NAFO Sci. Coun. Studies, 9: 139-142

Comparative Life History Adaptations of Some Myopsid and Sepiolid Squids

William C. Summers
Huxley College of Environmental Studies, Western Washington University
Bellingham, Washington, USA 98225

Abstract

The inadequacies of data for determination of life-history models are discussed. A close functional comparison is noted for myopsid (particularly *Loligo pealei*) and sepiolid squids. Although the latter squids are small and strictly nektobenthic, they are capable of laboratory cultivation and provide excellent models for experimentation. With appropriate cultivation techniques, it is now possible to test seasonal physiological changes relevant to various hypotheses on the life spans of squids and to examine social interactions and the proposed role of elective spawning. A qualitative myopsid-sepiolid life-history summary is presented to illustrate present ecological knowledge on the subject.

Introduction

This paper contrasts the author's experiences in cultivating sepiolid squids with field work on the myopsid *Loligo pealei*. These experiences involved studies of two species representing different genera of sepiolids, one each in Sweden and on the Pacific coast of the United States, and *L. pealei* in the western North Atlantic. Some aspects of the paper 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.

There is 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 closely identified systematically, and the latter look like the oceanic oegopsid squids (Summers, 1983a). The appearance is misleading, because oegopsids never escape the functional constraints of a planktonic-pelagic life, sepiolids (and most of the sepiids) live only as nektobenthic forms on the continental shelves, and myopsids share the same waters with a life stage like each of the two preceding groups. These functional groups of squids have a counterpart in several species of *Octopus*, which have come to be known as large-egged and small-egged forms.

Information on complete life histories of cephalopods is quite limited. Certainly, among the squids, few have been studied alive and only *Loligo opalescens* (Yang *et al.*, 1983) and a few species of sepiolids (Boletzky and Hanlon, 1983) have been cultivated. Much information has been inferred from indirect sampling, e.g. quantification of dead or dying animals captured in trawls. Population modeling techniques so far have been of limited value when applied to squid. Hence, a mythology exists which indicates that squid grow continuously, spawn only once, show latitudinal gradients, have low egg mortality, etc. In the midst of this uncertainty is the present need to establish fishery management goals. Data for a thorough management strategy are obviously lacking, and it is appropriate to examine how best to proceed.

It has been the author's inclination to gather more exact information on life histories of squids, even if the data were not from the target species. Study of sepiolids in the laboratory has bearing on the adult life stage of myopsids, such as *L. pealei*. Other approaches must be formulated to study the planktonic and pelagic life stages, but those will not be anticipated 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 the stage. Myopsids may provide both ends of the planktonic "black box" through egg counts and demersal recruitment data, but neither of these is well documented at present.

General Considerations

Some comparisons

Sepiolid squids lay approximately 100 large eggs (3–10 mm in diameter) which develop into young of proportionate size that immediately assume the adult mode of life. Swimming is labored and interrupted by long periods of lying on or being covered up on the bottom. Long migrations are very improbable. They tolerate crowding well, and one might risk calling them "social". These characteristics contribute to their adaptability in aquarium cultivation.

The myopsid (*L. pealei*) may lay up to 10,000 eggs (eliptical diameters of 1.0 and 1.6 mm) which develop quickly and hatch as planktonic juveniles. Little is known about their activities and whereabouts for one month prior to the assumption of a demersal form of life (Summers, 1983b). Because of selectivity, small to medium-sized squid are not readily caught in trawls, and those that are caught are usually injured. Mortality of adults in trawls is also high, but some survive and can be maintained in laboratory aquaria (Summers *et al.*, 1974). In captivity, they are often competitive or aggressive and swim most of the time, and their cultivation has not been successful.

Large-egged species of *Octopus* have been sufficiently well studied to warrant development of a model (relating nutrition, light intensity and temperature) which explains variations in life span and spawning size (Van Heukelem, 1979). The model has evidently not been tested on other cephalopods, but it seems to be consistent with the majority of individual observations from the literature. There is good reason to believe that the model would apply to some squids, perhaps especially to the sepiolids. Boletzky (1981) addressed the ecological significance of cephalopod reproduction.

Growth

The commercial value of squid is related to their length (usually reported as dorsal mantle length) and weight, and these parameters have been reported for large samples of *L. pealei*. Because ageing was not possible in the past, size was taken as being directly proportional to age (Summers, 1971). This is the basis of nearly all growth models which have been used for estimating life span, management strategy, etc.

