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The effects of an extraordinary El Niño / La Niña event on the size and growth of the squid *Loligo opalescens* off Southern California

Abstract The population structure of the California market squid *Loligo opalescens* was studied for the Channel Islands region off Southern California between June 1998 and March 2000. During this time Californian waters were exposed to an extraordinary El Niño event that was possibly the most dramatic change in oceanographic conditions that occurred last century. There was then a rapid transition to record cool La Niña conditions. Statolith increments were used to determine age parameters and increment periodicity was validated for the first 54 days of life. Based on statolith increment counts, the oldest males and females were 257 and 225 days respectively and individuals matured as young as 129 and 137 days respectively. No distinct hatching period was detected. There was a general trend of increasing body size throughout the study period. Squid that hatched and grew through the El Niño were strikingly smaller and had slower growth rates compared to squid that grew through the La Niña. This was related to oceanography and associated productivity. There was a positive correlation between squid mantle length and upwelling index and a negative correlation between mantle length and sea temperature. The 'live-fast die-young' life history strategy of squid makes them ideal candidates for following the effects of the dramatic changes in oceanographic conditions off California. We propose that squid can serve as ecosystem recorders and

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productivity integrators over time and space and are useful organisms to tie oceanography to biology.

Introduction

A major characteristic of squid populations is their short life spans, high growth rates and early maturity. The population dynamics of cephalopods generally appear to be driven principally by phenotypic plasticity in response to environmental variability (Boyle and Boletzky 1996). Individual growth rates have been shown to vary considerably and can be strongly influenced by temperature (Forsythe 1993, Forsythe et al 2001, Hatfield et al. 2001) and food availability (Jackson and Moltschaniwskyj 2001a), especially during the juvenile growth phase.

The rapid 'live-fast, die-young' strategy of squid appears to be due to a unique combination of features that include: (1) efficient digestion coupled with a protein based metabolism; (2) sustaining continued growth using a combination of an increase in muscle fibre size (hypertrophy) along with continual recruitment of new muscle fibres (hyperplasia); (3) efficient use of oxygen and (4) low levels of antioxidative defence (Jackson and O'Dor 2001). This unique growth strategy can result in squid changing their life-history features considerably in concert with seasonal changes in their environment. This is especially apparent in the Loliginidae that are subject to fluctuating near-shore environments as have been shown in seasonal statolith ageing studies (e.g., *Loligo vulgaris*, Raya et al. 1999; Rocha and Guerra 1999; *L. gahi*, Hatfield 2000; *L. pealei*, Brodziak and Macy 1996; Macy and Brodziak 2001; *Lolliguncula brevis*, Jackson et al. 1997; *Sepioteuthis lessoniana*, Jackson and Moltschaniwskyj 2002; *Loliolus noctiluca*, Jackson and Moltschaniwskyj 2001b, and *Loligo forbesi*, Boyle et al. 1995; Rocha and Guerra 1999). For example, Jackson and Moltschaniwskyj (2002) found that the Indo-Pacific squid *S. lessoniana* displays two different growth

strategies, a 'hot' strategy, shown in equatorial waters, of short life span and small body size and a 'cool' strategy, shown in sub-tropical waters, of longer life span and a much larger body size. These strategies were expressed both regionally (equatorial vs. sub-tropical) as well as seasonally (winter vs. summer) within an intermediate location. The plasticity of these strategies was further revealed in an alternation of generation with the 'cool' population producing 'hot' offspring and vice versa.

The growth physiology of squid thus enables them to respond rapidly to environmental changes. Furthermore, because food intake is directly converted into growth rather than storage (O'Dor and Webber 1986), squid should therefore rapidly reflect and record changes in the environment. Such changes in age and growth rates are recorded in the statolith increments.

In this study we examined the age and growth parameters of the California market squid *Loligo opalescens* (Berry 1911) from the Channel Islands region off Southern California. Our squid sampling program spanned a period of significant oceanographic and meteorological change in the Southern California region. The west coast of North America was exposed to an extraordinary El Niño during 1997–1998 that was considered to be the largest event of the century (Freeland 2000).

In the tropical Pacific there was a sharp transition to El Niño conditions in early 1997 with rising temperatures, and strong El Niño conditions obvious by April–May, and near-maximum values by July–August 1997 with very warm temperatures. These conditions lasted until April 1998 after which there was a rapid decline and a transition to La Niña conditions with cooler than average temperatures evident by July–August 1998 (Hayward 2000).

In Californian coastal waters there are several indices that indicate El Niño conditions. Firstly, anomalously warm water along with low levels of upwelling are indicative of El Niño. Secondly, these prevailing conditions lead to low levels of primary productivity and subsequently low levels in macrozooplankton. Previous El Niño's in Californian waters have been associated with substantial declines in macrozooplankton. The macrozooplankton biomass during 1998 was the lowest recorded from 1951 to 1998 (Hayward 2000). From mid-1997 through to much of 1998, Californian coastal waters were warmer and subject to lower than normal upwelling rates, while during late 1998 and into 1999 higher than normal upwelling was featured (Hayward et al. 1999; Hayward 2000; Bograd et al. 2000). From October 1998 to the spring of 1999 temperatures were generally cooler than normal. There was a dramatic change off Southern California in both the chlorophyll concentration and macrozooplankton biomass from late 1998 to the first half of 1999. The transition to cooler water conditions with increased upwelling resulted in a marked increase in both primary and secondary productivity. Macrozooplankton biomass levels during 1999 were as much as 3 times the

levels during 1998; and chlorophyll levels during 1999 showed up to a 5-fold increase compared to 1998 (Hayward 2000).

The ecology and fishery of *L. opalescens*

Loligo opalescens is an important component of the marine ecosystem off Southern California. Its latitudinal distribution is extensive ranging from Baja California to southeastern Alaska (Hixon 1983) and no detectable population differentiation has been detected over ~2,500 km of the North American west coast (Reichow and Smith 1999, 2001). Squid fishing has taken place in Californian waters since the late 1800s, however, there was a major increase in fishing effort during the 1990s and *L. opalescens* became the main California catch both in terms of tons landed and dollar value (Vojkovich 1998). This resulted in increased attention given to the need to obtain biological information in order to understand the role of *L. opalescens* off the California coast and in order to effectively manage a growing fishery. During the period of increasing catches an international meeting was convened (Hanan 1998) to focus on the research needs of *L. opalescens* and legislation was approved to direct funds for squid research (Vojkovich 1998). However, concomitant with this increased interest and recognised need for obtaining squid information was a developing El Niño of massive proportions (Bograd et al. 2000).

