 2000-01 to 2006-07 there was a decrease in mean opalescent squid DML and mass in all areas (Figure 10a-d). In 1999-00 opalescent squid size was the largest for the northern Channel Islands and Catalina Island. Opalescent squid size was the smallest during the 2004-05 fishing season for southern California. Body size then increased in 2005-06 for sites south of Point Conception, but size decreased even further in 2005-06 and 2006-07 in Monterey for all opalescent squid.

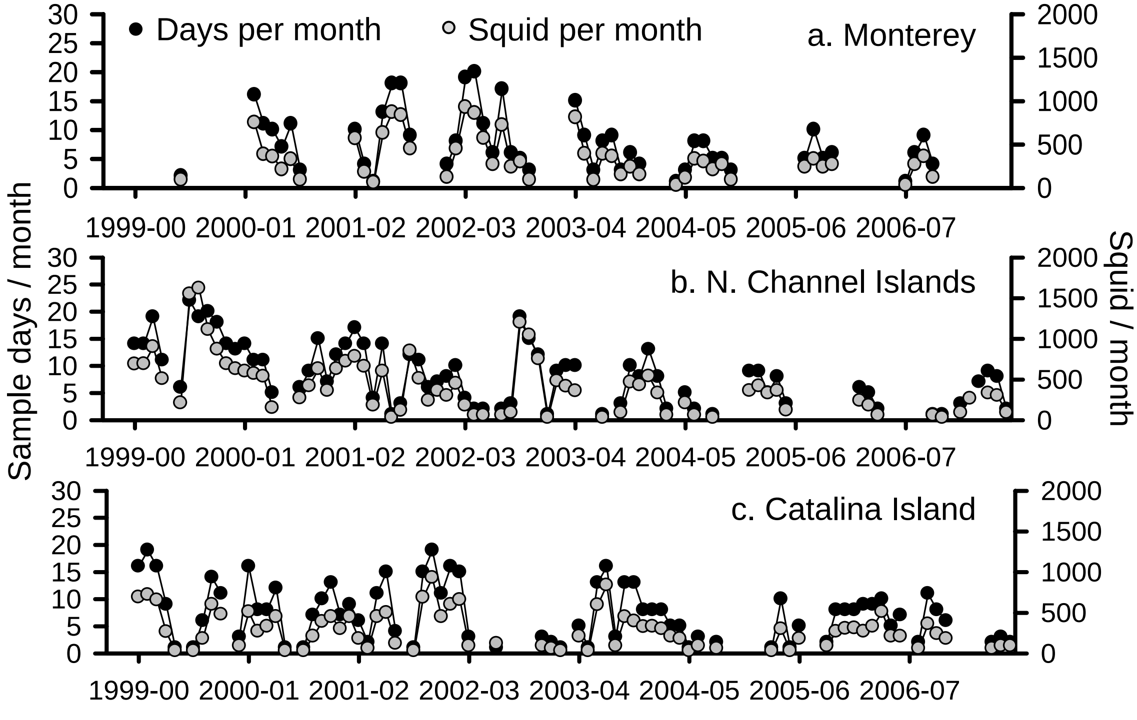

Figure 9a-b The number of sample days and number of opalescent squid sampled per month for 3 regions from 1999-00 to 2006-07 (data source *See Table 1*)

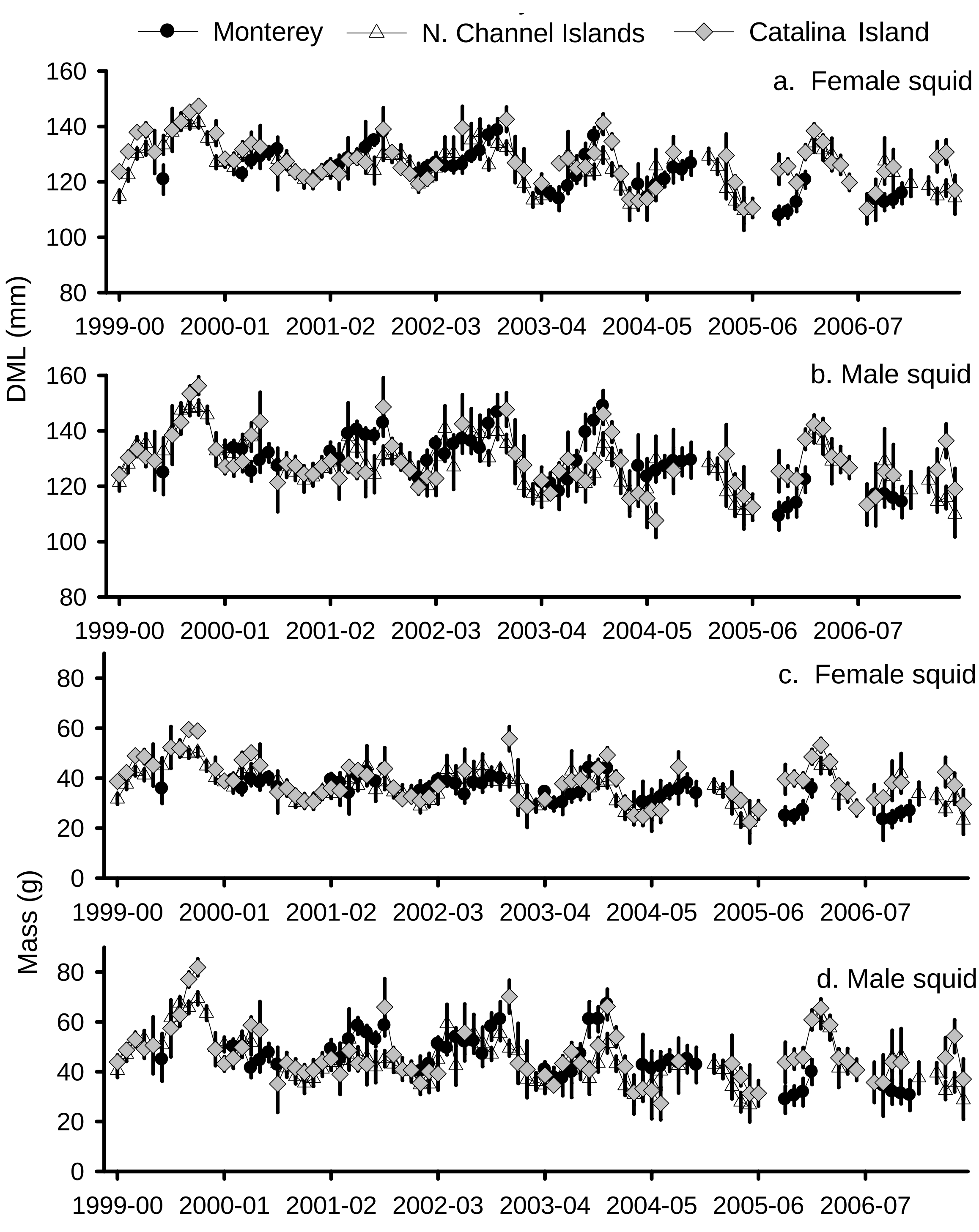

Figure 10a-d Mean DML and mass with corresponding 95% CI for 3 regions

from 1999-00 to 2006-07 (data source *See Table 1*)

Within a fishing season, mean opalescent squid body size oscillated from month to month (see Figure 10a-d). In Monterey, mean DML started at a certain size in the beginning of the regulatory fishing season (April) each year, and then increased on a monthly time scale until the end of the spawning period, sometime during the summer or fall. In southern California, opalescent squid size followed a pattern similar to Monterey when compared on a monthly time scale (see Figure 10a-d). In southern California, the spawning period usually began in October (instead of April in Monterey). Therefore, in the southern fishery, mean sizes were greatest at the beginning of the fishery, and then decreased in size until about the time when fishing stopped in the spring. Mean DMLs and masses were relatively small in the spring months and then increased through the summer months to the winter. This pattern occurred in Monterey, the northern Channel Islands, and Catalina Island. Mean DMLs were significantly correlated among the 3 regions for each month indicating that the pattern in mean opalescent squid size was similar among regions, although masses from Monterey did not correspond with the northern Channel Islands (Table 5).

Table 5 Pearson correlation coefficients of mean DML and mass by month between regions from 2000-01 to 2006-07

	Monterey vs. N. Channel Islands	Monterey vs. Catalina	N. Channel Islands vs. Catalina
Female DML (mm)	**0.44***	**0.69*****	**0.81*****
Female mass (g)	0.31	**0.54****	**0.81*****
Male DML (mm)	**0.35***	**0.52****	**0.80*****
Male mass (g)	0.36	**0.53****	**0.80*****

*$P<0.05$, **$P<0.01$, ***$P<0.001$

In most months, males from all 3 areas for 1999-00 to 2006-07 dominated sex ratios of opalescent squid captured in the fishery (Figure 11a-c). For the majority of the months, the proportion of males was within the 95% CI for a sample size of 30. In some months the proportion of males was significantly greater than the proportion of females (Table 6a-c). Past studies in Monterey found sex ratios to be equal from 1948 to 1962 (Fields 1965) and from 1989 to 1994 (Leos 1998) and not equal in 1974 (Evans 1976) – the results of this study indicate that sex ratios were equal in some months but not the majority. In Monterey, there was a general increase in the proportion of males from 1999 to 2006, although this increase was not evident in the southern California sites.

If female opalescent squid are captured before they have an opportunity to spawn, they will have a greater standing stock of eggs in their bodies, whereas females that have spawned will contain fewer eggs. Potential fecundity of female opalescent squid is dependent on DML (Macewicz et al. 2004); therefore, the temporal pattern in potential fecundity was the same as DML. Moreover, because DML decreased in Monterey from 1948 to 2006, potential fecundity decreased. To estimate the fraction of potential fecundity a female had released into the environment at the time of capture, the ratio of oocyte standing stock to potential fecundity was subtracted from 1. It appears that released fecundity increased from 1999-00 to 2002-03 (Figure 12). In Monterey from 2001-02 to 2002-03, the fraction of released fecundity increased through the fishing season from April to the fall, which matches the patterns in maturity index from 1989 to 1994 when there was a greater proportion of spent individuals later in the fishing season (see Figure 8a-b).

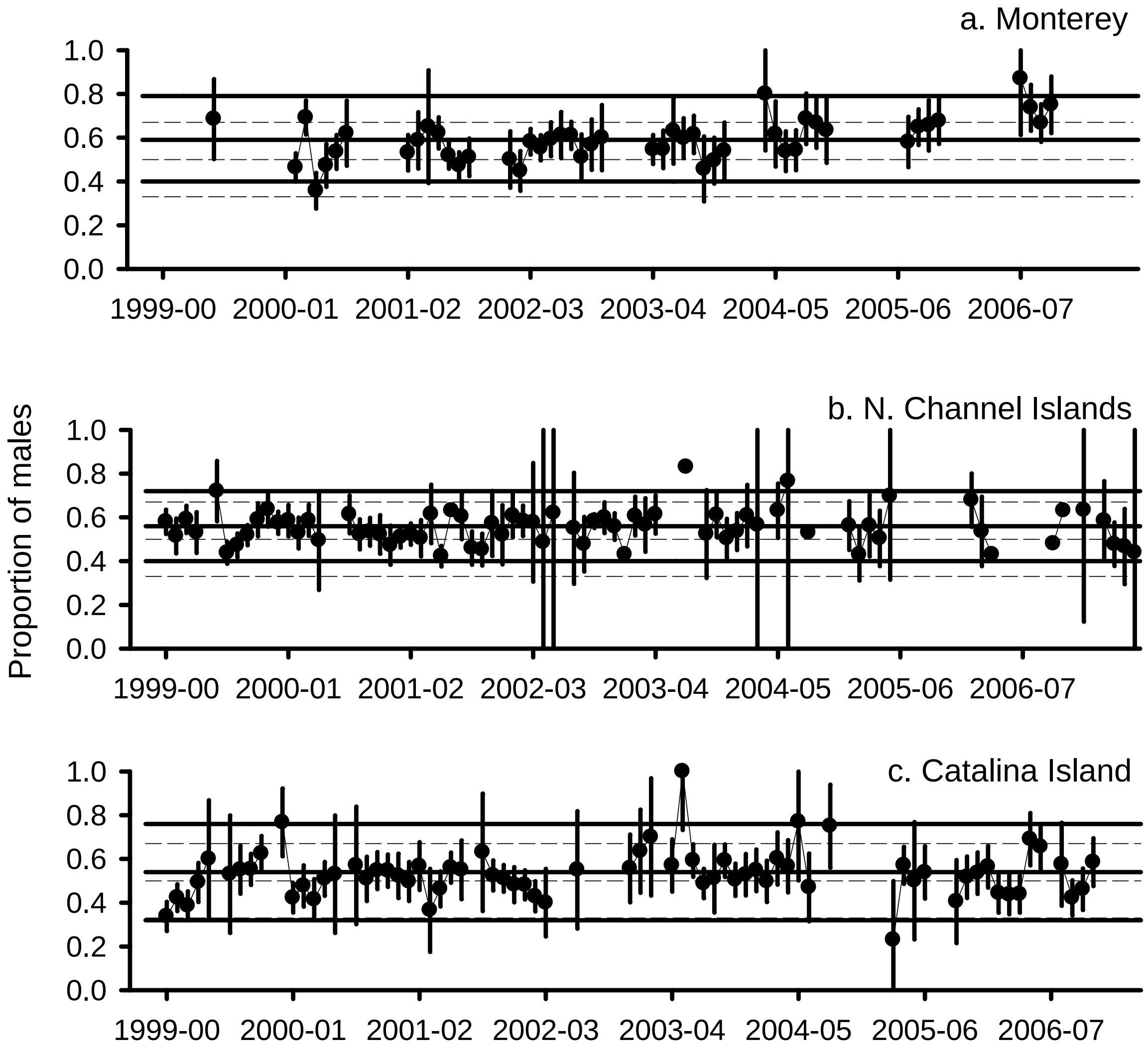

Figure 11a-c Mean proportion of males with corresponding 95% CI by month for 3 regions from 1999-00 to 2006-07. The upper and lower solid lines depict the 95% CI for the entire period, and the middle solid line depicts the mean. The upper and lower dashed lines show the 95% CI for a daily sample size of 30 squid; the middle dashed line signifies a sex ratio of 1:1. (data source *See Table 1*)

