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Properties of *Illex illecebrosus* Egg Masses Potentially Influencing Larval Oceanographic Distribution

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Abstract

Visual observations and video-tape records of the spawning of captive *Illex illecebrosus* show that this species can produce gelatinous egg masses 50 cm or larger in diameter while swimming in open water. Measurements of the density of the eggs and the changes in water density which are necessary to lift egg masses indicate that the masses have densities about 0.005% greater than the water used to make the gel, whereas the eggs are more than 5% denser than typical seawater. The gel thus appears to function as a buoyancy mechanism which prevents eggs from sinking. Measurements of rates of temperature equilibration between egg masses and the surrounding water indicate that complete density equilibration requires many days under most conditions. If spawning occurs pelagically, common oceanographic situations where density increases with depth, due either to decreasing temperature (e.g. North Atlantic Central Water) or increasing salinity (e.g. the Gulf Stream), could allow the egg masses to be suspended in the mesopelagic zone. Such a mechanism, which could retain pelagically-spawned eggs of *Illex* and other oegopsids, particularly ommastrephids, in a zone where temperatures are adequate to allow embryonic development, helps to explain why there are so few records of ommastrephid eggs in nature.

Introduction

Because there are to date no observations of the egg masses of *Illex illecebrosus* in nature, knowledge of this critical life history phase comes from scanty information on egg masses of other oegopsid squids and from laboratory observations on captive populations of *Illex* itself. Although a few oegopsid egg masses have been found floating on the surface of some of the world's oceans (Okiyama, 1965; Clarke, 1966; Okiyama and Kasahara, 1975), their occurrence is too rare to account for the large number of oegopsids that exist. Reports to date indicate that egg masses of the ommastrephid *Todarodes pacificus* are normally demersal and are either attached to the bottom or deposited in crevices (Hamabe, 1962, 1963).

Captive *I. illecebrosus* have been studied for several years in the Aquatron Laboratory of Dalhousie University, Halifax, Nova Scotia (O'Dor *et al.*, 1977). During studies in 1981, the extrusion of an egg mass by a swimming female was observed and the complete process was video-taped. In this paper, these observations are described and discussed in relation to changes in seawater density that are required to render the egg masses neutrally buoyant. When these observations are considered in conjunction with data on the rates at which temperature and salinity equilibration causes the masses to change their density, they allow prediction of conditions in which open-sea spawning and midwater development of eggs could be key features in the reproductive biology of *I. illecebrosus* and other oegopsids, particularly ommastrephids.

Materials and Methods

The squid were held in a circular pool (15 m diameter and 3 m deep) at the Aquatron Laboratory under conditions which were previously described by O'Dor *et al.* (1977). Characteristics of the egg masses were reported by Durward *et al.* (1980).

The spawning sequence was recorded on 31 October 1981 with a hand-held television camera (RCA TC 2011/N) from the surface. Photographs of the video monitor were taken with a recorder (Sony SLO-323) in pause mode at f4 and 1/60 sec with Ilford XP-1 film.

Estimates of egg density were obtained by dropping eggs into sodium chloride solutions of increasing density until they did not sink. Series of progressively narrower density ranges were used to refine the estimates.

Estimates of the density of egg masses are based on incidents where increases in the density of water in the pool caused masses on the bottom to "lift off". These events usually resulted from wind-forced advection of colder, higher salinity water to the intakes of the seawater system. Daily measurements of temperature and salinity of seawater in the pool were used to calculate density changes associated with "lift-offs" which were noted in daily records of egg masses throughout the spawning season. Usually, the egg masses were at the surface by the time the lift-offs were noticed. In a few cases, when the masses were suspended in midwater, temperature and salinity of the water above and below the masses were taken.

During the 1982 spawning season, techniques were developed to remove intact egg masses from the pool and to incubate them at controlled temperatures. A triangular-shaped funnel (1 m on a side at the outer edge) with a long handle was used to scoop an egg mass off the bottom and direct it into a bag (0.5 m diameter and 1 m long) which was made of black nylon window-screen. The bag was attached to the funnel with Velcro strips. When the mass was raised to the surface, the open end of the bag was detached from the funnel and sealed. A 200-liter polyethylene container was lowered beneath the enclosed mass and then lifted out of the pool, with the enclosed mass still suspended in water. For studies on the rate of egg development, the enclosed mass was left suspended in the container and a gentle flow of constant-temperature water was introduced.

