The spawning dynamics of California market squid (*Doryteuthis opalescens*) as revealed by laboratory observations

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ABSTRACT

California market squid (*Doryteuthis opalescens*) are fast-growing, semelparous and short-lived, making them the archetypal live-fast, die-young species. They form spawning aggregations that are targeted by a wide variety of predators and the largest commercial fishery in California. Despite their ecological and economic importance, relatively little is known about the life history of spawning *D. opalescens*. To gain insight into this life stage we performed controlled observational experiments on groups of mature *D. opalescens* collected from the spawning grounds. In all trials we observed extreme synchrony in egg-deposition and subsequent mortality. Importantly, we observed a prespawning period in which mature *D. opalescens* congregate on the spawning grounds for up to 2 weeks prior to spawning. During this period they are susceptible to predation and harvesting. We also present the first empirical estimates of postspawning mortality and egg-deposition rates. Taken together, our results suggest that the first day of spawning is critical to the viability of this species.

INTRODUCTION

Squid are well known to be ‘high-energy’ adapted—they grow rapidly, disperse widely and are short-lived (O’Dor & Webber, 1986). Many species attain weights in excess of 10 kg in less than 2 years and all are functionally semelparous (Boyle & Rodhouse, 2008). Spawning aggregations are thought to be a by-product of this high-energy lifestyle and complex spawning behaviour is common in squids. Perhaps no species is more emblematic of this life history than *Doryteuthis opalescens* (Berry, 1911), the California market squid. *Doryteuthis opalescens* lives for 6–9 months (Butler, Fuller & Yaremko, 1999), is distributed from Baja California to southeastern Alaska (Okutani & McGowan, 1969) and often forms large spawning aggregations on communal egg-beds (Fields, 1965).

*Doryteuthis opalescens* is also the most valuable fishery target in California, with recent annual landings exceeding 100,000 tonnes. However the fishery exclusively targets spawning aggregations, which is a notoriously risky strategy as catch-based abundance estimates from spawning aggregations tend to overestimate true abundance (Paloheimo & Dickie, 2001; Sadowy & Domeier, 2005). This results in the illusion of plenty during periods of scarcity. Despite this vulnerability, and the economic and ecological importance of this species, there are major knowledge gaps in our understanding of the spawning dynamics of *D. opalescens*.

Early observations of the spawning behaviour of *D. opalescens* were primarily qualitative. They described copulation positions, sex ratios and the presence of dead individuals after spawning (McGowan, 1954; Fields, 1965; Vaughan & Recksiek, 1979). It was noted that large spawning groups were common in the wild and that *D. opalescens* appeared to use a ‘big-bang’ strategy in which synchronized spawning occurred over only a few days (McGowan, 1954; Fields, 1965).

More recent studies have challenged this idea. *In situ* observational studies using ROVs concluded that *D. opalescens* uses a gradual spawning strategy where expansive egg beds are built up slowly over weeks (Forsythe, Kangas & Hanlon, 2004; Hanlon, Kangas & Forsythe, 2004). However, the presence of ‘mega-aggregations’ has been noted, in which heavy spawning takes place in a single night (Forsythe et al., 2004). Therefore, in locations of high population density (such as the southern California Bight), a spawning strategy more closely resembling a ‘big-bang’ may be prevalent. Unfortunately, it is difficult to quantify spawning vital rates in the field (e.g. mortality rates and total egg-deposition); therefore laboratory observations are necessary for additional insight.

In previous laboratory studies of *D. opalescens*, spawning occurred over several weeks and individuals died shortly after spawning (Yang et al., 1983, 1986). However, precocious maturation and spawning occurred in individuals of less than 80 mm dorsal mantle length. Similar precocious maturation has been observed in other squid maintained in the laboratory (Durward, 1980; Hanlon, Hixon & Hulet, 1983). Therefore, it is possible that the behaviour of squid observed in previous laboratory experiments was affected by the squid spending their entire life in captivity. In nature, individuals arrive on the spawning
grounds when they are sexually mature (Macewicz et al., 2004). However, the amount of time spent on the grounds prior to spawning is not known and the total duration of wild spawning has not been documented. Congeneric species exhibit multiple paternity within egg capsules, suggesting a highly competitive mating system (Buresch et al., 2003), and previous observations of spawning D. opalescens suggest a strong dominance hierarchy among males (Hurley, 1977). However, despite the competitive and physically intense nature of mating, protracted spawning periods (up to 40 d) have been documented in congeneric species, e.g. D. pealeii (Maxwell & Hanlon, 2000). Therefore, an important unresolved question is whether the spawning duration of D. opalescens is similar to that observed in other squids.