Table 6a-c Chi-square results for opalescent squid sex ratios compared to 1:1 ratio for 3 regions

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
a.							Monterey					
1999									**5.4***			
2000					**4.3***	**64.4***	**26.8***	0.6	1.6	**5.1***		
2001				3.3	1.8	**5.4***	**33.8***	0.8	1.2	0.6		
2002		0.0	**7.0***	**19.9***	**15.7***	**18.3***	**13.3***	**30.4***	0.2	**5.6***	3.6	
2003				**8.9***	1.8	**6.1***	**5.0***	**22.5***	2.7	0.6	1.0	
2004			**10.8***	**8.5***	**7.0***	2.6	**26.1***	**30.0***	**6.4***			
2005					**6.0***	**28.6***	**17.1***	**30.8***				
2006				**16.1***	**72.6***	**49.3***	**30.0***					
b.							N. Channel Islands					
1999				**17.6***	1.1	**29.6***	2.4		**42.1***	**24.8***	**4.5***	2.3
2000	**23.8***	**61.5***	**15.2***	**15.7***	0.7	**16.4***	0.0			**10.4***	0.2	2.5
2001	0.2	1.2	0.1	2.6	0.1	**5.0***	**12.3***	2.1	**6.2***	**14.0***	**8.0***	**9.6***
2002	2.3	**17.3***	**9.1***	2.2	0.1	3.3		0.6	0.2	**28.9***	**24.9***	**7.1***
2003	0.5	**32.0***	**6.0***	**13.7***			**13.3***		0.2	**19.0***	0.1	0.1
2004	**18.4***	1.1		**10.1***	**17.1***		0.1	**3.6***				
2005	**6.4***	0.0	**23.6***								**25.6***	0.8
2006	1.1						0.1	2.1	**6.4***			**3.9***
2007	2.4	0.0	2.8									
c.							Catalina					
1999				**66.4***	**18.1***	**31.2***	0.1	1.2		0.1	1.8	**7.3***
2000	**28.2***		**25.6***	**10.7***	0.0	**12.1***	0.8	0.1		0.5	0.1	2.3
2001	3.2	0.1	0.0	3.2	**4.3***	**1.3**	**6.1***	1.2		2.1	0.3	0.2
2002	0.1	0.1	**9.2***	3.6			1.0					1.1
2003	**4.3***	**4.8***		**8.4***	**30.0***	**20.0***	0.4	0.0	**14.3***	0.0	0.3	**5.1***
2004	0.1	**6.6***	**5.0***	**8.5***	0.4		**15.0***					
2005	**8.5***	**6.5***	0.0	2.2			1.6	0.2	0.6	2.5	3.6	**3.9***
2006	**6.2***	**24.7***	**19.2***		1.4	**8.1***	1.4	**5.0***				
2007	**7.5***	**14.4***	0.7									

*Sex ratios were significantly different from 1:1

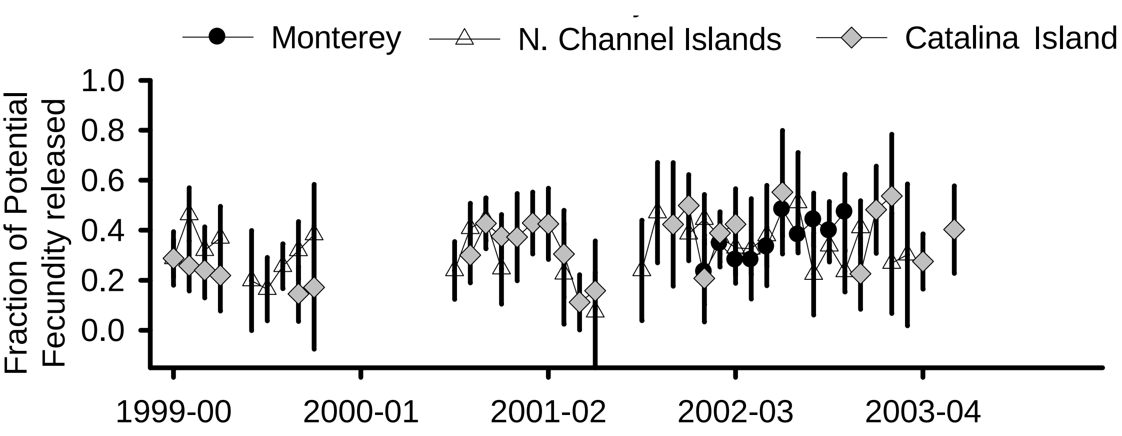

Figure 12 Fraction of potential female fecundity released with corresponding 95% CI for 3 regions from 1999-00 to 2003-04 (data source *See Table 1*)

Fishery and Environmental Data

The average catch-per-daily-vessel-landing was calculated from dealer receipts (Figure 13a-c). Calculating CPUE in this manner did not account for 0 take even if effort was expended, nor was the actual amount of fishing time used in analyses. CPUE in this instance was used as a relative measure of the amount of opalescent squid removed per standardized-unit-of-effort (one fishing vessel day) through time and among different geographic regions. From 1950-01 to 1953-54 and from 1969-00 to 1989-90 in Monterey, the average catch-per-landing was never greater than 10 mt, and from 1990-91 to 2006-07, CPUE was greater than 10 mt in some years (see Figure 13c). In 2002-03, even though the number of landings remained low, the average CPUE was greater than 20 mt per landing, signifying a potential increase in opalescent squid abundance during that fishing season (see Figure 13a-c).

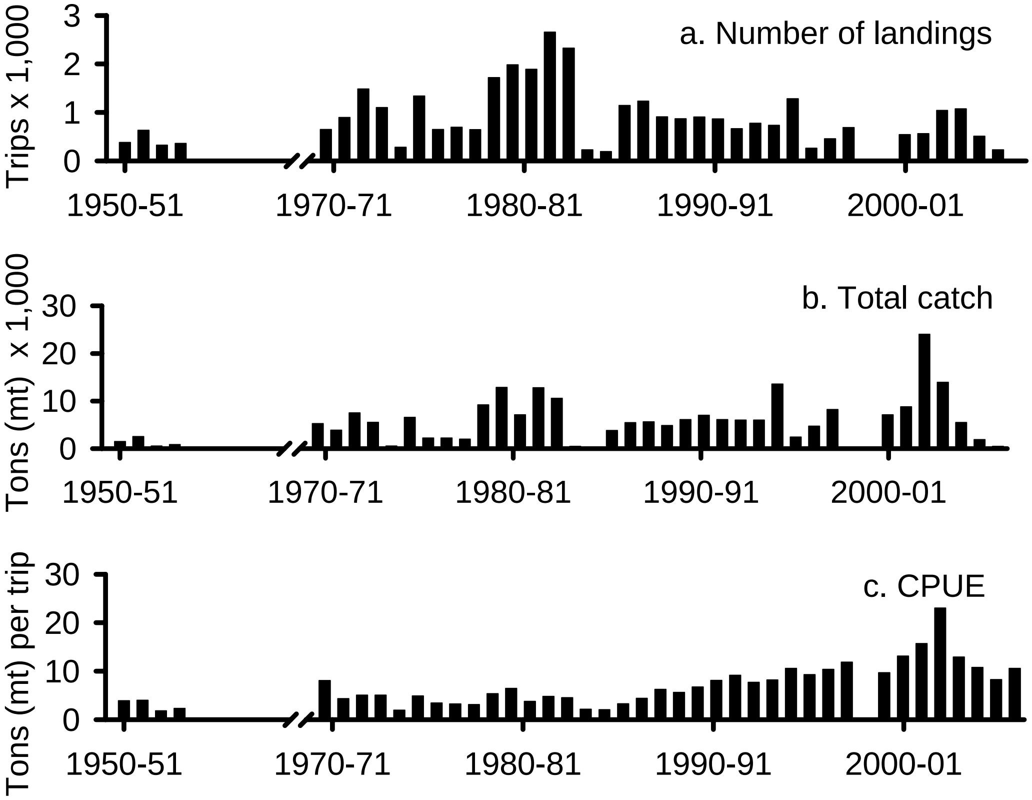

Figure 13a-c Monterey area fishery data from 1950-51 to 2006-07

(data source, *See Table 1)*

From 1998-99 to 2006-07, total catch and CPUE were considerably greater in southern California than in Monterey (Figure 14a-c). In 1999-00 there were higher landings from the northern Channel Islands than from Catalina Island and in 2005-06, the opposite trend occurred. In years when landings were relatively small in Monterey, landings were greater in the southern California sites.

In Monterey, the fishing season usually began within the month of April when mean opalescent squid sizes were relatively small (Figure 15a-b). Total catch reached a maximum in May or June and then declined through the rest of the summer as mean opalescent squid sizes increased. In southern California, the fishing season usually began in October when opalescent squid were relatively large. Total catch increased as mean DML decreased from November to March (Figure 15c-d). Through the summer months, mean opalescent squid DML declined as total catch decreased. It appears that in Monterey, the fishery captured relatively smaller opalescent squid as the season began, whereas in southern California larger opalescent squid were caught at the beginning of the fishing season (see Figure 15a-d).