Squid catches peaked in California during the 1996–1997 season at over 113,000 tons with a value of approximately $ 41 million. Squid catches in the northern Channel Islands region usually occur during late autumn to early spring (November–March). However, with the arrival of the extraordinary El Niño event in 1997 the squid fishery all but disappeared with virtually no squid landings in the Channel Islands fishery in the winter of 1997–1998. Squid catches however, resumed again during the spring of 1999 along with moderate catches throughout the first half of 1999 (Hayward 2000). However, a new record was set in squid catches during the 1999–2000 season when 117,890 tons was landed (Rogers-Bennett 2001) which apparently was due to a continuation of La Niña conditions (Durazo et al. 2001). Paralarval abundance of *L. opalescens* in Southern Californian waters also showed a marked increase from very low levels in 1999 to much higher levels during 2000 and 2001 in which squid paralarval concentrations were ~50 times that of 1999 (Zeidberg and Hamner 2002).

Preliminary statolith ageing work for *L. opalescens* was carried out by Jackson (1994a) who aged 12 individuals from the Monterey Bay region and compared this data to culture data from Yang et al. (1986). This suggested that individuals could live to over 300 days, which was much shorter than preliminary estimates by Spratt (1979). More recently, Butler et al. (1999) aged a larger sample of *L. opalescens* (192 individuals) off

Southern California during the 1998 El Niño, and found that individuals were short-lived with linear growth and maximum ages of 243 days and 238 days for males and females respectively. Ongoing research is showing that statoliths are valuable ageing tools for squid. Furthermore, daily increment periodicity has been documented in other loliginids (Jackson 1994b; Jackson and O'Dor 2001; Jackson and Forsythe 2002).

There is a need to undertake more extensive statolith ageing and population studies for *L. opalescens* covering as wide a spatial and temporal sampling as possible along with validation work on statolith increments (Jackson 1998). Our current study was focused on *L. opalescens* in the Channel Islands region of Southern California. We had the unique opportunity to track the response of squid growth during the extraordinary El Niño event and the subsequent cooler more productive La Niña conditions.

Materials and methods

Squid collections and hydrography data

Squid samples were collected from the Channel Islands region of Southern California. The main sampling site was off Catalina Island and squid were obtained for June 1998 and monthly (except for August) from January 1999 to March 2000. Additional samples were also obtained from off Laguna in December 1998, Santa Cruz in January 1999, and Santa Barbara in August 1999. Catches consisted predominantly of adults although a sample of juveniles was obtained off Carlsbad in July–August 1999. The majority of squid was from random sub-samples from commercial fishing vessels or collected using the Pfleger Institute of Environmental Research (PIER) vessel. The PIER samples were obtained using a 'crowder' net. This was similar to a short beach seine constructed of fine mesh [1.3 cm (1/2″) stretch mesh] stretched between two poles without a leadline. The net was lowered into the water under a light and then levered up out of the water when the squid congregated over the net.

Individuals ($n = 1,645$) were frozen and later examined at the PIER laboratory. Statoliths were removed from each individual and stored dry. Parameters taken from each individual included dorsal mantle length (ML) in mm, total weight (g) sex, maturity stage (after Lipinski 1979) and it was noted whether females had mated.

Mean monthly sea surface temperature was obtained from the National Data Buoy Center (http://www.ndbc.noaa.gov/index.shtml) from buoy 46023 (34°42′50″N, 120°58′00″W). The monthly upwelling index values were taken from the Pacific Fisheries Environmental Laboratory: (http://www.pfeg.noaa.gov/index.html) for 33°N, 119°W.

Hatchling rearing and validation

Egg capsules laid in captivity from two different collections of adult squid were used for rearing experiments. The first collection occurred during February 1998, egg capsules laid in captivity from these squid were removed and placed in 1,150 l flow-through rearing tanks at PIER, and maintained at ambient seawater temperatures (varied from 17 to 18°C). Tanks were located outdoors under shade cloth resulting in ambient day/night cycle. Hatching took place over three nights from 17 to 19 March 1998 and hatch-date was taken as the mean of these three dates (18 March). Hatchlings ($n = 8$) were fed wild zooplankton and were sacrificed periodically for up to 22 days post hatching (PIER 1). The second squid collection occurred during May 1998. Egg capsules laid from these squid were incubated for 10 days at the PIER, and then sent to the National Resource Center for Cephalopods, University of Texas Medical Branch, Galveston. Hatching for this experiment took place on 18 June 1998 and individuals ($n = 18$) were sacrificed periodically for up to 45 days post hatching. These were raised in a 2,600 l tank in a recirculating seawater system (Yang et al., 1983; Vidal et al. 2002) maintained at $16° \pm 0.5°C$ and provided with a day/night cycle using artificial light (Galveston 1). Paralarvae were fed on a mixed diet of wild zooplankton, enriched *Artemia* sp. Nauplii and mysid shrimp *Americamysis almyra* (Vidal et al. 2002). Feeding and survival are reported in Vidal et al. (2002), experiment 1. Five 54-day-old paralarvae were also obtained from growth experiment 4 (January-February 1999) conducted by Vidal et al. (2002) (Galveston 2). All paralarvae were preserved in 95% ethanol prior to examination of statoliths.

Statoliths were removed from individuals on a microscope slide in a pool of ethanol and mounted directly on the slide in the thermoplastic cement Crystal Bond. Increments were observed and counted within the statolith microstructure without any further preparation. Observing the size and shape of statoliths from newly hatched individuals facilitated the identification of the natal check. Although this helped to define the natal check in older paralarvae, there were often several prominent checks that sometimes made identification of the natal check difficult and there appeared to be some variability in natal check size.

Statolith examination

Statolith ageing was undertaken for a sub-sample of 295 squid ($n = 132$ females, 151 males, 12 juveniles). Statoliths were mounted in Crystal Bond and ground on the anterior and posterior surfaces using 1,200 grade carborundum paper and polished using a Leco Leccloth with 0.05 μm alumina powder (see Jackson 1994a). *Loligo opalescens* has a relatively good statolith increment structure (see Jackson 1998) and this technique produced a clear increment structure from the hatching check to the outer margin in most instances. For six individuals the outermost increments had to be extrapolated (Jackson and Choat 1992).

