SIZE DIFFERENCES, BY SEX, OF ADULT MARKET SQUID (*LOLIGO OPALESCENS*) AT-HARVEST IN DISTINCT TEMPERATURE AREAS NEAR THE CHANNEL ISLANDS

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Abstract—We examined adult market squid, *Loligo opalescens*, from two significantly different temperature areas (northern and southern Channel Islands) of intense squid fishing within the Southern California Bight (SCB) to determine the effects of temperature on size at-harvest. Dorsal mantle length (DML) and body mass by sex, and female gonad mass were compared over a four-year period (1999–2002). For males, there were no significant differences in mean monthly DML or body mass between the two areas. In contrast, there were significant differences in female DML and body mass. No difference was detected for female gonad mass, possibly due to sample size ($n = 7$). Temperature at-harvest was positively correlated with DML and body mass of males and females; however, an opposite and stronger trend was apparent when hatch temperature was correlated with the growth parameters (DML, body mass, and gonad mass). Gonad mass at-harvest was negatively correlated with water temperature at-hatch. Differences in squid size at-harvest relative to hatch temperature translate into differences in reproductive potential. We suggest that reduced reproductive potential from warm water events be considered in management strategies for harvest.

Keywords: age, growth, Loligo opalescens, squid, temperature

INTRODUCTION

Loligo opalescens[1] (Berry 1911), commonly referred to as market squid, is one of the most important fisheries in California based on biomass landed and revenue. *Loligo opalescens* taken in the fishery average 186 days of age (range 174– 302 days; Butler et al. 2001) and are believed to be semelparous, dying shortly after spawning (Fields 1965). The commercial fishery targets spawning aggregations close to shore, primarily over shallow (<100 m) sandy substrates (McGowan 1954) where females attach egg capsules to the bottom substrate; on average females produce 20 capsules each containing approximately 200 eggs (Fields 1965). Hatch interval, dependent on water temperature, usually starts at 35 days (Isaac et al. 2001) and paralarvae remain close to shore for up to a month after hatching (Zeidberg and Hamner 2002).

The distribution and/or abundance of *L. opalescens* appear subject to environmental conditions as evidenced by landing records from California Department of Fish and Game (CDFG). These records indicate that squid harvests plummet with warmer waters associated with El Niño events. Less than 10,000 metric tons of squid were landed during the 1997–1998 El Niño event while the highest seasonal catch (114,700 metric tons) for the Southern California Bight (SCB) occurred during the 1999–2000 cool water La Niña event.

Loligo opalescens is a semi-annual species that relies on reproductive success throughout the year. Sensitivity to temperature fluctuations, such as a decline in egg deposition, combined with fishery interactions, including disturbance to egg beds, could become problematic for the species. A worldwide decline in commercially valuable squid species (e.g., *L. gahi*) resulted in an increased demand for *L. opalescens* and a four-fold expansion

1.The genus *Doryteuthis* was officially proposed to replace *Loligo* in a loliginid workshop in 2004. The recommendations from this workshop will be published in a proceedings to be published in early 2005.

of the fishery in the SCB during in the 1980s. Since 1990, landings south of Point Conception have comprised almost 90% of total California catch. Unfortunately, unanswered questions about life history, its relation to environmental perturbations and resilience to fishing pressures are cause for concern. The primary goal of this project was to examine the relationship between water temperature and size at-harvest of *L. opalescens* in an area of recent intense fishing. We used size parameters (dorsal mantle length (DML), body mass, and gonad mass) of *L. opalescens* landed by commercial fishing vessels to compare size at-harvest between two significantly different temperature areas within the SCB.