To understand this life stage better, we performed controlled observational experiments on groups of wild-caught D. opalescens held in the laboratory. We measured the duration of the pre-spawning period as well as the mortality rate, egg-deposition rate, egg-development rate and the weight loss incurred due to spawning. We conclude with implications for the sustainability of California’s largest fishery.

MATERIAL AND METHODS

Doryteuthis opalescens were jig-caught by the authors in La Jolla, California, on 26 August, 12 November and 1 December 2013, at depths of 25–30 m. All squid were visually inspected to determine their maturation stage (following Macy, 1982) and it was found that only mature squid (stage 4 of Macy, 1982) were captured. In addition, all squid were caught on known spawning grounds in La Jolla and the presence of benthic egg capsules was verified using SCUBA observations within 7 d of squid collection. Squid were transported to the laboratory in a 121-l aerated barrel. Ten squid were collected in the August and November experiments and nine squid in the December experiment, to minimize accidental contact of the squid with the walls.

Upon capture each individual was measured, weighed and sexed (by visual inspection) and these measurements were taken again on the day of its death. Squid were fed 20% of their initial body weight per day, following Yang et al. (1986). The main food source was live mysid shrimp. The mysid shrimp were collected in La Jolla twice per week and were supplemented with hippolytid shrimp. Squid were fed each morning and the presence of free-swimming prey in the tank was confirmed twice per day. Water temperature, squid mortality and egg-deposition were recorded each morning between 8 am and 11 am. Eggs were removed each morning and subsampled eggs were transferred to individual holding tanks for the egg development observations. The average number of eggs per capsule was estimated by sampling 30 capsules from each experiment and counting all eggs under a dissecting microscope. Instantaneous mortality of spawning adults was estimated using the exponential decay model: \( \log(y) = b_0 + b_1x \), where \( y \) is the abundance of squid on spawning day \( x \), and \( b_0 \) and \( b_1 \) are estimated by linear regression. All experiments were grouped together for the analysis providing a total sample of 29 individuals. All statistical analyses were performed in the R computing language.

To assess egg development rates, up to three eggs capsules were subsampled from each spawning day during the November and December experiments. Each egg capsule was placed in an individual 5-l rectangular tank with flow-through ambient seawater. Egg capsules were suspended above the bottom of the tank by tying the capsule anchor to the central standpipe with a short piece of string (following Vidal et al., 2002). A low flow-rate and weak aeration were provided to ensure that all eggs received sufficient oxygen for normal development. Newly hatched squid were counted each morning and removed. Unhatched eggs were counted 2 weeks after hatching terminated, to ensure that all eggs had an opportunity to hatch. The mean temperature of the ambient seawater was 16.5 °C and 16.0 °C, for the November and December experiments, respectively.

RESULTS

In all experiments, we observed an initial prespawning period of up to 11 d in which individuals continued to feed but did not copulate or spawn (Fig. 1A, C). After this prespawning period, the squid terminated feeding and copulation began. Copulation was observed to be exclusively in the parallel position, in which the male grasps the female’s mantle while both are orientated in the same direction (Drew, 1911). The extended mating embrace of D. opalescens as described by Hanlon et al. (2004) typically began the day immediately before the mass-spawning event. Initial mating embraces persisted for several hours, after which the females were released and only embraced intermittently. In all experiments, on the night following the first observed copulation, a large spawn occurred which accounted for ca. 90% of the total eggs deposited (Fig. 1B, D). Immediately after egg deposition, dominant males exhibited egg-guarding behaviour similar to that described in previous studies (e.g. Hurley, 1977). This was followed by mortality of all squid within 11 d (Fig. 1A, C).

