Does the California market squid (*Loligo opalescens*) spawn naturally during the day or at night? A note on the successful use of ROVs to obtain basic fisheries biology data

John Forsythe

National Resource Center for Cephalopods
University of Texas Medical Branch at Galveston
301 University Blvd
Galveston, Texas 77555-1163
E-mail address: john.forsythe@utmb.edu

Nuutti Kangas

Roger T. Hanlon

Marine Resources Center
Marine Biological Laboratory
Woods Hole, Massachusetts 02543

The California market squid (*Loligo opalescens* Berry), also known as the opalescent inshore squid (FAO), plays a central role in the nearshore ecological communities of the west coast of the United States (Morejohn et al., 1978; Hixon, 1983) and it is also a prime focus of California fisheries, ranking first in dollar value and tons landed in recent years (Vojkovich, 1998). The life span of this species is only 7–10 months after hatching, as ascertained by aging statoliths (Butler et al., 1999; Jackson, 1994; Jackson and Domier, 2003) and mariculture trials (Yang, et al., 1986). Thus, annual recruitment is required to sustain the population. The spawning season ranges from April to November and spawning peaks from May to June. In some years there can be a smaller second peak in November. In Monterey Bay, the squids are fished directly on the egg beds, and the consequences of this practice for conservation and fisheries management are unknown but of some concern (Hanlon, 1998). Beginning in April 2000, we began a study of the *in situ* spawning behavior of *L. opalescens* in the southern Monterey Bay fishing area.

The prevailing thought is that the majority of spawning activity takes place at night because fishermen have observed these squids mating under their bright lights (which are used to attract and capture squids) and because television documentaries have revealed mating and spawning activity in large aggregations at night. The scientific literature on reproductive behavior is sparse. There are some cursory observations of actively spawning *L. opalescens* during diver surveys of egg beds (McGowan, 1954; Fields, 1965; Hobson, 1965; Hurley, 1977). Some daytime spawning has been seen both in southern and northern California but Fields (1965) and Hixon (1983) suggested indirectly that most spawning occurs at night. Shimek et al. (1984) also suggested night spawning by *L. opalescens* in Canada. Other loliginid squids whose natural behavior has been studied in the field were found to be daytime spawners (e.g., *L. pealeii*, *L. vulgaris reynaudii*, *Sepioteuthis sepioidea*; summarized in Hanlon and Messenger, 1996).

To help resolve this issue, we conducted three field expeditions (28 April–8 May 2000, 10–17 September 2000, and 16–21 August 2001) using remotely operated vehicles (ROVs) deployed either from the RV *John Martin* (Moss Landing Marine Laboratory) or the commercial squid FV *Lady J*. The ROVs were tethered vehicles with onboard video cameras and lights. Live video signals were transmitted by the tether to shipboard VCRs where observational data were viewed and recorded. For the first field trip, a large S4 Phantom ROV was used; it was outfitted with a video camera and zoom lens with tilt capability, and the video was recorded on Hi8 format video decks. For the second and third trips, a smaller S2 inspection-class Phantom ROV on loan from the NOAA Sustainable Seas Expeditions was used; this ROV had a customized fiber-optic tether and the video data were recorded on mini-digital video cassettes. Our goal was to make ROV dives each day from approximately dawn to dusk and to make a few comparable all-night surveys. A combination of adverse weather conditions and technical problems with the ROVs rarely allowed continuous video observations. During dives, if squids were encountered, we used video to conduct focal animal samples on females (which were paired) for as long as squids were present, or as long as we could keep track of the same individuals. Unless absolutely necessary to see the squids (for instance at night or at depths greater than 30 m in turbid daytime conditions), lights were not used for video taping in an effort to minimize their impact on the mating squids. Squids acclimated within minutes to the ROVs. After the expeditions, the videotapes were studied and the behavioral and biological data were quantified on a multimotion playback VCR.

By "mating" we refer to the peculiar mating behavior of this species that is unique among loliginid squids. The male firmly grasps the female from her ventral side and holds her for minutes or hours in a "copulatory embrace" in a nearly vertical position. Both copulation (i.e., transfer of spermatophores) and deposition of egg capsules occur in this posture. For example, as the female exudes a new egg capsule, the male and female lower themselves in unison to the egg bed where the female deposits the egg capsule in the sand. We have reported elsewhere on egg-

Manuscript approved for publication
20 January 2004 by Scientific Editor.