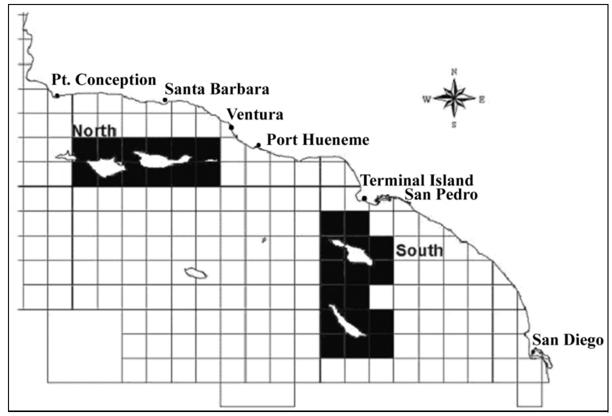

Figure 1. Location of the two study areas: north (California Department of Fish and Game block numbers 684–689 and 707–712) and south (California Department of Fish and Game block numbers 741–742, 760–762, 806–808, 828–829, 848–850 and 866–868) in the Southern California Bight.

MATERIALS AND METHODS

Study Area

Commercial squid fishers report the area of their harvest by assigned CDFG block numbers. Each block corresponds to an area of 10 × 10 nautical miles. This study targeted landings from primary fishing grounds for *L. opalescens* with a focus on two areas within the SCB. The northern area encompassed the fishing grounds near Anacapa, Santa Cruz and Santa Rosa Islands, and was defined as CDFG fishing block numbers 684–689 and 707–712. The southern area included the waters around Santa Catalina and San Clemente Islands and comprised CDFG fishing block numbers 741–742, 760–762, 806–808, 828–829, 848–850 and 866–868 (Fig. 1). The blocks selected correspond to areas within one mile of each island where the vast majority of the squid fishing occurs within the SCB (CDFG unpubl. data).

Sea Surface Temperature

Monthly composites of sea surface temperature (SST) satellite data were obtained online from the NOAA CoastWatch West Coast Regional Node website for July 1998 through December 2002 (http://coastwatch.pfel.noaa.gov/). CoastWatch SST Images are produced from Advanced Very High Resolution Radiometer (AVHRR) data four times daily for the coastal waters of the United States using data from NOAA Polar Operational Environmental Satellites. Average monthly temperatures were extracted using the temperature recorded for the CDFG block center (based on latitude and longitude); a monthly mean value was calculated for each study area using the mean value calculated for each block. On occasion, satellite error or poor weather conditions prevented accurate temperature readings for a block or a particular month and mean monthly temperatures were calculated without these values. A paired *t*-test was used to compare means and determine the level of significance.

Port Sampling

CDFG began a port-sampling program in 1998 to characterize squid harvested in California. This program required collecting a maximum of two squid samples daily at the major ports (Santa Barbara, Ventura, Port Hueneme, Terminal Island and San Pedro) where commercial fishing vessels land squid. A sample comprised 30 randomly selected squid from a single squid boat. No vessel was sampled more than once daily. Boats were selected opportunistically, with an effort made to sample as many different vessels throughout the season as possible. Squid were collected throughout the offloading process and taken from different areas and depths within the vessel's hold. Samples were kept on ice until processed later that same day at the lab.

Laboratory Analyses

The squid collected were processed daily. All specimens were sexed; DML was recorded to the nearest mm and body mass to the nearest 0.1 g. A subset of female squid gonads was preserved in a solution of 10% formalin for later processing. From January 1999 to July 2000, the subset consisted of 10 randomly selected squid; during July 2000, the subset was reduced to the first five females measured in the daily sample. As time permitted, the mass of these preserved gonads was recorded to the nearest 0.001 g. Because *L. opalescens* are sexually dimorphic (males larger than females; Fields 1950, 1965), monthly means were calculated for each month by sex. Paired *t*-tests were used to determine the level of significance of variables between the study sites by month. The Pearson correlation was used to measure the relation between temperature and DML, body mass and gonad mass.