The same system was used (often with the same egg masses) to measure the heat transfer through the gel. Before starting the flow of heated water, a thermal probe was inserted carefully into the center of the confined mass and the core temperature was continuously recorded as it approached the desired incubation level. In some cases, unfertilized egg masses were subjected to several cycles of heating and cooling to provide additional data.

Results

Spawning

During the experimental program in the autumn of 1981, several egg masses were spawned, and, in one instance, a female was observed during the spawning activity (Fig. 1). Mating had occurred previously and spermatophores in the mantle cavity were visible through the translucent mantle. Just prior to the depicted scenes, the female had spent about 15 min slowly circling the pool away from the rest of the school. Extrusion of the egg mass began while the squid was swimming. Figure 1A shows the small translucent spherical egg mass being formed and held within the arms. Outlined against one of the black grid lines on the bottom of the pool, the mass is clearly visible. Extrusion progressed rapidly, and, in approximately 15 sec, the sphere expanded and became sufficiently tenuous that it is not directly visible (Fig. 1C). However, its presence is indicated in Fig. 1D by continued expansion of the arms. During the spawning process, the fins beat powerfully at frequencies up to 90 beats per minute. Despite these high frequencies which are 2–3 times the rate during normal swimming, the squid and egg mass sank steadily. Figure 1E, which was taken as the egg mass touched bottom (near a water intake of the pool), shows the normal arm cone reforming as the arms withdrew from the mass of gel. The entire sequence lasted for a period of 2 min.

The observations on the egg mass, which was 30–40 cm diameter (Fig. 1), clearly illustrate the process by which egg masses are formed in midwater. The females apparently release 10,000–100,000 eggs (Durward *et al.*, 1980) into a concentrated gel from the nidamental glands. Mixed with the gel are sperm from the spermatophores and possibly intact spermatophores which broke loose from the mantle wall (Durward *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 with the gel by the mantle pump. The process is similar to blowing up bubble gum, except that the expanding egg mass contains a uniform mixture of gel and eggs. During the preparatory period, the squid continued to use its jet propulsion system and swam normally, but fin movements provided the only method of propulsion during the period of gel extrusion. The squid apparently could not maintain position with fin movement only, and so it sank to the bottom of the pool. In the ocean, however, the slow rate of sinking would be of little consequence.

Buoyancy

The specific gravity of individual eggs is about 1.10, and thus the egg masses must always be slightly denser than the water which makes up most of their volume. A typical spherical mass with diameter of 50 cm has a volume of approximately 65.5 l. A typical female squid weighing 400 g produces about 100 g of eggs and spawns about half of them in several masses. If 12.5 g of eggs were extruded in each of four masses, the concentration of eggs within a mass would be about 1 egg/ml, which is typical. If the egg mass contained water with density of 1025.000 kg/m^3, the density of the mass would be increased only to 1025.014 kg/m^3 by addition of the eggs. The gelling agent from the nidamental glands could potentially increase the density further but not greatly, because the total weight of the glands is only 20–30 g.

Changes in density of the inflowing seawater occasionally lifted the egg mass off the bottom of the pool (Fig. 2). Measurements of such changes (Table 1) confirm the very slight negative buoyancy of the masses relative to the water in which they are spawned. Evidently, three of these differences exceeded the minimum value that was required to lift the egg masses, because a change as small as 0.05 sigma-t units prevents the mass from sinking, and the densities in the preceding paragraph indicate that the change may be as small as 0.02 sigma-t units.

Because of the difference in density between the egg mass and the surrounding water depends primarily on temperature and salinity of the water within the mass, the rate of temperautre and ionic equilibration determine how long a mass will stay suspended after an influx of denser water. Direct observations indi-

