Fecundity, egg deposition, and mortality of market squid (*Loligo opalescens*)

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Abstract—*Loligo opalescens* live less than a year and die after a short spawning period before all oocytes are expended. Potential fecundity (E_P), the standing stock of all oocytes just before the onset of spawning, increased with dorsal mantle length (L), where $E_P = 29.8L$. For the average female squid (L of 129 mm), E_P was 3844 oocytes. During the spawning period, no oogonia were produced; therefore the standing stock of oocytes declined as they were ovulated. This decline in oocytes was correlated with a decline in mantle condition and an increase in the size of the smallest oocyte in the ovary. Close agreement between the decline in estimated body weight and standing stock of oocytes during the spawning period indicated that maturation and spawning of eggs could largely, if not entirely, be supported by the conversion of energy reserves in tissue. *Loligo opalescens*, newly recruited to the spawning population, ovulated about 36% of their potential fecundity during their first spawning day and fewer ova were released in subsequent days. *Loligo opalescens* do not spawn all of their oocytes; a small percentage of the spawning population may live long enough to spawn 78% of their potential fecundity.

Loligo opalescens are taken in a spawning grounds fishery off California, where nearly all of the catch are mature spawning adults. Thirty-three percent of the potential fecundity of *L. opalescens* was deposited before they were taken by the fishery (December 1998–99). This observation led to the development of a management strategy based on monitoring the escapement of eggs from the fishery. The strategy requires estimation of the fecundity realized by the average squid in the population which is a function of egg deposition and mortality rates. A model indicated that the daily total mortality rate on the spawning ground may be about 0.45 and that the average adult may live only 1.67 days after spawning begins. The rate at which eggs escape the fishery was modeled and the sensitivity of changing daily rates of fishing mortality, natural mortality, and egg deposition was examined. A rapid method for monitoring the fecundity of the *L. opalescens* catch was developed.

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Many loliginid squid populations depend entirely upon the reproductive output of the preceding generation because individuals live less than a year (Yang et al., 1986; Hatfield, 1991, 2000; Natsukari and Komine, 1992; Arkhipin, 1993; Arkhipin and Nekludova, 1993; Jackson, 1993, 1994; Jackson et al., 1993; Boyle et al., 1995; Jackson and Yeatman, 1996; Jackson et al., 1997; Moltschaniwskyj and Semmens, 2000; Semmens and Moltschaniwskyj, 2000). In California waters, *Loligo opalescens* (market squid, also known as the opalescent inshore squid [FAO]) live only 6–12 months (Butler et al., 1999) and die after spawning (McGowan, 1954; Fields, 1965). Thus, fecundity of *L. opalescens* is a critical life history trait and, in addition, must be known in order to estimate the biomass with either egg deposition or larval production methods (Hunter and Lo, 1997). *Loligo opalescens* is one of the most valuable fishery resources in California waters and is monitored under the Coastal Pelagics Species Fishery Management Plan of the Pacific Fishery Management Council as market squid.

Laptikhovsky (2000) pointed out that squid fecundity estimates would be biased if the females spawned ova prior to capture, if oocytes remained in the ovary after death, or if some of the standing stock of oocytes were lost because of atresia. Previous field work on squid fecundity has been limited to the traditional method of simply counting oocytes or ova (or both) of animals taken on the spawning grounds, and none of the biases identified by Laptikhovsky (2000) have been evaluated (Boyle and Ngoile, 1993; Coelho et al., 1994; Guerra and Rocha, 1994; Boyle et al., 1995; Collins et al., 1995; Moltschaniskyj, 1995; Lopes et al., 1997; Laptikhovsky, 2000). On the other hand, laboratory studies (Ikeda et al., 1993; Bower and Sakurai, 1996; Sauer et al., 1999; and Maxwell and Hanlon, 2000) have indicated that oocytes remain in the ovaries after spawning and death. Additionally, atresia was found to occur in all stages of oocytes of *Loligo vulgaris reynaudii* (Melo and Sauer, 1998). Modern approaches to estimating lifetime fecundity in fishes take the potential biases of past spawning history, residual fecundity, and atresia into account (Hay et al., 1987; Hunter et al., 1992; Macewicz and Hunter, 1994; Kjesbu et al., 1998). The initial objectives of the present study were to estimate the fecundity of *L. opalescens* by using a modern approach that considers such biases, and to provide a histological description of those aspects of ovarian structure upon which modern fecundity analyses are based. As our work progressed, we realized that it might be practical to manage the market squid fishery by monitoring egg escapement based on fecundity measurements. Thus, we added two new objectives: to conduct a preliminary evaluation of the use of egg escapement as a tool for management of the market squid fishery; and to develop a method

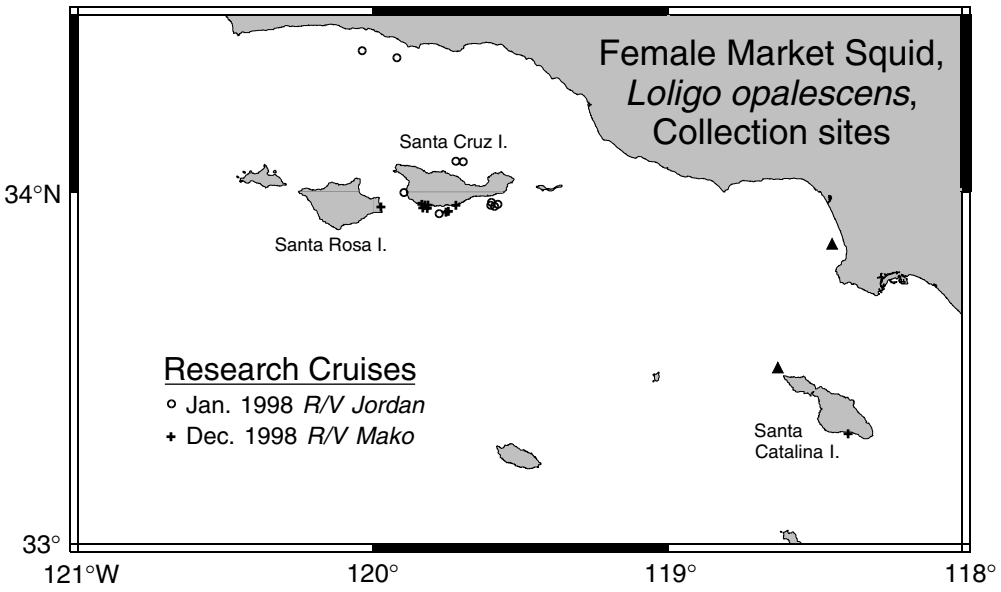

Figure 1

Collection locations for female *Loligo opalescens* during two joint research cruises during 1998 by California Department of Fish & Game (CDF&G) and National Marine Fisheries Service (NMFS) and for three immature females (triangles) collected during February 2000 (CDF&G).

to monitor the fecundity of the catch that avoids the costly process of counting all oocytes and ova.

In this study we consider four aspects of the fecundity of *L. opalescens*: potential fecundity, minimum residual fecundity, maximum fecundity, and the fecundity deposited by the average female in the population. *Potential fecundity,* or *potential lifetime fecundity,* is the standing stock of all oocytes in the ovary just before the onset of the first ovulation. Because *L. opalescens* are semelparous, the standing stock of all oocytes in the ovary just before first ovulation equals their potential lifetime fecundity. Clearly, once ovulation and spawning (deposition of ova in egg capsules on the sea floor) begin, the standing stock of oocytes can no longer be considered a measure of the potential fecundity of the female. *Minimum residual fecundity* is the minimum number of oocytes that might be expected to remain in the ovary at death. Because ovaries of dying *L. opalescens* contain oocytes (Knipe and Beeman, 1978), only a portion of the potential fecundity will be spawned in their lifetime. We use ancillary information on *L. opalescens* (an index of mantle condition and extent of ovarian development) to project what the minimum residual may be. *Maximum fecundity* (potential fecundity less the minimum residual fecundity) is the maximum number of eggs a female might be expected to deposit in a lifetime. We also estimate the fraction of the potential fecundity deposited by the average female, a key vital rate we approximate by modeling the daily rates of total mortality and egg deposition. Lastly, the term "standing stock of oocytes" is used throughout this article to indicate the total number of oocytes at all stages in an ovary. Whether the standing stock of a particular female is to be considered a potential fecundity, a residual fecundity, or something in between, depends upon ancillary information (i.e., presence of postovulatory follicles in the ovary, ova in the oviduct, mantle condition, or the level of ovarian maturity).

Materials and methods

We collected *Loligo opalescens* during two southern California research cruises in 1998 (7–15 January and 3–10 December) (Fig. 1). Most specimens were taken at night by using trawls, jigging, or by removing them from commercial purse-seine catches at sea; some specimens were collected during the day by using bottom trawls. We measured dorsal mantle length (mm), weighed the whole body (g), and classified the ovary and preserved it with viscera and oviduct attached in 10% neutral buffered formalin. To determine reproductive state we decided not to use the familiar ovary classification systems but rather tabulated gross anatomical characters and, later on, selected the most useful characteristics. See Table 1 for characters selected for scoring.

Preserved ovaries and oviducts were reclassified in the laboratory and weighed (to nearest 0.001 g). A piece of the preserved ovary from each of the 135 female *L. opalescens* from January and the 117 females from December was sectioned and stained (hematoxylin and eosin). Analyses of the histological sections included identification of the oocytes in the various development stages (I–VI) as described by Knipe and Beeman (1978), and identification of atresia and postovulatory follicles (Fig. 2). We use the term "ova" to indicate an ovulated mature oocyte (stage VI).

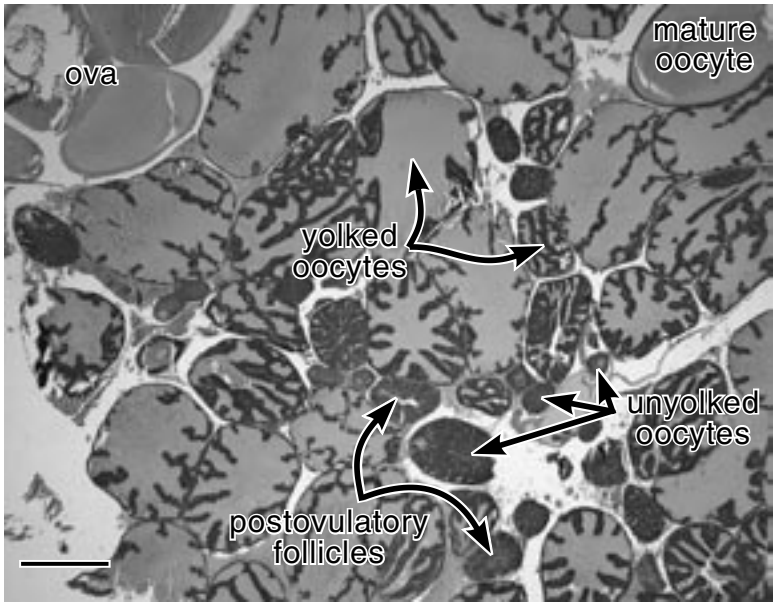

Figure 2

Slide of the ovary (stained with hematoxylin and eosin) of a mature spawning female *L. opalescens*. Bar = 1.0 mm.