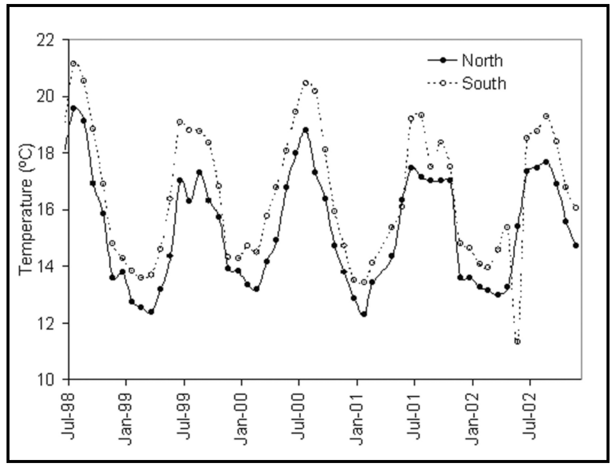

Figure 2. CoastWatch Advanced Very High Resolution Radiometer (AVHRR) mean monthly sea surface temperature (SST) for the north and south study areas in the Southern California Bight, July 1998 through December 2002.

RESULTS

From January 1999 through December 2002, the mean monthly SST was significantly different between the northern and southern areas (t = -8.27; df = 46; P < 0.001). Temperatures were consistently warmer in the southern area with values averaging 1.4ºC higher than the northern area (Fig. 2). One exception occurred in June 2002 when mean temperatures were higher in the northern study area. We also tested for temperature differences between the northern and southern areas for the period corresponding to the hatch temperature of harvested squid, based on a life span averaging six months (July 1998 through June 2002). Again, we found that the temperatures were significantly different between the two areas (t = -8.3; df = 46; P < 0.001).

From 1 January 1999 through 31 December 2002, 1,415 samples were collected from vessels that harvested squid in our study areas: 858 samples from the northern and 557 samples from the southern areas (Table 1) produced 35 months of comparable data. As expected, the DML (t = 17.1; df = 1412; P <

Table 1. Mean annual dorsal mantle length (DML) and body mass of squid collected from January 1999 through December 2002 by sex and area within the Southern California Bight.

	Male DML (mm)			Female DML (mm)			Male body mass (g)			Female body mass (g)		
Area/Year	N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD
North												
1999	336	133.3	13.74	336	130.3	11.26	336	52.6	13.99	336	43.4	9.85
2000	177	135.7	10.02	176	130.7	6.80	177	52.8	12.09	176	41.0	7.37
2001	189	128.9	6.22	189	125.8	4.34	189	43.0	6.09	189	35.1	4.18
2002	156	131.4	9.27	156	128.1	7.59	156	46.7	9.25	156	38.2	6.39
Average	858	132.5	11.13	857	129.0	8.79	858	49.5	12.12	857	40.2	8.42
South												
1999	161	129.5	12.75	161	130.0	9.98	161	48.8	14.70	161	42.3	10.17
2000	136	136.5	12.45	135	132.5	8.20	136	54.4	15.38	135	42.5	9.65
2001	170	127.6	5.75	170	125.5	4.13	170	42.8	5.42	170	35.2	5.75
2002	90	124.5	7.97	90	122.5	6.41	90	40.1	8.41	90	32.8	6.31
Average	557	129.8	11.03	556	128.0	8.35	557	47.0	12.92	556	38.6	9.25
All years	1,415	131.4	11.16	1,413	128.6	8.63	1,415	48.5	12.50	1,413	39.5	8.78

