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Comparative Life History Adaptations of Some Myopsid and Sepiolid Squid

by

William C. Summers

Huxley College of Environmental Studies, Western Washington University  
Bellingham, Washington 98225, USA

#### ABSTRACT

The inadequacies of population data in the determination of squid life history models is discussed. A close, functional comparison is noted for myopsids (Loligo pealei in particular) and the sepiolid squids. Though the latter are small and strictly nekto-benthic, they are capable of laboratory cultivation and provide excellent models for experimentation. It is now possible to test the physiological changes which support the seasonality of Mesnil's model and to examine the role of elective spawnin --as proposed here--and social interactions. A qualitative myopsid-sepiolid life cycle summary is presented to illustrate present ecological knowledge on this subject. The subject is briefly discussed in terms of squid fishery management in general.

#### INTRODUCTION

At the outset, I must observe that my title is fairly broad and that at most I will speak to only a few topics fitting within that heading. In particular, I want to contrast my experiences cultivating sepiolid squid with earlier field work with Loligo pealei. In the former I have now cultivated two species representing different genera, one each in Sweden and Washington State. In the latter, I worked on L. pealei for five years in the Atlantic, briefly in the Gulf of Mexico and variously on several other species of cephalopods. Some aspects of this report will apply to more diverse species, such as Illex illecebrosus, because cephalopods share a number of ecological characteristics--probably as a result of their comparatively long, evolutionary history.

Among these similarities, I see a functional commonality between the sepiolids and the adult forms of myopsids, even though the former share a body form with cuttlefish (with which they are most closely identified, systematically) and the latter look like the oceanic, oegopsid squid (Summers, 1983a). I suggest

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that the appearance is misleading; oegopsids never escape the functional constraints of a planktonic-pelagic life, sepiolids (and most of the other sepiolids) live only as nekto-benthic forms on continental shelves--myopsids share those same waters with one life stage like each of the above. These functional groupings of squid have a counterpart in the several species of *Octopus* which, in some circles, have come to be known as large-egged and small-egged forms.

Our information on life histories of cephalopods is necessarily limited. Certainly, among the squids, few have been seen alive and with the exception of *L. opalescens* (Yang et al, 1983), only a few species of sepiolids have been cultivated (Boletzky and Hanlon, 1983). Most data has been inferred from indirect sampling--quantification of the dead or dying animals brought up in trawls. Other fisheries methods so far have proven of limited value when applied to squid. Hence, a mythology exists which states that squid grow continuously, spawn only once, show latitudinal size gradients, have low egg mortality, etc. In the midst of this uncertainty is the present need to establish fisheries management goals. It seems obvious to me that we lack the data for a thorough management strategy and might well examine how best to proceed.

My inclination has been to gather more exact data on squid life histories, even if it was not from the target species. A proposal to examine sepiolids in the laboratory has bearing on the predominant life stage of, say, *L. pealei*. (Other approaches must be formulated to address planktonic and pelagic life stages and I will not anticipate those here.) The lack of a model for one life stage is not critical in population ecology so long as reasonable quantitative estimates exist at either end of that stage. If our mythology is correct, myopsids may provide both ends of the planktonic "black box" through egg counts and demersal recruitment data, though neither of these is well documented at present.

#### **Some Comparisons**

Sepiolid squids lay a few large eggs (approximately 100 that are 3-10mm in diameter) which produce young of proportionate size that immediately take up the adult mode of life. Swimming is labored and interrupted by long periods of sitting on, or being covered up on the bottom. Long migrations seem very improbable. They tolerate crowding well and one might risk calling them social. All of these characteristics contribute to their adaptability in aquarium cultivation.

The myopsid, *L. pealei*, may lay 10,000 eggs (I think fewer) which are 1.0 x 1.6mm in size and relatively quickly hatch as planktonic juvenile squid. Their activities and whereabouts are little known for the roughly one month previous to the assumption of a more demersal life form (Summers, 1983b). Cultivation of planktonic juvenile squid is very difficult. Because of trawl selectivity, small to medium sized squid are not readily caught and/or usually injured in sampling. Adult mortality in trawls is also high, but some survive and can be maintained in larger aquaria (Summers, et al, 1974). They are often competitive or aggressive in captivity and swim most of the time. They have not been cultivated.

### **Growth**

The commercial value of squid is related to their size (usually reported as dorsal mantle length) and weight. The two parameters have, of course, been reported for large samples of L. pealei. Because aging has not been possible in the past, size has been taken as directly proportional to age. This is the basis of nearly all growth models, hence the means for estimating life span, management goals, etc.

In laboratory cultures, feeding is usually not limiting and my observations based on regular photographs of sepiolids is that size is linearly related to age (differing for the two sexes) until maturation—at which point it stops. We have correlated different measurements with these photographic data and come to about the same conclusion. I will also cite the article last June proposing that Nautilus may live more than 20 years including 5-10 years past maturation (Saunders, 1984). Both sources suggest caution in the strict use of a proportional model. So far as I know, there is no experimental data on growth with limited food availability or relating the effects of migration on growth; these could be simulated in the laboratory. In addition, there is some progress on aging from statoliths. (Rosenberg et al, 1981). Obviously, growth is not a simple matter and requires further study.