Table 1

Classification system for the gross anatomical characteristics of the reproductive system of female market squid (*Loligo opalescens*).

Female organs	Character	Grade
Nidamental gland	length	millimeters
Accessory nidamental gland	color	0=clear, 1=whitish, 2= pink, 3=peach, 4=reddish-orange
Oviduct	number of large clear eggs	1=none, 2=1–20, 3=21–200, 4=>200
Ovary	number of large clear oocytes	1=none, 2=1–20, 3=21–200, 4=>200
Ovary	number of opaque or white oocytes	1=none, 2=1–20, 3=21–200, 4=>200

Postovulatory follicles were classified as either new, degenerating, or very degenerative. We assigned the females to one of the following reproductive categories on the basis of the histology of their ovaries (numerical stages in Knipe and Beeman, 1978):

Immature — Ovary contains only unyolked oocytes; oocyte development ranged from stages I (oogonia) to IV (follicular invagination oocyte) and requires microscopic examination.

Mature preovulatory — No postovulatory follicles are present. Ovaries contain oocytes with yolk (stage V, yolking begins about 1.1 mm in size); ovary usually contains unyolked oocytes.

Mature spawning — Ovary contains postovulatory follicles (POFs) of any degree of degeneration (none to extensive); more than one degenerative POF class may be present. Oocyte development stages III–VI are often present but stages Ic–II are rare. (2% of the ovaries have late stage Ic oocytes and none have any of the earliest stages, Ia or Ib.)

In some histological sections of ovaries we saw 1–10 yolking oocytes (development stage V) with a broken follicle layer, and the yolk seemed to be oozing out between the other oocytes. Because this may have been an artifact of handling, we did not use such females to estimate fecundity.

We used the gravimetric method (Hunter et al., 1985, 1992) to estimate the standing stock of oocytes in 98 *L. opalescens* ovaries. The gravimetric method overestimated the total number of oocytes of *Loligo pealeii*, but the difference between a count of all oocytes and a weight-based estimate was slight (Maxwell and Hanlon, 2000). We did not compare our estimates with a count of all oocytes in the ovary because we used a portion of the ovary for our histological examinations, and each value is the mean of the counts from two tissue samples (average coefficient of variation between samples was 0.12). All oocytes in each tissue sample were macroscopically classified (Fig. 3) as either unyolked, yolked, mature, or atretic; they were then counted by class and all stages were summed. "Atretic" was defined as oocytes in the alpha stage of atresia (Hunter and Macewicz, 1985b), recognizing, however, that poor preservation can create oocytes of similar macroscopic appearance. The number of ova in the oviduct was also counted directly (usually when n was less than 300) or the mean number was estimated from two tissue samples by using the gravimetric method. To illustrate the form of the oocyte-size distribution in the ovary, we measured (to 0.01 mm) the major axis of all the oocytes in one tissue sample from each ovary of six females by using a digitizer linked by a video camera to a dissection microscope. In all other ovaries used for fecundity estimation, we measured only the smallest and largest oocyte in the sample. The length of the major axis of the smallest oocyte (D) was used as an index of the extent of ovarian maturity. D is a crude index of time elapsed during the spawning period—as long as oocyte maturation continues throughout the spawning period and no new oocytes are produced—both of which appear to be true for *L. opalescens*.

To monitor body condition we cut a tissue sample disc from the mantle using a number 11 cork borer (area of 251.65 mm^2) and removed the outer dermis and the inner membrane. The mantle sample discs were frozen and subsequently dried at 56°C to a constant weight. An index of mantle condition (C) was calculated as the weight of the dry mantle in milligrams divided by disc surface area and is expressed as mg/mm^2.

We evaluated the extent that body reserves might be used to support egg production by comparing dry weight of the eggs and capsules to prespawning female body dry weight. For these calculations we made the following measurements: 1) the mean dry weight of one squid egg was 0.00177 g, including a fraction of the egg capsule because the value is based on the dry weight of 34 egg capsules (1–2 days old) containing 2 to 403 eggs each (total of 7341 eggs, capsules collected from La Jolla Canyon 6 July and 11 September 2000); 2) the relationship of dorsal mantle length (L) and whole-body wet weight (W_w) for immature and mature preovulatory females of $W_w = 0.000051L^{2.8086}$, where W_w is in grams and L is in mm (Fig. 4); and 3) the mean wet weight to dry weight conversion factor of 0.24 (2SE=0.001), based on the wet and dry weights of mantle tissue sampled from 214 mature females. The latter conversion factor was constant regardless of mantle condition index; apparently, in *L. opalescens*, starvation does not result in the replacement of muscle tissue with water as it does in fishes (Woodhead, 1960).

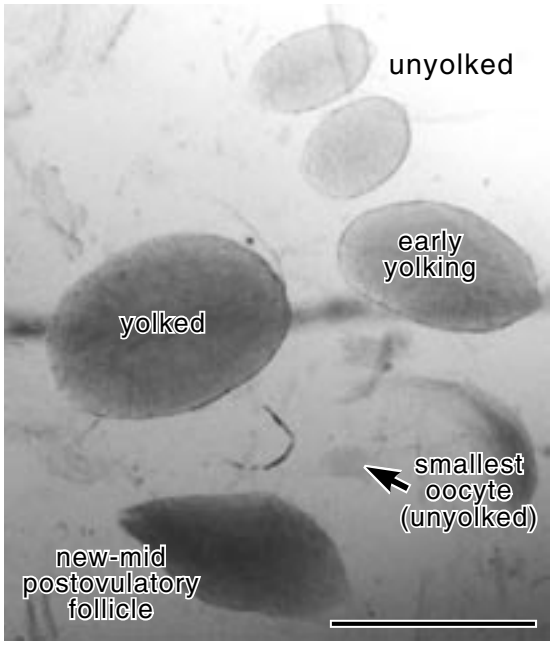

Figure 3

Whole *L. opalescens* oocytes as viewed under a dissection microscope used for counting and classifying oocytes. Bar = 1.0 mm.

In addition to the specimens taken during the research surveys, we also estimated the fecundity of 60 *L. opalescens* from the commercial catch sampled by California Department of Fish & Game (CDF&G) during 1998 and 1999. Landed specimens were not analyzed histologically because their ovarian tissues had begun to deteriorate before preservation. The 60 females were selected by dorsal mantle length and mantle condition index to provide a wide and uniform distribution of length and mantle condition. The number of oocytes in the ovaries was estimated (as described above) and the number of ova in the oviducts were predicted from oviduct weight (Fig. 5). CDF&G also provided data on the dry mantle disc weights of 1275 mature females taken from the catch from December 1998 through December 1999 as random samples taken during the Southern Californian Bight market squid fishery. About 100,000 tons of market squid were landed during this sampling period .

Modeling egg deposition

To identify egg deposition and mortality rates most consistent with our current understanding of spawning biology, we developed a model to estimate the proportion of the potential fecundity deposited by a cohort in its lifetime. The mean proportion of the potential fecundity deposited is the proportion of eggs deposited weighted by the propor-

tion of the cohort that died. Both the proportion of eggs deposited and squid that died were expressed as negative exponential functions. The cumulative eggs deposited up to elapsed time t (days) for a mature female *L. opalescens* is the difference of two terms: $E_{SP,t} = E_P - E_{YD,t}$ where $E_{SP,t}$ is the total eggs deposited by one female up to time t, E_P is the potential fecundity, and $E_{YD,t}$ is the standing stock of oocytes in the ovary plus the standing stock of ova in the oviduct remaining in the body at time t. If we assume that $E_{YD,t}$ declines at an exponential rate from E_P: $E_{YD,t} = E_P e^{-vt}$, where v is the daily rate of eggs deposited, then $E_{SP,t} = E_P(1-e^{-vt})$. We constructed the cumulative egg deposition curve as $Q_{SP,t} = E_{SP,t}/E_P = 1-e^{-vt}$. Assuming the mortality (survival) curve for the squid is e^{-zt}, where z is adult daily total mortality rate ($z=m+f$, where m is natural and f is fishing mortality), we computed the mean fraction of the potential fecundity deposited ($Q_{SP,t}$):

$$Q_{SP} = \frac{\int_0^{t_{\max}} ze^{-zt}(1-e^{-vt})dt}{\int_0^{t_{\max}} ze^{-zt}dt} \quad (1)$$

$$= 1 - \frac{z(1-e^{-(z+v)t_{\max}})}{(z+y)(1-e^{-zt_{\max}})} \cong \frac{v}{z+v} \text{ for large } t_{\max},$$

where $t_{\max}$ is the total elapsed time (days).

The mean fraction of the potential fecundity that remains in the average female (standing stock of oocytes and ova) over her lifetime is $1 - Q_{SP}$, and mean Q_{SP} is always less than one because of mortality. The mean duration of the spawning period in days is computed as the elapsed time corresponding to the mean fraction of eggs deposited (Q_{SP}: Eq. 1 and by setting $Q_{SP}=1-e^{-vt}$):

$$t_{Q_{SP}} = \ln(1-Q_{SP})/(-v). \quad (2)$$

We evaluated various rates of adult daily total mortality (z) and egg deposition (v) using these models to determine the combination of rates that would provide estimates of fecundity nearest to our observed field data.

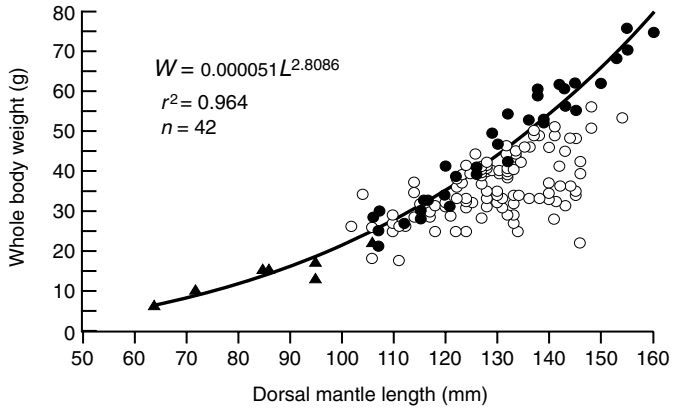

Figure 4

Female squid whole body weight (W) as a function of dorsal mantle length (L) for the 158 females with fecundity analyses. The line expresses the length-weight relation of females before weight losses associated with spawning and was fitted to the combined data for immature females (solid triangles), mature preovulatory females (solid circles), and mature females judged by their mantle condition to be new recruits to the spawning ground (solid circles). Open circles indicate females that have spawned.

