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## **To cite this version:**

William C. Summers. ECOLOGICAL IMPLICATIONS OF LIFE STAGE TIMING DETERMINED FROM THE CULTIVATION OF ROSSIA PACIFICA (MOLLUSCA : CEPHALOPODA). Vie et Milieu / Life & Environment, 1985, pp.249-254. hal-03022197

# **HAL Id: hal-03022197 <https://hal.sorbonne-universite.fr/hal-03022197v1>**

Submitted on 24 Nov 2020

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#### *VIE MILIEU,* 1985, 35 (3/4) : 249-254

## ECOLOGICAL IMPLICATIONS OF LIFE STAGE TIMING DETERMINED FROM THE CULTIVATION OF *ROSSIA PACIFICA* (MOLLUSCA : CEPHALOPODA)

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**ECOLOGY TIMING CULTIVATION**  *ROSSIA PACIFICA*  **SEPIOLID SQUID CEPHALOPODA** 

**ÉCOLOGIE RYTHMES ÉLEVAGE**  *ROSSIA PACIFICA*  **SEPIOLIDAE CEPHALOPODA** 

northeast Pacific océan and brought into the laboratory where it is currently in cultivation. At seasonally varying temperatures, the generation is two years; 18-19 months from hatching to a spawning-related death, and 5-6 months for embryonic development. Growth in dorsal mantle length was slow for the initial one-half year, but increased at the time of spawning and death of the preceding year class. It continued through maturation to spawning at différent rates for each sex. Repeated spawning was observed. Hatching of the eggs appeared to be keyed to the new moon and extended over more than two months. Low seawater temperatures may affect this process. The ecological significance of lunar cuing is discussed relative to predation. Long-term observation of overlapping, two-year life cycles from field data confirms measured growth in cultivation and suggests that two relatively independent year classes coexist on the same ground with little compétition. The early life is characterized by low growth, adaptability and a conservative strategy. It is released by the semelparous death of the preceding year class to become more opportunistic, grow faster and become sexually mature. This life pattern may be homologous to other squid species.

ABSTRACT. — The sepiolid squid, *Rossia pacifîca* Berry 1911, was trawled in the

RÉSUMÉ. — La durée d'une génération de *R. pacifîca* soumise aux variations saisonnières de températures est de 2 ans : 18 à 19 mois de l'éclosion à la reproduction (suivie de la mort), et le développement embryonnaire se déroule en 5 à 6 mois. La croissance linéaire est lente pour les six mois suivant l'éclosion, puis augmente pendant la période où la « classe » de l'année précédente se reproduit et meurt. Après cette augmentation du taux de croissance, les taux divergent pour les deux sexes. Une même femelle peut pondre plusieurs fois en l'espace de quelques semaines. L'espèce peut être élevée en aquarium si des Crevettes vivantes de taille appropriée sont disponibles comme nourriture. Un fond de sable et un renouvellement continu de l'eau de mer dans les bacs d'élevage sont souhaitables. L'éclosion des jeunes semble liée aux phases lunaires et peut se prolonger sur plusieurs mois si les températures sont basses. L'influence de facteurs liés aux conditions artificielles doit également être prise en considération dans le déclenchement de l'éclosion.

### **INTRODUCTION**

There are at least two compelling reasons for the détermination of squid life cycles and the factors that cause them to progress. The most immediate of these is for the rational management of squid fisheries based on an assumption that conservation is desirable and that the squid stocks are not infinite. The second is more basic; it seeks to détermine the ecological role of squid in marine ecosystems, noting that they are ubiquitous, ancient and never higher

than penultimate predators (Packard, 1972, Summers, 1983). The scientific establishment also places demands on squid as a source of giant axons (Baker, 1984) and as models for other biomédical research (National Research Council, 1985). Descriptions of a few, better-known squid life cycles (Boyle, 1983) suggest a partial dichotomy — some species have many small eggs and planktonic young that change form at relatively distinct life stages. Others have a few large eggs and hatch as functionally small adults (Boletzky, 1981). The former group is least well known.

The sepiolids are among the species with large eggs and an apparent direct development. They are widely distributed and can be cultivated (Boletzky and Hanlon, 1983). Furthermore, the sepiolids basically have only one life stage between hatching and death, and it is one that can be identified as a functionally generalized squid pattern, at least as far as neritic squids are concerned. Though more limited in sizes than some other squids, sepiolids cannot be considered small when compared with the majority of marine organisms. Because of cultivation, sepiolids may provide an experimental homology for the larger stages of other squid species.