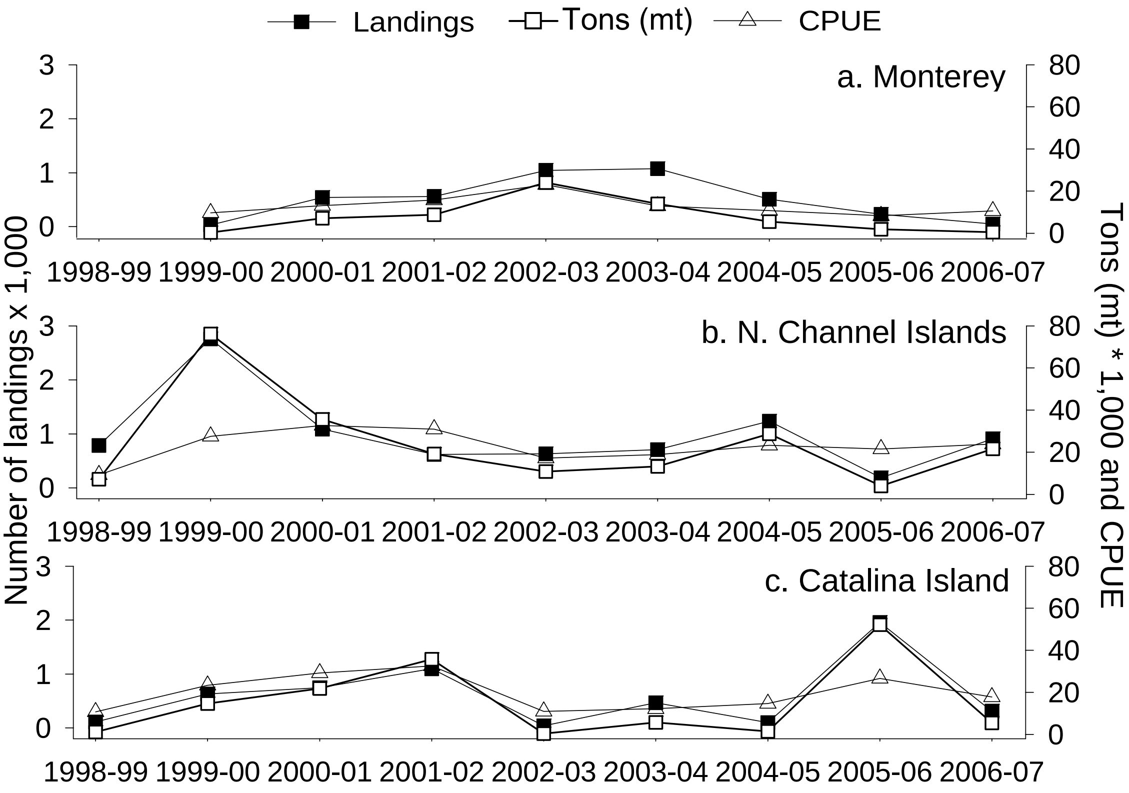

Figure 14a-c Regional fishery data from 1998-99 to 2006-07

(data source, *See Table 1)*

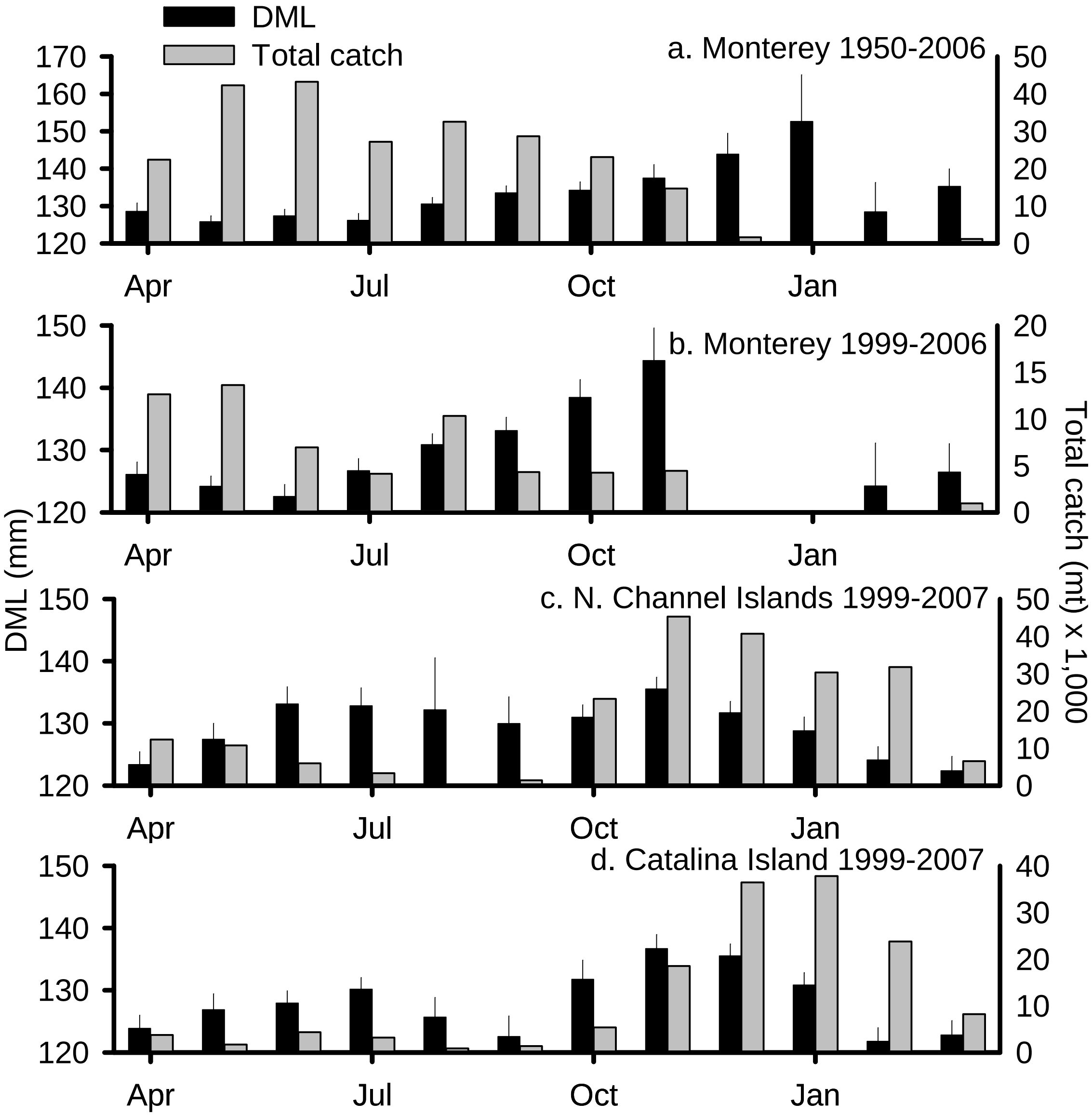

Figure 15a-d Total catch summed for each month throughout each time period and overall mean DML by month (data source *See Table 1*)

The 1976-77 regime shift caused SST to increase and upwelled nutrients to decrease along California. The monthly average SST recorded at Hopkins Marine Station near Monterey was 13.3°C (CI = 0.09) from 1947 to 2006; SST warmed 0.5°C. The seasonal pattern in SST – where SST is warm in the summer and cool in the winter – did not falter, but the SST of the summers and winters were warmer after the 1976-77 regime shift (Figure 16a-l). The strength of upwelling did not change considerably (Figure 17a-l); nutrients that would normally be upwelled were reduced due to an increase in water column stratification (McGowan et al. 2003; Kim and Miller 2007).

Environmental conditions differed between central and southern California. Mean monthly SSTs were consistently cooler near Monterey than in southern California during the summer months, whereas, SSTs were more similar during winter months (Figure 18a-b). The strongest upwelling occurred in spring and summer in both areas (Figure 18c). In Monterey, upwelled water provided a source of nutrients from bathymetric depths and in southern California, nutrients were upwelled from the continental slope (Venrick et al. 2006). Upwelling values overlapped in both areas throughout the year. During the 1998-99 La Niña, a shift to a cool regime phase was predicted, but instead of the shift being permanent, in 2002, SST became warm and upwelling relaxed. In addition, the timing of seasonal events shifted. For example, the spring transition that usually occurred in Monterey during March was offset to summer months in the 2005-06 (Peterson et al. 2006) and 2006-07 seasons (Goericke et al. 2007). Oceanographic conditions in southern California were near the long-term average during this alternative period (Bograd et al. 2000; Durazo et al. 2001).

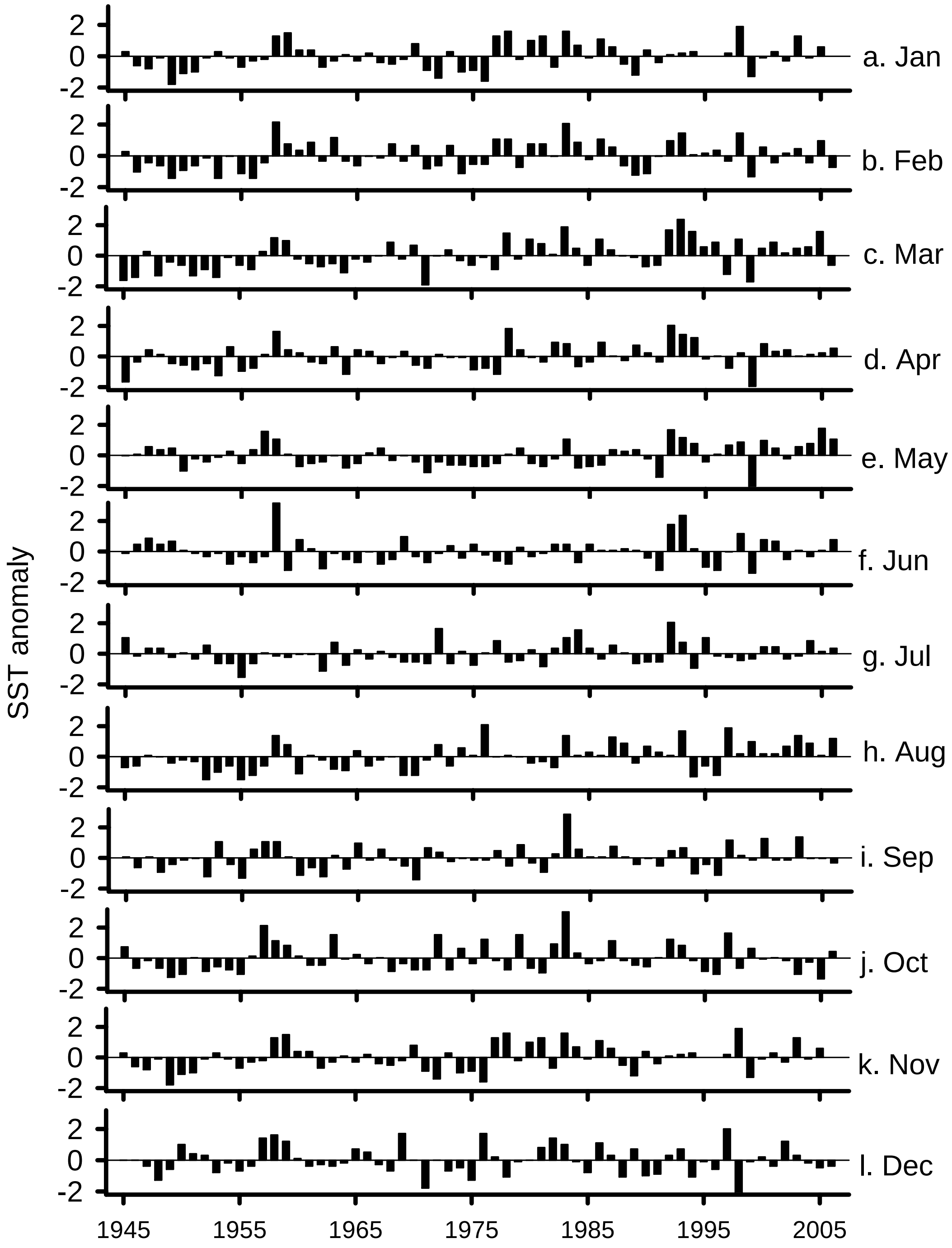

Figure 16a-l Monterey SST anomalies from the long-term annual mean from 1945 to 2006 (data source *see Table 1*)

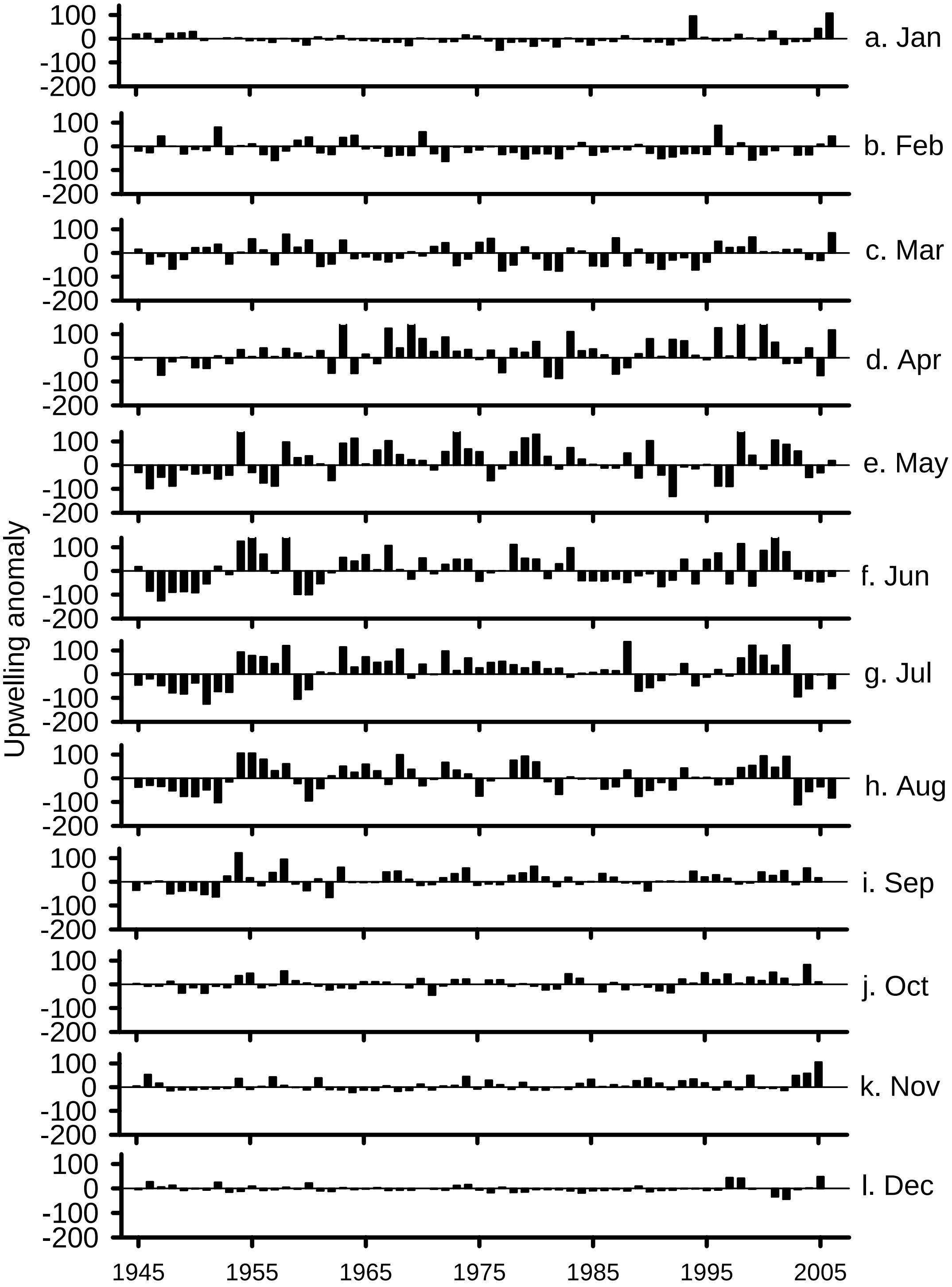

Figure 17a-l Monterey upwelling anomaly from 1945 to 2006 (data source *see Table 1*)