Manuscript received 25 January 2004
at NMFS Scientific Publications Office.

Fish. Bull. 102:389–392 (2004).

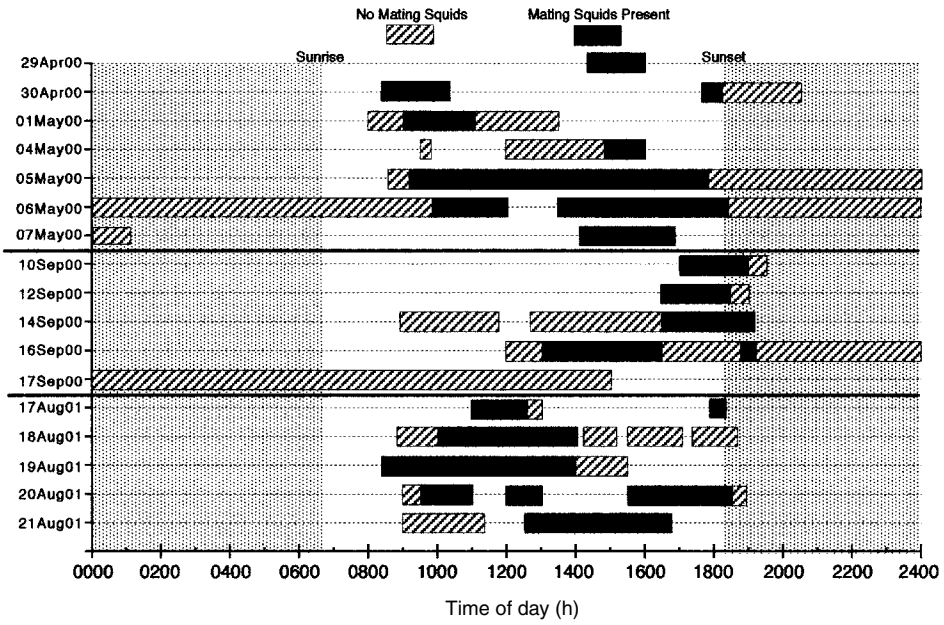

Figure 1

A summary of 154 spawning groups of *Loligo opalescens* showing the daily presence or absence of mating squids on egg beds in Monterey Bay, California. The horizontal bars represent the time periods when a ROV was on the bottom searching for mating squids during three different expeditions. Note three occasions in which operations were conducted continuously through the day and night, and also that spawning ceased at dusk.

laying frequency (Hanlon et al., in press). Only very rarely did we observe females laying eggs while unattended by a male; in these cases the female was moribund and laying her last few egg strands.

Results and discussion

We examined 28 hours of videotape recorded during 50 ROV dives over 18 days (divided into three expeditions). Figure 1 illustrates the relative presence or absence of mating *Loligo opalescens* throughout 24-hour periods. The large gaps in the daytime observation record were due to ROV problems. Although observation times varied daily, it is clear that normal mating and egg-laying behaviors were exclusively observed during daylight hours (ca. 0800–1800 hours but with some seasonal variation) and concluded near dusk. In all instances in Figure 1 where egg-laying extended into the early evening, these mating assemblages had formed during daylight hours and persisted slightly past sunset and the number of participating squids constantly decreased as sunset approached and passed. Observations were made throughout the night on three nights. Not only were no mating squids ever encountered around the egg beds at night, but generally no squids were encountered at all near the seabed, despite large aggregations that were present higher in the water column. Thus the 200–400 watt lights on the ROVs never induced any artificial spawning behavior because there were no squids present.

Figure 2 provides some quantification of Figure 1. This graph is based on 154 spawning groups that were videotaped and includes all three trips as well as the three "all night observations" illustrated in Figure 1. We were studying discrete groups of squids to examine mating dynamics and thus were sometimes biased to smaller groups of squids that could be kept in view. Overall, we observed that squids were present in greatest numbers in mid to late afternoon and absent during the night.

Our findings strongly indicate that the extensive egg beds produced at depths of 20–60 m in southern Monterey Bay (just beyond the kelp beds) are the result of daytime aggregations of mating *Loligo opalescens*. These benthic aggregations begin forming in the early morning hours and tend to be larger in the afternoon. Reproductive activity begins to wane toward sunset and comes to a near halt at sunset. We could find no evidence that egg laying occurs naturally during the night. All observations that we are aware of (mainly television documentaries) have occurred in the presence of artificial light sources near the surface provided either by fishermen or cinematographers. In the absence of artificial lighting, *L. opalescens* in South Monterey Bay does not aggregate into mating and spawning groups at night. Thus, we conclude that all significant egg deposition in the Monterey Bay fishery is the result of daytime aggregations of squids.