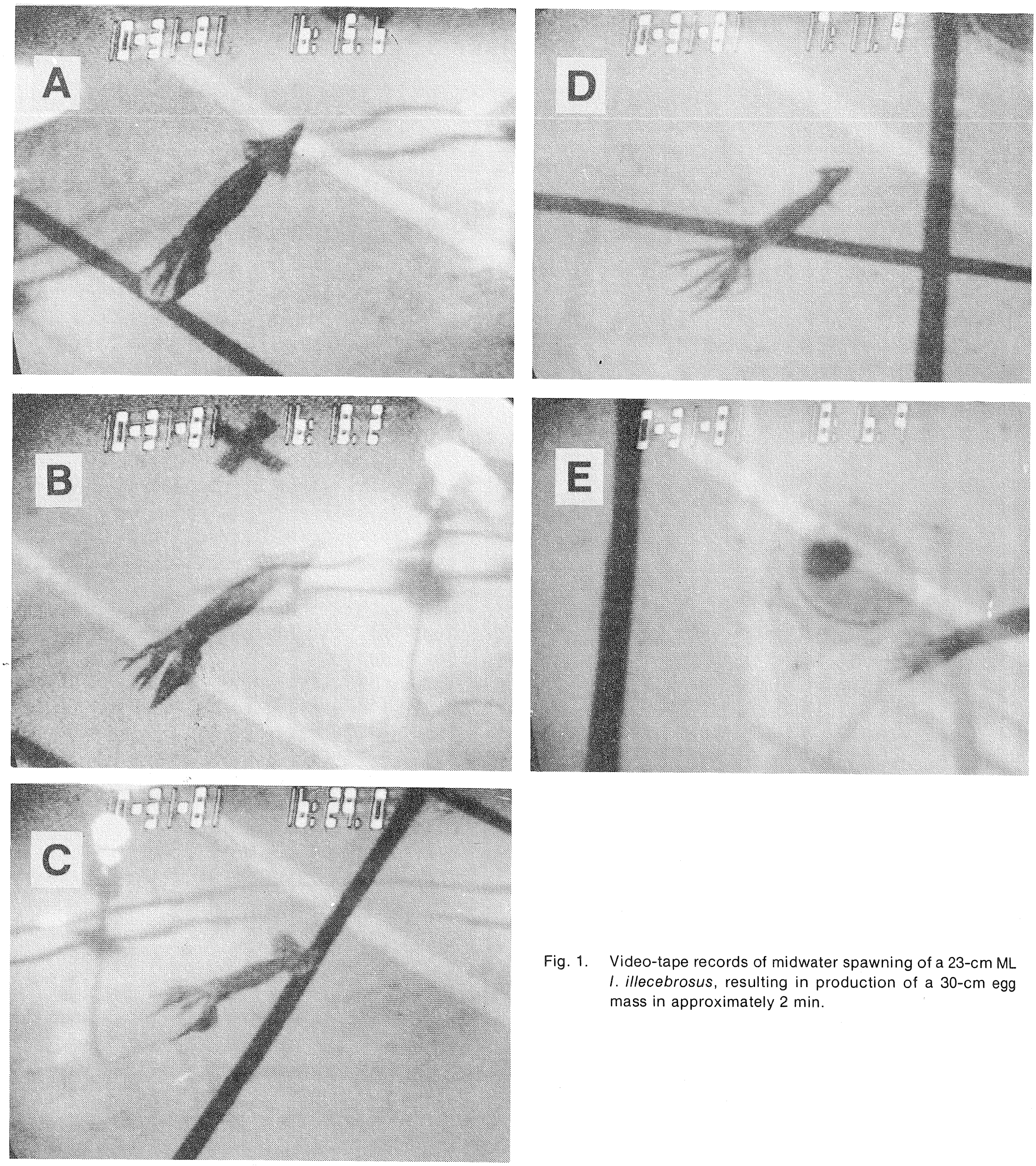

Fig. 1. Video-tape records of midwater spawning of a 23-cm ML *I. illecebrosus*, resulting in production of a 30-cm egg mass in approximately 2 min.

cated that the egg masses continued to float in the pool for a week or more, and measured rates of heat transfer allowed reasonably accurate estimation of equilibration time under various conditions. Figure 3 shows the changes in central temperature with time for an intact 50-cm egg mass after transfer from 10.5° to 25°C water. The curve was generated by using the equation for heat flow in a sphere (Ingersoll *et al.*, 1954):

$$\frac{T_c - T_s}{T_o - T_s} = 2(e^{-x} - e^{-4x} + e^{-9x} - \ldots)$$

with $x = \pi^2 At/R^2$, where T_c is central temperature, T_s is surface temperature, and T_o is initial mass temperature, t is time in seconds, R is radius of the mass in centimeters, and A is thermal diffusivity. The best fit