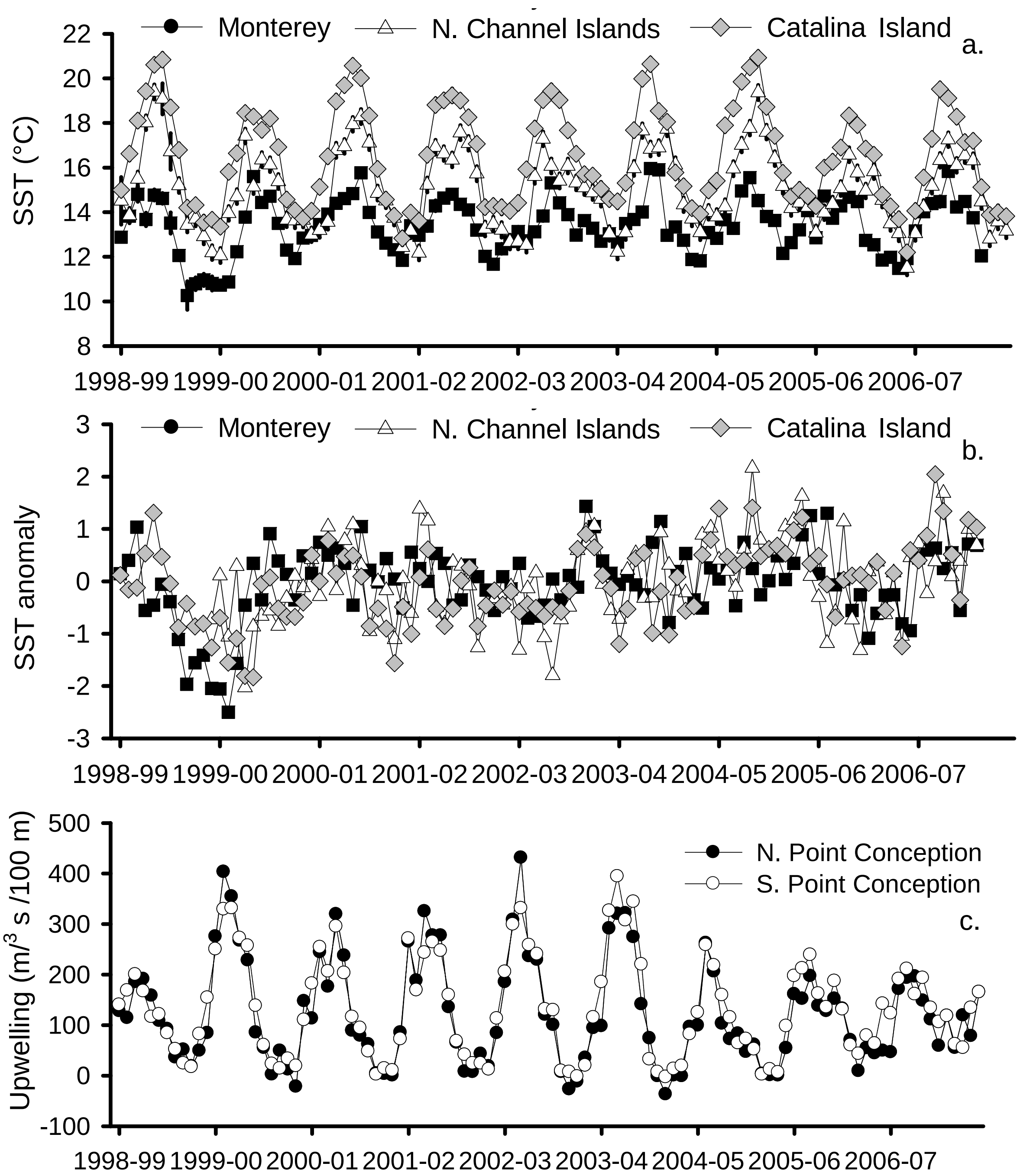

Figure 18a-c Mean SST with corresponding 95% CI, SST anomaly, and upwelling by month for 3 regions from 1998-99 to 2006-07 (data source *See Table 1*)

Causes for the decline in opalescent squid size are not well-known. For Monterey from 1948 to 2006, the PDO shifted from a cool regime to a period of warm water in 1976-77 and then to an alternative period in 1999, and there were numerous ENSO events (see Figure 4a). Opalescent squid DML was larger during the cool PDO and in years immediately following strong La Niña events, whereas warmer water led to comparatively smaller individuals (See Figure 4a). Correlations between biological characteristics and fishing pressure were not as strong as correlations between opalescent squid size and environmental variables for Monterey from 1948-49 to 2006-07. Mean DMLs for females and males were negatively correlated with landings 8 months prior to capture (Table 7a-b). CPUE 7 to 12 months before capture had a negative effect on female DML, but there were no significant correlations between male size and CPUE (see Table 7a-b). Total catch was negatively correlated with female DMLs at 8 to 12 months before capture (see Table 7a-b). A correlation with a 12-month lag indicates that the catch 1 year before opalescent squid were captured will have an effect on the size of individuals from a generation 1 year later unless opalescent squid live to 12 months.

Different results were found for the 3 geographic regions from 1999-00 to 2006-07 (Table 8a-b). There were no significant correlations between mean DMLs and the number of landings in Monterey, but instead positive correlations occurred from 7 to 9 months before capture in the northern Channel Islands for females and males. CPUE was positively correlated with DML at time of capture for males in the Monterey, but there were minor significant correlations between mean DML and CPUE for the southern California sites (see Table 8a-b).

Table 7a-b Pearson correlation coefficients for mean DML versus fishery and environmental variables by month for Monterey from 1948-49 to 2006-07

Lag	Landing	CPUE	Catch	SST	SST Anomaly	Upwelling	Upwelling Anomaly
a.	Female						
0	-0.01	-0.23	-0.08	**-0.25***	**-0.22****	**-0.42****	-0.13
1	0.01	-0.17	-0.08	-0.09	**-0.35****	**-0.34****	-0.18
2	0.01	-0.05	-0.04	-0.03	**-0.35****	-0.14	-0.19
3	0.13	-0.05	-0.01	0.09	**-0.32****	0.07	-0.20
4	0.13	-0.09	-0.04	0.09	**-0.29****	**0.24***	-0.13
5	0.18	-0.11	0.04	0.10	-0.19	**0.30****	-0.17
6	0.06	-0.32	-0.01	-0.06	-0.19	**0.30****	-0.25
7	-0.07	**-0.37***	0.10	**-0.27***	-0.23	0.16	**-0.28***
8	**-0.37***	**-0.39***	**-0.39***	**-0.38****	-0.21	-0.14	**-0.33****
9	-0.34	**-0.44***	**-0.38***	**-0.43****	-0.21	**-0.30****	-0.23
10	-0.25	**-0.38***	**-0.32***	**-0.48****	**-0.32****	**-0.39****	-0.16
11	-0.19	**-0.30**	-0.29	**-0.37*****	**-0.27***	**-0.45****	-0.11
12	-0.19	**-0.31***	-0.33*	-0.14	-0.19	**-0.45*****	-0.18
b.	Male						
0	0.08	-0.13	0.01	-0.23	**-0.32****	**-0.33****	-0.01
1	0.10	-0.06	0.01	-0.07	**-0.32****	**-0.25****	-0.10
2	0.08	0.01	0.03	0.02	**-0.33****	-0.08	-0.12
3	0.16	0.02	-0.07	0.07	**-0.31****	0.09	-0.15
4	0.15	-0.06	-0.01	0.06	**-0.31****	**0.25***	-0.06
5	0.15	-0.11	0.02	0.02	-0.23	**0.28***	-0.14
6	0.09	-0.27	0.02	-0.10	-0.22	**0.29***	-0.18
7	-0.10	-0.34	-0.06	**-0.26***	-0.21	0.17	-0.20
8	**-0.39***	-0.30	-0.34	**-0.33****	-0.15	-0.10	-0.24
9	-0.33	-0.29	-0.30	**-0.38****	-0.17	**-0.23***	-0.11
10	-0.18	-0.29	-0.25	**-0.41****	**-0.25***	**-0.31***	-0.06
11	-0.16	-0.21	-0.23	**-0.35****	**-0.26***	**-0.33****	-0.05
12	-0.09	-0.20	-0.27	-0.12	-0.17	**-0.34****	-0.05

$^{*}P<0.05$, $^{**}P<0.01$, $^{***}P<0.001$

Table 8a-b Pearson correlation coefficients for mean DML versus fishery variables by month for Monterey from 2000-01 to 2006-07 and two southern California sites from 1999-00 to 2006-07

	Monterey			N. Channel Islands			Catalina		
Lag	Landing	CPUE	Catch	Landing	CPUE	Catch	Landing	CPUE	Catch
a.	Female								
0	0.11	**0.55***	0.26	0.16	0.30	0.26	0.09	0.19	0.09
1	0.03	**0.44***	0.19	0.06	0.12	0.15	-0.08	0.07	-0.07
2	-0.06	**0.49***	-0.10	-0.02	0.20	0.12	-0.15	-0.16	-0.15
3	-0.07	0.38	0.01	-0.05	0.13	0.07	-0.21	-0.11	-0.23
4	-0.12	0.20	0.20	-0.07	0.04	-0.01	-0.32	-0.14	-0.34
5	0.26	-0.05	0.30	0.15	0.14	0.13	-0.31	-0.20	-0.30
6	0.44	-0.16	0.22	0.30	0.14	0.24	-0.18	-0.15	-0.15
7	-0.29	-0.15	-0.24	**0.44****	0.20	0.34	-0.02	0.06	0.01
8	-0.25	-0.22	-0.20	**0.48****	0.11	**0.37***	0.08	0.07	0.10
9	-0.24	-0.40	-0.14	**0.44****	0.05	0.31	0.13	0.15	0.14
10	-0.22	-0.17	-0.24	0.34	-0.01	0.22	0.22	0.14	0.19
11	-0.35	-0.04	-0.32	0.23	-0.01	0.13	0.12	0.16	0.13
12	-0.43	0.02	-0.24	0.22	-0.09	0.10	-0.01	0.07	0.04
b.	Male								
0	0.20	0.62	0.35	0.19	**0.36***	0.28	0.22	0.29	0.22
1	0.11	0.52	0.36	0.10	0.14	0.18	0.05	0.22	0.05
2	-0.01	0.52	0.20	0.05	0.20	0.19	-0.06	0.09	-0.05
3	0.01	0.43	0.01	0.09	0.18	0.20	-0.15	-0.02	-0.17
4	-0.09	0.15	0.12	0.07	0.08	0.12	-0.27	-0.08	-0.28
5	0.19	-0.12	0.29	0.24	0.17	0.22	-0.27	-0.16	-0.27
6	0.44	-0.14	0.23	**0.42***	0.16	**0.37***	-0.18	-0.14	-0.15
7	0.32	-0.22	-0.17	**0.47****	0.18	**0.38***	-0.02	0.03	0.01
8	-0.16	-0.15	-0.10	**0.37***	0.02	0.27	0.09	0.15	0.12
9	-0.11	-0.19	-0.06	0.36	-0.05	0.21	0.14	0.18	0.15
10	-0.10	-0.09	-0.11	0.32	-0.09	0.16	0.23	0.13	0.21
11	-0.21	0.14	-0.24	0.25	-0.09	0.07	0.13	0.19	0.14
12	-0.33	0.20	-0.19	0.21	-0.13	0.06	0.01	0.15	0.05

*$P<0.05$, **$P<0.01$

Environmental factors including mean SSTs and upwelling were significantly correlated with mean DMLs in Monterey from 1948-49 to 2006-07. There was a negative correlation between mean DML or mass with monthly SST at time of capture and from 7 to 11 months before opalescent squid were sampled, which should coincide with their hatch-month (Figure 19a-b). Additionally, there was a positive correlation between mean DML and mass versus upwelling approximately 4 to 6 months before capture (Figure 19c-d). Anomalies for monthly mean SST, upwelling, and opalescent squid sizes were correlated to determine if relatively stronger or weaker environmental variables would have an even greater effect on opalescent squid size. Correlations between the anomalies for monthly mean DML and SST, indicate an actual negative correlation existed that was not just an artifact of seasonality (see Table 7a-b).

Similar patterns existed for Monterey, the northern Channel Islands, and Catalina Island from 1999-00 to 2006-07 (Tables 9-12). In Monterey from 1999-00 to 2006-07, mean DML and SST were negatively correlated between 8 to 10 months before capture and positively correlated 1 to 4 months before being collected. Anomalies for monthly mean SSTs and opalescent squid DMLs were not significantly correlated. These patterns for Monterey from 1999-00 to 2006-07 do not match the results from 1948-49 to 2006-07 probably because the sample size was considerably less due to the shorter time period. In southern California, similar correlations were significant probably because the sample size was larger due to the fishery being more active throughout the fishing season. In the northern Channel Islands, monthly mean DMLs were negatively correlated with mean SSTs from 5 to 8 month for females and from 6 to 8 months for males before time of capture (see Table 9a-b). Correlations between the monthly mean anomalies for SST and DML also were significant for 2 to 4 months for females and males (see Table 9a-b). Near Catalina Island, mean DML and SST were negatively correlated for lags of 6 to 9 months for females and from 7 to 10 months for males, and correlations between the corresponding anomalies were significant (see Table 9a-b).