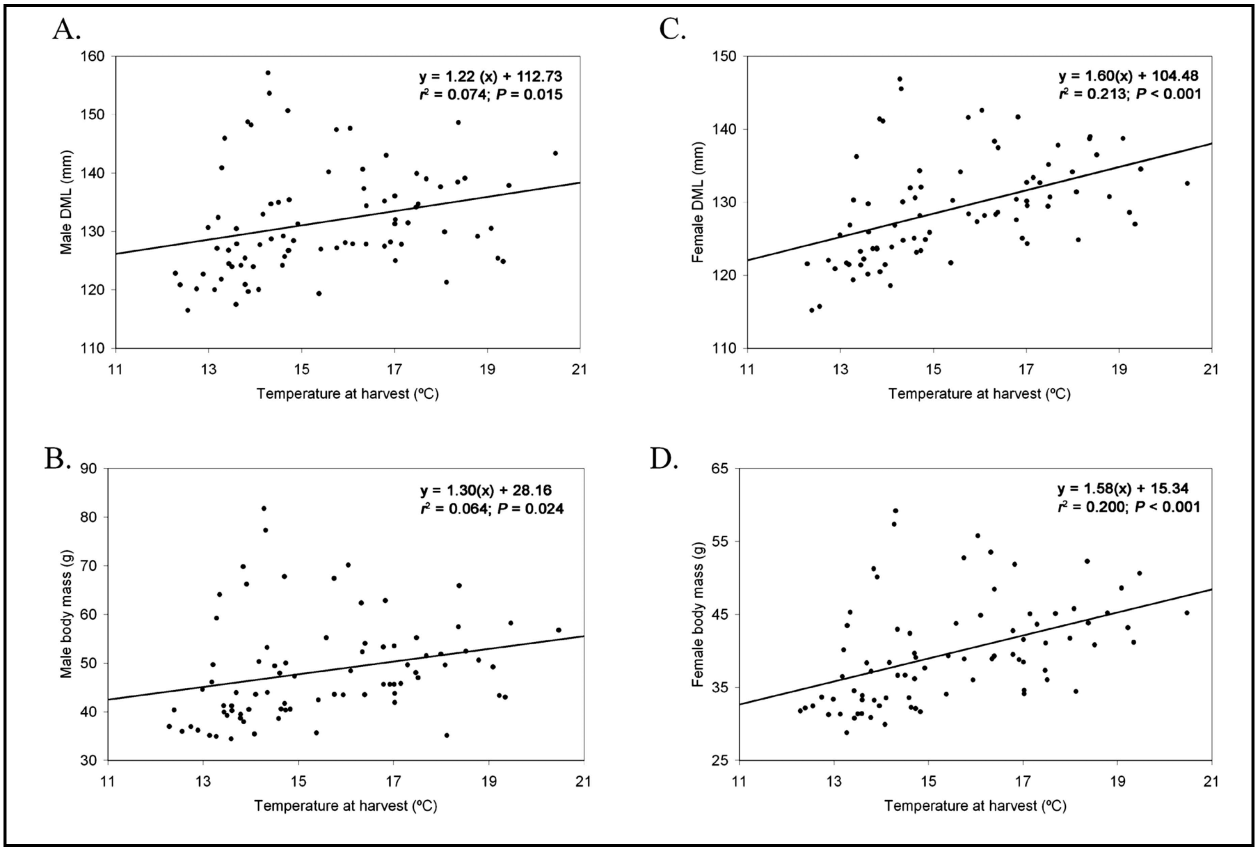

Figure 3. Monthly mean harvest sea surface temperature (SST) vs. male dorsal mantle length (DML) in millimeters (mm) (A); male body mass in grams (g) (B); female DML (mm) (C); and female body mass (g) (D) for market squid harvested in the Southern California Bight, January 1999 through December 2002.

0.001) and body mass (t = 47.3; df = 1412; P < 0.001) of male *L. opalescens* were significantly greater than female squid in our samples.

Comparisons of the monthly mean size parameters of male *L. opalescens* revealed no significant difference in either DML (t = 0.12; df = 34; P = 0.9) or body mass (t = -1.1; df = 34; P = 0.3) between the two areas. However, there was a significant difference in the monthly mean DML (t = -1.4; df = 34, P = 0.044) and body mass (t = -1.9; df = 34, P = 0.021) of females. Although there were significant differences between the areas, no clear trend in size at-harvest between the two areas was evident.

Female gonads from 249 gonad samples were processed, producing seven months of comparable data. Although gonads were consistently heavier in the southern area (mean = 5.99 g ± 2.15) versus the northern area (mean = 4.99 ± 1.23 g), there was no statistical difference between the two study areas (t = -0.9; df = 6; P = 0.4).