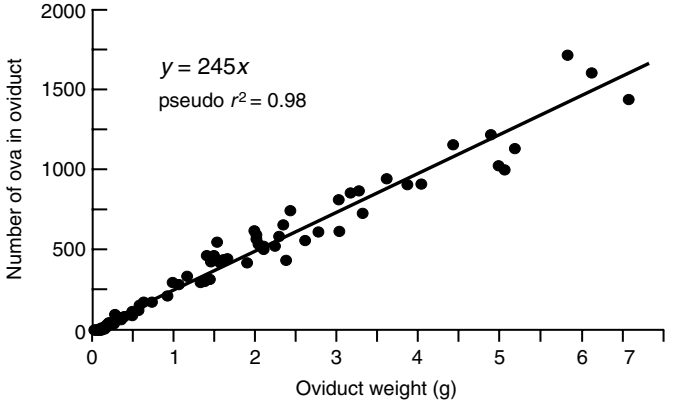

Figure 5

Number of ova in each oviduct shown as a function of the oviduct weight; n equals 91 mature females, pseudo r^2 = 1 – *residual ss/total ss.*

Modeling the effect of fishing effort on egg escapement

In theory we could manage the market squid fishery by monitoring egg escapement, that is, the fraction of the fecundity realized by the average female. Under such a management scheme, egg escapement would be maintained at a specified level by changing fishing effort whenever escapement of eggs fell below it. In this section we develop a model to explore the relative effects of fishing effort on egg escapement. We use this model to discuss some of the biological issues related to using egg escapement as a management tool.

In the modeling process, we follow one cohort of spawners. The elapsed time 0 is defined as the time when squid start spawning. The total escapement of eggs for a given elapsed time (t_k in days) is the sum of three sources of egg escapement: E_C, the total number of eggs deposited by mature females in the catch; E_M, the total number of eggs deposited by mature females dying of natural causes; and E_A, the total number of eggs deposited by females

alive and not taken by the fishery up to time t_k, and $t_k < t_{\max}$. The egg escapement rate, R_{e,t_k}, up to time t_k is the sum of the three sources of egg escapement divided by the total number of eggs that would have been spawned if no fishery existed (E):

$$R_{e,t_k} = \frac{E_C + E_M + E_A}{E}. \quad (3)$$

Egg escapement rate at the maximum elapsed time ($t_{\max}$) is

$$R_{e,t_{\max}} = \frac{E_C + E_M}{E}, \quad (4)$$

where $t_k = t_{max}$.

Because there are no survivors at time $t_{\max}$, no eggs can be deposited and E_A is zero.

Each term in Equation 3 can be expressed as functions of the mean cumulative number of eggs deposited up to time t_k, $\overline{E_{SP,t_k}} = \overline{E_P} - \overline{E_{YD,t_k}} = \overline{E_P}(1-e^{-vt_k})$, and total mortality ($z$) of the cohort; z includes both natural morality (m) and fishing mortality (f). For practicality, we considered cases when $t_k = t_{\max}$, where E_A is zero. For formulas of any t_k, see appendix. The total number of eggs deposited by the females in the catch (E_C) is

$$E_C = \int_0^{t_{\max}} \overline{E_{SP,t}} N_0 e^{-(m+f)t} f dt = \overline{E_P} N_0 \int_0^{t_{\max}} (1-e^{-vt}) e^{-(m+f)t} f dt \quad (5)$$

$$= \overline{E_P} N_0 f \frac{v}{(m+f)(m+f+v)}, \quad (6)$$

where $\overline{E_P}$ = the mean number of oocytes in the ovary per mature female prior to spawning; and
N_0 = the number of mature females at time 0.

From the fishery data, we can estimate the total number of eggs deposited by the females in the catch (E_C) as

$$\hat{E}_C = N_C\left(\hat{\overline{E_P}} - \hat{\overline{E_{YD}}}\right), \quad (7)$$

where $\hat{\overline{E_P}}$ and $\hat{\overline{E_{YD}}}$ = sample estimates from the catch; and
N_C = the total number of spawners in the catch.

The total number of eggs deposited by *L. opalescens* prior to death due to natural mortality (E_M) is

$$E_M = \int_0^{t_{\max}} \overline{E_{SP,t}} N_0 e^{-(m+f)t} m dt = \overline{E_P} N_0 \int_0^{t_{\max}} (1-e^{-vt}) e^{-(m+f)t} m dt \quad (8)$$

$$= \overline{E_P} N_0 m \frac{v}{(m+f)(m+f+v)}. \quad (9)$$

The total eggs that would be deposited for the cohort without fishing mortality is

$$E = \int_0^{t_{\max}} \overline{E_{SP,t}} N_0 m e^{-mt} dt = \overline{E_P} N_0 \int_0^{t_{\max}} (1-e^{-vt}) m e^{-mt} dt \quad (10)$$

$$E = \overline{E_P} N_0 \frac{v}{m+v}, \quad (11)$$

where $t_{\max}$ (days) = the maximum elapsed time; and
time 0 = the time at the onset of egg deposition.

Egg escapement based on Equation 4 is

$$R_{e,t_{\max}} = \frac{f\frac{v}{(m+f)(m+f+v)} + m\frac{v}{(m+f)(m+f+v)}}{\frac{v}{v+m}} = \frac{m+v}{m+f+v}. \quad (12)$$

Thus, egg escapement reduces down to a simple ratio, $\left(\frac{m+v}{m+f+v}\right)$ involving three daily instantaneous rates: natural mortality (m), egg deposition (v), and fishing mortality (f). $R_{e,t_{\max}} = 1$ when there is no fishing and thus $R_{e,t_k}<1$ with fishing mortality. The lower bound of the egg escapement rate for the cohort is equal to the ratio of the eggs escaping the fishery (E_C) to the total eggs deposited if no fishery existed (E):

$$R_e = E_C / E. \quad (13)$$

Results

Oocyte maturation and production

Immature ovaries contain many small unyolked oocytes with a pronounced peak at about 0.15 mm in size distribution (Fig. 6A). As development continues and vitellogenesis begins, the peak diminishes and shifts to a larger size class of unyolked oocytes (Fig. 6B). Just before the onset of spawning, the size distribution of oocytes becomes relatively flat without pronounced modes (Fig. 6C) and remains so through the rest of the spawning period (Fig. 6, D–F). The standing stock of oocytes declines throughout the spawning period. The minimum size of oocytes in the ovary gradually increases after the onset of yolking, indicating that new oocytes are not produced. We saw no primary oogonia in our histological sections of mature ovaries, another indication that new oocytes are not produced in mature ovaries. Knipe and Beeman (1978) reached the

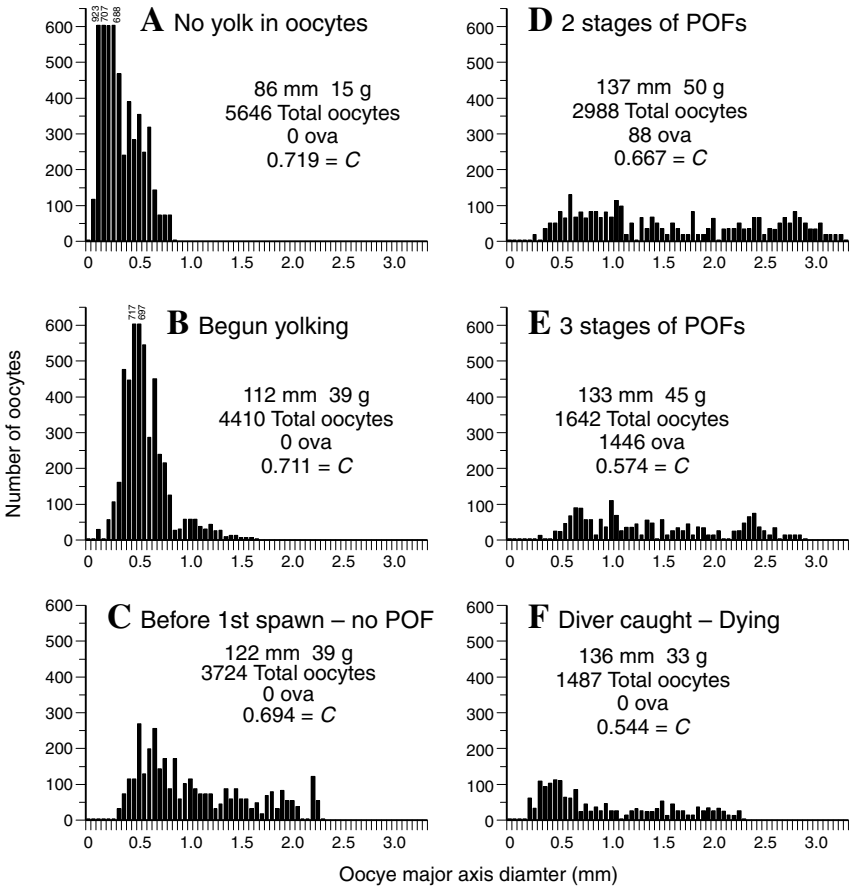

Figure 6

Oocyte-size distribution for six female *Loligo opalescens*. Dorsal mantle length (mm), body weight (g), the total number of oocytes in the ovary, and the number of ova are indicated for each specimen. (**A**) Female that is immature. (**B** and **C**) Females that are considered to be mature and preovulatory because neither has postovulatory follicles (POFs) in their ovaries nor ova in their oviducts. Although the oocytes have just begun yolking in the ovary of female B, female C has well-yolked oocytes and is close to its first ovulation. (**D**–**F**) Females are mature spawning females and their ovaries contained postovulatory follicles. Female F was caught by a scuba diver and appeared to be dying.

same conclusion from their histological analysis of *L. opalescens* ovaries. Thus, potential fecundity in *L. opalescens* probably becomes fixed near the onset of spawning. Not all oocytes are deposited, however, because all spawning females had some oocytes and many oocytes were counted in the ovary of a dying female (Fig. 6F).

In *L. opalescens* the migration of the oocyte nucleus begins early in the maturation process shortly before the onset of vitellogenesis, whereas in fishes, migration is near the end of vitellogenesis. The follicle of a migratory-nucleus-stage oocyte (late stage IV) of *L. opalescens* has a very large granulosa cell layer (in relation to the size of the oocyte) and is highly folded and perhaps fully developed. Subsequent maturation of the oocyte seems to consist primarily of the massive addition of yolk and fluid and the consequent stretching and unfolding of the follicle, ending with the formation of a chorion. Apparently, the formation of the chorion compacts the yolk because many mature oocytes (endpoint of stage V) have a smaller major axis than advanced yolked oocytes prior to chorion formation. Thus, maximum oocyte size is not a good proxy for oocyte maturation in *L. opalescens* and is not an indicator of the time remaining before spawning of the next batch. More importantly, the ovary of *L. opalescens* seems well adapted for rapid oocyte vitellogenesis, maturation, and spawning because nuclear migration and follicle cell proliferation is completed at an early stage.

Ovulation appears to occur in small batches. The distribution of oocyte sizes in spawning *L. opalescens* was flat (e.g., Fig. 6, D–F) and lacked the separate and distinct mode of hydrated oocytes that is typical in fishes. Batch sizes of mature oocytes ranged from 5 to 246 and averaged 50 (n=72

females). The maximum number of mature oocytes (246) was never close to the maximum number of ova (1726) in the oviduct. In addition, spawning females with 900 or more ova in their oviduct had in every case three or more distinctly different stages of postovulatory follicles in their ovaries (Table 2). Thus the oviduct is probably filled by a series of ovulation bouts separated by enough time to produce distinct age classes of degenerating follicles in the ovary.