An alternative to laboratory evaluation exists in long-term field studies where population statistics subtitute for precise determinations from known individuals. This approach is traditional in fisheries research and still necessary for those species that cannot be cultivated (e.g., Summers, 1971). The field study approach is inefficient and introduces possible errors due to sampling and migration; laboratory studies are prone to artifacts due to unnatural conditions.

In a recent paper, the author calls into question the widely used practice of equating size with the age of squid and raises the issue of elective behavior of individual squid at the latter stages (Summers, 1985). The purpose of this report is to describe some new information on life stage timing obtained during the first cultivation of *Rossia pacifîca.* The ecological importance of timing is discussed.

#### MATERIALS AND METHODS

The common northeast Pacific sepiolid squid, *Rossia pacifîca* Berry 1911, was caught regularly in Burrows Bay, Skagit County, Washington in June and July of 1983. Specimens were collected in 40 to 60 m depth with commercial shrimp trynets (10 foot otter trawls) from the R/V Leona III operated by personnel from the Shannon Point Marine Center. Examinations of about 30 specimens showed two distinct size groupings, the larger of which had a clear sexual dimorphism (females larger than maies). Some of these were transferred to the laboratory near Anacortes, Washington and maintained in running seawater for a few weeks. Ail of the healthy animais fed readily on shrimp (approximately the same size as the squid), particularly various pandalid species. When sand was provided in the aquaria, the *Rossia* spent large portions of the daylight hours on the bottom covered with sand.

#### *Cultivation*

Seven of the smaller squid were placed together in a rectangular fiberglass aquarium with coarse sand (dimensions : 55  $\times$  40 cm, filled to a depth of 35 cm). These were maintained together until March 1984, at which time sexual maturity was evident and pairs or individuals were isolated in various aquaria of the same or smaller dimensions  $(40 \times 30 \text{ cm},$ filled to 30 cm depth) until all of them had died (a period extending from 10 April to 29 June, 1984). Of the seven, two were maies and five females. One pair copulated on or shortly before 7 May; the female laid about 50 eggs (1 cm in diameter) on the aquarium wall approximately <sup>1</sup> June, and (after both were moved to a controlled temperature aquarium of about 95 L volume) another 35 eggs on 21 June. This female died four days later followed by the maie five days after that.

Monthly mean temperatures varied seasonally from 6 to 12 °C. The controlled temperature aquarium was maintained at 10 °C, which is the approximate year-round mean temperature. This aquarium had regular, partial replacement of seawater rather than running seawater. Standard water quality parameters remained consistently high over the course of the cultivation (e.g., dissolved oxygen 7-11 ppm, pH 7.7-8.3, and both total and carbonate alkalinities 1.85-2.25 meq/liter).

Running seawater aquaria were situated in a north facing, roofed, but otherwise open and unheated room connected to the laboratory building. Artificial illumination was used irregularly during working hours, and rarely at night. Clear plastic sheeting was used to provide weather protection of the room during the most severe winter months. The temperature controlled aquarium was immediately adjacent to this room, but inside the building in a heated space. It received illumination through large Windows and daytime artificial illumination. This aquarium was, in general, somewhat darker than the running seawater aquaria.

The animals were subjected to weekly photographie documentation, with a few lapses which include the period of embryonic development, beginning <sup>3</sup> August, 1983. Squid were photographed vertically from about one-half meter distance in shallow glass dishes placed on millimeter graph paper. The procédure was conducted quickly and with little apparent trauma using photoflood illumination. By later projection of color slides, it was possible to reliably measure dorsal mantle length (and other dimensions) to less than one millimeter. It should be noted that this produces a good relative measure, but one which is foreshortened by the squid's upright posture and, to a lesser extent, by the photographie geometry.

The reliability of the photographie method was tested through a series of repeated photographs in a randomized complete block ANOVA design when the squid were half-grown (mean dorsal mantle length of 22 mm). As expected, the blocks (individual squid) were highly significant in photographie size déterminations, but individual measurements of the same specimen did not vary significantly. Persons taking the measurements had a small, but consistent effect on the results.

Eggs were disturbed as little as possible, but were occasionally flushed with the flow of water from the intake hose to dislodge sediment and diatoms. The range of temperatures measured in the running seawater tank was from 15 to 6 °C over the period of embryonic development, with the greatest daily variation occurring in the summer. The temperature-controlled aquarium remained within one degree of the preset, 10°C.