Age was estimated by taking the mean of two replicate counts that varied less than 10% from the mean. Statolith increments were viewed at 400× using either an Olympus B×60 microscope with an Olympus OLY-750 triple chip camera with a Pentium computer using a Flashpoint digitising card, or an Olympus CH microscope with a Jai CV-M50 monochrome chip camera with a high resolution monochrome monitor.

Statistical analysis

Regression and paired *t*-test analyses were used to compare the statolith age counts to the known age of individuals from the three validation experiments. A chi-square (χ^2) test of independence was used to determine if the sex ratios of the monthly samples were significantly different than 1:1. Population trends were analysed using mean ML, mean weight or mean age, grouped according to month of capture. All analysis of mature individuals included stage 5 and stage 6 individuals. Pearson correlation was used to determine relationships between paired parameters. Due to problems of an increased probability of type I error rates when using the same data in multiple correlations, probability values were used as a guide.

Due to the limited length range in the data sets it was not possible to compare growth curves between different hatch seasons. A growth curve could only be fitted for the spring 1999 hatch season. In order to analyse growth between the six hatch seasons we compared the average length and average weight of individuals for each hatch season aged between 150–200 days, using a two-way analysis of variance followed by a Tukeys HSD test.
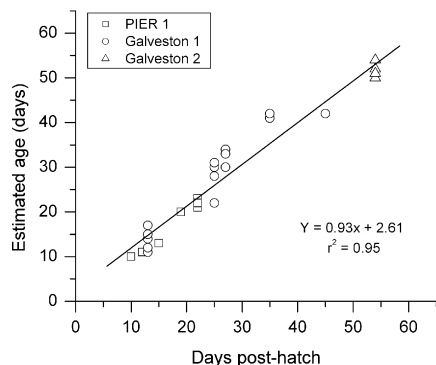
Fig. 1 The relationship between the number of days post-hatch and the estimated age determined by statolith increment counts for paralarvae of *Loligo opalescens* reared in captivity for the three experiments

We were also interested to see if we could correlate differences in individual body size to changes in physical parameters off Southern California during the El Niño / La Niña period. It is expected that physical influences are particularly relevant to an individual's early growth period. We therefore grouped the ML of individuals at capture according to their hatch month. Relationships between mean monthly ML and mean monthly sea surface temperature; and mean monthly ML and mean monthly upwelling index were determined using Pearson's correlation for males and females separately.

Results

Statolith increment validation

The relationship between the number of days post-hatching and the statolith increment counts (Fig. 1) resulted in a highly significant positive relationship $r^2 = 0.95$, $P < 0.001$, $n = 31$) and the slope (0.93) was not significantly different than one (95% confidence interval 0.85–1.02). A paired *t*-test also revealed that there was no significant difference between the number of elapsed

days and the number of statolith increments ($t = -1.34$, $P = 0.19$, *df* 30). We were thus able to show that statolith increments are laid down daily for at least the first 54 days post hatching. For the purpose of this study we are assuming daily periodicity throughout the life span but this will require further validation studies.

Population biology

The majority of the squid captured were mature (stage 5) and only very few immature individuals were caught (Table 1). A total of 27 squid (12 females, 15 males) were classified as spent (stage 6). Furthermore, most females collected throughout the year had also mated. Out of 642 females that were examined for deposited spermatophores, 543 (85%) had mated. This suggested probable spawning activity throughout the year. Six of the 17 months showed a 1:1 F:M ratio, however for the remaining months there was considerable skewness in the F:M ratio for either males or females (Table 1). In some instances there were considerably more males (September 1999 1:11.7, November 1999 1:6.2, January 2000 1:6.6) or alternatively more females (March 1999 1:0.3, May 1999 1:0.3, December 1999 1:0.6).

The ML frequency over time at Santa Catalina Island revealed a general pattern of a narrower range in ML for females than for males for any particular month (Fig. 2). The only clear fine scale pattern of modal progression in ML could be seen from April-June 1999. There was, however, a broader-scale pattern of an increase in ML throughout the study period with smaller individuals captured in early 1999 and much bigger specimens in late 1999–early 2000.

The pattern in the change in size over time could be better visualised by plotting the mean monthly ML and weight of mature individuals. The mean monthly ML and weight shows a general increasing trend in the size

Table 1 Details on the individuals of *Loligo opalescens* collected in this study at Santa Catalina Island including additional samples from off Laguna (December 1998) and off Santa Barbara (August 1999). Numbers in parentheses indicate the percent of individuals from the sample that were mature (stage 5 + 6). The χ^2 statistic was used to determine if the sex ratio differed significantly from 1:1