Potential fecundity (E_P)

Potential fecundity (E_P) is the standing stock of oocytes of all stages in the ovary of a mature female just prior to the first ovulation. Finding females at this point in their reproductive cycle was difficult because nearly all specimens had already ovulated. The ovaries of 94% of the 247 mature females, from our research cruises, contained postovulatory follicles, indicating that they had recently ovulated and would not be suitable for estimating E_P. As can be seen in Figure 7A, spawning females had fewer oocytes in their ovaries than did mature preovulatory females. The relation between fecundity and squid size is best expressed in terms of dorsal mantle length (L) because *L. opalescens* lose weight during spawning (Figs. 4, 7C). The data from thirteen mature preovulatory females were used to establish the relationship between potential fecundity and L:

$$E_P = 85.62L - 6715, \qquad [r^2 = 34.3\%] \tag{14}$$

where L = dorsal mantle length in mm.

Because the constant was not significant (P=0.146) and the coefficient was (P=0.036), we forced the regression through zero which resulted in the equation

$$E_P = 29.8L. \tag{15}$$

Thus, the average female (129 mm) according to Equation 15 had a potential fecundity of 3844 oocytes (SE=317).

Clearly it would be preferable if the sample size for the estimate of potential fecundity were larger because thirteen females may not accurately represent the *L. opalescens* stock. Although the landed catch provides an unlimited supply of specimens, histological detection of postovulatory follicles is not possible because of deterioration of the ovaries. An alternative approach is to use mantle condition of mature females from the catch as a proxy for the preovulatory state. As can be seen in Figure 7C, the mantle condition index (C) of mature females declines as oocyte maturation continues and females deposit eggs. The mature preovulatory females (n=11, two discs were lost) had a mean C of 0.73 mg/mm^2 (SE=0.02). We believe that the twenty-two mature females from the landed catch with $C \geq 0.7$ mg/mm^2 had not begun to deposit eggs (Table 3). Because many of them had ovulated, we combined our estimates of the standing stock of oocytes (E_Y) with those of ova (E_D) to calculate total fecundity ($E_Y + E_D = E_{YD}$), and then regressed total fecundity on length. Although the regression was not significant, the average total fecundity of 3890 oocytes (Table 3) was within 5% of the potential fecundity of 4083 oocytes computed by substituting the mean length of the twenty-two females (137 mm) in Equation 15. The close agreement between these two values increases our confidence that the potential fecundity equation is accurate despite the low n. On the other hand, this rough comparison is not a substitute for increasing the sample size of specimens analyzed histologically, because females from the catch may have spawned some of their ova before they were captured.

Table 2

Percentage of spawning female market squid classed by the number of eggs in their oviducts and by the number of ages (stages of degeneration) of postovulatory follicles (POFs) in their ovaries.

Number of eggs in the oviduct	Number of females	Percentage of females	
		1 or 2 ages of POFs	≥3 ages of POFs
0	1	100	0
1–300	36	22	78
301–600	20	35	65
601–900	10	20	80
901–1200	7	0	100
1201–1500	2	0	100
1501–1800	2	0	100

Maximum fecundity ($E_P - E_R$)

Few if any *L. opalescens* live to realize their full potential fecundity (E_P). The literature on *L. opalescens* indicates that females that were described as "spawned out," dying, or dead had oocytes in all stages of development except the earliest previtellogenic stage (Knipe and Beeman 1978). In addition, all the spawning females that we collected had some oocytes in their ovaries. Thus, the maximum fecundity that *L. opalescens* might be expected to realize is the potential fecundity less an estimate of the number of oocytes that might be left in the ovary at death (residual fecundity [E_R]). To estimate residual fecundity we examined the relationship of the standing stock of oocytes in the spawning period with mantle condition index (C), size of the smallest oocyte (D), and dorsal mantle length (L).

The standing stock of oocytes in ovaries of mature females declines rapidly with decreasing mantle condition, between a C of 0.8 and 0.6 mg/mm^2, and more gradually over lower mantle conditions (Fig. 7C). A curvilinear relationship also exists between oocyte standing stock and the size of the smallest oocyte (Fig. 7B). Thus the number of past spawnings (decline in oocyte standing stock) appears to be inversely correlated with C and directly correlated with the extent of ovarian maturation as measured by D. To quantify how the standing stock of oocytes changes during the spawning period we fitted a nonlinear model to the fecundity data of 75 mature spawning females (Fig. 7) from our research cruises:

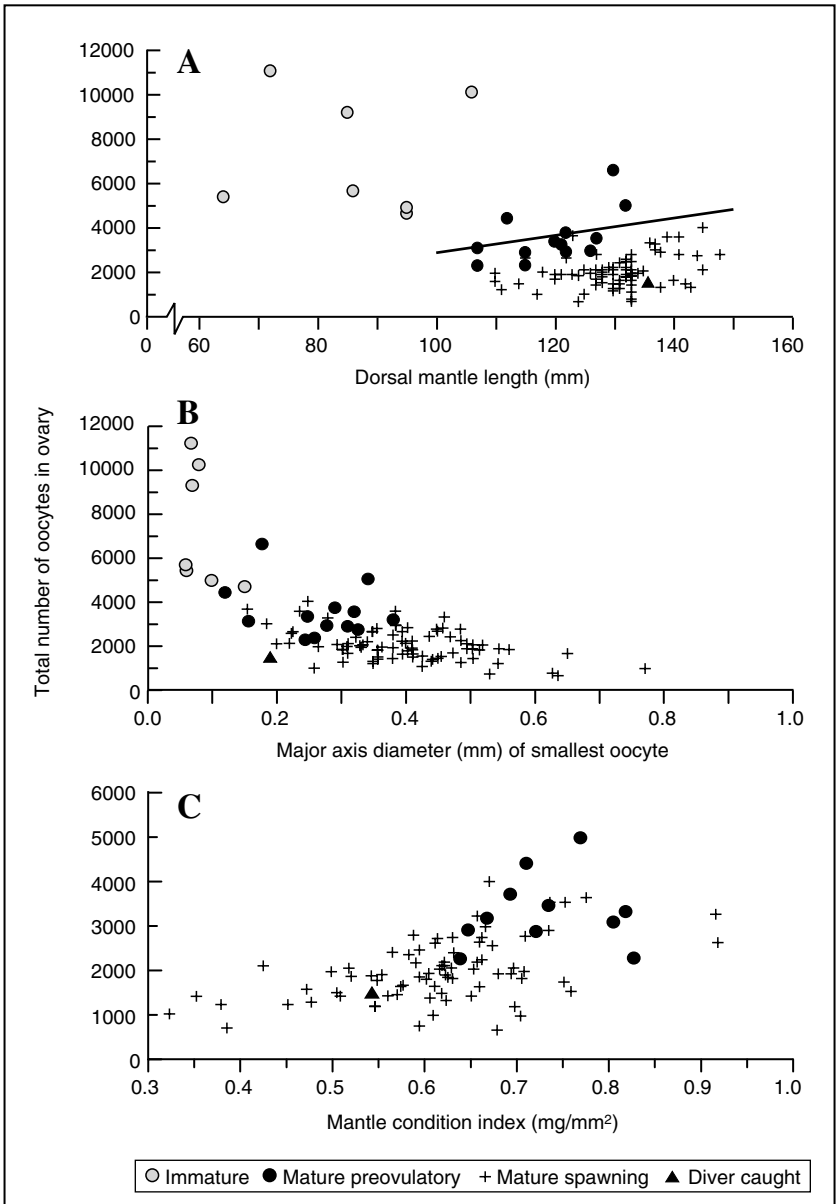

Figure 7

The number of oocytes in ovaries of 98 *Loligo opalescens* as a function of dorsal mantle length (**A**) and the diameter of the major axis of the smallest oocyte (**B**). In (**C**), the number of oocytes is plotted as a function of mantle condition index (the dry weight per surface area of a mantle tissue disc) for 87 mature females (4 discs were lost and the 7 immature were not included). Line in A expresses potential fecundity as a function of length (E_P=29.8L) for the 13 mature preovulatory females (solid circles); open circles represent immature females; plus signs represent spawning females; and the triangle represents a dying mature female.

$$E_R = 30283e^{(-1.24D - 6.19C - 0.024L + 0.059LC)}, \quad (16)$$

where C = mantle condition index;
D = size of the smallest oocyte; and
L = dorsal mantle length.

Substituting into the model (Fig. 8) the maximum observed D (0.771 mm) and the minimum observed C (0.323 mg/mm^2) from our research survey data set, we estimated that a female *L. opalescens* with L of 129 mm may have a minimum residual fecundity of 834 oocytes (CV=0.12).

Table 3

Mean fecundity, gonad weight, and dorsal mantle length for 60 mature female market squid (*Loligo opalescens*) sampled at the ports December 1998 to December 1999.

Mantle condition index (mg/mm^2)		Fecundity (mean number)			Mean gonad weight (g)	Dorsal mantle length (mm)		Number of females
Class	Mean	Oocytes in ovary (E_Y)	Ova in oviduct (E_D)	Total (E_{YD})		Mean	Range	
0.347–0.499	0.432	1134	231	1365	2.215	132	106–146	22
0.500–0.699	0.613	2072	522	2594	4.959	125	102–154	16
0.700–0.951	0.824	2589	1301	3890	8.988	137	106–160	22
0.347–0.951	0.624	1917	701	2618	5.397	132	102–160	60

A 129-mm *L. opalescens* with a potential fecundity of 3844 oocytes would have a maximum fecundity of 3010 eggs (3844–834 eggs) or about 78% of the potential fecundity. Very few females would be expected to deposit 78% of their potential because this maximum is based on extreme values for both mantle condition index and ovarian maturation. In a much larger set of mantle samples from the catch (Table 4), only 1.5% of the females had values of C less than 0.35 mg/mm^2. Clearly very few squid live to deposit 78% of their potential fecundity.

Another approach is to count the number of oocytes remaining in the ovaries of females presumed, from their behavior and appearance, to be dying. Although *L. opalescens* has been observed to be dying or dead on the bottom on video from a remotely operated vehicle (Cossio[1]), capturing such females was not attempted at the time. A female *L. opalescens* (136 mm) believed to be dying was opportunistically collected by a diver 6 July 2000 on the La Jolla Canyon spawning grounds (McGowan, 1954). There were no ova and the ovary contained 1487 oocytes—substantially more oocytes than our estimate of the minimum residual fecundity. In fact, the female had deposited only about 63% of her potential fecundity.

Table 4

Distribution of mantle condition index for 1275 mature female *L. opalescens* sampled from the landed catch from December 1998 to December 1999.