Using the exponential decay model we estimated a daily spawning mortality rate of 0.21. This is within the range of rates previously assumed in population-dynamics models of D. opalescens (Macewicz et al., 2004; Dorval, Cron & McDaniel, 2013). In contrast, egg deposition did not follow a smooth exponential model as has been previously assumed; rather it more closely resembled a short-duration spike in which nearly all eggs are deposited in a single event (Fig. 1B). The average total number of capsules deposited per female was 19.7 and the average number of eggs per capsule was 102.4, therefore each female deposited c. 2000 eggs before death (similar to reports by Fields, 1965, and Macewicz et al., 2004).

Both females and males exhibited dramatic weight loss associated with spawning (Fig. 2). The average weight loss for females was 43%, while males lost 27% of their body weight. The difference in weight loss was strongly significant (t-test, \( P < 0.001 \)). Importantly, the prespawn and postspawning weight distributions for females were nonoverlapping, which supports our hypothesis that the females were captured prior to spawning. The observed weight loss is likely due to the termination of feeding during spawning, as well as the high energy expenditures associated with mating and the deposition of egg capsules.

In agreement with previous studies (Fields, 1965), males were slightly longer and heavier than females on average, however the difference was not statistically significant. Small males, which may have been ‘sneaker’ males (Zeidberg, 2009), were present. Also in agreement with previous research (Zeidberg et al., 2011), the majority of individuals hatched during the first week of hatching (Fig. 3). Hatching typically terminated within 2 weeks, although it persisted in two capsules for up to 22 d. Similar to previous studies (Zeidberg et al., 2011), the time to first hatch was significantly correlated with mean temperature during incubation (linear regression, \( R^2 = 0.74, P < 0.001 \)).
The mean number of unhatched eggs per capsule was 11.6, corresponding to a mean hatching success of 83.3%.

**DISCUSSION**

Our results suggest that *Doryteuthis opalescens* aggregates on the spawning grounds for up to 2 weeks prior to spawning. Copulation occurs after this prespawning period and egg-deposition commences within the following 24 h. To our knowledge this is the first evidence of prespawning aggregation behaviour in *D. opalescens*. Similar prespawning behaviour has been observed in other loliginids (e.g. Sauer *et al.*, 1997) and was associated with complex lek-like behaviour. A lek-mating system has not been observed in *D. opalescens*, however the prespawning period provides ample opportunity for the formation of a dynamic mating arena where intensive sexual selection may occur. It may also serve to increase group size to achieve predator satiation during spawning, as heavy predation on spawning squid is well known (Morejohn, Harvey & Krasnow, 1978; Francis *et al.*, 1991; pers. obs.).

Once spawning begins, *D. opalescens* exhibits highly synchronous egg-deposition, primarily within 24 h, followed by rapid mortality. Strong postspawning mortality has been documented in other loliginids (e.g. Hanlon *et al.*, 1983; Rocha, Guerra & Gonzalez, 2001), however the degree of synchrony observed here appears to be the most extreme example of this phenomenon. The rapid postspawning mortality may be due to the extended mating embrace, described by Hanlon *et al.* (2004), which is unique to this species. Females showed significant mantle damage as a result of the embrace and this physical trauma likely shortens the spawning duration of *D. opalescens* compared with other loliginids. Males also experienced a high level of physical trauma while competing for females; this behaviour is likely driven by *Loligo* β-microseminoprotein pheromone emitted by females and egg capsules (Cummins *et al.*, 2011). The large proportion of eggs spawned on the first day, combined with the low survival thereafter, suggest that the initial day of spawning is critical to the successful propagation of the population, while each additional day is of decreasing value.

A concern in any laboratory study is the degree to which the artificial environment affects the animal's behaviour. Nevertheless, we believe the observed prespawning period is unlikely to be an artefact of the laboratory environment for the following reasons. First, *D. opalescens* terminates feeding while spawning (Fields, 1965; pers. obs.) and all squid in this study were jig-caught (hooked on their tentacles) on the spawning grounds, suggesting they were actively feeding in the wild. Second, the squid continued to feed actively in the laboratory during the pre-spawning period and only terminated feeding once spawning began. Third, all individuals were of high mantle quality when

