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Laboratory Observations of Midwater Spawning by *Illex illecebrosus*

by

R. K. O'Dor

Biology Department, Dalhousie University
Halifax, Nova Scotia, Canada

and

N. Balch

Institute of Oceanography, Dalhousie University
Halifax, Nova Scotia, Canada

and

T. Amaratunga

Invertebrates Division, Department of Fisheries and Oceans
Halifax, Nova Scotia, Canada

Abstract

Visual observations and video-tape records were made for the first time of mid-water spawning by *Illex illecebrosus* in the Aquatron Laboratory pool tank. Coupled with data on the density of egg masses, they allow some conclusions to be drawn concerning possible mid-water spawning sites in nature.

Introduction

Since there are to date no observations of the egg masses of *Illex illecebrosus* in nature, our understanding of this critical life history phase comes from scanty information on egg masses of other oegopsid squid and from laboratory observations on captive populations of *Illex* itself. Although there are a few records of egg masses of oegopsids found floating on the surface of several of the world's oceans (Clarke, 1966), these occur too rarely to account for the large number of oegopsids that exist. Floating egg masses of *Todarodes pacificus*, for example, have been reported (Okiyama, 1965); but the other evidence suggests that they are normally demersal and are either attached to the bottom or deposited in cavities (Hamabe, 1962; 1963).

During the 1981 experimental period with captive squid in the

Aquatron Laboratory pool tank, observations were made of the extrusion of an egg mass by a female while swimming and the complete process was video-taped. Together with data on the buoyancy of several egg masses, these observations suggest that open ocean spawning and mid-water development may be key features in the reproductive biology of Illex and perhaps other oegopsids.

Material and Methods

Squid were held to sexual maturity in the 15 m diameter, 3 m deep pool at the Aquatron Laboratory under conditions previously described (O'Dor et al., 1977). The spawning sequence was recorded with a hand-held TV camera (RCA TC 2011/N) from the surface. Prints were prepared from 35 mm photographs of the video monitor with the Sony SL0-323 Recorder in pause mode taken at f4 and 1/60 sec. with Ilford XP-1 film.

Results

During the experimental program in the fall of 1981, several spawned egg masses were formed; and in one instance a female was observed during the spawning activity. The female squid shown in Figure 1 had previously mated, and spermatophores present inside her mantle cavity were visible through her translucent mantle. Just prior to the scenes depicted, she had spent about 15 minutes slowly circling the pool away from the rest of the school. The egg mass extrusion began while she was swimming. Frame (a) shows the small translucent spherical egg mass beginning to be formed and held within the arms. Outlined against one of the black grid lines on the pool bottom, the mass is clearly visible. The extrusion progressed rapidly and in approx. 15 seconds the sphere has expanded and become sufficiently tenuous that it is no longer visible directly (frame (c)); however, the continued extension of the arms mark the outline of the expanding mass through frame (f). Figure 1b diagrammatically represents the estimated proportions in different frames. During the spawning process the fins beat powerfully at frequencies up to 90 beats per minute. This is 2 to 3 times the frequency in normal swimming, but despite this the squid and mass sank steadily. Frame (g) was taken just as the mass touched bottom (near a water-inlet port of the tank) and shows the arms withdrawing from the

mass of gel. In frame (h) the normal arm cone is reforming as the squid jets away. The sequence covered a period of 2 min.

The mass formed in Figure 1 was only 30 to 40 cm in diameter, but clearly illustrated the process by which masses are formed in mid-water. The females apparently release 10^4 to 10^5 eggs into a concentrated gel from the nidamental glands which is mixed with sperm released from spermatophores and/or intact spermatophores broken loose from the mantle wall (O'Dor *et al.*, 1980). After some delay, possibly to ensure fertilization, the gel mixture is moved into the funnel and a large volume of water is mixed into the gel by the mantle pump. The process is similar to blowing up bubble gum, except that it results in a relatively uniform mix of gel and eggs. During the preparatory period, the animal can continue to use its jet propulsion system and swim normally, but during the period that the gel is being extruded, fin movements provide the only method of propulsion. The squid apparently cannot maintain position this way and so sinks to the bottom of the pool. The small amount of sinking which occurs would be of little consequence in the ocean.

The individual eggs have a specific gravity of about 1.10 (unpublished data) and the mass that is formed is always slightly denser than the surrounding water. However, this difference is so small that the egg masses can achieve neutral buoyancy at normal seawater densities. The mass shown in Figure 2 was lifted up by a change in the density of the seawater of the pool after a storm had brought high-salinity water to the source of the laboratory seawater.

Discussion

Our studies of captive Illex illecebrosus in the Aquatron Laboratory pool tank (O'Dor *et al.*, 1977; Durward *et al.*, 1980), have enabled us to make observations of over 30 egg masses since 1978. Although no prior observations of the actual egg-laying process had been made, the behaviour of mature females resting on the bottom of the tank suggested that the species is a demersal spawner. This conclusion was strengthened by the fact that most egg masses were first observed on the bottom of the tank. Although several masses have been seen floating at the surface or in mid-water, this was usually explained by changes in the den-

sity of the water in the tank or by the formation of air bubbles in the egg mass gel caused by supersaturation resulting from warming of the water. We now know that I. illecebrosus can spawn pelagically.