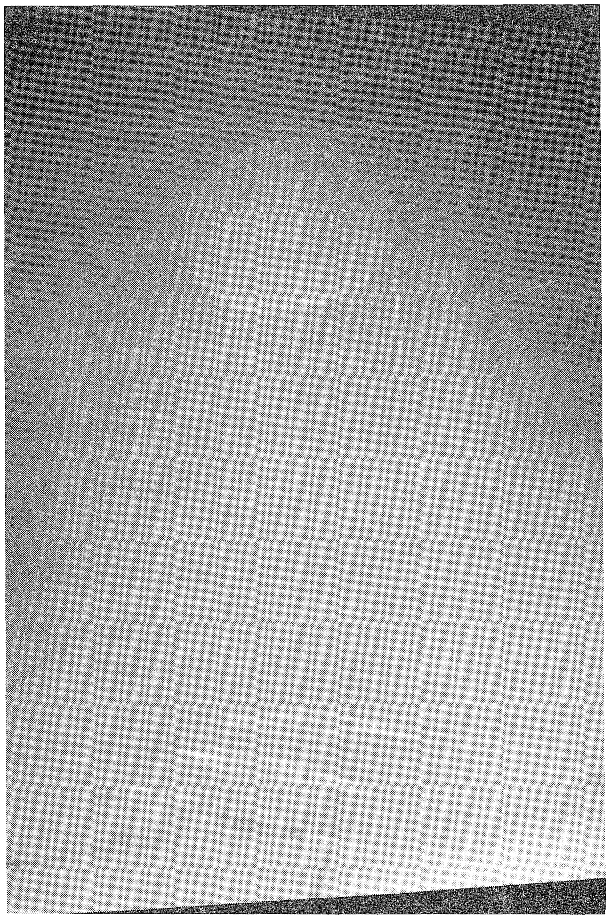

Fig. 2. A 50-cm egg mass of *I. illecebrosus*, spawned *in situ* and suspended on a pycnocline in the Aquatron Laboratory pool (15 m diameter and 3 m deep). (Photo by R. W. M. Hirtle, Dept. of Biology, Dalhousie University.)

was achieved with A = 0.0036 cm²/sec. This value is 2.5 times the diffusivity constant for water, indicating that the heat transfer in the mass was greater than that which would be produced by pure conduction but much less than that which would occur by convection. Thus the gel seems to restrict mixing and transfer of heat by convection. Part of the difference from pure conduction may be attributable to damage to the gel structure by the thermal probe and to overestimation of the central temperature because the probe was not truly a point. Under laboratory conditions, the structure of the mass degenerates with time and the apparent diffusivity increases. The mass which yielded the data in Fig. 3 was in good condition and gave one of the lowest diffusivities that were recorded, but its rate of equilibration was still probably higher than that of an undisturbed mass in nature.

Discussion

Studies of captive *I. illecebrosus* in the Aquatron Laboratory (O'Dor *et al.*, 1977; Durward *et al.*, 1980)

TABLE 1. Changes in seawater density in the Aquatron Laboratory pool which rendered egg masses positively or neutrally buoyant.

Date	Sigma-t		
	Minimum	Maximum	Difference
25 Sep 1981	22.64	23.09	0.45
30 Sep 1981	22.96	23.17	0.21
20 Oct 1981	21.78	21.83	0.05
08 Dec 1982	23.33	23.68	0.35

have involved observations on nearly 50 egg masses since 1978. Although no prior observations of the actual spawning process had been made during these studies, the behavior of mature females resting on the bottom of the pool was taken as evidence that the species may be a demersal spawner, as had been inferred from limited observations on other species (Clarke, 1966; Hamabe, 1962, 1963; Boletzky *et al.*, 1973). Although several egg masses were observed floating at the surface or in midwater, this was usually explained by changes in density of water in the pool or by the formation of air bubbles in the gel due to supersaturation from heating of the water. The present observations do not rule out bottom spawning, but it is now clear that *I. illecebrosus* can spawn pelagically.

Whether pelagic spawning is the only or the most common spawning mode, and hence what the role of this type of spawning may be, can only be determined by direct observations in nature. However, since there have been no observations of *I. illecebrosus* egg masses in nature, some speculation may help in the search. Water temperatures above 13° C are necessary for successful embryonic development (O'Dor *et al.*, 1982). Because near-surface waters are commonly warmer than waters at depth, appropriate temperatures for pelagic spawning are much more widespread than those suitable for demersal spawning. Squid which leave the feeding grounds at Newfoundland in late autumn have to travel 2,000 km or more southwestward to find suitable temperatures if spawning occurs on the bottom, but they need to swim only a few hundred kilometers southward to reach such temperatures in the Gulf Stream. Spawning in the Gulf Stream could have important consequences for larval distribution, as discussed by Trites (1983). From the foregoing information on physical properties of egg masses, it should be possible to predict the behavior of an egg mass under various oceanographic regimes. The following assumptions relate to three scenarios which are discussed in this paper:

1. The initial density of the egg mass is 0.03 sigma-t units higher than the water from which it was made.
2. The thermal diffusivity is 0.0036 cm²/sec, which means that, if the temperature of the surrounding water changes, the average temperature in the

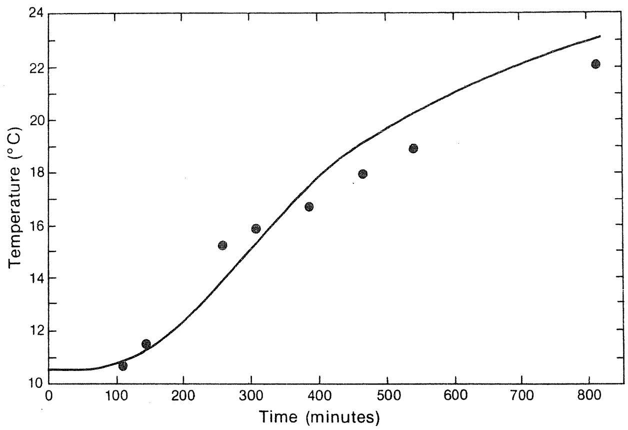

Fig. 3. Central temperature equilibration of a 50-cm egg mass in 25° C water following a change from the initial 10.5° C water. (The curve represents theoretical temperature changes for a sphere with a thermal diffusivity of 0.0036 cm²/sec.

mass will be 90% equilibrated in about 10 hr (Ingersoll *et al.*, 1954).

3. The diffusion of ions into the mass occurs at a rate proportional to the ratio of the diffusivity constants for heat and sodium chloride in water, where salinity differences between the mass and the environment take about 130 times longer to equilibrate than temperature differences (i.e. about 50 days). This is probably conservative, because the "skin" of the egg mass may be much more of a barrier to ions than to heat. This effect is probably negligible, because the life of a mass is generally less than 16 days.
4. The mass behaves hydrodynamically like a rigid sphere. The terminal velocity of a 50-cm egg mass, which sinks in water of constant density and has a density of 0.03 sigma-t units higher than the surrounding water, is estimated to be about 1 m/min from standard equations, if the drag coefficient is assumed to be 0.4 which is relatively constant for rigid spheres over the appropriate range of Reynold's numbers (Blake, 1983).

North Atlantic Central Water

This water mass is quite stable throughout the year. Fuglister (1963) recorded a typical April profile at a position east of Bermuda (33° 00'N, 52° 27'W), with temperature decreasing from about 20° C at the surface to about 13° C at 700 m (i.e. a rate of decrease of 1° C/100 m). The combination of temperature and salinity changes produces a sigma-t gradient of about 0.15 units/100 m. With the changing drag coefficients, rates of temperature equilibration, and gradients of temperature and salinity, actual calculation of the sinking rate is extremely complex, but it is quite simple to demonstrate an upper limit by assuming a stepwise descent. An egg mass that is formed at the surface would sink about 20 m before reaching an isopycnic level. This would require only about 40 min at an average velocity of 0.5 m/min. At this level, the water temperature would have decreased by about 0.2° C. The average change in sigma t with temperature over the range from 20° to 13° C is 0.16 units/° C, and so the 90% temperature equilibration would return the mass to its original relative density in about 10 hr. If this cycle is repeated for every 20 m of sinking, it would take about 16 days for the mass to sink to the depth where the water is less than 13° C. Because the development time for the eggs is 16 days at 13° C and only 12 days at 16° C (O'Dor *et al.*, 1982), eggs spawned in this area would have a reasonable prospect of hatching. Recent studies on the vertical swimming ability of newly-hatched larvae indicated that they would have no difficulty in moving to the surface (O'Dor *et al.*, 1985). It is not clear, however, what they would eat or how they would get to the northern edge of the Gulf Stream where most of the larvae and juveniles have been found (Amaratunga *et al.*, MS 1980; Hatanaka *et al.*, 1985).