Following hatching late in 1984 and early in 1985, the young squid were transferred to floating plastic containers within the aquaria. After a few days the squid were released into all-glass aquaria of about 100 L capacity with a clean sand bottom. The squid in the temperature controlled aquarium were simply released in that tank which had coarse shell-sand as a bottom filter. Cultivation of second generation squid is continuing as of December, 1985.

### RESULTS

The photographic sizes of the seven specimens and a representative number, or all, of the second generation is shown in Figure 1. A mean photographie dorsal mantle length is given in the figure; this should be taken as 80-90 % of the directly measured dorsal mantle length in relaxed live squids or fresh dead ones. It progresses from a measured hatching size of 6 mm dorsal mantle length (photographed at 80 %) to the largest females of 50 mm (photographed at 90 %). The photographie size range also increased from 2 mm during the hatching period to 12 mm at spawning; the last mostly due to sexual dimorphism.



Fig. I. — Growth of *Rossia pacifîca* over a two-year life span. The figure is a transposition of mean dorsal mantle length data (photographic measurements) for seven specimens captured in June and July of 1983 (shown as stars) and all or a representative number of the subsequent generation (shown as squares). The ultimate sizes of the original seven are shown at the time of death as F (female) and M (maie); one pair laid two batches of eggs as indicated. Monthly mean seawater températures are shown at the top-two data points in July represent a warmer season in 1985 compared with 1983. Filled squares are conservative size estimates from recent measurements.

Growth (Fig. 1) was continuous but not at the same rate through the one and one-half year life life span. Even after size correction for the photographie method — if such is necessary — it is clear that growth rates increase with âge and size. This is opposite to the von Bertalanffy growth model. Field data and specimens of *R. pacifica* collected in the immediate area over the last decade readily fit this laboratory observation and further confirm that two âge groups are typical. Food did not appear to be limiting in the laboratory because the numbers of shrimp consumed by the squid remained relatively constant throughout the cultivation (roughly 3/squid/week). In running seawater temperatures were seasonal and cycled twice over the total generation (life span plus embryonic development).

The cultivation determined that sexual maturity presages death in both sexes — with or without copulation and spawning. Thus, *R. pacifîca* is semelparous as are other cephalopods (Boletzky, 1981) and it may spawn on more than one occasion over a period of weeks. Boletzky (personal communication) reported that *Rossia macrosoma* spawned over a period of two months.

#### *Hatching of Eggs*

Those eggs laid in a single egg mass in the running seawater aquarium about <sup>1</sup> June, 1984 began hatching on 25 October and continued, sporadically, for 62 days (41 squid). A number of fully developed eggs remained, but did not hatch (seawater temperature was then 6 °C). One was mechanically induced by rupturing the chorion at about two week intervais through 25 February, 1985. No viable eggs remained at mid-March (seawater temperatures had risen to about  $7^{\circ}$  C). The egg mass laid on 21 June, 1984, in the temperature controlled aquarium contained few healthy eggs. Six squid hatched from this mass from 14 to 30 November, 1984, and no more viable embryos were found. Only one of thèse squids survived and it continues to thrive.

There was very little activity in this part of the laboratory during the hatching episode so that extraneous stimuli were minimized. The following pattern was observed : On a daily basis, hatching tended to occur late at night or around daybreak. Overall, hatching was associated with lunar cycles, occuring especially around the time of the new moon (Fig. 2). Statistical analysis of the hatching data for the lunar cycle was very highly significant when the data were treated as a circular distribution. The estimated mean hatching time was one day after the new moon (approximately equal to the reporting delay based on 4-5 observations per week) with a standard déviation less than 6 days. Hatching in the temperature controlled aquarium spanned the new



Fig. 2. — A polar diagram of hatching times of *Rossia pacifîca* eggs relative to moon phases. Bar lengths may be compared with the scale to détermine the number hatched in three-day intervais, which are indexed to the day of the new moon. The natural hatching from one egg mass, as represented in the figure, extended over three consecutive new moons. The relationship to the lunar cycle is statistically very highly significant.

moon, and began 3 weeks after those in running seawater. The différences in numbers prevents meaningful comparisons of temperature effects on embryonic development times, but it can be reported that under seasonally varying temperatures, and at 10°C, the minimum hatching times were 4 3/4 months.

#### DISCUSSION

#### *Growth and Stage Timing*

The long generation time of the genus *Rossia* was anticipated by Boletzky and Boletzky (1973). In their work, the eggs of *R. macrosoma* were collected in the western Mediterranean Sea, and maintained at 15 °C. A few specimens were raised at 15 °C and, later,  $20-22$  °C over a period of 240 days. These hatched at 6 mm mantle length and had reached 20 mm in 166 days. The increasing growth rate that is reported here was not observed in Boletzky's work.