![Figure 1. Spawning and survival curves of *Doryteuthis opalescens* in all experiments. Each line represents a separate experiment. In all experiments there was a prespawning period of at least one week (**A**, **C**), after which spawning occurred (**B**), followed by rapid mortality. The first two nights of spawning accounted for at least 80% of the total spawned eggs (**D**).](https://academic.oup.com/mollus/article-abstract/82/1/37/2459933/The-spawning-dynamics-of-California-market-squid/821/37/2459933/fig1.png)
captured; postspawning squid have severely depleted mantle condition (Macewicz et al., 2004). Therefore we feel confident that the squid captured in this study were prespawning individuals. Laboratory effects cannot be ruled out however, and future work is needed to provide additional observations of field-estimated spawning rates (i.e. building upon Hanlon et al., 2004). In this regard, field-tagging studies similar to those by Sauer, Lipinski & Augustyn (2000) may be useful.

Previous estimates of total fecundity of *D. opalescens* were c. 50–70 capsules per female (Hanlon et al., 2004). However, our observations of 19.7 capsules per female more closely agree with the estimate of 21.25 by Fields (1965). Our results also suggest that estimates of spawning taking place for up to 1 week (e.g. Macewicz et al., 2004) are probably overestimates, as most fecundity appears to be expended on the first day of spawning. The removal of egg capsules each morning may have decreased the rate of egg-deposition compared to that in the wild, as the presence of eggs stimulates spawning in *D. opalescens* (Fields, 1965; Hurley, 1977; Yang et al., 1986). Therefore our spawning rate estimate may be viewed as conservative.

Our experimental setup utilized a flow-through seawater system; therefore the water temperature in our experiment was equivalent to the ambient surface water temperature in the coastal ocean near La Jolla at that time. Squid on the spawning grounds utilize the entire water column (Hanlon et al., 2004), therefore they would experience similar temperatures in the wild as in our experiment. However, the bottom temperature at the egg beds is 4–5 °C colder than that of our experiments (unpublished data) and it is not known if this impacted the squid’s behaviour. In the egg-hatching observations the increased temperature led to a predictable decrease in egg-incubation times (Zeidberg et al., 2011).

Recently, an egg-escapement model has been proposed for estimating the effect of harvesting on spawning *D. opalescens* (Macewicz et al., 2004; Dorval et al., 2013). An egg-escapement model estimates this effect by measuring the number of eggs remaining in harvested females (residual fecundity) and comparing that with the number of eggs expected in a female that dies naturally. Years in which females have high residual fecundity correspond to years of high harvesting rates, and vice versa. Here we provide the first empirical estimates of previously unknown vital rates on which the model relies. Encouragingly, our mortality rate estimate is similar to that assumed previously. Our estimate of egg-deposition rate appears to be significantly higher than that previously assumed, although our estimated spawning duration of 1–2 d agrees with previous estimates (1.67 d; Macewicz et al., 2004). Therefore, the results of this study could be incorporated into an updated egg-escapement model with a higher egg-deposition rate.

The rapid mortality of postspawning individuals and the high proportion of early-deposited eggs suggest that females can

Figure 2. Histogram of individual weights of *Doryteuthis opalescens* before and after spawning. Individuals from all experiments are shown. Bar height represents the number of individuals at each weight. Light grey bars are prespawn measurements, dark grey bars are postspawn measurements and medium grey bars are overlapping prespawn and postspawn measurements. Females exhibited large losses in weight associated with spawning, losing c. 50% of their body weight (A). Males also exhibited substantial weight loss (B), although less than females.
achieve a high percentage of their reproductive potential if they are allowed to complete just one day of spawning. However, the presence of individuals on the spawning grounds for up to 2 weeks prior to spawning suggests that there is a high probability of mortality immediately prior to spawning due to predation and harvesting. During periods of high abundance this is less likely to be a concern, as predator satiation will occur due to the immense number of squid in the spawning aggregations. However, at low abundance, it is possible that spawning aggregations may be extirpated before realizing their full reproductive potential. Under the current fishery management strategy, harvesting is prohibited at weekends, which increases the probability that individuals will spawn prior to being captured. However, given that the abundance of several important predators of squid is at or near historical highs (e.g. California sea lions and harbour seals; Carretta et al., 2014), further conservation measures may be required during periods of low squid abundance.

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