Mantle condition index (mg/mm^2)	Mature females	
	Number	Percentage
0.263–0.299	4	0.3
0.300–0.349	15	1.2
0.350–0.399	29	2.3
0.400–0.449	54	4.2
0.450–0.499	91	7.1
0.500–0.549	128	10.0
0.550–0.599	207	16.2
0.600–0.649	210	16.5
0.650–0.699	216	16.9
0.700–0.749	137	10.7
0.750–0.799	94	7.4
0.800–0.849	53	4.2
0.850–0.899	18	1.4
0.900–0.949	10	0.8
0.950–0.999	6	0.5
1.000–1.043	3	0.2

Role of body reserves

We used weight relationships to evaluate the extent to which body reserves might be used to support the reproduction of spawning female *L. opalescens*. In these crude energetic calculations we did not include metabolism, conversion efficiencies, or caloric values of tissues. We used the average dry weight of squid eggs, length to body weight conversion, potential fecundity equation, and the conversion factor from wet to dry mantle weight. We assumed preovulatory mantle condition index (C) for an average mature female of 130 mm was 0.798 mg/mm^2, the mean for values (n=41) of $C \geq 0.700$ mg/mm^2 in the our fecundity data set. We calculated that the potential fecundity of a 130-mm *L. opalescens* (i.e., 3874 encapsulated eggs) has a dry weight of 6.86 g which is equivalent to 64.8% of the whole-body dry weight (10.58 g) of that female just before spawning. If mantle condition is reduced in proportion to the dry weight of all the eggs, our hypothetical female would have a C of about 0.281mg/mm^2 ($0.798 \times [(10.58-6.86)/10.58]$). This end point ($C$=0.281, egg=0) and the beginning point for the mature preovulatory female (C=0.798, eggs=3874) create a hypothetical

[1] Cossio, A. 2000. Personal commun. Southwest Fisheries Science Center, National Marine Fisheries Service, 8604 La Jolla Shores Dr., La Jolla, CA 92037

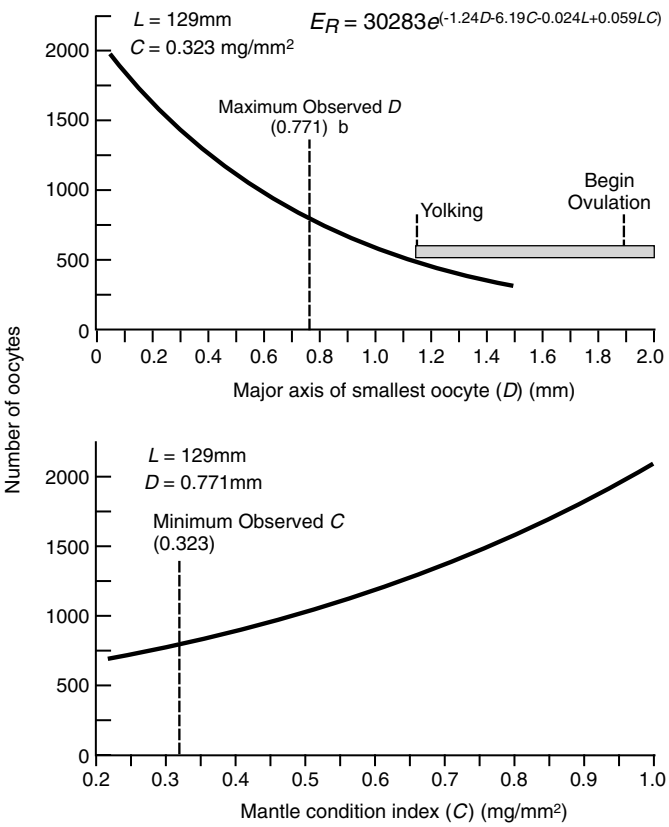

Figure 8

Changes in the standing stock of oocytes predicted by Equation 16 (equation also given at top of panel) when major axis of smallest oocyte (D) is varied and mantle condition index (C) held constant (upper panel), and when C is varied and D held constant (lower panel). The major axis size of oocyte when yoking begins and when ovulation begins is also indicated, as are the maximum observed D and minimum observed C. Substitution of the latter two values into the equation yields the standing stock of oocytes of females close to the end of their reproductive activity and is considered to be a minimum estimate of residual fecundity.

line that expresses oocyte standing stock for the average mature female of 130 mm as a function of mantle condition. In addition to the hypothetical line, we plotted the total standing stock of oocyte and ova (E_{YD}) and mantle condition index for all 147 mature females used for direct fecundity determinations (Fig. 9). Our hypothetical line, based on direct proportionality between egg dry weight and body dry weight, follows the general trend in the data, indicating that energy reserves in mantle tissue may largely support the production and spawning of eggs. Of course, actual energy costs would be higher because metabolism, other somatic tissue, and conversion efficiency of mantle tissue to eggs are not considered. The lowest observed C in the fecundity data set was 0.323 and the lowest C observed in the 1275 mature females from the landed catch was 0.263. Using the above preovulatory C (0.798 mg/mm^2), we determined that these values of C are equivalent to 60% and 67% losses in body dry weight for these individuals. Fields (1965) suggested body wet weight declined by as much as 50%, which is consistent with our results.

These rough calculations support the long held belief that oocyte maturation is supported primarily by body reserves. Some feeding occurs during spawning; *L. opalescens* has been observed feeding under lights at night on the spawning grounds (Butler[2]). Maxwell and Hanlon (2000) observed *L. pealeii* feeding between egg-laying bouts when they were held in the laboratory. Feeding between spawning bouts by the more robust spawners that may migrate on and off the grounds each day seems quite

[2] Butler, J. 2000. Personal commun. Southwest Fisheries Science Center, National Marine Fisheries Service, 8604 La Jolla Shores Dr., La Jolla, CA 92037.

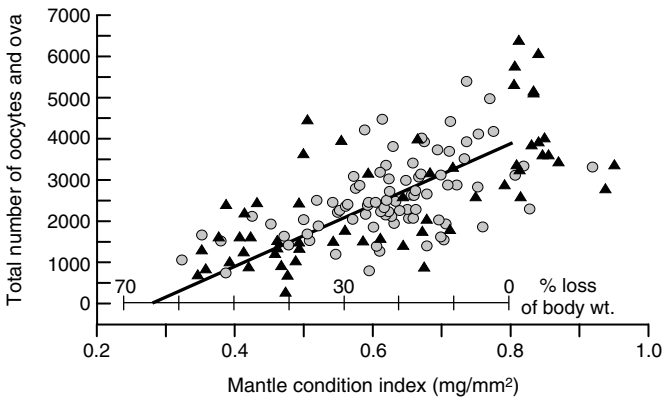

Figure 9

Standing stock of oocytes and ova as a function of mantle condition index for 60 mature females taken in the fishery (triangles) and 87 mature females taken in research surveys (circles). The line (not drawn to the data points plotted) represents a possible relation if losses in body weight were equivalent to the weight of the spawn released, computed for an average female (130 mm) where the starting point is her potential fecundity of 3874 oocytes and ends with 0 eggs and a mantle condition index of 0.281 mg/mm^2.

possible, but it seems unlikely for the nearly exhausted *L. opalescens* that are near the end of their life.

Longevity and egg deposition rates

Inferences regarding the longevity of adult spawning *L. opalescens* are the best proxy we have for the mortality rates of spawning adults. Previous observers (McGowen, 1954; Fields, 1965) suggested that females deposited all their eggs in one night and death soon followed. On the other hand, it is unreasonable to expect that a reduction of 60% in body weight and the maturation and deposition of up to 78% of the potential fecundity could take place in 24 hours. Our data on fecundity and mantle condition show an initial rapid decline in the number of oocytes followed by a more gradual decline (Fig. 7C), indicating an initial period of intense egg laying may be followed by a longer one where fewer eggs are deposited. It is also important to recognize that ovaries of spawning animals contain a wide range of oocyte sizes (Fig. 6), including many small unyolked oocytes (0.3–1 mm) that may mature and be deposited during the spawning period. It is unlikely that all these processes (body resorption, dynamic changes in rates of egg deposition, and maturation of small unyolked oocytes) could occur in one 24-hour period. Spawning periods longer than two weeks also seem unlikely because mature *L. opalescens* females may require extensive feeding periods and prolonged absences from the spawning grounds; these behaviors are inconsistent with our energetic analysis in the preceding section. Our analysis indicated that the observed reduction in eggs can be fairly well explained by the observed reduction in squid dry weight.

Egg deposition rates provide another way to infer the longevity of spawning squid. The best evidence for the rate of egg deposition is provided by females judged, on the basis of their high mantle condition ($C \geq 0.700$ mg/mm^2), to be new recruits to the spawning grounds. Considering only those new recruits that have ovulated (postovulatory follicles present or ova in the oviduct), the difference between their average oocyte standing stock (E_Y=2571) and their average potential fecundity (E_P=4020) was equivalent to a reduction of 1449 oocytes or 36% of their potential fecundity (Table 5). If the difference is spawned in 24 hours or less, then 36% can be considered as an average for the first day of egg deposition. Instead of using the reduction of oocyte standing stock, one could consider the standing stock of ova (E_D) to be equivalent to the first day (24-hour period) of spawning in these new recruits. Their average E_D was 1073 or 27% of their potential fecundity. Thus depending on the criteria, the first day of spawning might be 27% to 36% of the potential fecundity. We prefer 36% because it is unaffected by any losses due to egg deposition.

The standing stock of ova (E_D) of spawning females with lower mantle condition (C<0.7 mg/mm^2) averaged 9% of their potential fecundity. If the average E_D from these females is a crude measure of daily egg deposition rates after the first day, then we calculate it would take seven additional days [(100%–36%)/9%] to use up the remaining potential fecundity or a total spawning period of eight days. Eight days is an extreme value because an adult *L. opalescens* has never been taken with zero oocytes. The minimum residual fecundity was 22% of the potential which is roughly equivalent to about two days of egg deposition. Thus, six days may be a better guess of the maximum longevity of spawning *L. opalescens*.

Table 5

The mean fecundity for various classes of mantle condition for spawning *Loligo opalescens* and the grand mean weighted by the frequency of mantle condition classes in fishery samples 1998–99.

Class of mantle condition (mg/mm^2)	Number of spawning females	Mean fecundity (SE)			Dorsal mantle length in mm	Mean potential fecundity[1] (SE)	Number of eggs deposited $E_{SP} = E_P - E_{YD}$	Weighting factors (Table 4)
		Oocytes in ovary (E_Y)	Ova in oviduct (E_D)	Total (E_{YD})	Mean (SE)			
≤0.499	31	1212 (93)	207 (40)	1419 (100)	133 (2.08)	3954 (384)	2535	0.151
0.500–0.699	70	2008 (84)	437 (49)	2496 (100)	128 (1.20)	3813 (340)	1317	0.597
≤0.700	34	2571 (202)	1073 (109)	3657 (210)	135 (2.37)	4020 (385)	363	0.252
0.323–0.951	135	1967 (83)	544 (47)	2541 (102)	131 (1.01)	3897 (336)	1356	
				2599[2]	129.5	3859 (320)	1260[3]	

[1] Potential fecundity (E_P) estimated by $E_P = 29.8L$, where L = dorsal mantle length in millimeters.

[2] Product of population E_P and weighted average of the fraction of potential fecundity remaining in spawners):
3859× [(1419/3954×0.151) + (2496/3813×0.597) + (3657/4020×0.252)] = 2599; or the population E_P less $E_{SP(weighted)}$ which is 3859–1260.

[3] Weighted average of the number of eggs deposited [(2535×0.151) + (1317×0.597) + (363×0.252)].

Probably very few females would be expected to survive six days because only a small percentage of the spawning population (Table 4) met the mantle criteria for minimum residual fecundity.