Next, we examined the association between SST and size at-harvest. Data were pooled for further analysis because there was no statistical difference between means for DML, body mass, and gonad mass for our study areas. We found a significant positive correlation between the mean monthly harvest SST and male DML (r^2 = 0.074, P = 0.024) and body mass at-harvest (r^2 = 0.064, P = 0.015; Fig. 3A-B). Also, a significantly positive correlation between the mean monthly harvest SST and DML at-harvest (r^2 = 0.213, P < 0.001) and body mass (r^2 = 0.200, P < 0.001) at-harvest was found for females (Fig. 3C-D). There was no correlation between mean monthly harvest SST and female gonad mass (r^2 = 0.007, P = 0.654; Fig. 4).

We back calculated the mean monthly hatch temperature for our samples based on an average life span of six months for harvested *L. opalescens* (Butler et al. 2001). The mean monthly hatch SST was negatively correlated with size at-harvest for male DML (r^2 = 0.148, P < 0.001) and body mass (r^2 = 0.137, P < 0.001) and female DML (r^2 = 0.287, P < 0.001) and body mass (r^2 = 0.300, P < 0.001; Fig. 5A-D). The mean monthly hatch SST accounted for a greater proportion of the variance of size at-harvest for both males and females than the temperature at-harvest. Lastly, we found a negative correlation (r^2 = 0.172, P = 0.023) between the temperature at-hatch and gonad mass at-harvest (Fig. 4).

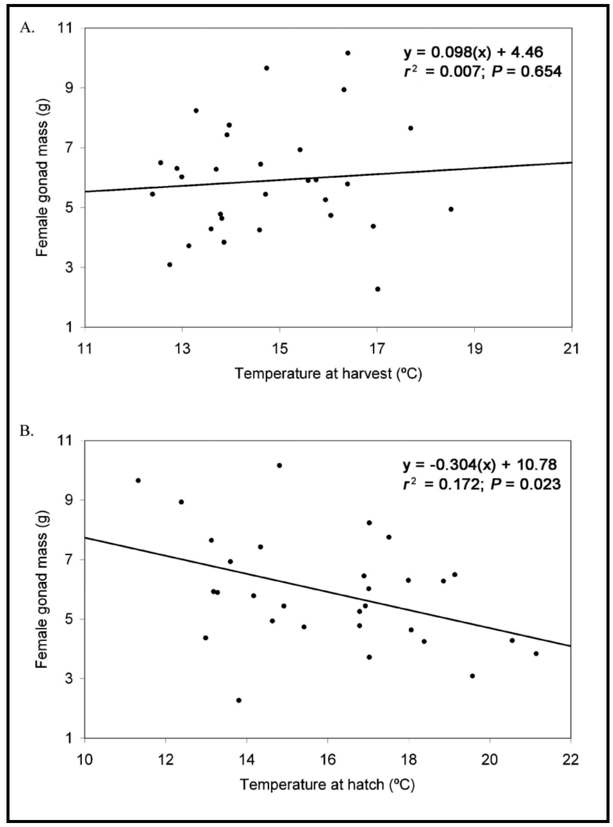

Figure 4. Monthly mean harvest sea surface temperature (SST) vs. female gonad mass (g) (A) and monthly mean hatch sea surface temperatures vs. female gonad mass (g) (B) for market squid harvested in the Southern California Bight, January 1999 through December 2002.

DISCUSSION

There were consistently warmer temperatures in the southern study area compared to the northern area. There was no significant difference in the male squid size at-harvest between the two sites. The data for female squid were confounded; although *t*-tests showed a significant difference in size at-harvest between the two sites, there was no clear trend for larger or heavier squid in one area compared to the other. The DML for the southern area females was larger in 57% of the months and body mass heavier in 60%. Males displayed a similar trend with 51% of the monthly DML means greater in the southern area and 57% heavier. A χ^2 test indicated that these values did not differ from unity.