| Capture month	Number of males/ percent mature	Number of females/ percent mature	Sex ratio F:M	χ^2 statistic
June 1998	25 (84)	18 (100)	1:1.4	1.14 n.s.
Dec 1998 (Laguna)	38 (100)	19 (63)	1:2	6.333*
Jan 1999	57 (100)	49 (96)	1:1.2	0.604 n.s.
Feb 1999	89 (100)	29 (100)	1:3.1	30.508***
Mar 1999	26 (100)	87 (100)	1:0.3	32.929***
Apr 1999	44 (100)	60 (100)	1:0.7	2.462 n.s.
May 99	31 (100)	89 (100)	1:0.3	28.033***
June 1999	61 (100)	39 (100)	1:1.6	4.84*
July 1999	50 (100)	50 (100)	1:1	0.000 n.s.
Aug 1999 (Santa Barbara)	37 (0)	36 (0)	1:1	0.014 n.s.
Sept 1999	94 (100)	8 (100)	1:11.7	72.51***
Oct 1999	52 (100)	48 (98)	1:1.1	0.16 n.s.
Nov 1999	87 (100)	14 (100)	1:6.2	52.762***
Dec 1999	36 (100)	64 (100)	1:0.6	7.84 **
Jan 2000	92 (99)	14 (100)	1:6.6	57.396***
Feb 2000	61 (100)	40 (100)	1:1.5	4.366*
Mar 2000	75 (99)	26 (100)	1:2.9	23.772***
Total	955 (95)	690 (93)	1:1.4	68.59***
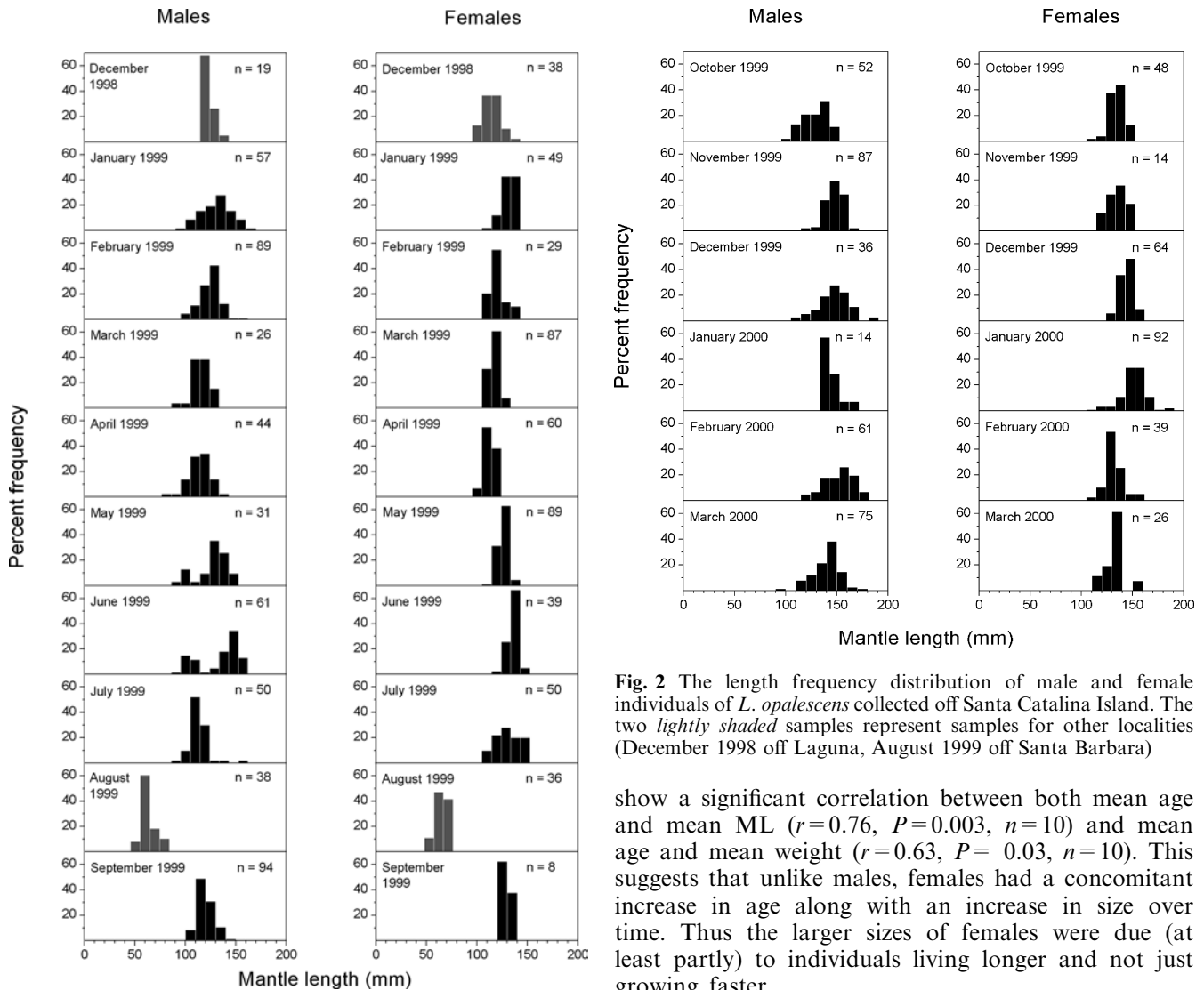
Fig. 2 The length frequency distribution of male and female individuals of *L. opalescens* collected off Santa Catalina Island. The two *lightly shaded* samples represent samples for other localities (December 1998 off Laguna, August 1999 off Santa Barbara)

of captured squid from June 1998 to early 2000 (Fig. 3). Mature squid captured during the El Niño (June 1998) had the smallest mean ML and weight for both males and females of all the samples. The longest and heaviest mature males were caught in January 2000. The longest females were also caught in January 2000 although the females peaked in weight the month earlier (December 1999).

Monthly mean age data provided a further insight into the observed size increase with time (Fig. 3). Although there were fewer data points compared to the size data it still revealed patterns in age over time. The correlations between both mean age and mean ML ($r = 0.53$, $n = 9$), and mean age and mean weight ($r = 0.45$, $n = 9$) for mature males were not significant. This indicates that even though there was a significant increase in mean size of males over the period there was not a corresponding increase in age. Rather, individuals achieved their larger size due to an increase in growth rates as conditions changed from El Niño to La Niña. In contrast, mature females did
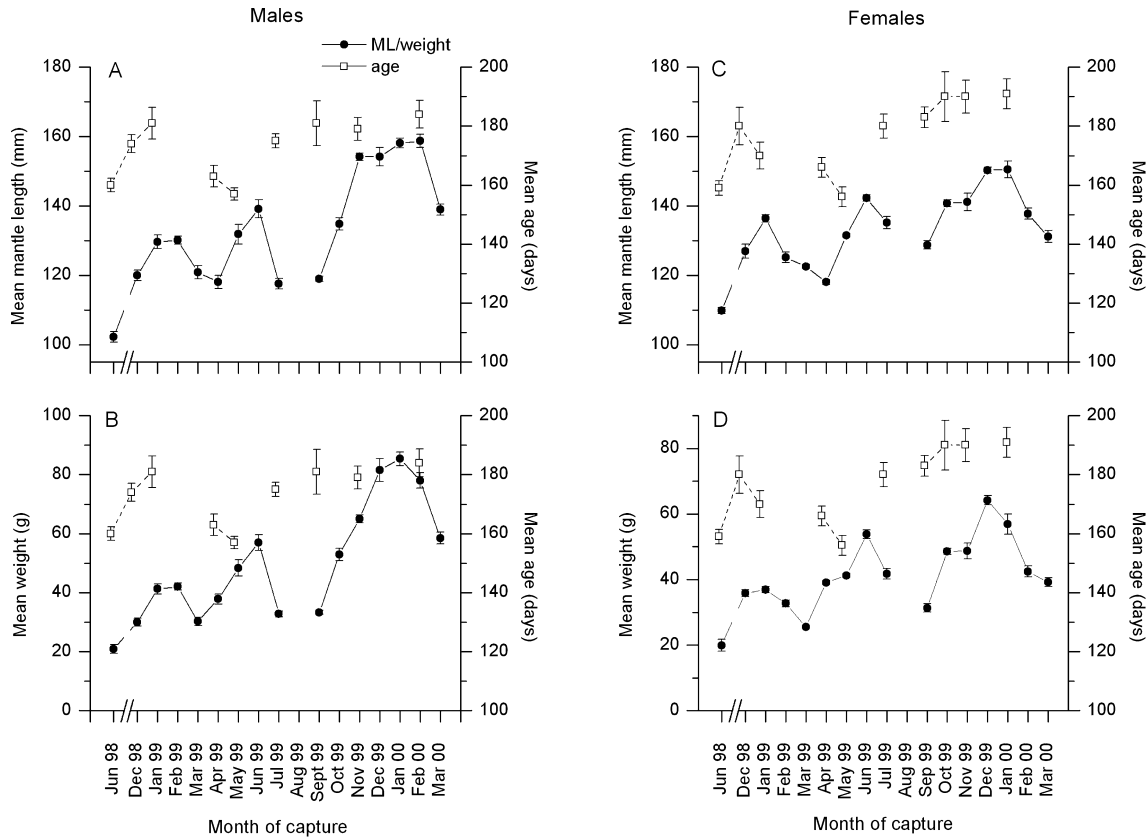
show a significant correlation between both mean age and mean ML ($r = 0.76$, $P = 0.003$, $n = 10$) and mean age and mean weight ($r = 0.63$, $P = 0.03$, $n = 10$). This suggests that unlike males, females had a concomitant increase in age along with an increase in size over time. Thus the larger sizes of females were due (at least partly) to individuals living longer and not just growing faster.