In summary, our best guess of the maximum longevity of squid on the spawning grounds is about six days. Our best description of daily egg deposition is a rate that ends the first day with 36% of the potential fecundity deposited and averages about 9% of the potential per day over the remaining five days and where only a small percentage of the females live to deposit 78% or more of their potential fecundity.

Egg escapement

We examine the spawning dynamics of *Loligo opalescens* from the standpoint of possibly using fecundity of the catch to monitor and ultimately regulate escapement of eggs from the fishery. The key variable in this approach is the fraction of the potential fecundity that is actually deposited as eggs on the bottom because this value can be directly estimated from the fecundity of the catch. Two other important parameters are the daily rate of total mortality (z) on the spawning grounds and the daily rate of egg deposition (v). Neither of these parameters can be directly estimated but they are approximated by values that are most consistent with our observations by using a model (Eq. 1). Our observations consist of the fecundity of the catch and the inferences regarding longevity and egg deposition, presented in the previous section. We use our approximations for egg deposition and total mortality in a second model (Eq. 12) to gain an idea of how natural mortality and fishing mortality may affect egg escapement. Lastly, we present a rapid method for monitoring the fecundity of the catch which does not require direct counting of oocytes or ova.

Fraction of the potential fecundity spawned (Q_{SP}) In a spawning population of *L. opalescens*, the mean standing stock of oocytes and ova ($\overline{E_{YD}}$), when expressed as a fraction of potential fecundity, is equivalent to the fraction of the potential fecundity of the population that remains in the spawners ($\overline{E_{YD}}/\overline{E_P}$). When subtracted from one ($1-[\overline{E_{YD}}/\overline{E_P}]$), the difference becomes the fraction of the potential fecundity of the population that is actually spawned (Q_{SP}). For this interpretation to be correct, samples must be randomly drawn from the population and represent all spawners according to their abundance on the spawning grounds—from the newly recruited to those that have been spawning for extended periods.

Neither the females taken from our research cruises nor those used to estimate fecundity from the landed catch were random samples of the spawning population. First, not all of the specimens taken during the two research cruises were from the spawning grounds. Second, the 60 females from the commercial catch were not randomly chosen but were selected to represent a full range of L and C. However, by weighting our fecundity estimates by a random sample of mantle condition from the fishery, it was possible to approximate a random fecundity sample of spawners. The population we used for weighting was based on the mantle condition index (C) of 1275 randomly taken specimens from the commercial catch sampled December 1998 through December 1999 (Table 4). The weighted and unweighted mean standing stocks of oocytes and ova ($\overline{E_{YD}}$) were similar (Table 5), indicating that our previous selection of specimens by C did not introduce a large bias. For the unweighted data, $\overline{E_{YD}}$ was 2541 and was 2599

Table 6

Estimates of number of days of egg deposition, the mean number of eggs deposited, mean standing stocks of oocytes and ova remaining in female *L. opalescens*, mean number of eggs deposited at the end of the first night (all means are expressed as a fraction of the potential fecundity), for various combinations of possible egg deposition (v) and total adult mortality (z) rates. Model provided estimate nearest observed data when $z = 0.45$, $v = 0.25$, and $t_{max} = 8$ days.

Daily total mortality (z)	Daily egg deposition rate (v)	Fraction of potential fecundity deposited Q_{SP} (Equation 1)	Fraction of potential fecundity remaining in females $(1 - Q_{SP})$	Mean number of nights of egg deposition $t_{Q_{SP}}$ (Equation 2)	Fraction of eggs deposited at the end of the first night $(1 - e^{-v})$	Days to reach 78% eggs deposited
0.2	0.25	0.458	0.542	2.45	0.221	6.057
0.2	0.45	0.617	0.383	2.13	0.362	3.365
0.2	0.65	0.706	0.294	1.88	0.478	2.329
0.45	0.25	0.341	0.659	1.67	0.221	6.057
0.45	0.45	0.486	0.514	1.48	0.362	3.365
0.45	0.65	0.580	0.420	1.33	0.478	2.329
0.8	0.25	0.237	0.763	1.08	0.221	6.057
0.8	0.45	0.359	0.641	0.99	0.362	3.365
0.8	0.65	0.447	0.553	0.91	0.478	2.329
Observed		0.326 (SE 0.075)	0.674		0.36	6.0

when the data were weighted by the distribution of mantle conditions in the catch. The mean fraction of the potential fecundity deposited (Q_{SP}) by *L. opalescens* was 0.326 (1–2599/3859). That much of the fecundity had escaped (eggs were deposited) before the market squid were taken by the fishery does not seem unreasonable because 22–36% of E_P may be deposited during the first day of spawning. The mean Q_{SP} is an important index because it measures egg escapement as a fraction of potential fecundity over its lifetime (Eq. 1). It is used in subsequent sections to identify a daily total mortality rate and egg escapement rate for the average female in the population that best characterizes the sampled *L. opalescens* population.

Preferred mortality and egg deposition rates We used Equation 1 to evaluate which combination of a range of plausible values for the rates of daily total mortality (z of 0.2, 0.45, and 0.8) and daily egg deposition (v of 0.25, 0.45, and 0.65) provides an estimate closest to observed Q_{SP} ($\overline{E_{SP}}/\overline{E_P}$) (Table 6). The combination of an adult daily total mortality (z) rate of 0.45, a daily egg deposition (v) rate of 0.25, and using a $t_{\max}$ of 8 days gave an estimate that was most consistent with the observed value for Q_{SP} of 0.326 (Table 6, Fig. 10). This combination of rates also gave an egg depletion of 78% of the potential fecundity in 6 days which was consistent with our best guess for maximum longevity and maximum fecundity. On the other hand, the model (using $1–e^{-vt}$ and t=1) predicts that about 22% of the potential is deposited by the end of the first 24 hours (day 1) which is less than our preferred estimate (36%) based on the reduction in standing stock of oocytes but is closer to the one based on the standing stock of ova (27%). A possible biological explanation for the difference might be that some of the ova produced during the first day of deposition might remain in the oviduct and then be deposited on the second day. Regardless of the uncertainties regarding the fit for the initial day of egg deposition, a daily total mortality rate of 0.45 and daily egg deposition rate of 0.25 are most consistent with the field data known at the present time. This means that the average spawning period is very short; the average female lives only 1.67 days after spawning begins (ln(0.659)/–0.25; Eq. 2). It is interesting that 1.67 days for the average animal is not a radical departure from Fields's (1965) original conclusion of a single night of spawning.

Egg escapement from the fishery In *L. opalescens*, where the fishery targets spawning adults that die after spawning, it is important to know the effect of fishing mortality on the egg escapement rate with respect to the lifetime fecundity deposited, $R_{e,t_{\max}}$ (Eq. 12). However, not all terms in Equation 12 are observable and it may be practical to manage the fishery by monitoring the fraction of the potential fecundity that is deposited on the bottom (Q_{SP}= $1-[\overline{E_{YD}}/\overline{E_P}]$). Nevertheless, we examined the potential effects of fishing mortality (f) on the egg escapement rate, $R_{e,t_{\max}}$, when natural mortality (m) is 0.1, 0.25, or 0.4, and egg deposition (v) is 0.25, 0.45, or 0.65 (Fig. 11). Because our preferred rates from the previous section are v = 0.25 and z = 0.45, then m is <0.45 with fishing because $z = m + f$. If we use v = 0.25 and set daily natural mortality rate high (m=0.4), then f is 0.05 and $R_{e,t_{\max}}$ is 93%. Doubling the fishing mortality (to 0.1) produces an absolute difference of 6% in egg escapement (Fig. 11C). Thus at a high m of 0.4, escapement is relatively insensitive to changes in daily

fishing mortality. At lower natural mortalities, a change in fishing mortality has a greater effect on escapement. At m = 0.1 and f = 0.35 $R_{e,t_{\max}}$ is 50%. Doubling the fishing morality to 0.7 $R_{e,t_{\max}}$ would be 33%, producing a loss of 17% in escapement (Fig. 11A). Increasing the rate of daily egg deposition (v) from our preferred value of 0.25 to 0.65 also diminishes the effect of fishing mortality on escapement but the effect of fishing on egg escapement is most marked at the low natural mortality of m = 0.1 and is relatively minor when natural mortality reaches m = 0.4. Thus, uncertainties regarding the true initial values of egg deposition seem relatively unimportant at these high mortality rates. It is important to remember that in this discussion that we are discussing daily mortality rates that last only a few days or weeks of the life of a semelparous animal; hence the rates are very high and resemble the typical daily mortality rates of small pelagic fish eggs (Alheit, 1993) that also exist for short periods.

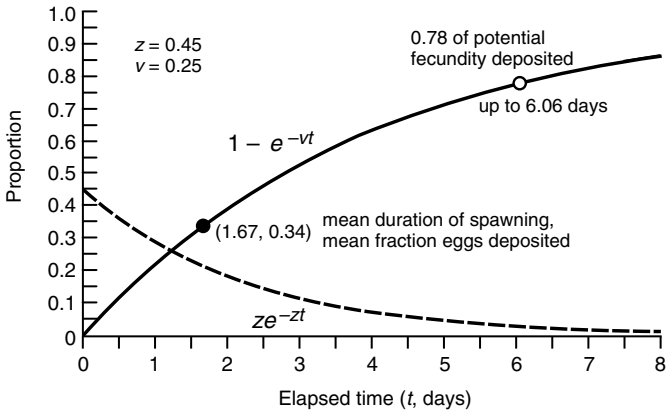

Figure 10

The cumulative egg release curve (solid line) and the density function of longevity on the spawning grounds of adult females (dashed line) of *Loligo opalescens* for a total mortality rate (z) of 0.45 and a egg release rate (v) of 0.25. The plotted solid circle represents mean egg deposition estimated by the model as a proportion of the potential fecundity and model estimate of the mean duration of the spawning period.

Cost effective methods for monitoring fecundity If egg escapement were adopted as a monitoring and management tool for the market squid fishery, a cost-effective method for monitoring fecundity of *L. opalescens* would be needed. A direct estimation of the standing stock of oocytes in an ovary by using a microscope and video system (as preformed in this study) is too time consuming for routine monitoring of the fishery because it takes about 4 hours per specimen.

Our first approach for an indirect estimator was to use the measurements routinely taken by CDF&G staff who sample the catch. These measurements were dorsal mantle length, mantle condition index, and an oviduct classification system for approximating the numbers of ova. To estimate the oocyte standing stock (E_Y) of the catch females, using only length and mantle condition, we fitted a nonlinear model to the data for all squid classed as mature (spawning individuals and pre-ovulatory) in our 1998 research survey data set. This yielded the equation

$$E_Y = 220.453e^{(1.99C + 0.0079L)}, \quad (17)$$

where L = dorsal mantle length; and
C = mantle condition index.