Several studies have shown that temperature most influences growth of loliginid species during the early stages of development in their life cycle (Hatfield 2000, Oosthuizen et al. 2002, Vidal et al. 2002, Jackson and Domeier 2003). Similar to these findings, our analyses found that *L. opalescens* hatched in cooler waters reached spawning grounds at a larger size than those individuals hatched in warmer waters, and that temperature at-hatch may be a potential tool to estimate the mean squid size at-harvest. The negative correlations between hatch SST and size presented here agree with trends described by Jackson and Domeier (2003) who noted temperature and size relationships for *L. opalescens* in the SCB. Squid hatched in comparatively cooler temperatures would arrive at spawning grounds at a larger size and presumably a higher reproductive potential. Because of the cyclic nature of temperature within the SCB, these progeny would hatch at warmer temperatures and we would expect them to be comparatively smaller with a reduced reproductive potential. Variation in their reproductive potential due to temperature may be offset by the presence of multiple cohorts within any year (Maxwell 2001). Fluctuating environmental conditions and food supply select for phenotypic plasticity and indeed, this seems to be well suited to the semi-annual lifespan of *L. opalescens*.

Temperature is a critical factor in the life history of loliginid squid (Jackson et al. 1997, Perez and O'Dor 1998, Forsythe et al. 2001, Hatfield et al. 2001). Yet temperature at-hatch only accounted for a portion of the variability (≤30%) evident in squid size at-harvest. Hatch temperature affects squid growth and likely acts as a proxy for food abundance. The cooler water temperatures in the SCB are indicative of upwelling and often result in increased primary productivity. Coastal upwelling events in the SCB, usually driven by local winds, cause a sudden decline in sea surface temperatures (Dorman and Palmer 1981)