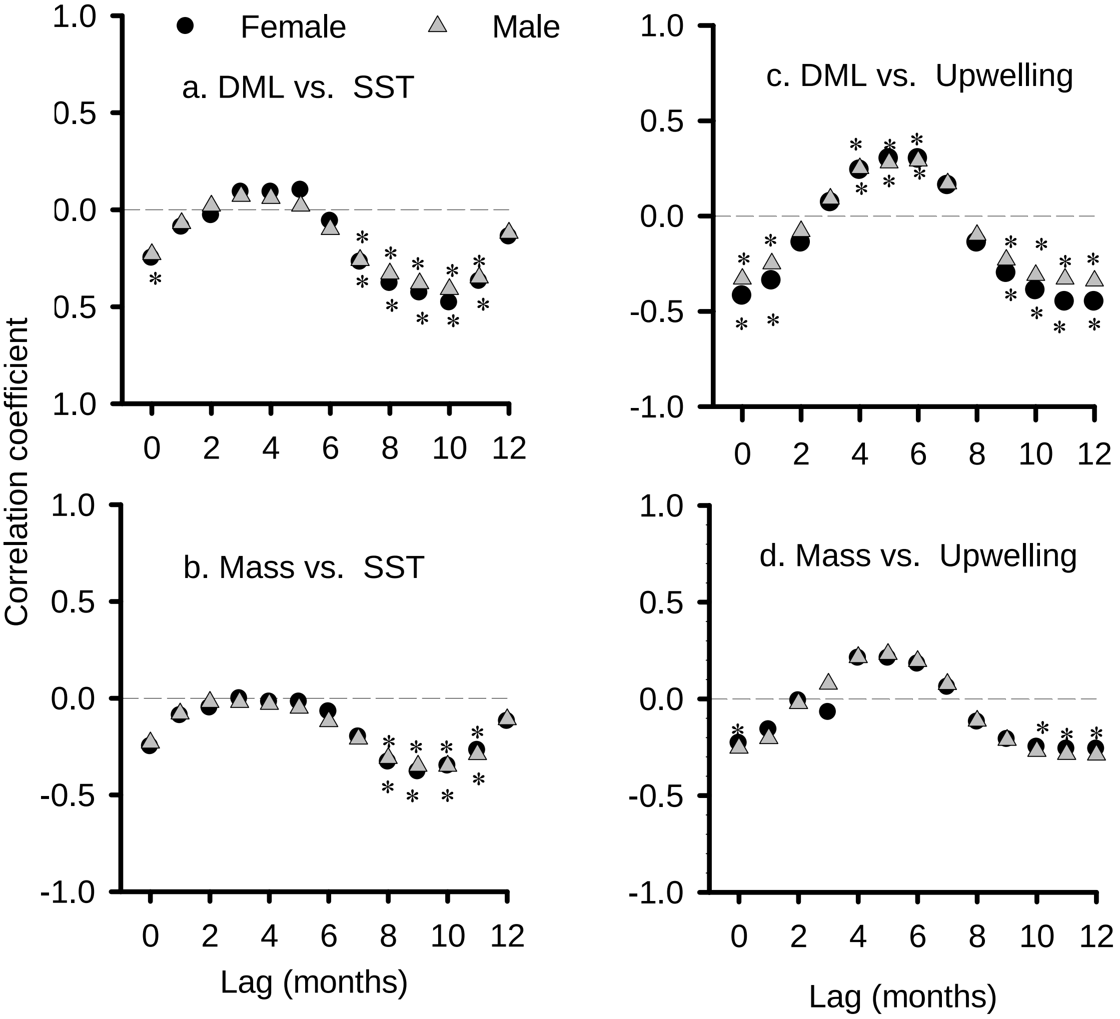

Figure 19a-d Pearson correlation for monthly mean DML and mass versus environmental variables for Monterey, 1948 to 2006; *$P<0.05$

Table 9a-b Pearson correlation coefficients for mean DML versus SST by month for Monterey from 2000-01 to 2006-07 and two southern California sites from 1999-00 to 2006-07

	DML vs. SST			DML anomaly vs. SST anomaly		
Lag	Monterey	N. Channel Islands	Catalina	Monterey	N. Channel Islands	Catalina
a.			Female			
0	0.08	**0.41****	0.26	-0.20	-0.18	-0.27
1	**0.40***	**0.34***	**0.39****	-0.11	-0.20	**-0.36***
2	**0.57****	0.14	**0.46*****	-0.06	**-0.39****	**-0.32***
3	**0.57****	-0.10	**0.35****	-0.11	**-0.49****	**-0.37***
4	**0.41***	-0.28	0.13	-0.22	**-0.43****	**-0.41****
5	0.27	**-0.39****	-0.11	-0.16	-0.20	**-0.34***
6	-0.03	**-0.54****	**-0.41****	-0.06	-0.21	**-0.51****
7	-0.28	**-0.55****	**-0.59*****	0.07	-0.23	**-0.51****
8	**-0.49****	**-0.46****	**-0.55*****	0.08	-0.31	**-0.31***
9	**-0.55****	-0.16	**-0.38*****	0.25	-0.18	-0.20
10	**-0.49****	0.16	-0.13	0.17	-0.01	-0.09
11	-0.16	**0.37***	0.07	0.06	-0.16	-0.17
12	0.19	**0.47****	0.25	-0.15	-0.02	-0.13
b.			Male			
0	0.02	0.28	0.11	-0.14	-0.12	-0.16
1	0.26	0.19	**0.32***	-0.17	-0.13	-0.27
2	0.41	-0.02	**0.45****	-0.13	**-0.43****	**-0.33***
3	**0.43***	-0.20	**0.45****	-0.19	**-0.51****	-0.31
4	0.28	-0.31	**0.28**	-0.20	**-0.46****	**-0.38****
5	0.13	-0.37	0.06	-0.23	-0.30	**-0.33***
6	-0.04	**-0.43***	-0.25	-0.08	-0.22	**-0.46*****
7	-0.15	**-0.41****	**-0.50*****	0.15	-0.25	**-0.43*****
8	-0.33	**-0.32****	**-0.57*****	0.17	-0.31	-0.26
9	-0.37	-0.07	**-0.51*****	0.28	-0.17	-0.20
10	-0.36	0.18	**-0.31***	0.17	-0.02	-0.11
11	-0.20	0.30	-0.15	-0.03	-0.01	**-0.26***
12	0.09	0.33	0.10	-0.16	0.03	-0.09

**P*<0.05, ***P*<0.01, ****P*<0.001

Table 10a-b Pearson correlation coefficients for mean DML versus upwelling by month for Monterey from 2000-01 to 2006-07 and two southern California sites from 1999-00 to 2006-07

	DML vs. upwelling			DML anomaly vs. upwelling anomaly		
Lag	Monterey	N. Channel Islands	Catalina	Monterey	N. Channel Islands	Catalina
a.			Female			
0	-0.23	0.06	-0.07	**0.49***	-0.01	0.15
1	0.10	0.30	0.17	0.38	-0.07	0.13
2	**0.49****	**0.46****	**0.40****	0.38	-0.02	0.17
3	**0.64****	**0.50****	**0.47****	0.16	0.10	0.06
4	**0.74****	**0.40****	**0.46*****	0.18	0.15	0.01
5	**0.73****	0.22	**0.36****	0.09	0.09	-0.01
6	**0.48****	0.09	0.28	-0.07	0.25	0.12
7	-0.01	-0.14	0.09	-0.12	0.26	0.14
8	-0.30	**-0.36***	-0.20	0.01	0.29	0.15
9	**-0.40****	**-0.41****	**-0.42*****	0.31	0.22	0.20
10	**-0.46****	**-0.35***	**-0.45*****	0.35	0.05	0.25
11	**-0.44****	-0.11	-0.28	**0.46***	0.05	0.35
12	-0.33	0.16	-0.05	0.36	0.15	0.34
b.			Male			
0	-0.11	0.07	-0.26	**0.48***	-0.08	0.10
1	0.16	0.19	-0.03	**0.45***	-0.15	0.09
2	0.43	0.32	0.22	**0.43***	0.01	0.07
3	**0.55***	0.33	**0.38****	0.25	0.12	-0.01
4	**0.60****	0.23	**0.48*****	0.21	0.01	-0.02
5	**0.60****	0.18	**0.47*****	0.04	0.20	-0.01
6	**0.40***	0.12	**0.45*****	-0.04	0.30	0.18
7	-0.01	-0.04	0.24	-0.14	0.32	0.14
8	-0.22	-0.16	-0.09	0.03	0.35	0.13
9	-0.28	-0.23	**-0.38***	0.16	0.24	0.12
10	-0.30	-0.19	**-0.50*****	0.34	0.11	0.12
11	-0.25	-0.01	**-0.41****	**0.51***	0.07	0.25
12	-0.19	0.18	-0.26	0.39	0.12	0.19

*$P<0.05$, **$P<0.01$, ***$P<0.001$

Table 11a-b Pearson correlation coefficients for mean mass versus SST by month for Monterey from 2000-01 to 2006-07 and two southern California sites from 1999-00 to 2006-07

	Mass vs. SST			Mass anomaly vs. SST anomaly		
Lag	Monterey	N. Channel Islands	Catalina	Monterey	N. Channel Islands	Catalina
a.			Female			
0	0.11	__0.43**__	__0.39**__	-0.16	-0.17	-0.23
1	0.39	0.27	__0.45***__	0.05	-0.30	-0.30
2	__0.47*__	-0.05	__0.39**__	0.05	__-0.47**__	-0.30
3	__0.46*__	-0.15	0.20	0.01	__-0.43**__	-0.33
4	0.37	__-0.35*__	-0.09	-0.02	__-0.39**__	__-0.45**__
5	0.28	__-0.51**__	-0.33	-0.02	__-0.32**__	__-0.37**__
6	0.02	__-0.59**__	__-0.56*__	-0.08	-0.26	__-0.45***__
7	-0.15	__-0.50**__	__-0.64***__	0.27	-0.19	__-0.39**__
8	-0.34	__-0.32*__	__-0.51***__	0.20	-0.17	-0.19
9	-0.38	-0.05	__-0.24***__	0.33	-0.13	-0.11
10	-0.34	0.18	0.04	0.22	-0.15	-0.06
11	-0.08	__0.38*__	0.27	0.02	-0.16	-0.05
12	0.11	__0.50**__	0.41	-0.28	0.04	-0.03
b.			Male			
0	0.02	0.27	0.18	-0.12	-0.13	-0.14
1	0.25	0.16	__0.35*__	-0.15	-0.23	-0.25
2	0.41	-0.05	__0.42**__	-0.09	__-0.49**__	-0.32
3	__0.44*__	-0.19	__0.37**__	-0.12	__-0.48**__	-0.29
4	0.28	-0.32	0.15	-0.13	__-0.45**__	__-0.43**__
5	0.12	__-0.42**__	-0.07	-0.21	__-0.40**__	__-0.35*__
6	-0.03	__-0.46**__	__-0.35*__	-0.02	-0.28	__-0.42**__
7	-0.12	__-0.42**__	__-0.53**__	0.21	-0.27	__-0.34*__
8	-0.28	-0.29	__-0.55***__	0.24	-0.24	-0.19
9	-0.34	-0.03	__-0.44***__	0.32	-0.12	-0.14
10	-0.33	0.16	-0.22	0.19	-0.06	-0.07
11	-0.19	0.28	-0.03	-0.03	-0.04	-0.18
12	0.05	0.32	-0.19	-0.20	-0.03	-0.04

*P<0.05, **P<0.01, ***P<0.001

Table 12a-b Pearson correlation coefficients for mean mass versus upwelling by month for Monterey from 2000-01 to 2006-07 and two southern California sites from 1999-00 to 2006-07

	Weight vs. upwelling			Weight anomaly vs. upwelling anomaly		
Lag	Monterey	N. Channel Islands	Catalina	Monterey	N. Channel Islands	Catalina
a.			Female			
0	-0.07	0.16	0.10	**0.48****	0.02	0.09
1	0.19	**0.39***	**0.32***	0.39	0.01	0.04
2	**0.45***	**0.52****	**0.52*****	0.31	0.04	0.12
3	**0.53****	**0.47****	**0.49*****	0.10	0.04	-0.06
4	**0.61*****	0.35	**0.41****	0.19	0.03	-0.05
5	**0.49****	0.18	0.25	-0.07	0.13	0.02
6	0.28	0.04	0.09	-0.14	0.30	0.12
7	-0.11	-0.21	-0.11	-0.23	0.29	0.17
8	-0.27	**-0.36***	**-0.37****	0.03	0.33	0.13
9	-0.27	**-0.38***	**-0.52*****	0.38	0.26	0.14
10	-0.31	-0.25	**-0.42****	0.35	0.17	0.20
11	-0.26	0.01	-0.16	**0.48****	0.12	0.26
12	-0.14	0.24	0.14	**0.42***	0.08	0.22
b.			Male			
0	-0.07	0.10	-0.16	**0.50****	-0.02	0.19
1	0.20	0.23	0.06	**0.51****	-0.07	0.04
2	**0.43***	**0.34***	0.31*	**0.46***	0.06	0.09
3	**0.54*****	0.32	**0.41****	0.26	0.10	-0.05
4	**0.58*****	0.22	**0.48*****	0.22	0.06	-0.02
5	**0.56***	0.19	**0.43****	-0.01	0.20	0.03
6	0.37	0.10	**0.37***	-0.06	0.29	0.21
7	-0.04	-0.04	0.13	-0.18	0.32	0.16
8	-0.23	-0.16	-0.17	0.02	0.33	0.14
9	-0.28	-0.23	**-0.42***	0.25	0.23	0.13
10	-0.28	-0.16	**-0.49*****	0.34	0.15	0.11
11	-0.23	-0.01	**-0.34***	**0.50****	0.08	0.24
12	-0.15	0.17	-0.17	**0.41***	0.10	0.14

*$P<0.05$, **$P<0.01$, ***$P<0.001$

Correlations between monthly mean upwelling and opalescent squid DMLs were significantly positive in Monterey, the northern Channel Islands, and Catalina Island for females for lags of 2 to 6 months (see Table 10a). For males, however, the positive correlation between mean DMLs and upwelling was only significant in Monterey and Catalina Island (see Table 10b). Anomalies for DML and upwelling were significant in Monterey from 0 to 2 months; however, there were no significant correlations between anomalies for upwelling and DMLs in southern California (see Table 10b). Similar to DML, mean body mass was negatively correlated with SST and positively correlated with upwelling (see Tables 11-12). When SST was warm during potential hatch-months of opalescent squid, then adult body mass was relatively smaller than if SST had been cool during the early life stages.