In laboratory experiments, where feeding is usually not limited, observations on sepiolids indicate that size is linearly related to age (differing by sex) until maturation, at which point growth stops. From mark-recapture studies, Saunders (1984) reported that *Nautilus* may live more than 30 years, including 5–10 years beyond maturation. Both sources indicate caution in the strict use of a proportional model. There have been few, if any, experimental studies on the effects of limited food availability on growth or the effects of migration on growth, both of which could be simulated in the laboratory. Recently, there has been some progress on ageing squid from statoliths (e.g. Rosenburg *et al.*, 1981), but techniques are still being developed (Morris and Aldrich, 1985; Dawe *et al.*, 1985). Obviously, growth of squids is not a simple process and further studies are required.

Maturation and spawning

At some point, the physiology of a growing squid is changed to promote sexual maturation. Wells and Wells (1959) showed that this was governed by the optic gland in *Octopus*, and Wodinski (1977) experimentally manipulated growth and maturation in animals of the same genus. Mesnil (1977) used physiological data from cuttlefish responses to the light and temperature effects of a winter-to-summer period to show how maturation and spawning of *L. pealei* and *I. illecebrosus* could be promoted. Maturation appears to be a one-way change because the reverse process has not been reported. This process may occur regularly in some species over a brief period, but the triggering events are not fully understood.

Copulation must occur during the period of maturation, but its timing may not be critical because female squid have the ability to store sperm for long periods. However, the males and females of some species aggregate (and copulate) when in the process of spawning. In the laboratory, some sepiolids refrain from copulaton and die unspawned. In fact, reports on maintenance of sepiolids often end with death at the time of maturation or the likely time of spawning. Without blaming the investigator for inattention in such cases, it is important that allowance be made for more elective or discretionary participation by individual squid in the later stages of maturation, especially mate selection, copulation and eventual spawning. Thus, squid should be thought of as being "fickle". This phenomenon is simply the response of an intelligent, sensitive animal to its particular situation rather than to conscious decision-making. Some squid will copulate and spawn at a predictable time, but others will not. The latter are the fickle ones.

Life span

The capacity for individual choice in squid behavior is subject to selection. If the "fickle" characteristic is unevenly distributed throughout the range of a species, referring particularly to *L. pealei*, it would lead to races and possibly new species. In the present context, it is a mechanism which allows the alternate life-span model, proposed by Mesnil (1977), to fit the differing description of *L. pealei* populations throughout the broad and varied range of the species. However, the Mesnil model of long and short life spans, by itself, 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. Each line is exposed to the risks of every life stage, and there is no accounting for oversized individuals or latitudinal gradients in size.

The problem with the Mesnil (1977) model is that it does not account for variability of individuals. Because selection works at the level of individuals rather than at the level of groups such as populations or species, an accounting for variability is necessary. At the risk of undoing some progress in squid biology, a more realistic interpretation is proposed until the data become available. In the case of *L. pealei*, there is good reason to accept the existence of ages one, two and even three years on the basis of size, to assume that some of these individuals missed the predictable spawning time because they were fickle, and to expect different races in some samples. Borrowing again from the sepiolid data, the somatic growth of squids appears to be species-specific and independent of water temperature (Boletzky, 1975). Thus, the larger *L. pealei* in the higher latitudes must be older and probably more often fickle than those in the lower latitudes, where, in the absence of harsh winters and according to the sepiolid cultivation model, they tend to spawn and/or die at the first opportunity.

There are some experimental options which have utility. A recent study, by the author and associates, of the complete life cycle of *Rossia pacifica* in the laboratory indicates a life span of about 2 years. Other sepiolids have much shorter laboratory life spans, roughly 5–9 months (e.g. *Sepietta oweniana* was cultivated by the author and associates in about 9 months). None of these cases fits a simple annual model and all can be manipulated, especially through temperature effects at the egg stage.

A Qualitative Life Cycle Model

The myopsid-sepiolid life cycle model is restated below in qualitative terms in order to focus attention on the range of options available to individual squid.

1. Winter conditions over much or all of the range of a species may preclude spawning and/or may be partly avoided by migration. Maturation is enhanced during this season, and squid which already have matured may copulate. Growth generally continues, but maturation and migration may result in growth arrests.
2. The longer days and higher temperatures of spring promote both copulation and spawning, which are more exhaustive after 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 devoted largely to feeding and growth, but some large individuals will mature sexually and spawn over a protracted period. It is at this time of the year that squid are potentially most fickle.
4. Egg mortality is very low and hatching times are strongly influenced by water temperature. Small-egged species hatch quickly and produce planktonic young. The young of species with large eggs immediately take up the adult demersal or nektobenthic form after hatching.
5. The chance of formation of aggregations is directly related to the potential for squid to be fickle, and these phenomena occur at different times of the year, in seasonal climates. The production cycle may, to some extent, substitute for a seasonality in physical parameters.
6. The largest squid (about twice the usual size) may produce distinctive year-class components. These may directly populate peripheral regions, or they may spawn in various combinations with recently-matured squid.
7. The social interactions of squid are largely unknown.