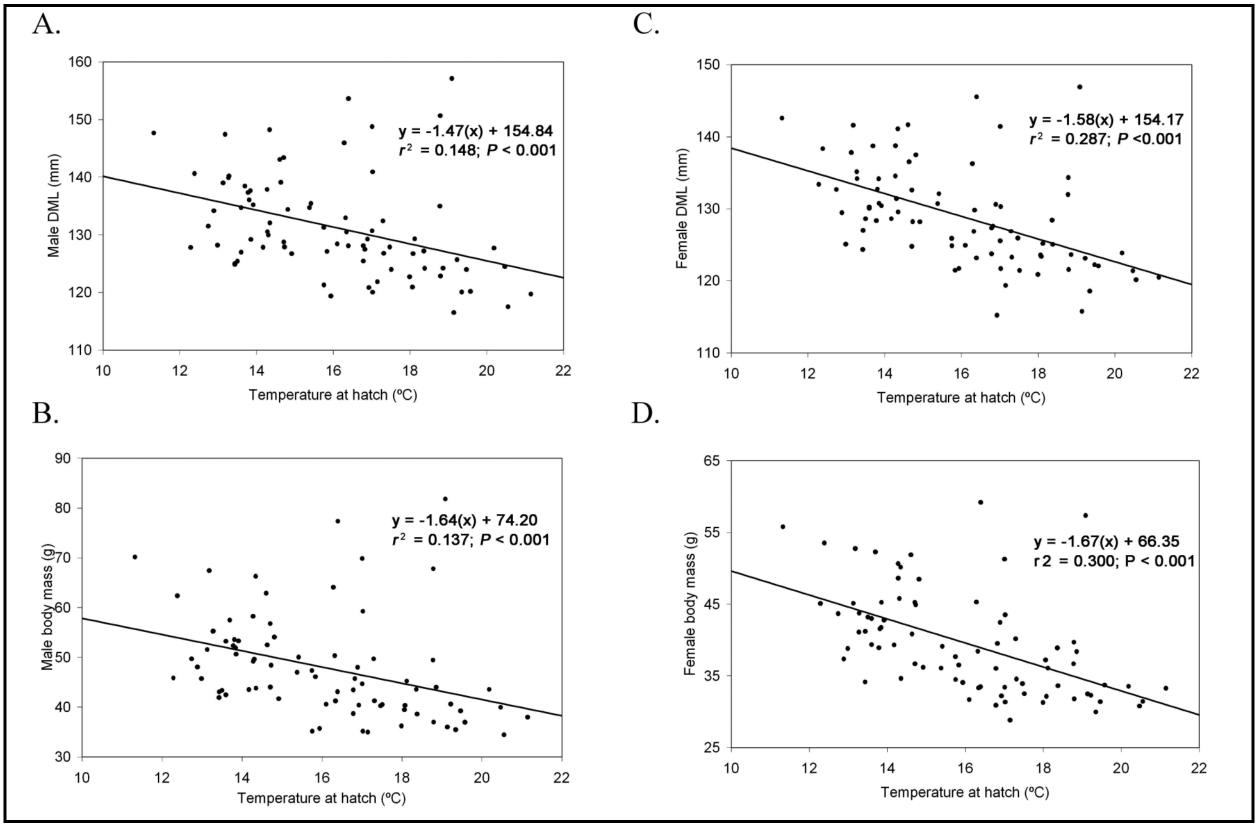

Figure 5. Monthly mean hatch sea surface temperature (SST) vs. male dorsal mantle length (DML) in millimeters (mm) (A); and male body mass in grams (g) (B); female DML (mm) (C); and female body mass (g) (D) for market squid harvested in the Southern California Bight, January 1999 through December 2002.

accompanied by rapid growth of phytoplanktonic diatoms (Tont 1981). Hardy (1993) noted that declines in sea surface temperatures of 2.5°C were often associated with an increase of four orders of magnitude in the standing stock of diatoms. Further, Moser et al. (2000) reported that plankton volumes in the California Current region are historically higher during the colder ocean conditions than warmer periods. Because temperature affects other variables that likely contribute to squid size at harvest, an ecosystem approach to management for this species should be considered.

Their spawning grounds are well documented and it has been shown that *L. opalescens* remain close to shore during the first month after hatch (Zeidberg and Hamner 2002). Still, we do not have a good idea of their distribution or migration during the intervening period. For our study, we assumed that *L. opalescens* exhibit site fidelity, implying that squid hatched in the northern or southern study areas return to the same general area to spawn. It is likely that there is some mixing of *L. opalescens* within the Bight, however, to what degree is unknown. Unquestionably, this mixing is reflected in our r^2 values. Further research, particularly stable isotope analysis of statoliths, should resolve this theory.

Presently, there is no estimate of squid biomass and California catch limits are based on previous record landings. To assure sustainability, the market squid fishery in California is currently being monitored through an egg escapement method (PFMC 2002). This method is based on ensuring a proportion of eggs (30%) are deposited prior to harvest. Potential fecundity is a function of DML (Macewicz et al. 2004). Our study found differences in squid size at-harvest relative to hatch temperature within the SCB which translates into potential reproductive differences. The DML of a squid hatched at 12ºC should reach 135 mm at-harvest; the DML of a squid hatched at 19ºC should reach 124 mm at-harvest. Because the relationship between DML and potential fecundity is linear, this results in an 8.9% decline to potential fecundity. We suggest that the reduced reproductive potential from warm water events needs to be considered in fishery management strategies for commercial harvest.

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REFERENCES

Berry, S. S. 1911. Notes on some cephalopods in the collection of the University of California. University of California Publications of Zoology 8:301–310.

Butler, J., J. M. Wagner and A.E. Henry. 2001. Age and Growth of *Loligo opalescens*. Pacific Fishery Management Council (PFMC) Squid Stock Assessment Review. Southwest Fisheries Science Center, La Jolla, CA, 14 pp.

Dorman, C.E. and D.P. Palmer. 1981. Southern California summer coastal upwelling. Pages 44–56. *In*: Richards, F.A. (ed.), Coastal Upwelling. American Geophysical Union, Washington, D.C.

Fields, W.G. 1950. A preliminary report on the fishery and on the biology of the squid, *Loligo opalescens*. California Fish and Game 36:366–377.

Fields, W.G. 1965. The structure, development, food relation, reproduction, and life history of the squid, *Loligo opalescens*, Berry. California Department of Fish and Game Fish Bulletin 131. 108 pp.

Forsythe, J. W., L.S. Walsh, P.E. Turk and P.G. Lee. 2001. Impact of temperature on juvenile growth and age at first egg-laying of the Pacific reef squid *Sepioteuthis lessoniana* reared in captivity. Marine Biology 138:103–112.