Despite the general trend of increasing size from June 1998 to early 2000, the age data reveals that the sampling did not follow a cohort through time. The length frequency data suggested that the modal progression between April and June 1999 might have indicated growth of a cohort. However, the age data revealed that this was not the case and in fact this was a period of decreasing mean ages for both sexes (Fig. 3). Even though there were periods where the age of either males or females increased over a 1 or 2-month period, these increases were considerably less than the number of days. The age data therefore indicated that the sampled population of squid at Santa Catalina Island consisted of waves of cohorts moving into the region rather than a resident population.

Age structure

Individuals were grouped according to season of hatch for assessing age and growth (Fig. 4). Growth in ML and weight was best modelled with a power curve

Fig. 3 The relationship between mean monthly mantle length and mean monthly weight at capture (*solid circles*) for mature males (**a**, **b**) and mature females (**c**, **d**) of *L. opalescens*. Also shown is the mean monthly age (*hollow squares*) for selected months for mature males (**a**, **b**) and mature females (**c**, **d**). All samples are from Santa Catalina Island except for December 1998, which is from off Laguna. *Error bars* are standard errors

for both males (ML $y = 0.0259x^{1.6492}$, $r^2 = 0.93$, weight $y = 7*10^{-9}x^{4.3625}$, $r^2 = 0.94$) and females (ML $y = 0.0464x^{1.5251}$, $r^2 = 0.95$, weight $y = 7*10^{-8}x^{3.8724}$, $r^2 = 0.95$, for the spring 1999-hatched individuals. Males showed more variability in both ML and weight for a given age than did females. The age range for both sexes was similar with all individuals in this study < 260 days and the majority of individuals aged between 140–220 days (Fig. 4).

The spring juveniles ranged in age from 77–128 days and from 31 to 60 mm ML. Immature males ranged in age from 144 days (93 mm ML) to 173 days (99 mm ML). The youngest mature male, which had grown through El Niño conditions, was from the June 1998 sample and was 129 days and 110 mm ML, while the oldest mature male was collected during the La Niña (January 2000) and was 257 days (178 mm ML). Immature females ranged in age from 73 days (34 mm ML) to 201 days (122 mm ML). The youngest mature female was from the April 1999 sample and was 137 days (115 mm ML) while the oldest mature female captured in November 1999 was 225 days (152 mm ML).

The 2-way ANOVA revealed that the average weight and length of individuals between 150–200 days was dependent upon hatch season for both sexes (sex × hatch season interaction) $F_{ML} = 3.44$, $P = 0.005$, df 5,227; $F_{weight} = 3.89$, $P = 0.002$, df 5,227 (Fig. 5). There was a consistent trend of El Niño hatched individuals (winter 1997–1998) having the lowest mean sizes while the summer 1999 La Niña samples had the largest individuals. There were also significant differences in average sizes of individuals within the same seasons for the different years. From winter 1997–1998 to winter 1998–1999, males were 20% longer and 84% heavier while females were 22% longer and 87% heavier. From summer 1998 to summer 1999, males were 31% longer and 173% heavier while females were 19% longer and 65% heavier (Fig. 5).

Statolith ageing revealed that squid hatched during two periods, December 1997–February 1998 and June 1998–August 1999 (Fig. 6). The peaks in percent frequency were directly related to numbers of squid aged from particular samples rather than indicative of peaks in hatching activity. The results indicate that spawning activity takes place during all seasons and months of the year.