Two measures of female fecundity for spawning adults were tested for correlations with fishery landings projected from 1 to 12 months into the future around Catalina Island from 1999-00 to 2002-03. The first measure of fecundity that was tested was the mean fraction of released potential fecundity for each month of adult female opalescent squid. This measure was not significantly correlated with fishery landings that occurred 1 to 12 months later. The second measure of female fecundity, the standing stock of oocytes, however, did have a positive correlation with fishery catch 4 to 7 months after samples were taken (Table 13). These results indicate that oocyte standing stock may be used as a proxy to predict fishery landings projected up to 7 months into the future.

Table 13 Pearson correlation coefficients for a measure of fecundity (standing stock of oocytes) versus total catch for Catalina Island from 1999-00 to 2002-03

Projection (month)	Oocytes vs. Catch
0	-0.24
1	-0.27
2	-0.30
3	-0.05
4	**0.42*****
5	**0.61*****
6	**0.73*****
7	**0.58****
8	0.23
9	-0.12
10	-0.25
11	-0.26
12	-0.09

**P*<0.01, ****P*<0.001

DISCUSSION

Having access to original, historic, biological data to statistically evaluate long-term trends is uncommon. Although the opalescent squid fishery began in the mid 1800s and the biological samples for this study were not collected until the 1940s, sampling did begin just as fishing pressure was substantially increasing in California. The results of this study offer insight into long-term trends in the biology of the fished population of California's opalescent squid.

Biological characteristics of opalescent squid tend to oscillate over time; for instance a significant decrease in opalescent squid body size and an increase in the proportion of males were evident in this study. Although, monthly mean opalescent squid DMLs may fluctuate in excess of 20 mm within a fishing season, recorded sizes have yet to reach the maximum average sizes of the past. Given that opalescent squid are a valuable commodity for California's economy and that numerous marine organisms depend on opalescent squid as a food source, it is important to identify potential causes for the decline in opalescent squid body size from 1948 to 2006 and the increase in the proportion of males captured in the fishery from 1999 to 2006.

The presence of smaller opalescent squid in fishery landings may be from individuals recruiting to the fishery at a younger age, indicating that individuals are maturing earlier. Many exploited species have undergone such changes in age (Trippel 1995). One cause for an earlier age-at-maturity is the compensatory response where fishing reduces population density, thereby fostering a less competitive environment for food resources and allowing more food intake and faster growth. The explanation that an increase in food availability may have increased growth rates in the opalescent squid population is somewhat weak because there has been a decline in food availability over the long-term (Roemmich and McGowan 1995). The ages of harvested opalescent squid were not available for this analysis. Past ageing studies indicate, however, that the longevity of opalescent squid may have decreased from the 1940s to the 2000s (Fields 1965; Spratt 1979; Butler et al. 1999; Jackson and Domeier 2003; Reiss et al. 2004).

Another factor that may have caused the decline in opalescent squid size in Monterey could be a change in how individuals were sampled or captured by the fishery. Since the inception of the opalescent squid fishery, a change in gear types made fishing more efficient, fishermen's knowledge about the behavior of opalescent squid improved, technology for finding aggregations became more sophisticated, and regulations changed. There was a shift from lampara to purse or drum seine nets in Monterey in the late 1980s when the ban on purse seine nets was lifted. Gear types, including lampara, purse, and drum seine nets, did not have the same mesh size and may have selectively captured certain sizes of opalescent squid. Even though on average there was a larger mesh size used from the 1940s to late 1980s than from the early 1990s to the mid 2000s, this still does not explain why the maximum size in opalescent squid declined. In fact, relatively smaller individuals (both DML and mass) were captured in the later study periods although the mesh size was larger. Since opalescent squid from the largest sizes were missing, the decline in monthly mean DMLs and masses cannot be solely an effect of mesh size or gear type. In addition, the use of purse seine nets led to a decrease in actual fishing time. Identifying opalescent squid aggregations became easier as improvements in sonar technology allowed fishermen to discriminate between different schooling species. With all of these improvements, fishermen have harvested a greater amount of opalescent squid in the more recent years, thus allowing more opportunities to sample – yet the maximum sizes were still missing from the samples.

A fishing regulation that could have affected opalescent squid size was a ban on using lights as an attractant from 1959 to 1989 in Monterey (CDFG 2005). Considering that in most fishing seasons opalescent squid DML was above the long-term mean from the 1940s to the 1970s and that the ban on lights began in the middle of that time period, lights probably did not have a significant effect on opalescent squid size.

From 1950 to 2007, total catch in Monterey increased starting in the mid 1980s. Some may argue that with larger catch volumes, a greater number of relatively smaller opalescent squid have been sampled, thereby causing the mean size to decline. This could be the case for samples taken in 2000, but RS for Excel was used when the sampling sizes were greatly unequal, thereby reducing the bias of sample size and unequal variances. In addition, with more individuals being sampled from the environment by the fishery, there should have also been a greater likelihood that the largest individuals would be captured, but instead they were non-existent in samples taken from the 1980s to the 2000s.

The fishing fleet may have been intercepting opalescent squid before they actually reached the spawning grounds. This would have caused mean DMLs of sampled opalescent squid to be smaller. The fishery occurs mainly during the night; in recent years, however, there has been an increase in daytime fishing (unpublished DFG logbook data). The data on maturity collected from the 1980s to the 1990s was fairly constant through time. Even though a direct measure of maturity was not taken for the samples from the 2000s, it was noted whether the sex was discernable. The percentage of unknown sex in opalescent squid samples did not change, indicating that the fishery did not intercept opalescent squid earlier in their life history or at smaller sizes.

Size-selectivity by the fishery may have played a role in the decline in opalescent squid size. The fishing fleet captures only the largest opalescent squid, thereby leaving the smaller individuals to reproduce and spawn offspring that may grow to a size that is similar to their parents. The fishing industry usually targets the largest individuals because buyers often will not accept relatively small opalescent squid. If the fishing industry knows that spawning opalescent squid are too small, then they will not put forth the effort to catch them, thereby leaving the smaller opalescent squid to spawn. The offspring of the smaller opalescent squid may live to spawn individuals that may grow to a size that is similar to their parents. This form of size-selective mortality leads to a population that spawns smaller larvae through time (Conover and Munch 2002; Melville-Smith and de Lestang 2006). Fishermen usually target the largest opalescent squid, thus leaving the smaller individuals to reproduce, therefore the likelihood of size-selectivity shaping the biological aspects of the opalescent squid population is also a potential factor leading to a change in size through time. This effect could compound the gradual decrease in food availability caused by the warm, nutrient-poor cycle of the PDO and the increased frequency of El Niños. The cumulative affect of fishing may interfere with the natural ability of opalescent squid to counteract the effects of a warmer, low-nutrient environment (Jackson et al. 2001).

Among the different environmental and fishery aspects that were tested as potential factors causing the decrease in mean opalescent squid DML, SST had the greatest correlation with body size, which supports the findings of other studies (Jackson and Domeier 2003; Reiss et al. 2004). When SST was warm, relative to long-term averages, mean DML was relatively smaller from 7 to 11 months later; and when SST was cold, mean DML was larger within the same time lag. Interestingly, the correlation was significant up to 11 months before the time of capture, which could potentially mean that some individuals were as old as 11 months, although the most recent ageing studies have estimated opalescent squid to live to a maximum of 10 months (Butler et al. 2001). According to the results of this study, not only was DML smaller with a warmer hatch-month, but DML was even smaller during months that were anomalously warmer.

Opalescent squid body size was not just fluctuating with SST as a coincidence – either SST or something related to SST, like food supply, caused some of the variability in opalescent squid size. Opalescent squid that were estimated to hatch in cool months of early spring grew even larger if SSTs were anomalously cooler. When SST was warmer than usual, DML was relatively smaller. In addition to the short-term effects of SST on opalescent squid size, a longer-term effect also was taking place. As SST increased decadally from the 1940s to the 2000s, mean opalescent squid DML and mass decreased.

The most probable causes for the observed decline in opalescent squid size were the limiting nature of SST and food supply during the earlier life stages of opalescent squid. The California Current was less productive and warmer from 1977 to 2007 than it was from 1948 to 1975. In the California Current system, SST can be inversely related to nutrients and plankton (Roemmich and McGowan 1995). When SST increases, zooplankton (one of the main food items of opalescent squid) decreases. Zooplankton and pelagic finfish, the main prey items of opalescent squid (Fields 1965; Cailliet et al. 1979; Karpov and Cailliet 1979; CDFG 2005), have decreased since the 1950s (Roemmich and McGowan 1995; Chavez et al. 2003). Not only has the SST during the past 60 years increased, but food availability for opalescent squid also has decreased.

Upwelling and opalescent squid DML were positively correlated from 2 to 6 months and negatively correlated from 8 to 11 months, or at the beginning of the lifespan of opalescent squid. A negative correlation for upwelling during the hatch-month may correspond more to the movement of water and passive larvae transport from nursing grounds rather than with nutrients (Zeidberg and Hamner 2002). Upwelling and opalescent squid DML were positively correlated during their growth stage (2 to 6 months), which corresponds to the time when they would be actively feeding on zooplankton. Upwelling would bring nutrients to the surface, causing a bloom in phytoplankton and zooplankton, thereby increasing the food source of juvenile opalescent squid. The absence of significant correlations between the anomalies for upwelling and body size may signify that anomalously high upwelling within a particular season is unlikely to correspond to larger opalescent squid DMLs.

Sampling concurrently within different geographic regions began in 1998 during an El Niño when there happened to be a considerable decline in landings. The lack of opalescent squid and samples continued in Monterey through the 1999-00 season; however, CDFG samplers obtained samples from southern California during the 1999-00 La Niña. Opalescent squid DMLs and masses were significantly larger than in other years in southern California during the first season of sampling; probably due to the increase in nutrients and drop in SST from the 1999-00 La Niña. There was a considerable reduction in body size in 2004-05 in Monterey, most likely due to a decrease in food availability because there was a delay in the onset of upwelling, which was associated with weaker winds (Goericke et al. 2005). In 2005-06, upwelling was again reduced in Monterey, causing the size of opalescent squid to decline even further, whereas mean DMLs and masses increased in both of the southern California sites as the SST was in a cool state (Peterson et al. 2006).

Although the primary spawning periods in Monterey and southern California occurred at different times, mean DMLs and masses fluctuated on a monthly basis in the same pattern. Size was usually at a minimum in early spring and at a maximum in late fall and early winter. Ageing studies conducted in southern California during 1998 (Butler et al. 1999) and from July 1998 to March 2000 (Jackson and Domeier 2003) indicated the oldest opalescent squid were from 225 to 257 days (7.5 to 8.5 months), and they matured as early as 129 to 163 days (4.3 to 5.4 months). Based on opalescent squid being between 6 to 10 months old (Butler et al. 2001), the relatively largest individuals captured in November, December, and January would have been born from February to July during relatively cool to medium SSTs and during periods of increased food supply due to upwelling. Relatively smaller opalescent squid caught in March, April, and May would have been hatched from July to November during a nutrient low period with months that were warm due to summer heat.

As shown in the correlations between opalescent squid DML and mass and environmental variables, SST explained up to 60% of the variation in size during potential hatch-months and upwelling was related more to the juvenile period. The lack of a significant correlation in Monterey from 2000 to 2006 between opalescent squid body size and environmental factors was probably due to a smaller sample size north of Point Conception versus southern California. Due in part to a relatively short life span and low fat content, when opalescent squid consume nutrients, the energy is used for growth instead of being stored for later use (O'Dor and Webber 1986). Growth was influenced primarily by SST and food availability due to the rapid response opalescent squid have to fluctuations in these factors (Jackson and Domeier 2003; Reiss et al. 2004). Interestingly, although SST was consistently cooler in Monterey than southern California, opalescent squid size overlapped for each of the locations, even though opalescent squid in Monterey should be larger due to the cooler SSTs. This signifies that SST explains just a portion of the variation in size and that other variables like age, food supply, and fishing pressure should be considered.