Two other ascribed characteristics of *L. opalescens* spawning are mass aggregations at the sea floor and subsequent die-offs after squids have spawned. Mass aggregations can be detected by standard fathometers used by commercial fishermen, who report that mass aggregations on the sea floor are rare in Monterey Bay. During our ROV operations we encountered only one large aggregation, which occurred on 21 August 2001. We estimated from our video recordings that there were approximately 3000–4000 squid in a 50-m^2 area on the sea floor and that intermittent egg laying was occurring over an area of ca. 2000 m^2 during a period of about 3 hours. Collectively, then, we recorded 154 very small spawning groups and one large spawning group. There was no mass die-off during or after this large spawning aggregation. Instead, we consistently observed in all spawning groups that females actively broke the embrace of the paired male and jetted strongly upwards away from the spawning groups and rejoined large schools in the upper water column. Thus, squids that dispersed from the egg beds were consistently in excellent condition — certainly not senescent or moribund. These observations corroborate the results of other studies on loliginid squids that spawn intermittently (Moltschaniwskyj, 1995; Maxwell and Hanlon, 2000). Twice we encountered large numbers of dead squids on the sea floor in the early morning, but in both instances the squid fishing fleet had been working in the same area the night before and it appeared as though these mortalities were associated with the purse-seine fishery; there were few eggs in those localities. McGowan (1954), Hobson (1965), and Cousteau and Diole (1973) reported that squids died after spawning in S. California. Various *Loligo* spp. are noted for flexible reproductive strategies (*cf.* Hanlon and Messenger, 1996) so it should not be surprising if *L. opalescens* occasionally engaged in large reproductive events. Our data suggest that small groups of squids (20–200 individuals) generally descend during the day and lay eggs for several hours before rejoining squids in the water column. We encourage other researchers to use ROVs or SCUBA without lights and with stealthy approaches to determine the natural diurnal spawning of *L. opalescens* throughout its range. Given our findings that active sexual selection processes are occurring during the day and that there is vertical migration between the large schools of squid in the water column and the small spawning groups at the substrate, it would be prudent, at the very least, to restrict daytime fishing directly over egg beds or to create protected spawning areas in southern Monterey Bay. This strategy would allow the complex mating system of *L. opalescens* to be played out without direct disruption by fishing activity. In such a short-lived species, annual recruitment to the population is necessary; thus sufficient eggs must be laid for each new generation to ensure a viable living resource.

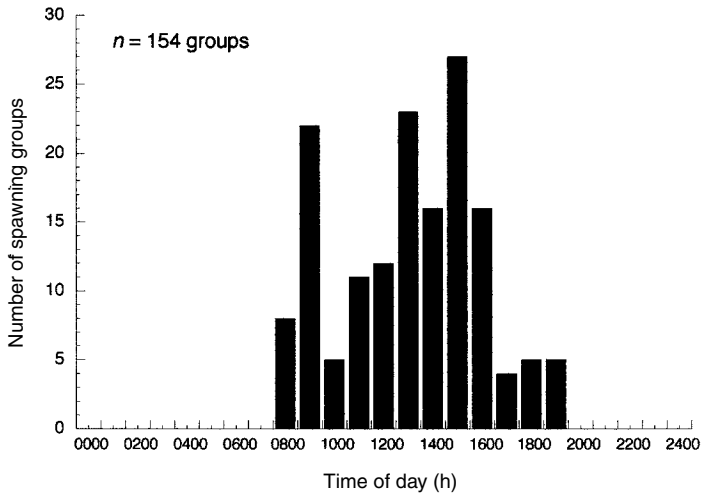

Figure 2

The number of squid spawning groups at the egg beds at different times of day (data pooled from three expeditions over 2 years; n=154 groups). A group is defined as a group of two or more mating pairs. These data correspond hour by hour with data in Figure 1.