Squid growth in relation to physical parameters

Upwelling

The upwelling index showed a peak in June 1998 with a trough in January 1999 followed by a period of continuing increase in upwelling activity from January 1999
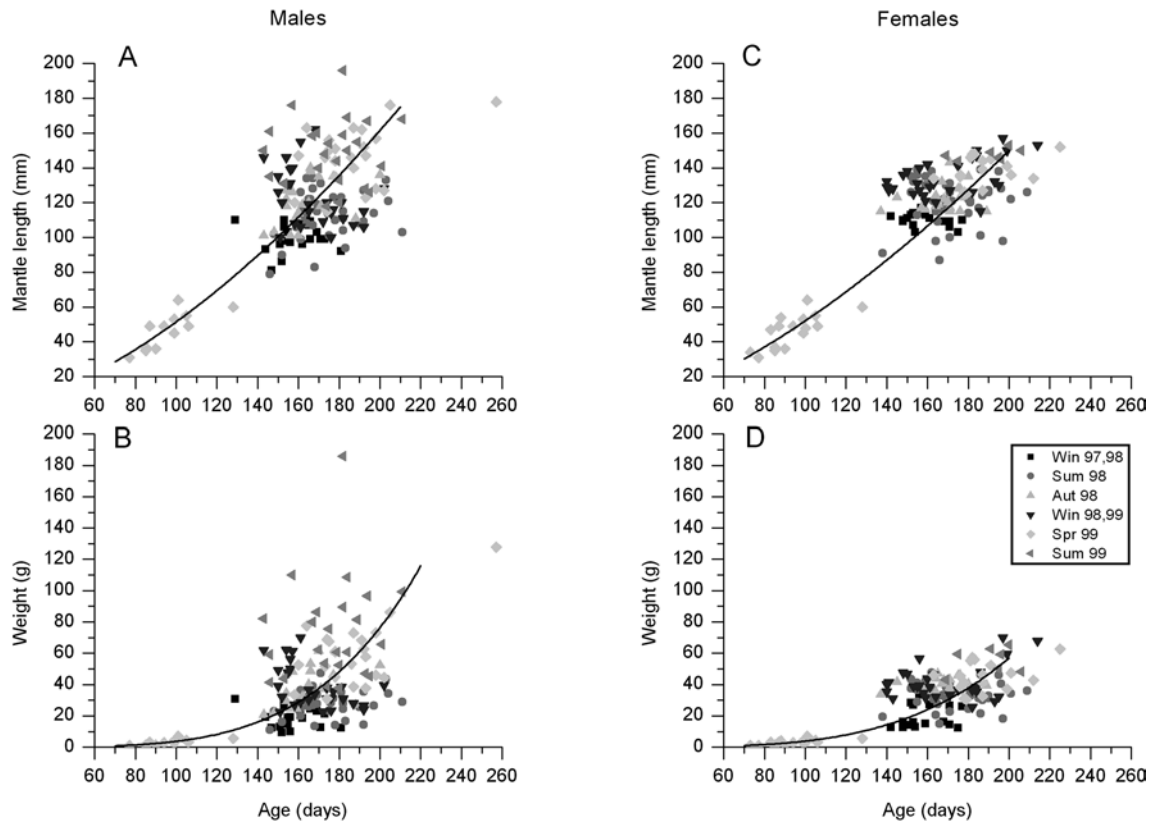
Fig. 4 The relationship between age and mantle length, and age and weight for male (**a**, **b**) and female (**c**, **d**) individuals of *L. opalescens* grouped according to hatch season. The *growth curves* show the power curves for the spring 1999 sample that included juvenile squid

to June 1999 (Fig. 7). There is a good relationship between the mean ML of males grouped according to hatch month with the upwelling index (Fig. 7). The period of increasing upwelling from January 1999 was mirrored closely with the male ML data, and they were significantly correlated ($r = 0.81$, $P < 0.001$, $n = 16$). The female ML data was not as highly correlated with upwelling, as was the male data (Fig. 7) although it was also significant ($r = 0.65$, $P = 0.008$, $n = 15$).

Water temperature

Sea surface temperatures provided another comparison to the ML pattern in *L. opalescens*. Temperatures in the Channel Islands region were relatively high until around September 1998 then dropped considerably with the winter cooling from September 1998 to May 1999 with a subsequent rise to the summer of 1999 (Fig. 8). However, the seasonal temperatures of 1999 were considerably less than corresponding seasons in 1998. For example, the mean temperature of August 1998 (17.02°C) was 24% greater than August 1999 (13.78°C), while the mean temperature of January 1998 (15.65°C) was 21% greater than January 1999 (12.97°C).

Mean ML of males and females grouped by month of hatching showed an inverse relationship with the corresponding temperature experienced during the juvenile growth phase (Fig. 8). There was a significant negative correlation between the average length of both males ($r = -0.61$, $P = 0.013$, $n = 16$) and females ($r = -0.72$, $P = 0.002$, $n = 15$) in relation to temperature. This suggests that during periods of high temperature through the El Niño period, individuals were growing slower while during the cooler La Niña period, they were growing faster.

Discussion

The value of this study is that we not only had an extended squid data set during a period of anomalous oceanographic conditions but the associated physical parameters from a well-studied marine region. Major environmental changes were recorded in sea temperature, upwelling and macrozooplankton abundance. We correspondingly recorded significant changes in squid body size and growth rates that tracked the oceanographic conditions. This study suggests that the special demographic features of squid (and their importance in the food chain) make them ideal ecosystem recorders of oceanographic change.

The increased size and accelerated growth rates of squids during the La Niña period appear to be directly related to productivity. Squid achieved larger sizes
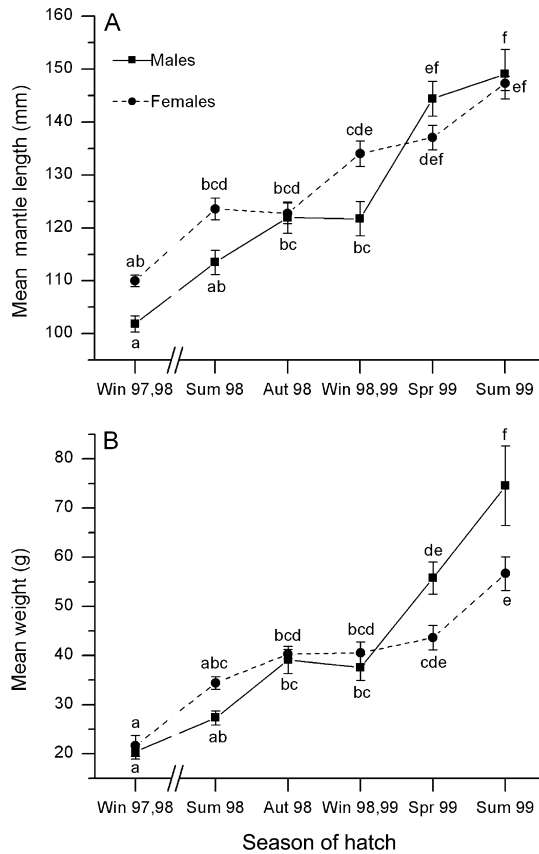
Fig. 6 The back-calculated hatch month for all aged individuals of *L. opalescens*

Fig. 5 The mean monthly mantle length (**a**) and mean monthly weight (**b**) at capture for mature males (*squares*) and mature females (*circles*) of *L. opalescens* grouped according to hatch season. The *letters* over each *symbol* are results from Tukey's post hoc test, different *letters* represent samples that are statistically different. *Error bars* represent standard errors

during periods of enhanced upwelling (and associated lower temperatures). Greater upwelling then produced a remarkable burst in productivity and macrozooplankton abundance in Southern California compared to the previous El Niño period (Hayward 2000) that recorded extremely low levels of productivity (Bograd et al. 2000).