The lifting of masses off the bottom has been a common occurrence in the pool, and has followed density increases of as little as 0.004 g cm^{-3} (i.e. a change in sigma-t ($\Delta\delta_t$) of 4). Vertical profiles in the ocean show increased density with depth, and density gradients of this magnitude can be found in the upper 200 m at the interface between Slope and Gulf Stream water (Fuglister & Worthington, 1951). Less pronounced gradients could effectively serve to reduce the sinking velocity of an egg mass. Data from Amaratunga et al (1980) show the presence of early stages of I. illecebrosus in and near the Gulf Stream where values for $\Delta\delta_t$ between 0 m and 600 m were between 1.0 and 1.6. Since the gel of an egg mass once formed apparently retains its density and does not mix further with ambient seawater, an egg mass could have its sinking rate slowed as it encountered water of increasing density with depth. Upwelling could similarly serve to reduce sinking velocities. These mechanisms could maintain the egg mass in the relatively warm surface waters of the Gulf Stream or North Atlantic Central water mass long enough to allow normal embryonic development. Water temperatures above 13°C are important for successful embryonic development (O'Dor et al., 1982).

The density of the egg masses may thus be a critical feature of the species' life history. Squid leaving the feeding grounds in Newfoundland in late autumn would have to travel over 2000 km to find suitable temperatures if spawning were to occur on the bottom, but need only swim a few hundred kilometers to reach such temperatures for mid-water spawning. The near neutral buoyancy of the gel mass would then keep the eggs from sinking below the thermocline.

If oegopsid egg masses normally accumulate at mid-water pycnoclines, it would explain why they are rarely seen or collected. The gel is too tenuous to be recovered by trawls, and plankton nets would be little better. Even in the pool, it is difficult to catch masses in plankton nets since a small pressure wave will push them aside. The occasional appearance in nature of masses on the surface might result from entrainment in water moving to the surface from storm-induced turbulence or from upwelling processes such as those associated with the edge of the

Gulf Stream (Neumann, 1952; Yoder et al., 1981).

Since egg mass recovery in nature using nets will be difficult, the most promising method for making observations may be the use of submersibles, divers or underwater television. Such techniques have been employed for underwater observations of similarly fragile gelatinous zooplankton some of which have mucous webs 2 m across. (Hamner et al., 1975). However, even these techniques would have to be used with special care, particularly with respect to lighting, because the egg masses are difficult to observe even under the optimum conditions existing in the laboratory.

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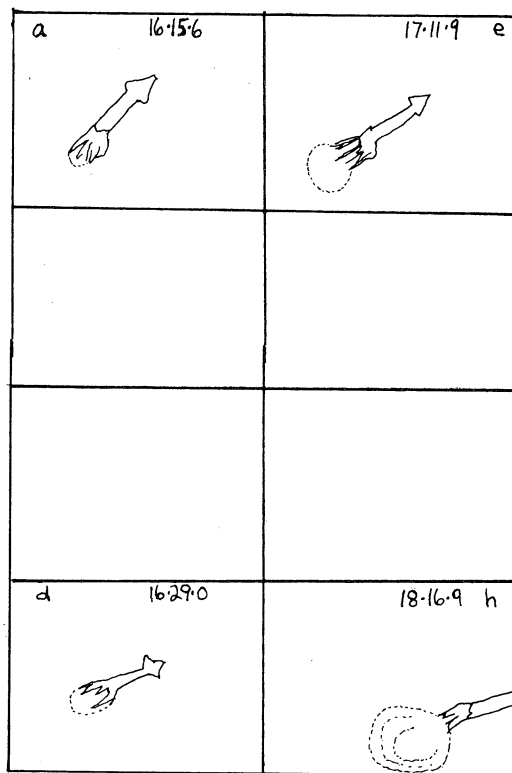
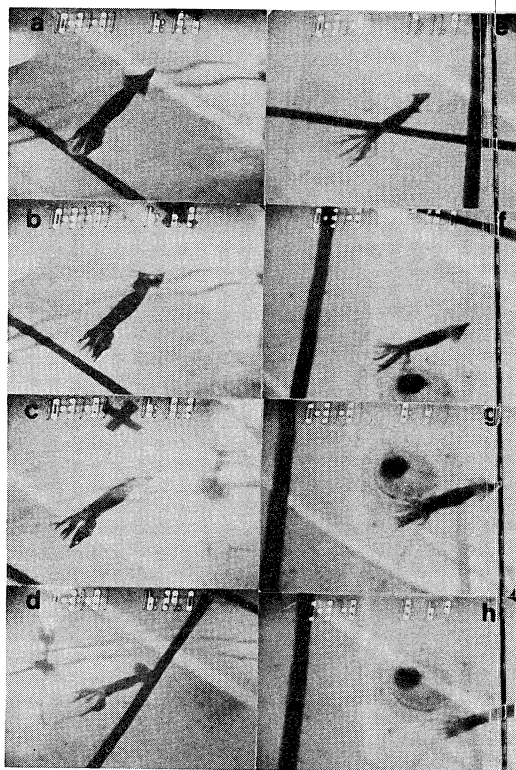


Fig. 1. Single frames from a videotape recording of the inflation of a 30 cm egg mass by a 23 cm (mantle length) *Illex illecebrosus*. The diagram on the right depicts the probable size and form of the egg mass. The process required just over 2 min., as the time display indicates.



Fig. 2. An egg mass of *Illex illecebrosus* spawned *in situ* and suspended on a pycnocline in the Aquatron Pool (15 m diameter by 3 m deep) (Photo by R. W. M. Hirtle, Biology Department, Dalhousie University).