In a thesis dealing with the biology of *R. pacifîca*  in British Columbia, Brocco (1971) gave lengthweight information for maies and females larger than 10 mm mantle length. A scaling of those data suggests that the males have an increased ratio of weight to length at about 27 mm mantle length. This corresponds to Brocco's observation that 50 % had spermatophores at a size of 26 mm mantle length. Also, females had a more profound increase in the weight to length ratio at about 29 mm mantle length. He reported ovarian development beginning at 24 mm mantle length. Brocco speculated on a one year life span, which can be understood as an extrapolation of the right half of Figure <sup>1</sup> where the smaller specimens were not observed.

A seasonal growth pattern similar to Figure <sup>1</sup> is reported for North Sea plaice (Lockwood, 1974). Two separate von Bertalanffy growth curves were fitted to each âge group in that case. Growth models aside, the ecological effect is the same in both species — two âge groups live in close association with the bottom at the same time and place. They are distinctly différent in size and, thus can avoid compétition by partitioning the food resource. The North Sea plaice eventually migrates offshore and can live a long life and spawn repeatedly. *R. pacifîca*  invests ail of its final énergies in the production of a modest number of very large eggs. Apparently, it does not migrate far nor grow further except that dimorphism results in large females (for egg production).

In an ecological sensé the spawning and death of the larger animals releases the subsequent year class to exploit the whole food resource. During the period of embryological development, this class doubles its size and reaches sexual maturity. If seasonal growth — or, better seasonal lack of growth — does occur in *R. pacifîca,* it can only be attributed to the first half-year of very slow growth. Boletzky & Boletzky (1973) observed that newly hatched *R. macrosoma* live up to three months without feeding at 9 °C; these animals utilize muscle tissue for maintenance and neither grow nor survive. Perhaps *Rossia* has an unusually long life span precisely because, in an ecological sense, it hatches precociously, and it awaits a productivity opportunity before growing. One must question whether warmer or more favorable conditions promote early growth.

#### *Hatching Times*

The moon relationship in hatching was unexpected. Hatching occurred when day lengths were shortest (about 8 hours) and nights darkest. An animal vulnerable to visually oriented predators has maximum protection under these circumstances. Also of possible importance, lunar cuing spreads hatching over a long period, which provides an opportunity for areal distribution. Because the eggs are sizeable and the newly hatched animais are highly visible, a hatching strategy that minimizes vulnerability would be advantageous. An examination of data from an earlier cultivation of *Sepietta oweniana* (Bergstrôm and Summers, 1983) showed that half of the few day long hatching events observed were at the time of the new moon.

Secondary keying factors cannot be discounted in the hatching of *R. pacifîca.* The tidal amplitude, hence, water quality factors, cycle twice in each lunar cycle. Perhaps olfactory eues influence hatching. Mechanical stimulation may also occur as an indirect effect of tides, illumination or day length, perhaps through activity patterns of the embryos themselves. The unaided hatching was observed extending over three new moon events and may have been truncated by low seawater temperatures. Clearly, the hatching progressed at  $10^{\circ}$ C and continued to nearly 6 °C. Eggs were mechanically induced over the next two months at seawater temperatures below 7 °C, but did not hatch spontaneously. It should be noted that embryonic duration had reached 9 months at this point and that yolk reserves remained.

ACKNOWLEDGEMENTS. **—** Cultivation of marine organisms is labor intensive and requires long-term support and use of facilities. <sup>I</sup> am indebted to many people for their contributions to this work; most especially Dr. Carter Broad (acting director of the Shannon Point Marine Center) and his technical assistant, Paul Cassidy, who have been unstinting in their efforts. Several students have worked on this project for short periods of time, and one has made it a continuing personal commitment — <sup>I</sup> thank ail of them, and Larry Colvin in particular. <sup>I</sup> gratefully acknowledge the counsel and advice of colleagues at many différent points in this work.

Financial supports for parts of the project have been provided by the following agencies associated with Western Washington University : The Western Foundation, Research Advisory Council, Huxley College, Fairhaven College and the work/study program. The major portion of direct costs to date, however, has been borne by the author.

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*Reçu le 3 septembre 1985; received Seplember 3, 1985 Accepté le* 7 *décembre 1985; accepted December 7, 1985*