### **Maturation and Spawning**

At some point, the physiology of a growing squid is changed to promote sexual maturation. Wodinski (1977) showed that this was governed by the optic gland in Octopus and Mesnil (1977) quoted French physiological data (derived from cuttlefish response to the light and temperature effects of a winter to summer period) to show how this would promote maturation and spawning in L. pealei and I. illecebrosus. Maturation appears to be a one way change since dematuration is not reported. This progression may regularly occur in some species over a brief span of time, however, the triggering events are not fully understood.

Copulation must also occur in this interval, but its timing may not be critical owing to the ability of female squid to store sperm for long periods of time. But then why do some squid aggregate (and copulate) when in the process of spawning? In the laboratory, some sepiolids refrain from copulation and die unspawned. In fact, reports on sepiolid maintenance often end with death at the time of maturation or the likely time of spawning. Rather than blaming the investigator for inattention in these cases, I suggest that we need to allow for a more elective or discretionary participation by individual squid in the later stages of maturation, including especially mate selection, copulation and eventual spawning. In a word, squid should be thought of as "fickle." We need not attribute any conscious decision making to this phenomenon, it is simply the result of an intelligent, sensitive animal responding to its particular situation. Some will copulate and spawn as we have predicted, but some will not—these are the fickle ones.

### The Long and the Short of It, Again

The capacity for individual choice in behavior is subject to selection. If "fickle" is unevenly distributed through the range of a squid—I am particularly referring to L. pealei—it would lead to races and, possibly, new species. More immediately, it is a mechanism which allows the Mesnil (1977), alternate life span model to fit differing descriptions of L. pealei populations throughout its broad and varied range.

By itself, the Mesnil model of obligate long- and short life spans is too rigid to account for the observed variability in squid populations. Ecologically it is questionable because three separate lines must be present at all times and crossover mechanisms are inconsistent with the model. Every line is exposed to the risks of every life stage and, there is no accounting for latitudinal size gradients nor oversize individuals. Does this fit in low latitudes where, on the basis of size, only short cycle squid occur and these spawn year round, or in high latitudes where what I have called the fall brood has never been observed spawning?

The problem with this model is that it substitutes statistical individuals for reality—the variability of individuals and sexes does not appear as a part of the model. Selection works at the level of individuals, not on groups such as populations or species, so an accounting for variability is necessary. At the risk of undoing some progress in squid biology, I am proposing a more generous interpretation until the data are available. In the case of L. pealei, there is good reason to accept ages of one, two and even three years (based on sizes), to assume that some of these missed predictable spawning times because they were fickle and to expect races among some samples.

Borrowing again from the sepiolid data, the somatic growth of squids appears to be species-specific, but independent of water temperature (Boletzky, 1975). Thus in higher latitudes, the larger L. pealei must be older and probably more often fickle. The double sized individuals which are reported (Summers, 1983b) must be especially fickle. I am assuming that sepiolid cultivation is a good model for the lower latitude situation because harsh winters and migration have not been simulated, hence the squid tended to spawn and/or die at the first opportunity.

There are some experimental options which may also have utility. By the time of this meeting, I hope to be able to report a complete life cycle of Rossia pacifica in the laboratory; I expect that this will take about 15 months. Other sepiolids have much shorter laboratory life spans, roughly five to nine months. (Bo Bergstrom and I cultivated Sepietta oweniana in about nine months). None of these cases fits a simple, annual model and all can be manipulated, especially through temperature effects at the egg stage. Testing of the above mentioned factors is now possible in the laboratory with particular squid. The whole area of inclusive fitness indicating cohort selection needs to be examined. Why do squid occur in schools of all one size and how do they pair up when mating? These are unresolved questions.

### A Qualitative Life Cycle Model

I would like to recast the myopsid-sepiolid life cycle model in qualitative terms simply for clarification and in order to focus attention on the range of possible individuals responses.

- 1) Winter conditions over much or all of the range may preclude spawning and/or may be partly avoided by migration. Maturation is enhanced during this season and already mature squid may copulate. Growth continues over the longer term though both maturation and migration may result in growth arrests.
- 2) The return of longer days and warmer temperatures promotes both copulation and spawning. This is more seasonal and exhaustive following prolonged winter conditions. Death follows spawning for both sexes, but copulation may be repeated and several batches of eggs produced over a period of several days to a month. Larger squid lay more eggs.
- 3) The summer months are largely devoted to feeding and growth, but some large individuals will mature sexually and spawn at dispersed times. It is at this time of year that squid are potentially most fickle.
- 4) The egg mortality is very low and hatching times are strongly influenced by water temperature. Small-egged species hatch quickest and produce planktonic young. Those with large eggs hatch as young which take up the adult, demersal or nekto-benthic forms of life.
- 5) The chance of aggregation formation is directly related to the potential for squid to be fickle and these phenomena occur at different times of year, in seasonal climates. The production cycle may, to some extent, substitute for a seasonality in physical parameters.
- 6) The largest squid (circa twice usual sizes) may produce distinctive year class components, directly populating peripheral regions, or these may spawn in various combinations with recently matured squid.
- 7) The social interactions of squid are largely unknown.

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