Equation 17 for E_Y explains only 33% of the variability within the survey data set (n=90) and therefore is rather imprecise. Using this model we estimated E_Y to average about 2221 oocytes in the ovaries of the mature females

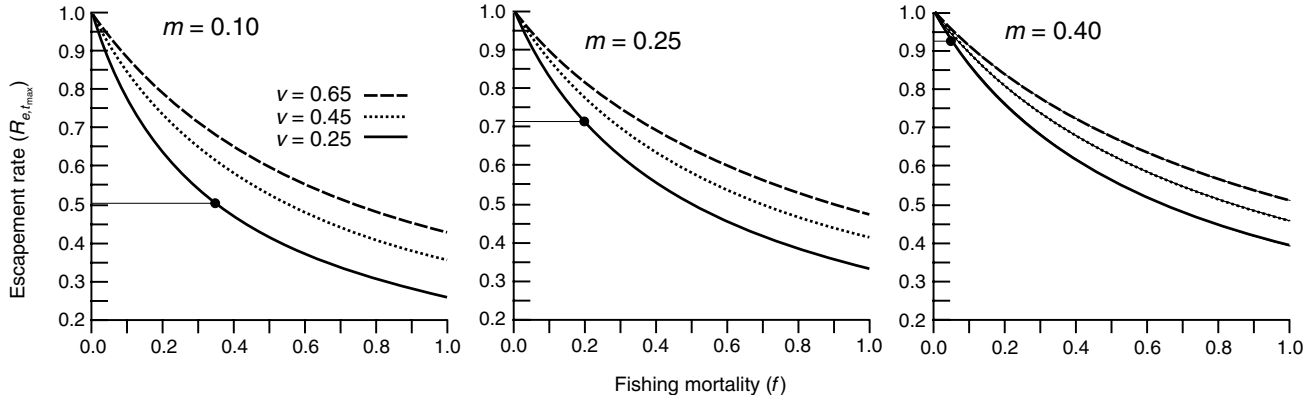

Figure 11

The egg escapement rate, $R_{e,t_{max}}$ (Eq. 12) of *L. opalescens* as a function of various daily natural adult mortality rates (m), daily egg deposition rates (v), and daily fishing mortality rates (f). In each panel, the solid circle indicates the f value for preferred values: z = 0.45 and v = 0.25.

(n=1275) sampled from catch during the period 1998–99 (Fig. 12); this estimate is equivalent to approximately 58% of the potential fecundity calculated from mean length (129 mm).

Our second approach was to estimate total fecundity (E_{YD}, standing stock of oocytes and ova) indirectly using the combined formalin wet weight of the ovary and the oviduct, in addition to mantle condition. Combining ovary and oviduct in one weight is more efficient than weighing them separately because much less time is required for dissection. Dorsal mantle length was also considered as a variable but it was not significant. The final equation for the total standing stock of oocytes and ova in a mature female squid is

$$E_{YD} = 378.28e^{(2.33C + 0.2447G - 0.24CG)}, \qquad (18)$$

where C = mantle condition index; and
G = gonad (ovary and oviduct) weight.

The predicted fecundity related well to the observed with a pseudo r^2 of 0.60 (df=143). We also used generalized additive models to estimate fecundity (GAM, pseudo r^2=0.64), as well as regression on the first principal component which explained 86% of the total variation (pseudo r^2=0.55). Although the GAM gave a slightly higher pseudo r^2 than the parametric nonlinear regression, we chose the later for easier interpretation and implementation. A pattern existed in the residuals from our model (Fig. 13); the model overestimated some fecundities at high mantle condition and underestimated fecundity at low mantle condition. This pattern in the residuals is probably related to the differences in density and size of oocytes in the ovary. Regardless of the minor problem with the residuals, this proxy (Eq. 18) for the standing stock of oocyte and ova is preferred because it gives a much more precise estimate at the minor additional cost of preserving and subsequently determining the combined weight of ovary and oviduct. Although formalin weight of ovary and oviduct are not presently monitored in the fishery, it is a variable that could be added to fishery protocols at a minor increase in cost. Another benefit of this more precise approach using E_{YD} is that oviduct is included in the estimate. If an estimate of the removal of fecundity by the fishery is needed, ova must be included. Because ova are not included in Equation 17, to add them requires using the oviduct classification system (Table 1) to estimate the average number of ova—a system that is imprecise but cheap. One could, of course, use Equation 17 for E_Y and either count the ova in the oviduct or weigh the oviduct, but that would take more work than applying Equation 18 for E_{YD}.

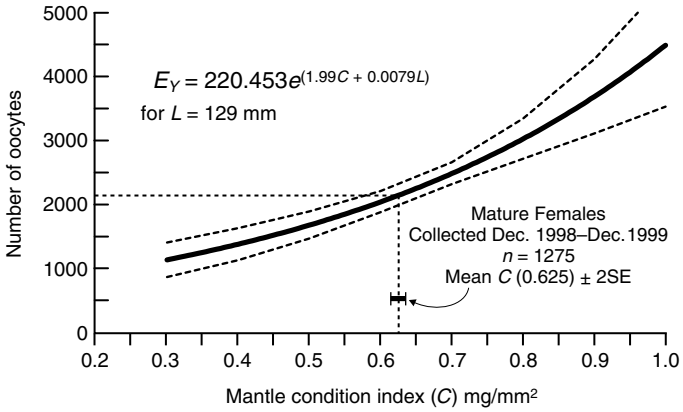

Figure 12

Standing stock of oocytes in the ovary (E_Y) as a function of mantle condition index (C) for a 129-mm mature female *L. opalescens* as predicted by Equation 17 (equation also given on top of panel; L is dorsal mantle length). Dashed lines are ±2SE. The mean E_Y for the females taken in the fishery was 2221 oocytes.

Discussion

Potential fecundity

Our estimate of *Loligo opalescens* potential fecundity is based on a regression of the standing stock of oocytes on dorsal mantle length for mature preovulatory females having yolked oocytes in their ovaries. The accuracy of this approach depends upon the assumption that these females are at the point in life when the standing stock of oocytes in their ovaries is equivalent to their potential lifetime fecundity. This key assumption would not hold if some of the mature squid classed histologically as preovulatory had in fact spawned. We do not know how long postovulatory follicles are distinguishable from atretic structures in the ovary of *L. opalescens* and, as far as we know, the rate of degeneration has not been determined for any loliginid. We know from our work on anchovy (Hunter and Goldberg, 1980; Hunter and Macewicz, 1985a), although it is not a cephalopod, that postovulatory follicles are distinguishable from atretic structures in the ovary of anchovy for about two to three days after spawning when the water temperature is about 16°C. This means that for undetected spawning to occur in *L. opalescens,* the interval between ovulation periods would likely need to exceed three days. This may be a minimum estimate because *L. opalescens* spawn at lower temperatures (9–13°C, Butler[2]) than do anchovy. Definitely a laboratory study on the rate of degeneration is necessary because postovulatory follicles in fish degenerate slower at lower temperatures (Fitzhugh and Hettler, 1995). In addition to the absence of postovulatory follicles, the oviduct must be empty for a spawning act to be undetected. Undetected ovulation and spawning seems unlikely because females with multiple stages of postovulatory follicles were common (87% of 247 mature females), females with only old postovulatory follicles were not detected, and the average life span on the spawning grounds may only be a few days.

Atretic losses of oocytes are another possible bias in estimating potential fecundity. Atresia (degeneration and resorption of an oocyte and its follicle) appears to be a

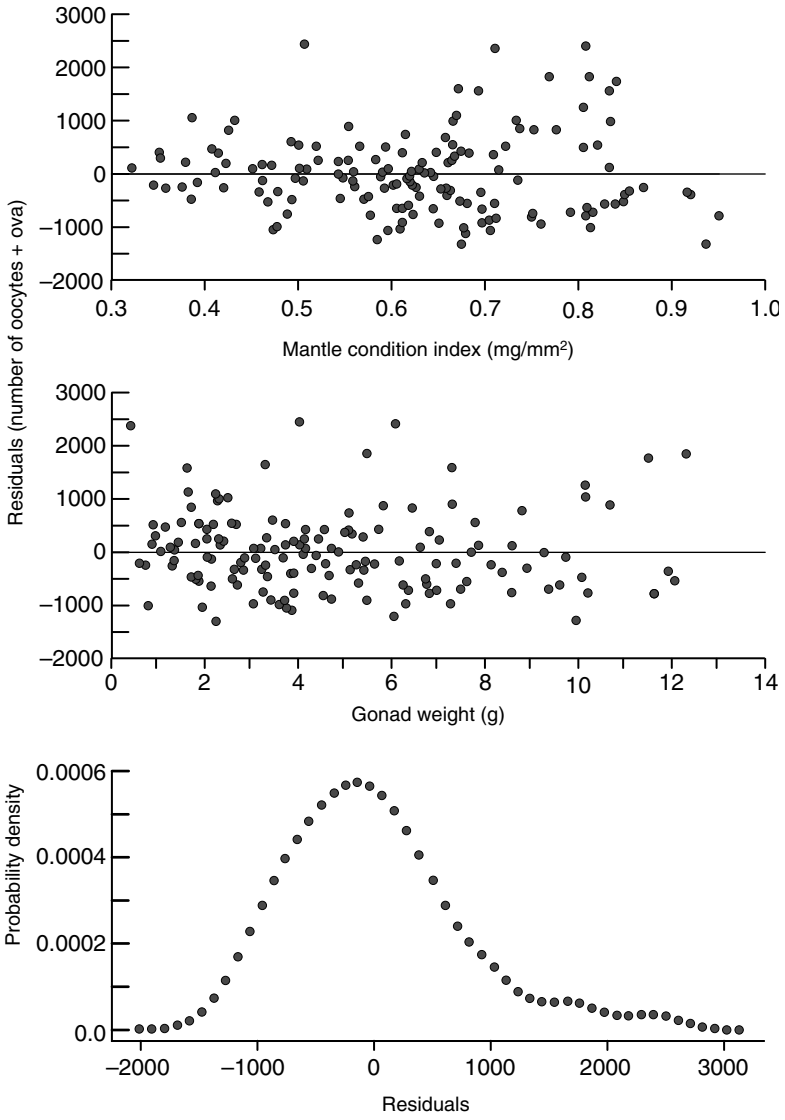

Figure 13

Residual plots of number of oocytes and ova from the equation $E_{YD} = 378.28e^{(2.33C + 0.2447G - 0.24CG)}$ (Eq. 18) where standing stock of oocytes and ova (E_{YD}) are predicted from mantle condition index (C) and gonad weight (G). Bottom panel shows probability density of residuals.

normal part of ovarian maturation in *L. oplaescens*, as it is the case for *L. v. reynaudii* (Melo and Sauer, 1998). Our evidence for this is that the standing stock of oocytes in immature female *L. opalescens* declines sharply as their ovaries mature (D increases, Fig. 7B). Clearly a narrow window of opportunity exists for an unbiased estimate of the potential fecundity of *L. oplaescens*. If the count is made too early in the ovarian maturation process, the count will either be low because extensive primary oogonia production may be still be occurring (64-mm female, Fig. 7A) or too high because additional oocytes will be absorbed before the female reaches maturity. If the count is made too late, it will be impossible to find a female that has not ovulated. Our selection criteria "presence of yolked oocytes" (which roughly begins at a oocyte size of about 1.1 mm) filtered out the very high counts of oocytes associated with immature ovaries.