Hardy, J.T. 1993. Phytoplankton. Pages 233–265. *In*: Daily, M.D., D.J. Reish, and J.W. Anderson (eds.), Ecology of the Southern California Bight: A Synthesis and Interpretation. University of California Press, Berkeley and Los Angeles, CA, 926 pp.

Hatfield, E.M.C. 2000. Do some like it hot? Temperature as a possible determinant of variability in the growth of Patagonia squid, *Loligo gahi* (Cephalopoda: Loliginidae). Fisheries Research 47:27–40.

Hatfield, E.M.C, R.T. Hanlon, J.W. Forsythe and E.P M. Grist. 2001. Laboratory testing of a growth hypothesis for juvenile squid *Loligo pealeii* (Cephalopoda: Loliginidae). Canadian Journal of Fisheries and Aquatic Sciences 58:845–857.

Isaac, G., H. Neumeister and W.F. Gilly. 2001. The effects of temperature on early life stages of the California Squid (*Loligo opalescens*). Pacific Fishery Management Council Squid Stock Assessment Review. Southwest Fisheries Science Center, La Jolla, CA, 15 pp.

Jackson, G.D., J.W. Forsythe, R.F. Hixon and R.T. Hanlon. 1997. Age, growth, and maturation of *Lolliguncula brevis* (Cephalopoda: Loliginidae) in the northwestern Gulf of Mexico with a comparison of length-frequency versus statolith age analysis. Canadian Journal of Fisheries and Aquatic Sciences 54:2907–2919.

Jackson, G.D. and M.L. Domeier. 2003. The effects of an extraordinary El Niño/La Niña event on the size and growth of the squid *Loligo opalescens* off California. Marine Biology 142:925–935.

Macewicz, B. J., J.R. Hunter, N.C.H. Lo and E.L. LaCasella. 2004. Fecundity, egg depositions, and mortality of market squid, *Loligo opalescens*. Fishery Bulletin 102:306–327.

Maxwell, M. R. 2001. Stock Assessment Models for the Market Squid, *Loligo opalescens.* Pacific Fishery Management Council Squid Stock Assessment Review. Southwest Fisheries Science Center, La Jolla, CA, 53 pp.

McGowan, J.A. 1954. Observations on the sexual behavior and spawning of the squid, *Loligo opalescens*, at La Jolla, California. California Department of Fish and Game Fish Bulletin 40:47–55.

Moser, G.H., R.L Charter, W.Watson, D.A. Ambrose, J.L. Butler, S.R. Charter and E.M. Sandknop. 2000. Abundance and distribution of rockfish (*Sebastes*) larvae in the Southern California Bight in relation to environmental conditions and fishery exploitation. California Cooperative Fisheries Investigations Report 41:132–147.

Oosthuizen, A., M.J. Roberts and W.H.H. Sauer. 2002. Temperature effects on the embryonic development and hatching success of the squid *Loligo vulgaris reynaudii*. Bulletin of Marine Science 71:619–632.

PFMC (Pacific Fishery Management Council). 2002. Fisheries Off West Coast States and in the Western Pacific; Coastal Pelagic Species Fishery; Amendment 10, Portland, OR, 52 pp.

Perez, J.A.A. and R.K. O'Dor. 1998. The impact of environmental gradients on the early life inshore migration of the short-finned squid *Illex illecebrosus*. South African Journal of Marine Science 20:293–303.

Tont, S.A. 1981. Temporal variations in diatom abundance off southern California in relation to surface temperature, air temperature and sea level. Journal of Marine Research 39:191–201.

Vidal, E.A.G., F.P. DiMarco, J.H. Wormuth and P.G. Lee. 2002. Influence of temperature and food availability on survival, growth, and yolk utilization in hatchling squid. Bulletin of Marine Science 71:915–931.

Zeidberg, L.D. and W.M. Hamner. 2002. Distribution of squid paralarvae, *Loligo opalescens* (Cephalopoda: Myopsida), in Southern California Bight in the three years following the 1997–1998 El Niño. Marine Biology 141:111–122.