In Monterey from 1948 to 2006, the proportion of males incrementally increased from the beginning of the fishing season in April to the end of the year, and then the number of females increased at the end of the fishing season. Patterns in monthly sex ratios indicated that one sex may have completed their spawning stage and died of natural causes before being caught by the fishery (Starr and McCrae 1984, 1985). In other species of *Loligo*, males recruit to the fishery before females (Boyle and Pierce 1994), which may cause the number of males present at the spawning grounds to increase if the presence of cohorts overlaps considerably.

There appeared to be an increase in the proportion of males in Monterey during the study. Whether this was due to a decline in the number of females or an increase in the number of males could not be determined due to the absence of an actual biomass estimate for this species. Past studies have identified the presence of smaller, lone males on the spawning grounds (Hanlon et al. 2004; Zeidberg 2008). These “sneaker” males insert their spermatophores into the mantle cavity of females mating with larger males. A decrease in opalescent squid size may be associated with an increase in the proportion of males being captured by the fishery and with the paternal effect of smaller males.

Additionally, changes in fishing methods may have also caused a shift in sampled sex ratios. Within the past few years, daytime fishing has increased, and perhaps those schools were dominated by a particular sex. Another possibility is that catch was dominated by males in a year when abundance was low; for instance in the 2004-05 and 2005-06 fishing seasons, catch was unusually small and sex ratios were dominated by males. In addition, lights may affect sex ratios if one sex is more phototropic (Leos 1998). A decline in the number of females present in the ecosystem would be of great concern because each cohort is dependent on the fecundity of females from past months.

Potential fecundity for females was directly related to DML (Macewicz et al. 2004). In Monterey, assuming that the relationship between DML and fecundity has not changed, there was an SST induced decrease in potential fecundity associated with the decline in body size from 1948 to 2006. Even if this may be the case, in some of the more recent years, opalescent squid landings greatly surpassed those from the past, which occurred because of an increase in food supply due to the presence of a La Niña and to greater effort on the part of the fishery.

In 2005-06, potential fecundity for opalescent squid in Monterey declined to an all time low as did the fishery for that season and the following 2006-07 season. The decline in female fecundity and landings can be attributed to the relatively warmer SST in Monterey and the delay and weakening in upwelling from 2004-05 to 2006-07. In southern California from 1999-00 to 2006-07, potential fecundity was relatively lower in

2004-05, but this rebounded in 2005-06 to values similar to previous seasons. Landings did not closely match the decline in DML or potential fecundity in southern California as was seen in Monterey. Although the Monterey fishery could extend from the Farallon Islands to Pt. Conception, it was mostly concentrated near Monterey. The southern California fishery covered a much greater area with fishing activity occurring along the coast from Pt. Conception to the Mexican border and around the offshore islands. A greater area of spawning grounds and a larger number of active fishing vessels in the fleet could explain why landings persisted through periods of lower female fecundity in southern California.

Identifying potential causes for long-term changes in opalescent squid size is imperative for effective fisheries management. The current management strategy for sustainable harvest in the opalescent squid fishery involves monitoring the amount of eggs released by females. In other words, one way for the fishery to be replenished is to ensure that enough females have laid enough eggs before being caught by the fishery. According to the current assessment of egg escapement by CDFG and NMFS, enough eggs (at least 30% of potential fecundity) are being released. However if size, which is directly related to fecundity and has been in an overall decline for at least the past 60 years, continues to decrease, there should be concern for the future health of the fishery.

One of the primary objectives of the MSFMP is to ensure the sustainable harvest of the species. According to statewide landings for the past decade, the fishery has done well – the resource appears to support the abundance the fishery extracts. For most species, CPUE is not considered a reliable index for abundance. For the opalescent squid fishery, however, fishermen only expend the effort to fish when opalescent squid aggregate in abundance. Therefore, CPUE does serve as an index of the available abundance of opalescent squid on well-known spawning grounds. CPUE in the opalescent squid fishery has in general increased thus signifying a supposed increase in relative abundance on the spawning grounds and perhaps an increase in the area fished. The resource may not be able to sustain such levels of fishing pressure especially when coupled with a decline in food availability, which may be revealed by a decline in opalescent squid size and the proportion of females captured in the fishery.

To ensure sustainable long-term conservation of the resource, current management for the opalescent squid fishery includes a host of measures that pertain to catch limits, gear restrictions, and closures. The seasonal catch limit, which was set at 107,047 mt in 2005 to prevent the fishery from over-expanding, was based on a multi-year average catch of previous seasons. To provide opalescent squid with a period of uninterrupted spawning, a weekend closure was enacted in 1984 for Monterey and then extended to southern California in 2000. Opalescent squid captured immediately following the weekend fishing closure tended to have spawned more than those caught later in the week (Leos 1998). Due to an increase in fishing pressure and the number of vessels participating in the fishery, a restricted access program was established in time for the 2005-06 fishing season. Gear restrictions pertain primarily to reducing any disturbance of lights on the local communities and wildlife, not on opalescent squid communities. In the past, however, lighting was restricted in Monterey from 1959-60 to 1987-88. Since then, lighting has been restricted to 30,000 watts.

In 1996-97, 1999-00, and 2000-01 landings surpassed the current catch limit, however, the majority of the catch came from south of Pt. Conception. Since 2002, statewide catch has not exceeded 74,000 mt, and within the past 3 fishing seasons, landings have been extremely low in Monterey. As shown by work done by Reiss et al. (2004), opalescent squid abundance naturally declines and then increases through time; however, it remains to be determined if in Monterey, where the habitat for spawning is concentrated in a relatively confined area, opalescent squid are no longer found in abundance because prolonged exposure to artificial illumination is having a negative effect, thereby causing a reduction in landings. The natural diel migration of opalescent squid allows them to feed in the shallows at night in the safety of darkness from visual predators; during the day, they remain at depth. When opalescent squid are on the spawning grounds and are targeted by fishing vessels, they are attracted to lights, or are phototropic.

Opalescent squid paralarvae hatch primarily during the night (Fields 1965; Vidal et al. 2002). Similar among squid species, recently hatched young are attracted to light and will actively swim towards any light source (Rugh 1950; Recksiek and Kashiwada 1979). Opalescent squid paralarvae, however, will not hatch when there is constant illumination (Vidal et al. 2002). A postponement in hatching due to the presence of lights would cause embryos to use nutrient resources from yolk globules that would otherwise serve as their food source during the first few days of their paralarval stage. In addition, if opalescent squid paralarvae hatch during the night and are then immediately exposed to artificial light they will be more prone to mortality as they swim towards the surface where nighttime predators are actively feeding. The effect lights have on opalescent squid paralarvae mortality should be further investigated to determine potential consequences for the adult population. In confined fishing areas, such as Monterey, restricting the use of lights for a pre-determined period or adding an additional weekday closure during the fishing season may be an alternative management option to establishing a full seasonal closure.

We have observed that the abundance of opalescent squid declines and size decreases in the event of anomalously warm water with the opposite occurring during cool periods. To offset any potential compounding impacts the opalescent squid fishery may have during nutrient-limited periods, a climate-based annual catch limitation might be used. If an El Niño event is forecasted for the central and southern California coast, then the capacity of a seasonal catch limit could be set in accordance to the predicted strength of the environmental anomaly (Agnew et al. 2005). Catch limits could be set based on strong, weak, or moderate El Niño events. This could protect the opalescent squid that are available and also reserve those opalescent squid for other species, such as marine mammals (Lowry and Carretta 1999), birds, and finfish, that depend on opalescent squid as a food source (Morejohn et al. 1978; Recksiek and Frey 1978). During cool periods, the HG could be increased to account for an increase in abundance and to provide an opportunity for the fishery participants to benefit from the improved conditions.

The central and southern California fisheries, however, do not respond to El Niño events in the same capacity. For instance, following the 1982-83 El Niño, which began in August 1982 and ended in June 1983, opalescent squid landings in southern California were significantly less than landings in Monterey for the 1982-83 fishing season. In the following two fishing seasons, 1983-84 and 1984-85, landings decreased in Monterey and continued to be reduced in southern California. During the 1997-98 El Niño, which began in April 1997 and ended in April 1998, landings first dropped in southern California as was seen in the 1982-83 El Niño. Then in 1998-99 and 1999-00, landings rose dramatically in southern California, but fell below 500 mt in Monterey. Therefore, a climate based seasonal catch limit could be assigned separately to fishing areas north and south of Pt. Conception. Because southern California usually experiences the effects of an El Niño first, the climate-based catch limit for their fishing season (October to March) could be set accordingly. In Monterey, the climate-based catch limit could be set for March to September for two seasons following the El Niño. If future studies indicate environmental factors are not the primary causal factor for changes in the biological aspects of opalescent squid, then management measures could be re-evaluated (Agnew et al. 1998).

Aside from the difference in landings in the central and southern fisheries that occurs because of El Niño events, the fishery could be managed according to region due to the noticeable difference in catch. According to the results of this study, opalescent squid from the two regions were not different from one another. We can see this in average monthly DML and mass. If patterns were to diverge in the future (as seen in sex ratios), then managing the two areas as separate regions could be considered. The seasonal catch limit of 107,047 mt could be modified to match an amount that represents the landings of the most recent past few years for each area, not statewide.

A management option that perhaps could be pursued in the near future would be to have a seasonal closure to protect the largest size classes of opalescent squid, thereby allowing the largest females to spawn without interruption within a 1 or 2 month period regardless of changing environmental conditions (Dawe and Beck 1997). In southern California, the seasonal closure could be set for November and/ or December, when opalescent squid are at their largest. In Monterey, the seasonal closure could be in August and/ or September when opalescent squid are being captured and relatively larger than earlier in the fishing season. These seasonal closures could protect the largest size class of opalescent squid, thereby allowing a greater proportion of spawning to occur, thus ensuring a more sustainable resource.

SUMMARY

Body size, sex ratios, and fecundity of opalescent squid captured in California's most valuable fishery were examined for spatial and temporal patterns and changes. Biological samples were collected in Monterey from 1948 to 2006 and from the northern Channel Islands and Catalina Island from 1999 to 2007. There was a significant decline in opalescent squid DML and mass in Monterey from 1948 to 2006. Monthly opalescent squid body size was similar among all three areas. Due to the fishing season occurring at different times of the year within each fishing region, the Monterey fishery captured larger individuals as the fishing season progressed from April to August, whereas the southern California fishery captured the largest opalescent squid in the beginning of the season in October.

According to past studies, opalescent squid live from 4 months to 4 years, although most recent ageing studies indicate they have an average lifespan of 6 months. The SST of their hatch-month can determine their ultimate size. For this study, there was a significant correlation between potential hatch-month SST and mean DML and mass that signified opalescent squid will be larger at catch when they are born in cooler water and grow through months with an abundant food source. This holds true for Monterey from 1948 to 2006 and for southern California from 1999 to 2007. Significant negative correlations between the anomalies for SST and body size for potential hatch-months indicated that if a winter was anomalously cooler, then opalescent squid DMLs would be even larger. Upwelling and body size were significantly correlated during the juvenile stage; stronger upwelling in the season would lead to larger individuals a few months later. The anomalies were not significantly correlated, which signifies that a relative increase in upwelling within a year will not lead to larger opalescent squid. In addition, when CPUE was high on adults, then the fishery probably removed a greater portion of larger individuals before they had a chance to spawn, thereby leaving smaller individuals to spawn and generate smaller offspring in the following fishing season. The proportion of males captured in the fishery has increased within the past 7 years in Monterey. The potential decline in the number of females present in the fishery and a decrease in DML are of significant concern for the sustainability of the opalescent squid population because females are producing fewer eggs.

REFERENCES

Agnew DJ, Baranowski R, Beddington JR, des Clers S, Nolan CP. 1998. Approaches to assessing stocks of *Loligo gahi* around the Falkland Islands. Fisheries Research 35:155-69.

Agnew DJ, Hill SL, Beddington JR, Purchase LV, Wakeford RC. 2005. Sustainability and management of southwest Atlantic squid fisheries. Bulletin of Marine Science 76(2):579-93.

Anderson FE. 2000. Phylogenetic relationships among loliginid squid (Cephalopoda: Myopsida) based on analyses of multiple data sets. Zoological Journal of the Linnean Society 130:603-33.

Beamish RJ, Noakes DJ, McFarlane GA, Klyashtorin L, Ivaov VV, Kurashov V. 1999. The regime concept and natural trends in the production of Pacific salmon. Canadian Journal of Fisheries and Aquatic Sciences 56:516-26.

Bograd SJ, Digiacomo PM, Durazo R, Hayward TL, Hyrenback KD, Lynn RJ, Mantyla AW, Schwing FB, Sydeman WJ, Baumgartner T and others. 2000. The state of the California Current, 1999-2000: forward to a new regime? CalCOFI Reports 41:26-52.

Boyle PR, Pierce GJ. 1994. Fishery biology of northwest Atlantic squid: an overview. Fisheries Research 21:1-15.

Butler J, Fuller D, Yaremko M. 1999. Age and growth of market squid (*Loligo opalescens*) off California during 1998. CalCOFI Reports 40:191-95.