It is interesting to note that similar calculations for the sinking rate of individual eggs give a terminal velocity of 1.2 m/min. Without the equilibration time, they would sink below the 13° C limit in only 10 hr. It is proposed that the slow rate of sinking of egg masses may play an important role in the life history of *I. illecebrosus*, and that the production of similar gelatinous egg masses may also be a critical adaptation for other oegopsids, particularly ommastrephids, which live in the open ocean.

Gulf Stream

An oceanographic regime with a subsurface salinity maximum would seem to be ideally suited to reducing the sinking rate of egg masses. In the western North Atlantic, such a feature is present in two areas. One is the Shelf Water–Slope Water frontal zone, where cold, low salinity Shelf Water often extends seaward over warmer, higher salinity Slope Water. However, in January–February when spawning presumably occurs, the temperature of these water masses are too low for egg development (i.e. less than 13° C). The second area is the Gulf Stream where there are consistently high temperatures and where there appears to be a salinity maximum at 100–200 m. Information on this feature is rather sparse, but some examples are summarized in Table 2.

An egg mass which is composed mainly of Gulf Stream surface water would sink and become neutrally buoyant at the subsurface salinity maximum. The much slower equilibration of salinity within the egg mass would permit it to remain there for many days and perhaps weeks, thus allowing adequate time for development of the eggs. In addition, there would be important consequences for transport, because the mass would be trapped in the fast-flowing part of the Gulf

TABLE 2. Some reported subsurface salinity maxima in the Gulf Stream.

General location in Gulf Stream	Number of station	Depth of salinity maximum (m)	Salinity difference from surface to maximum	Source
South of Nova Scotia	1	75	0.1	Smith and Petrie (1982)
South of Nova Scotia	11	90–190	0.028–0.342	Fuglister (1963)
Off Cape Hatteras	12	63–131	0.071–0.886	Richardson and Knauss (MS 1970)
Off Cape Hatteras	1	150	0.4	Lambert (1982)
Off Chesapeake Bay	8	100	0.020–0.350	Iselin (1936)

Stream, thereby resulting in egg-mass distributions similar to the larval distributions that were hypothesized by Trites (1983). The warm Gulf Stream water would also be an asset for development, because recent studies have shown that *I. illecebrosus* eggs will develop in as short a time as 6 days at temperatures up to, and perhaps higher than, 26° C (O'Dor *et al.*, 1985). In fact, larvae developed more fully (e.g. arm length, mouth parts) prior to hatching at temperatures above 20° C than at lower temperatures and may have a better chance of survival. If spawning occurs in warm water south of Cape Hatteras, the Gulf Stream would provide rapid transport of larvae to appropriate sites along the northern edge of the Stream where the food supply would be adequate and where *I. illecebrosus* larvae and juveniles have, in fact, been caught (Amaratunga *et al.*, MS 1980; Hatanaka *et al.*, 1985).

Gulf Stream-Slope Water front

The complex shear zone between the Gulf Stream and Slope Water, where features such as shingles, eddies and countercurrents are common and biological productivity is high, is also a potential spawning area. This zone is often characterized by relatively cool low-salinity water overlying warm high-salinity water where egg masses could be entrapped. This hydrographic feature is evident in two transects across the Gulf Stream-Slope Water frontal zone south of Halifax, Nova Scotia, in April 1979 (Fig. 4). Six of eight such transects showed subsurface salinity maxima, and *I. illecebrosus* larvae and juveniles were consistently present in the zone (Amaratunga *et al.*, MS 1980). However, these features are much more variable than in the Gulf Stream and North Atlantic Central Water. On the other hand, the rapid increase in temperature that would be experienced by squid in crossing the Shelf Water-Slope Water frontal zone during their southward migration from the continental shelf in late autumn could be the cue that triggers spawning. Even spawning in Slope Water north of Cape Hatteras may be less risky than it appears, because there is some evidence that low salinity water is entrained in the surface water of the Gulf Stream (Ford *et al.*, 1952). Presumably, any egg masses in such low salinity water would sink to isopycnic positions in underlying Gulf Stream water. South of Cape Hatteras, the boundary zone lies over the edge of the continental shelf, and the existence of bottom temperatures above 13° C in this region provides an additional safeguard for egg masses even if they sink completely to the bottom (Trites, 1983). In general, the larval transport mechanisms that were discussed by Trites are equally applicable to larvae from egg masses spawned in the Gulf Stream-Slope Water frontal zone.