Acknowledgments

We are most grateful for funding on NOAA grant UAF 98 0037 from the National Undersea Research Center (West Coast). Additional funding was provided by the David and Lucile Packard Foundation and the Sholley Foundation. J. Forsythe gratefully acknowledges financial support for travel from the National Institutes of Health, National Center for Research Resources (grant P40 RR0102423-23), and the Marine Medicine General Budget account of the Marine Biomedical Institute. N. Kangas gratefully acknowledges financial support from the Academy of Finland. We thank Sylvia Earle for loan of the Sustainable Seas ROV and we appreciate the professional efforts of Deep Ocean Exploration and Research (DOER) who supported the ROV operations. We especially thank John Rummel who helped begin this project, and Brett Hobson who kept it going at a critical juncture. We are thankful for expert shipboard assistance from the captains and crew of the RV *John Martin* and the FV *Lady J* (especially Captain Tom Noto). We benefitted from discussions with Bob Leos, Bill Gilly, Annette Henry, John Butler, Teirney Thies, and Sue Houghton.

Literature cited

Butler, J., D. Fuller, and M. Yaremko.
1999. Age and growth of market squid (*Loligo opalescens*) off California during1998. CalCOFI Rep. 40:191–195.

Cousteau J.-Y., and P. Diole.
1973. Octopus and squid: the soft intelligence, 304 p. Cassell, London.

Fields, W. G.
1965. The structure, development, food relations, reproduction, and life history of the squid *Loligo opalescens* Berry. Fish. Bull. 131:1–108.
Hanlon, R. T.
1998. Mating systems and sexual selection in the squid *Loligo*: How might commercial fishing on spawning squids affect them? CalCOFI Rep. 39:92–100.
Hanlon, R.T., N. Kangas, and J. W. Forsythe.
In press. Rate of egg capsule deposition, changing OSR and associated reproductive behavior of the squid *Loligo opalescens* on spawning grounds. Mar. Biol.
Hanlon, R. T., and J. B. Messenger.
1996. Cephalopod behaviour, 232 p. Cambridge Univ. Press, Cambridge.
Hixon, R. F.
1983. *Loligo opalescens*. *In* Cephalopod life cycles, vol. I, species accounts, 475 p. Academic Press, London.
Hobson, E. S.
1965. Spawning in the Pacific Coast squid. *Loligo opalescens*. Underwater Naturalist 3:20–21.
Hurley, A. C.
1977. Mating behavior of the squid *Loligo opalescens*. Mar. Behav. Physiol. 4:195–203.
Jackson, G. D.
1994. Statolith age estimates of the loliginid squid *Loligo opalescens*: corroboration with culture data. Bull. Mar. Sci. 54:554–557.
Jackson, G. D., and M. L. Domeier.
2003. The effects of an extraordinary El Nino/La Nina event on the size and growth of the squid *Loligo opalescens* off Southern California. Mar. Biol. 142:925–935.
Maxwell, M. R., and R. T. Hanlon.
2000. Female reproductive output in the squid *Loligo pealeii*: multiple egg clutches and implications for a spawning strategy. Mar. Ecol. Prog. Ser. 199:159–170.
McGowan, J. A.
1954. Observations on the sexual behavior and spawning of the squid, *Loligo opalescens*, at LaJolla, CA. Cal. Fish Game 40:47–54.
Moltschaniwskyj, N. A.
1995. Multiple spawning in the tropical squid *Photololigo* sp.: what is the cost in somatic growth? Mar. Biol. 124:127–135.
Morejohn, G. V., J. T. Harvey, and L. T.Krasnow.
1978. The importance of *Loligo opalescens* in the food web of marine vertebrates in Monterey Bay, California. *In* Biological, oceanographic, and acoustic aspects of the market squid, *Loligo opalescens* Berry (C. W. Recksiek and H. W . Frey, eds.), p. 67–98. Calif. Dep. Fish Game Fish Bull. 169.
Shimek, R. L., D. Fyfe, L. Ramsey, A. Bergey, J. Elliott, and S. Guy.
1984. A note on spawning of the Pacific market squid, *Loligo opalescens* (Berry, 1911), in the Barkley sound region, Vancouver Island, Canada. Fish. Bull. 82:445–446.
Vojkovich, M.
1998. The California fishery for market squid (*Loligo opalescens*). CalCOFI Rep. 39:55–60.
Yang, W. T., R. F. Hixon, P. E. Turk, M. E. Krejci, W. H. Hulet, and R. T. Hanlon.
1986. Growth, behavior, and sexual maturation of the market squid, *Loligo opalescens*, cultured through the life cycle. Fish. Bull. 84:771–798.