Acknowledgements

The author gratefully acknowledges partial support for continuing research from various sources associated with Western Washington University. The Shannon Point Marine Center and Wilson Library have been especially supportive of this work. The encouragement and advice of several colleagues has been invaluable. The personal contribution of a student, Larry Colvin, is particularly acknowledged.

References

BOLETZKY, S. V. 1975. The reproductive cyle of Sepiolidae (Mollusca, Cephalopoda). *Publ. Sta. Zool. Napoli*, **39**(suppl): 84–95.

BOLETZKY, S. V. 1981. Reflexious sur les strategies de reproduction chez les cephalopodes. *Bull. Soc. Zool. France*, **106**: 293-304.

BOLETZKY, S. V. and R. T. HANLON. 1983. A review of the laboratory maintenance, rearing and culture of cepholopod molluscs. *Mem. Nat. Mus. Vict.*, **44**: 147–187.

DAWE, E. G., R. K. O'DOR, P. H. ODENSE, and G. V. HURLEY. 1985. Validation and application of an ageing technique for short-finned squid (*Illex illecebrosus*). *J. Northw. Atl. Fish. Sci.*, **6**: (in press).

MESNIL, B. 1977. Growth and life cycle of the squids *Loligo pealei* and *Illex illecebrosus*, from the Northwest Atlantic. *ICNAF Sel. Papers*. **2**: 55–69.

MORRIS, C. C., and F. A. ALDRICH. 1985. Statolith length and increment number for age determination of *Illex illecebrosus* (Lesueur, 1821) (Cephalopoda, Ommastrephidae). *NAFO Sci. Coun. Studies*, **9**: 101–106 (this volume).

ROSENBERG, A. A., K. F. WIBORG, and I. M. BECH. 1981. Growth of *Todarodes sagittatus* (Lamarck) (Cephalopoda, Ommastrephidae) from the Northeast Atlantic, based on counts of statolith growth rings. *Sarsia*, **66**: 53–57.

SAUNDERS, W. B. 1984. *Nautilus* growth and longevity: evidence from marked and recaptured animals. *Science*, **224**: 990–992.

SUMMERS, W. C. 1971. Age and growth of *Loligo pealei*, a population study of the common Atlantic coast squid. *Biol. Bull. Mar. Biol. Lab. Woods Hole, Mass.*, **141**: 189-201.

1983a. Physiological and trophic ecology of cephalopods. *In*: The Mollusca (Chap. 6, p. 261–279), Vol. 6 (Ecology), W. D. Russell-Hunter (ed.), Academic Press, New York, N.Y., 695 p.

1983b. *Loligo pealei*. *In*: Cephalopod life cycles (Chap. 8, p.

115–142), Vol. 1 (Species accounts), P. R. Boyle (ed.), Academic Press, New York, N. Y., 475 p.
SUMMERS, W. C., J. J. MacMAHON, and G. N. P. A. RUPPERT. 1974. Studies on the maintenance of adult squid (*Loligo pealei*). II. Empirical extensions. *Biol. Bull. Mar. Biol. Lab. Woods Hole, Mass.*, **146**: 291–301.
VAN HEUKELEM, W. F. 1979. Environmental control of reproduction and life span in *Octopus*: an hypothesis. *In*: Reproductive ecology of marine invertebrates (p. 123–133), S. E. Stancyk (ed.), Univ. South Carolina Press, Columbia, S. Carolina, 283 p.
WELLS, M. J., and J. WELLS. 1959. Hormonal control of sexual maturity in *Octopus*. *J. Exp. Biol.*, **36**: 1–33.
WODINSKI, J. 1977. Hormonal inhibition of feeding and death in *Octopus*: control by optic gland secretion. *Science*, **198**: 948–951.
YANG, W. T., R. F. HIXON, P. E. TURK, M. E. KREJCI, R. T. HANLON, and W. H. HULET. 1983. Culture of the California market squid from hatching — completion of the rearing cycle to second generation hatchings. *Aquabiology*, **5**(5): 328–339, (in Japanese).