General considerations

Of the three areas discussed above, North Atlantic Central Water seems to be the least suitable for *I. illecebrosus*, because it requires maturing squid to migrate across the Gulf Stream where conditions are equally or more favorable, it is relatively poor in suitable food items, and it presents a problem for larvae which would have to perform a substantial horizontal migration to reach the northern edge of the Gulf Stream where they are commonly found. The evidence therefore suggests that the most probable spawning sites would be within or along the edge of the Gulf Stream.

For oegopsids in general, if egg masses normally become distributed mesopelagically, it would explain why they have been rarely seen or collected. The gel is too tenuous to be retained in trawls, and plankton nets would not be much better. Even in the laboratory pool, it is difficult to catch the egg mass in plankton nets because a small pressure wave pushes them aside. The occasional appearance in nature of egg masses at the surface (*Todarodes pacificus* by Okiyama, 1965; *Illex coindetii* by Naef, 1923, 1928) might have resulted from entrainment in water which moved to the surface due to storm-induced turbulence or upwelling processes such as those associated with the northern edge of the Gulf Stream (Yoder *et al.*, 1981; Lee *et al.*, 1981). In general, the mesopelagic zone seems to be a safer place for eggs to undergo development than either the surface or bottom waters, and the behavior of larvae is consistent with their movement to the surface (O'Dor *et al.*, 1985).

Recovery of egg masses in nature will be required in order to determine which, if any, of the strategies, outlined above, are used by *I. illecebrosus*. However, further studies of the environmental factors which induce spawning in adults and the temperature and salinity preferences of mature adults might help to

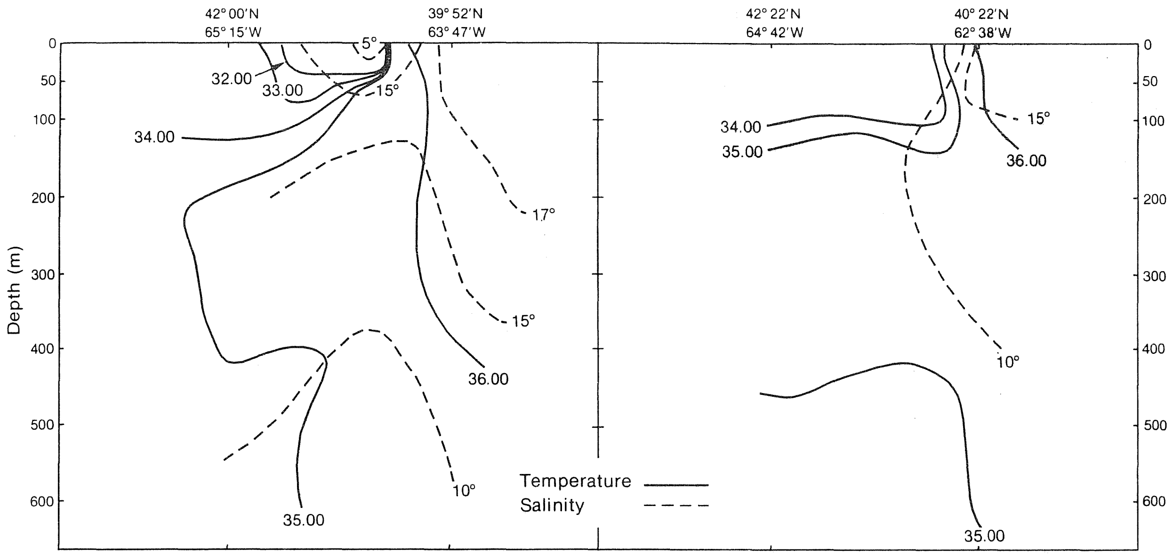

Fig. 4. Temperature and salinity transects across the Slope Water-Gulf Stream frontal zone south of Nova Scotia. (After Amaratunga *et al.*, MS 1980.)

narrow the search. If one of the more risky strategies is found to be used, it could explain the high variability in population size. For example, spawning in or along the edge of the Gulf Stream where cold-core eddies are formed could result in the transport of large numbers of larvae south of the Gulf Stream, thus reducing the probability of the movement of juveniles northward to the continental shelf areas.

Because of the difficulty in capturing egg masses in nature with nets, more promising methods for making observations may be the use of submersibles, divers and underwater television. Such techniques have been employed for underwater observations of similarly fragile gelatinous zooplankton, some of which have mucous webs up to 2 m in diameter (Hamner *et al.*, 1975). However, 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 which exist in the laboratory.

Acknowledgements

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