High temperature accelerates squid growth when food is not limited (Forsythe 1993; Forsythe et al. 2001; Hatfield 2000; Hatfield et al. 2001; Jackson et al. 1997; Jackson and Moltschaniwskyj 2002). Under experimental conditions, Forsythe et al. (2001) showed that squid growth rate was intrinsically tied to temperature. Perez et al. (1996) and Jackson and Moltschaniwskyj (2001a) were also able to show that food intake can be correlated to squid growth rate with an increase in feeding levels leading to a concomitant increase in growth rate. Our current study demonstrates that food availability in the field is an overriding factor to promote growth rates of *L. opalescens* despite cooler temperatures from the La Niña conditions. The smaller and younger mature females during the El Niño may also be due to acceleration in maturity due to both higher temperatures and reduced
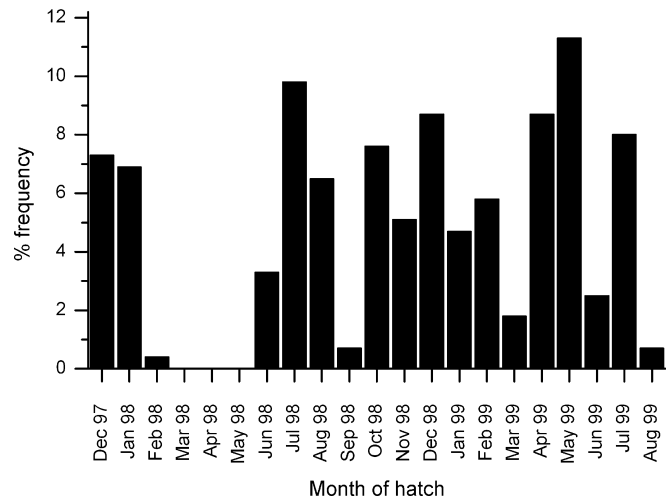
feeding rates (Mangold 1987) that would have occurred during this period. It is clear that both temperature and food are important factors influencing the growth dynamics and maturation rates of squids. Which factor has the greater influence may depend on environmental conditions experienced during the squid's life history.

It is likely that juvenile stages of squid are particularly susceptible to changes in oceanographic conditions. Older adult squid would be feeding on larger organisms (e.g., teleost fish) with life spans that number in years and would not respond as rapidly to environmental changes. In contrast, juvenile squid would be feeding on organisms with very short generation times (e.g., macrozooplankton). Thus, juveniles would be much more sensitive to rapid changes in productivity resulting from increased upwelling. This would have a more dramatic and immediate effect on these lower trophic organisms.

The dramatic change in physical conditions in the California Current as a result of the shift from the El Niño to La Niña conditions has been suggested as heralding a regime shift (a decadal-scale climate shift). This would lead to cooler conditions with enhanced upwelling and higher productivity off California (Bograd et al. 2000). This in turn could reverse the general trend of decreasing abundance in macrozooplankton biomass observed from 1951 to 1998 (see Hayward 2000, Fig. 12). The cool 1999 conditions may indicate a reversal in the general warming conditions experienced off California and may be the first sign of a shift in climate with the California Current returning to a former environmental and ecological state (Schwing et al. 2000).

There appears to be continuous recruitment and protracted spawning of *L. opalescens* off Southern California. This resulted in waves of new individuals entering the sampling region, as there was no dramatic difference in mean age between subsequent samples. The data also suggests that we were primarily sampling
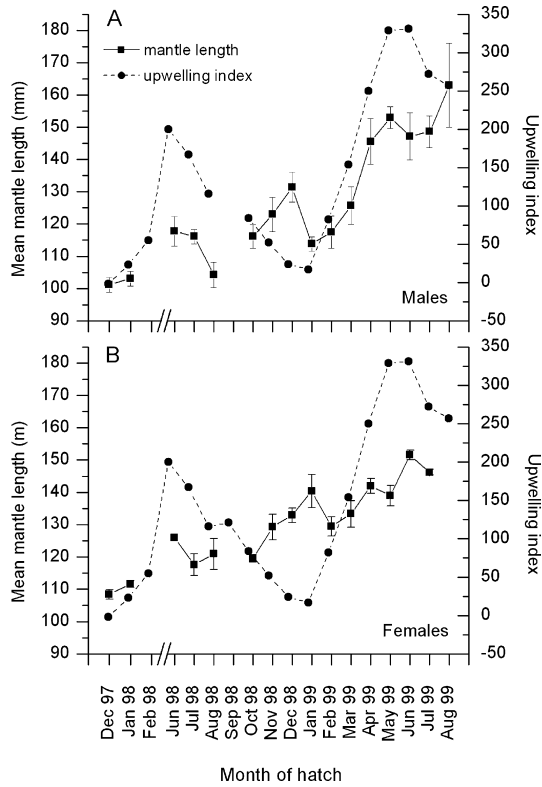
Fig. 7 The upwelling index plotted against mean mantle length of mature males (**a**) and females (**b**) of *L. opalescens* grouped according to hatch month. *Error bars* represent standard errors
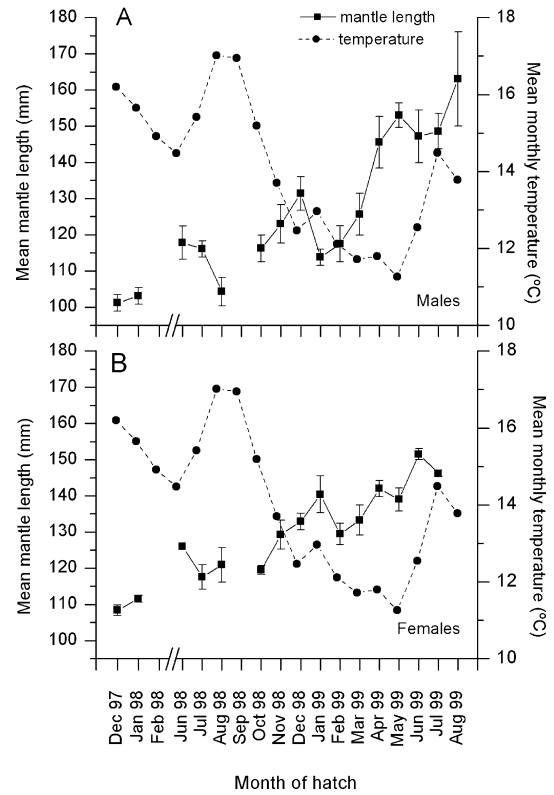
Fig. 8 The mean monthly temperature plotted against mean mantle length of mature males (**a**) and females (**b**) of *L. opalescens* grouped according to hatch month. *Error bars* represent standard errors