From the practical standpoint, dealing with atretic losses that may continue into the spawning period is much less important for *L. opalescens* than for *L. v. reynaudii* (Melo and Sauer, 1998; Sauer et al., 1999) or *L. pealeii* (Maxwell and Hanlon, 2000). In these squid, where the spawning period may last weeks or months, atresia may seriously bias potential fecundity estimates. In the pres-

ent study all atretic losses would be attributed, of course, to ovulation and spawning but the chances of this being a major error seem low. Because we counted atretic as well as normal oocytes, atretic losses would be erroneously attributed to spawning only if atresia had proceeded to the point that the atretic structure could not be identified as that of an oocyte in whole-mount preparations under a light microscope (64× power). The time at stage for atretic oocytes in *L. opalescens* ovaries, as well as other squid, is unknown. The duration of alpha-stage atresia of yolked oocytes in anchovy is about a week at 16°C (Hunter and Macewicz, 1985b) and we suspect for the larger *L. opalescens* yolked oocyte that the alpha-stage duration may be even longer. The disappearance of unyolked atretic oocytes, as an oocyte-like structure that would be counted, is more difficult to dismiss because so little is known about this atretic stage and its duration. If our estimate of the average longevity of spawning female is only about 1.67 days, then atretic losses of even small unyolked oocytes is probably not an important bias. It would be useful if a way could be found to estimate oocyte resorption rates in squid although it may be very difficult. It seems more important to validate our preliminary estimate of the average longevity of spawning squid, because if true, any concerns regarding atresia could be dismissed.

Mature females without postovulatory follicles in their ovaries made up only 6% of the 247 females examined histologically. The rarity of these females in our collections reduced the precision of our potential fecundity estimate. Only thirteen of the fifteen females classed as a mature preovulatory female were usable for estimating potential fecundity, further reducing the sample size. Such a small sample size not only results in a low precision but raises the concern that the sample may not be representative of the stock as a whole. The fact that the average total fecundity of females with high mantle condition from the catch was close to the predicted value based on the thirteen females, indicates that the latter estimate may not be biased. Clearly a larger sample size is needed, particularly if egg escapement is used to monitor the fishery. It would be helpful, in obtaining more samples, if we knew the reason for the apparent rarity of mature preovulatory *L. opalescens* females. One possibility is that females might pass rapidly from the initial vitellogenesis to ovulation, perhaps in the course of a single day or some fraction of it, and ovulation might begin sometime in the evening when *L. opalescens* are the most vulnerable to fishing. Another possibility is that mature preovulatory females aggregate in regions not heavily fished by either our trawl or the fishery.

Egg escapement

A practical suggestion from this study is the idea of managing spawning-ground loliginid fisheries by monitoring the fecundity of the catch and computing the fraction of the potential fecundity spawned. Monitoring the escapement of eggs from the fishery is an attractive approach for *Loligo opalescens* because costs are moderate, unlike the high cost for monitoring egg beds that cover many locations offshore and occur at any time of the year, and because traditional fishery assessment models are difficult to apply or inappropriate at the present time (PFMC, 2002). To proceed with escapement fecundity as a management tool, it would be necessary to set a target level for egg escapement and to relate escapement to egg-per-recruit analysis so that fishing effort could be adjusted to alter egg escapement rates. Conceptual work along these lines has been completed (Maxwell[3]).

As mentioned earlier, as a practical matter in applying the egg escapement method, one would need to use Q_{SP}, the mean fraction of the potential fecundity escaping (Eq. 1), as a proxy for the more comprehensive and more useful measure of egg escapement $R_{e,t_{\max}}$, the fraction of the expected lifetime fecundity deposited (Eq. 12). Obviously, Q_{SP} will always be lower than $R_{e,t_{\max}}$ because the denominator of Q_{SP} (the fraction $\overline{E_{SP}}/\overline{E_P}$) is potential fecundity which will always be larger than the denominator for $R_{e,t_{\max}}$, which is expected lifetime fecundity (E). Although quite a different value, Q_{SP} is a useful proxy for $R_{e,t_{\max}}$. If natural mortality (m) and egg deposition rates (v) are constant, changes in fishing mortality will result in changes in Q_{SP} that are proportional to the change in $R_{e,t_{\max}}$.

However, changes will not be proportional if either v or m varies. If there is reason to believe that m and v are varying significantly, the use of Q_{SP} as a proxy for $R_{e,t_{\max}}$ should be undertaken with caution.

A point of concern in applying this method is that it may be difficult to substantially change escapement of eggs by regulating fishing effort. Our model indicated that egg escapement may be relatively insensitive to changes in fishing mortality if natural mortality rates are as high as we believe them to be. Of equal importance to management is the need to protect egg beds from damage by nets and to monitor the catch to prevent any change that might result in the capture of significant numbers of female *L. opalescens* before they begin to deposit eggs. Thus the fraction of the catch that is immature females must be monitored if the stock is managed by using the egg escapement method. For simplicity, our calculations of escapement were based on only mature females because immature females were only 2.6% of the females in the catch (1998–99) and their inclusion had little effect on parameter estimates. Egg escapement would decrease with an increase in the fraction of immature in the catch. As none of the fecundity of a captured immature female escapes the fishery, a relatively small increase in the fraction of immature animals in the catch can have significant consequences.

From the standpoint of fishery management, the most important unanswered question regarding the reproductive biology of *L. opalescens* is "how long do they remain on the spawning grounds?" or the equivalent question "what

[3] Maxwell, M. R., L. D. Jacobson, and R. Conser. Unpubl. data. Managing squid stocks using catch fecundity in an eggs-per-recruit model. Southwest Fisheries Science Center, National Marine Fisheries Service, 8604 La Jolla Shores Dr., La Jolla, CA 92037.

is the daily natural mortality of the spawners?" *Loligo opalescens* have only one spawning period in their life time (McGowan, 1954; Fields, 1965; Butler et al., 1999) but how long that period lasts remains unknown. Melo and Sauer (1999) concluded that the spawning period of *L. v. reynaudii* consisted of more than one spawning bout but neither the number of bouts nor the duration of each spawning period is known. In a laboratory study of *L. pealeii* (Maxwell and Hanlon, 2000), the number of bouts varied from one to ten, the interval between bouts was highly variable, and the life span after the first spawning bout was from 3 to 50 days. Our best guess for *L. opalescens* under fishing conditions was an average life on the spawning grounds of only 1.67 days and a maximum longevity of about 6 days. These estimates were based on a simple exponential model, constrained by various proxies for egg deposition rate, longevity, and the fraction of the potential fecundity in the catch (the only directly measured value). We believe that two of our estimates, 36% of the potential fecundity is deposited in the first 24 hours of spawning and minimum residual fecundity is about 22% of the potential fecundity, are on relatively firm ground but our estimate of the maximum longevity on the spawning grounds as 6 days is speculative. New information on mortality is needed because, over a wide range of daily mortality rates, our model yields values that are consistent with observed average fraction of potential fecundity in the catch. Because direct measurement of mortality on the spawning grounds may be difficult, it may be useful to develop some indirect approaches. For example, a laboratory study could be designed to generate an energy-based model that converts squid mantle tissue loss to deposited eggs. This mantle-to-egg conversion rate could be used to assign an age (time elapsed after first egg deposition) to modes of mantle condition from fishery samples. Mortality could then be computed by following modes of mantle condition through time.

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Appendix I

Terms

E_P	potential fecundity (standing stock of oocytes in the ovary of mature females prior to spawning)
$E_{SP,t}$	the total eggs deposited on the bottom up to time t (t in days)
E_C	total number of eggs deposited by mature females in the catch or total number of eggs escaped
E_M	total number of eggs deposited by mature females prior to death due to natural mortality
E_A	total number of eggs deposited by females alive and not caught by fishery
E	total number of eggs that would have been spawned during a squid's lifetime if no fishery existed
E_Y	standing stock of oocytes in the ovary
E_D	standing stock of ova in the oviduct
E_{YD}	total fecundity, the sum of both the number of oocytes in the ovary and ova in the oviduct
E_{YD,t_k}	stocking stock of oocytes in the ovary plus those ova in the oviduct after spawning has begun and up to the elapsed time t_k, where t_k is ≤ $t_{\max}$
$t_{\max}$	maximum elapsed time with the time 0 being the time when mature females are about to ovulate or total elapsed time (in days) of spawners on the spawning ground
E_R	standing stock of oocytes remaining in ovary at death
m	daily adult natural mortality rate
f	daily fishing mortality rate for adults
v	daily egg deposition rate
$Q_{SP,t} = E_{SP,t}/E_P = 1 - e^{-vt}$	fraction of potential fecundity deposited up to time t
e^{-zt}	mortality (survival) curve
N_0	number of mature females at time 0
N_C	total number of spawners in the catch
R_{e,t_k}	egg escapement rate = ratio of eggs deposited to total number of egg which would be spawned if there was no fishery, at a given elapsed time (t_k)
$R_{e,t_{\max}}$	egg escapement rate up to the maximum elapsed time ($t_{\max}$)

Appendix II

For any elapsed time t_k, formulas for E_C, E_M, E_A and E:

$$E_C = \overline{E_P} N_0 f \left[\frac{1 - e^{-(m+f)t_k}}{m+f} - \frac{1 - e^{-(m+f+v)t_k}}{m+f+v} \right]$$

$$E_M = \overline{E_P} N_0 m \left[\frac{1 - e^{-(m+f)t_k}}{m+f} - \frac{1 - e^{-(m+f+v)t_k}}{m+f+v} \right]$$

$$E_A = (\overline{E_P} - \overline{E_{YD,t_k}}) N_k = N_0 e^{-(m+f)t_k} \overline{E_P} (1 - e^{-vt_k})$$

$$E = \overline{E_P} N_0 \left[\frac{v}{v+m} - e^{-mt_k} \left(1 - \frac{m}{v+m} e^{-vt_k} \right) \right].$$

The derivation for E_A is straight forward and the derivations for E_C, E_M, and E, similar among one another, are as follows:

$$E_C = \int_0^{t_k} \overline{E_{SP,t}} dC_t = \int_0^{t_k} \overline{E_P} (1 - e^{-vt}) dC_t$$

$$= \overline{E_P} N_0 \int_0^{t_k} (1 - e^{-vt}) e^{-(m+f)t} f dt,$$

where

$$C_t = N_0 \frac{f}{m+f} (1 - e^{-(m+f)t})$$

is the number of removals of the cohort due to fishing up to time t (Quinn and Deriso, 1999).

$$E_M = \int_0^{t_k} \overline{E_{SP,t}} dD_{m,t} = \int_0^{t_k} \overline{E_P} (1 - e^{-vt}) dD_{m,t}$$

$$= \overline{E_P} N_0 f \frac{v}{(m+f)(m+f+v)},$$

where

$$D_{m,t} = N_0 \frac{m}{m+f} \left(1 - e^{-(m+f)t} \right)$$

is the number of removals of the cohort due to natural mortality up to time t (Quinn and Deriso, 1999) and E (when no fishing takes place):

$$E = \int_0^{t_k} \overline{E_{SP,t}} dD_t = \int_0^{t_k} \overline{E_P}(1 - e^{-vt}) dD_t$$

$$= \overline{E_P} N_0 \int_0^{t_k} (1 - e^{-vt}) e^{-mt} m dt,$$

where $D_t = N_0(1 - e^{-mt})$ is the number of removals of the cohort due to natural mortality when no fishing takes place.