Butler J, Wagner J, Henry A. 2001. Age of harvested California market squid. In: Marine Region, editor. Status of the market squid fishery with recommendations for a conservation and management plan. Los Alamitos: California Department of Fish and Game; p E9-10.

Cailliet GM, Karpov KA, Ambrose DA. 1979. Pelagic assemblages as determined from purse seine and large midwater trawl catches in Monterey Bay and their affinities with the market squid, *Loligo opalescens*. CalCOFI Reports 20:21-30.

Cailliet GM, Vaughan DL. 1983. A review of the methods and problems of quantitative assessment of *Loligo opalescens*. Biological Oceanography 2(2-4):379-400.

CDFG. 2005. Final Market Squid Fishery Management Plan submitted to the California Fish and Game Commission March 25, 2005. Sacramento: California Department of Fish and Game Marine Region; p 525.

Chavez, F.P., Ryan J, Lluch-Cota SE, Niquen C M. 2003. From anchovies to sardines and back: multidecadal change in the Pacific Ocean. Science 299(5604):217-21.

Conover DO, Munch SB. 2002. Sustaining fisheries yields over evolutionary time scales. Science 297(5578):94-6.

Dawe EG, Beck PC. 1997. Population structure, growth, and sexual maturation of short-finned squid (*Illex illecebrosus*) at Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences 54:137-46.

Dickerson T, Leos R. 1992. California market squid. In: Leet WS, Dewees CM, Haugen CW, editors. California's living marine resources and their utilization. Davis: Sea Grant; p 36-9.

Durazo R, Baumgartner TR, Bograd SJ, Collins CA, De La Campa S, Garcia J, Gaxiola-Castro G, Huyer A, Hyrenbach KD, Loya D and others. 2001. The state of the CA Current, 2000-2001: a third straight La Niña year. CalCOFI Reports 42:29-60.

Evans RG. 1976. Analysis of squid (*Loligo opalescens*) samples from Monterey Bay and southern California for 1974 [master's thesis]. Moss Landing (CA): Moss Landing Marine Laboratories, p 88.

Fields WG. 1965. The structure, development, food relations, reproduction, and life history of the squid *Loligo opalescens* Berry. Fish Bulletin 131. Long Beach: California Department of Fish and Game; p 108.

Forsythe JW. 2004. Accounting for the effect of temperature on squid growth in nature: from hypothesis to practice. Marine and Freshwater Research 55(4):331-339.

Francis RC, Hare SR, Hollowed AB, Wooster WS. 1998. Effects of interdecadal climate variability on the oceanic ecosystems of the NE Pacific. Fisheries Oceanography 7(1):1-21.

Goericke R, Venrick E, Koslow T, Lara Lara JR, Gaxiola-Castro G, Weise MJ, Sydeman WJ, Valdez JG, Harvey JT, Schwing FB and others. 2007. The state of the California Current, 2006-07: regional and local processes dominate. CalCOFI Reports 48:33-66.

Goericke R, Venrick E, Mantyla A, Bograd SJ, Schwing FB, Hyuyer A, Smith RL, Wheeler PA, Hooff R, Peterson WT and others. 2005. The state of the California Current, 2004-2005: still cool? CalCOFI Reports 46:32-71.

Hanlon RT, Kangas N, Forsythe JW. 2004. Egg-capsule deposition and how behavorial interactions influence spawning rate in the squid, *Loligo opalescens* in Monterey Bay, California. Marine Biology 145:923-30.

Hare SR, Mantua NJ. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. Progress in Oceanography 47:103-45.

Hofmann EE, Powell TM. 1998. Environmental variability effects on marine fisheries: four case histories. Ecological Applications 8(1 Suppl):S23-32.

Hunt JC, Zeidberg LD, Hamner WM, Robison BH. 2000. The behaviour of *Loligo opalescens* (Mollusca: Cephalopoda) as observed by a remotely operated vehicle (ROV). Journal of Marine Biological Association of the United Kingdom 80:873-83.

Isaac G, Neumeister H, Gilly WF. 2001. The effects of temperature on early life stages of the California squid (*Loligo opalescens*). Monterey: California Department of Fish and Game, report; p14.

Ish T, Dick EJ, Switzer PV, Mangel M. 2004. Environment, krill and squid in the Monterey Bay: from fisheries to life histories and back again. Deep-Sea Research II 51:849-62.

Jackson GD. 1994. Statolith age estimates of the Loliginid squid *Loligo opalescens* (Mollusca: Cephalopoda): corroboration with culture data. Bulletin of Marine Science 54(2):554-7.

Jackson GD, Domeier ML. 2003. The effects of an extraordinary El Niño / La Niña event on the size and growth of the squid *Loligo opalescens* off Southern California. Marine Biology 142:925-35.

Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA and others. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293(5530):629-38.

Karpov KA, Cailliet GM. 1979. Prey composition of the market squid, *Loligo opalescens* Berry, in relation to the depth and location of capture, size of squid, and sex of spawning squid. CalCOFI Reports 20:51-7.

Keiper CA, Ainley DG, Allen SG, Harvey JT. 2005. Marine mammal occurrence and ocean climate off central California, 1986 to 1994 and 1997 to 1999. Marine Ecology Progress Series 289:285-306.

Kim H-J, Miller AJ. 2007. Did the thermocline deepen in the California Current after the 1976/77 climate regime shift? Journal of Physical Oceanography 37:1733-9.

Klyashtorin LB. 1998. Long-term climate change and main commercial fish production in the Atlantic and Pacific. Fisheries Research 37:115-25.

Kong C, Bishop TL, Larson ML, Kraus J, Taylor BL. 2004. A guide to port sampling, laboratory sampling procedures, and databases for the market squid fishery. Santa Barbara: California Department of Fish and Game, manual; p 87.

Law R. 2000. Fishing, selection and phenotypic evolution. ICES Journal of Marine Science 57:659-68.

Leos RR. 1998. The biological characteristics of the Monterey Bay squid catch and the effect of a two-day-per-week fishing closure. CalCOFI Reports 39:204-11.

Lowry MS, Carretta JV. 1999. Market squid (*Loligo opalescens*) in the diet of California sea lions (*Zalophus californianus*) in southern California (1981-1995). CalCOFI Reports 40:196-207.

MacCall AD. 1996. Patterns of low-frequency variability in fish populations of the California current. CalCOFI Reports 37:100-10.

Macewicz BJ, Hunter JR, Lo NCH, LaCasella EL. 2004. Fecundity, egg deposition, and mortality of market squid (*Loligo opalescens*). Fishery Bulletin 102:306-27.

Mantua NJ, Hare SR. 2002. The Pacific Decadal Oscillation. Journal of Oceanography 58:35-44.

Marinovic BB, Croll DA, Gong N, Benson SR, Chavez FP. 2002. Effects of the 1997-1999 El Niño and La Niña events on zooplankton abundance and euphasiid community composition wihtin the Monterey Bay coastal upwelling system. Progress in Oceanography 54:265-77.

Mason JE. 2004. Historical patterns from 74 years of commercial landings from California waters. CalCOFI Reports 45:180-90.

McGowan JA, Bograd SJ, Lynn RJ, Miller AJ. 2003. The biological response to the 1977 regime shift in the California Current. Deep-Sea Research II 50:2567-82.

McInnis RR, Broenkow WW. 1978. Correlations between squid catches and oceanographic conditions in Monterey Bay, California. In: Recksiek CW, Frey HW, editors. Biological, oceanographic, and acoustic aspects of the market squid, *Loligo opalescens* Berry. Fish Bulletin 169. Long Beach: California Department of Fish and Game; p 161-70.

Melville-Smith R, de Lestang S. 2006. Spatial and temporal variation in the size at maturity of the western rock lobster *Panulirus cygnus* George. Marine Biology 150:183-95.

Morejohn GV, Harvey JT, Krasnow LT. 1978. The importance of *Loligo opalescens* in the food web of marine vertebrates in Monterey Bay, California. In: Recksiek CW, Frey HW, editors. Biological, oceanographic, and acoustic aspects of the market squid, Loligo opalescens Berry. Fish Bulletin 169. Long Beach: California Department of Fish and Game; p 67-98.

Moser HG, Charter RL, Watson W, Ambrose DA, Butler JL, Charter SR, Sandknop EM. 2000. Abundance and distribution of rockfish (*Sebastes*) larvae in the southern California bight in relation to environmental conditions and fishery exploitation. CalCOFI Reports 41:132-47.

Moser HG, Charter RL, Watson W, Ambrose DA, Hill KT, Smith PE, Butler JL, Sandknop EM, Charter SR. 2001. The CalCOFI ichthyoplankton time series: potential contributions to the management of rockfy-shore fishes. CalCOFI Reports 42:112-28.

O'Dor RK, Webber DM. 1986. The constraints on cephalopods: why squid aren't fish. Canadian Journal of Fisheries and Aquatic Sciences 64:1591-605.

Parrish RR, Tegner MJ. 2001. California's variable ocean environment. In: Leet WS, Dewees CM, Klingbeil R, Larson EJ, editors. California's living marine resources: a status report. Oakland: University of California; p 21-8.

Peterson B, Emmett R, Ralston S, Forney KA, Benson S, Goericke R, Venrick E, Mantyla A, Lavaniegos BE, Weise M and others. 2006. The state of the California Current, 2005-2006: warm in the north, cool in the south. CalCOFI Reports 47:30-74.

Recksiek CW, Frey HW. 1978. Background of market squid research program, basic life history, and the California fishery. Biological, oceanographic, and acoustic aspects of the market squid, Loligo opalescens Berry. Fish Bulletin 169. Long Beach: California Department of Fish and Game; p 7-9.

Recksiek CW, Kashiwada J. 1979. Distribution of larval squid, *Loligo opalescens*, in various nearshore locations. CalCOFI Reports 20:31-4.

Reiss CS, Maxwell M, Hunter JR, Henry A. 2004. Investigating environmental effects on population dynamics of *Loligo opalescens* in the southern California Bight. CalCOFI Reports 45:87-97.

Roemmich D, McGowan J. 1995. Climatic warming and the decline of zooplankton in the California Current. Science 267(5202):1324-26.

RS. 2006. Resampling Stats Add-in for Excel user's guide. Arlington: Resampling Stats, Inc.; p 177.

Rugh R. 1950. The effect of x-radiations on squid larval tropisms. Biological Bulletin 98(3):247-53.

Scofield WL. 1924. Squid at Monterey. California Fish and Game 10:176-82.

Spratt JD. 1979. Age and growth of the market squid, *Loligo opalescens* Berry, from statoliths. CalCOFI Reports 20:58-64.

Starr RM, Cope JM, Kerr LA. 2002. Trends in fisheries and fishery resources associated with the Monterey Bay National Marine Sanctuary from 1981-2000. La Jolla: California Sea Grant; p 156.

Starr RM, Johnson KA, Laman EA, Cailliet GM. 1997. Fishery resources of the Monterey Bay National Marine Sanctuary. La Jolla: California Sea Grant; p 50-51.

Starr RM, McCrae JE. 1984. Squid resource assessment: annual report. Salem: Oregon Department of Fish and Wildlife; p 39.

Starr RM, McCrae JE. 1985. Market squid (*Loligo opalescens*) investigations in Oregon, 1983-85. Salem: Oregon Department of Fish and Wildlife; p 41.

Steneck RS, Wilson CJ. 2001. Large-scale and long-term, spatial and temporal patterns in demography and landings of the American lobster, *Homarus americanus*, in Maine. Marine and Freshwater Research 52(8):1303-19.

Trippel EA. 1995. Age at maturity as a stress indicator in fisheries. BioScience 45:759-72.

Vecchione M, Shea E, Bussarawit S, Anderson F, Alexeyev D, Lu C-C, Okutani T, Roeleveld M, Chotiyaputta C, Roper C and others. 2005. Systematics of Indo-west Pacific Loliginids. Phuket Marine Biological Center Research Bulletin 66:23-6.

Venrick EL, Reid FMH, Weinheimer A, Lange CB, Dever EP. 2006. Temporal patterns of silicious flux in the Santa Barbara Basin: the influence of north Pacific and local oceanographic processes. CalCOFI Reports 47:156-73.

VenTresca DA, Parrish RH, Houk JL, Gingras ML, Short SD, Crane NL. 1995. El Niño effects on the somatic and reproductive condition of blue rockfish, *Sebastes mystinus*. CalCOFI Reports 36:167-74.

Vidal EAG, DiMarco FP, Wormuth JH, Lee PG. 2002. Optimizing rearing conditions of hatchling loliginid squid. Marine Biology 140:117-27.

Vojkovich M. 1998. The California fishery for market squid (*Loligo opalescens*). CalCOFI Reports 39:55-60.

Zeidberg L. 2008. First observations of ‘sneaker mating’ in the California market squid, Doryteuthis opalescens, (Cephalopoda: Myopsida). JMBA2 - Biodiversity Records 5998:Published on-line.

Zeidberg L, Hamner WM, Nezlin NP, Henry A. 2006. The fishery for California market squid (*Loligo opalescens*) (Cephalopoda: Myopsida), from 1981 through 2003. Fishery Bulletin 104:46-59.

Zeidberg LD, Hamner WM. 2002. Distribution of squid paralarvae, *Loligo opalescens*, (Cephalopoda: Myopsida), in the southern California bight in the three years following the 1997-1998 El Niño. Marine Biology 141:111-22.