spawning individuals off Santa Catalina Island due to the predominance of mature animals in the samples. Sex ratio data also suggests that while sex ratios are often 1:1, during some periods there may be schooling of same-sex individuals.

The fact that there are waves of individuals moving through the Channel Islands region is a significant point for consideration when developing a policy for fisheries management. Fishing pressure is therefore not focused on a single cohort. A similar pattern has also been documented for the large loliginid *Sepioteuthis australis* in southern Australia (Jackson and Pecl 2003) and *Loligo pealei* off northeastern North America (Macy and Brodziak 2001). Such a strategy may be common in loliginid populations.

Despite the complex and confusing pattern of multiple cohorts through time there was a clear overall pattern in individual size throughout the study period. Individuals that lived through El Niño conditions were much smaller than those that lived through the subsequent La Niña conditions. There were also some differences between the sexes in their response to changing environmental conditions with males apparently tracking changes in the environment more closely than females. This is most likely due to the greater reproductive investment of females, with reproductive organs being 25–50% of total body weight, compared to males which invest only 4–7% in reproductive organs (Hixon

1983). Thus males are able to respond quickly to favourable changes in the environment without the energy costs of reproduction.

Possible ecosystem effects

The marked poor performance of squid as a response to anomalous environmental conditions has a potentially enormous down-stream effect on the rest of the ecosystem given the key role of squid in the California Current (Morejohn et al. 1978). Squid were not only experiencing reduced growth rates and smaller body sizes, but this was also paralleled with a catastrophic drop in squid biomass due to unfavourable environmental conditions (Hayward 2000; Zeidberg and Hamner 2002). Changes in *L. opalescens* size have been recorded previously. Fields (1965) noted a long-term trend where squid were small from 1948 through to 1961 in central California. It was not until 1962 that squid were as large as individuals caught some 14 years earlier in 1948. However, the reasons for this are still unclear.

A comparison to our study can be found in the results of Lowry and Carretta (1999) who also recorded notable changes in squid size in the diet of California sea lions (*Zalophus californianus*) between El Niño and non-El Niño periods. Sea lions consistently ate smaller squids during El Niño events (1982–1983 and 1992–1993)

compared to non-El Niño periods (1984–1991 and 1994–1995). At both San Clemente and Santa Barbara Islands squid consumed during El Niño periods were half the size (63 mm, 62 mm ML respectively) of squid consumed during non-El Niño periods (128 mm, 128 mm ML respectively). In contrast, sea lions on the furthest offshore island, San Nicolas, consumed both small and large squid (bimodal distribution) during the 1992–1993 El Niño compared to the non-El Niño period where mainly larger individuals were eaten. Lowry and Carretta (1999) suggested two possible mechanisms responsible for these patterns in sea lion predation: (1) the oceanographic changes associated with El Niño caused a delay in the spawning cycle of squid, or (2) growth rates were slowed as a result of nutritional stress due to a decline in prey of squid.

Our study helps clarify results from California sea lion diets during El Niño periods. The small size of squid during El Niño is due to decreased growth rates in association with low productivity in the water column. Squid just don't reach large sizes during El Niño periods at least in the inshore Channel Islands region. The situation of squid ingestion by sea lions at San Nicolas is interesting in that, although small squid are eaten, some large squid are also available during El Niño periods. Again this may be a response by squid to better conditions offshore. Lowry and Carretta (1999) indicated that waters around San Nicolas during the 1992–1993 El Niño were relatively cooler and more productive than the waters around Santa Barbara and San Clemente Island. Lowry and Carretta (1999) suggested that larger squid might have moved to more productive waters in response to El Niño. We suggest that the conditions around the offshore island were more conducive to increased growth rates in squid, producing larger mature individuals. Differences in oceanography off Central America between the 1997 El Niño and 1999 La Niña were found to strongly influence the distribution of the large ommastrephid squid *Dosidicus gigas* (Ichii et al. 2002). Squid populations moved to regions of greater productivity and enhanced upwelling as a response to El Niño induced changes in oceanography. Zeidberg and Hamner (2002) also suggested that squid in southern Californian waters could have been advected north during the El Niño conditions as has been shown for other species. Thus spawning aggregations might have taken place further north near Monterey and squid in the Channel Islands may have originated off Baja.

Forsythe et al. (2001) suggested that the sensitivity of squids to subtle temperature changes raised the question of how squid populations are impacted by both acute (El Niño / La Niña) and chronic (global warming) changes in ocean temperature. Based on our results we propose that in fact squids may prove to be effective ecosystem recorders to track change in the marine environment. The live-fast growth strategy of squid (Jackson and O'Dor 2001) means they can provide real-time monitoring of the ecosystem and serve as productivity integrators. Similarly, a much greater level of resolution may be obtained through the use of statoliths (e.g., Durholtz and Lipinski 2000; Villanueva 2000; Jackson and Moltschaniwskyj 2001a) and gladius (Perez et al. 1996) increment widths. If the California Current continues to experience a new climate of cooler/higher productive conditions reversing the almost half century trend of decreasing macrozooplankton biomass we can make some predictions about what to expect in the population dynamics of *L. opalescens*. We predict that squid biomass will increase, individual size will not decrease; rather growth rates will increase resulting in larger sized individuals at maturity with a downstream effect that is beneficial to higher predators, with larger individuals in the diet of California sea lions. We suggest that studies such as ours be extended to continue monitoring the dynamics of squid both growth temporally and spatially.

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