Pacific Science (1985), vol. 39, no. 4

The Common Occurrence of Oegopsid Squid Eggs in Near-Surface Oceanic Waters[1]

RICHARD EDWARD YOUNG,[2] ROBERT F. HARMAN,[2] AND KATHARINA M. MANGOLD[3]

ABSTRACT: A variety of egg types removed from near-surface plankton tows off Hawaii developed into young squids. Previously, the eggs of pelagic, oceanic squids were virtually unknown. Over 90% of these near-surface plankton tows taken with a 1-m net contained squid eggs. About 90% of the eggs were collected in the upper 100 m with most of these coming from the mixed layer. The eggs were separate rather than in masses. Two egg types have been identified. One belongs to the Enoploteuthinae, which are thought to spawn individual eggs. The other belongs to the Brachioteuthidae, whose spawning mode is unknown. Most squids are thought to deposit eggs in masses. Estimates, based on the abundance of the captured eggs, indicate that the chances of sampling an intact egg mass with a plankton net are small.

THE SPAWNED EGGS of marine animals can be useful guides for investigating life-history strategies and adult population parameters, and they can provide a source of young, undamaged animals for experimental purposes (Price 1974; Stearns 1976; Stauffer and Picquelle 1980). The eggs of pelagic, oceanic squids, however, are virtually unkown, even though most species have larvae in near-surface waters.

Squids belong to the cephalopod order Teuthoidea, which is divided into two suborders: Myopsida and Oegopsida. Members of the Myopsida (that is, the families Loliginidae and Pickfordiateuthidae) are almost exclusively neritic in habitat. Members of the most common myopsid genus, *Loligo*, deposit their eggs in many small masses on the shallow sea floor (McGowan 1954; Mangold-Wirz 1963; Waller and Wicklund 1968). During spawning, the eggs are coated with a layer of jelly from the oviducal glands which is, in turn, covered by large quantities of jelly from the nidamental glands (Jecklin 1934).

Members of the Oegopsida are predominantly oceanic species. Most of these squids possess nidamental glands and, therefore, are thought to produce egg masses. On several occasions oegopsid squids belonging to the Ommastrephidae have spawned in captivity (Hamabe 1961, 1963; Boletzky et al. 1973; O'Dor et al. 1982). The eggs were generally spawned in large masses (up to 100,000 eggs).

Very few records exist of naturally spawned eggs or egg masses from oceanic cephalopods. Most of the early reports (d'Orbigny and Ferussac 1839; Collingwood 1873; Grenacher 1874; Naef 1923 [Oegopsid X]; Sanzo 1929) described oegopsid egg masses of very similar appearance: large, gelatinous, cylindrical masses generally 60–90 cm long by 10–20 cm in diameter, containing rows of eggs which encircled the mass in a helix near its periphery. Sanzo (1929) attributed this type of egg mass to the large epipelagic squid *Thysanoteuthis rhombus* after raising the eggs to hatching and comparing the hatchlings to identified larvae taken from the plankton. In more recent years, this type of egg mass has been observed at localities throughout much of the tropical and temperate oceans of the world (Clarke 1966; Nesis 1975; Misaki and Okutani 1976; Suzuki et al. 1979; pers. obs.). Berrill (1966) published a beautiful color photograph of one of these egg masses which was misidentified as the pelagic tunicate *Pyrosoma*.

[1] This material is based on research supported in part by the National Science Foundation under Grant OCE 82-07754. Manuscript accepted May 1985.

[2] Department of Oceanography, University of Hawaii, 1000 Pope Rd., Honolulu, HI 96822.

[3] Laboratorie Arago, F-66650 Banyuls-sur-Mer, France.

Observations of other types of egg masses have been few. Akimushkin (1963) reported an unidentified, ribbonlike egg mass (70 × 30 × 5 cm) found "drifting at sea" south of Japan. Naef (1923) described embryos of an ommastrephid from an egg mass found in the Mediterranean Sea. Unfortunately, the egg mass was not described. Jatta (1896) reported similar eggs from the Mediterranean.

The abovementioned egg masses were sighted floating at the sea surface. A few reports exist of oegopsid eggs that were taken in nets. The number of eggs taken in a single tow was always rather low (generally between 1 and 200), indicating that individual eggs, rather than egg masses, were being caught. Sasaki (1914) attributed such eggs from the Sea of Japan to the enoploteuthid *Watasenia scintillans*, which spawns in near-shore waters. Similar eggs have been reported from the Sea of Japan by Nishikawa (1906), Shimomura and Fukutaki (1957), Yamada (1937), and Yamamoto (1943). These eggs generally were found in near-surface waters, were ovoid in shape (approximately 1.5 × 1.2 mm), and were coated with jelly. Another type of egg found by Yamamoto (1946) and Okiyama (1965) from the Sea of Japan, and by Shojima (1970, 1972) from the South China Sea, was also ovoidal and covered with jelly, but it was smaller (approximately 0.8–0.9 × 0.6–0.8 mm). Although these eggs were originally thought to come from the ommastrephid *Todarodes pacificus*, Okiyama and Kasahara (1975) concluded that the eggs were probably spawned by members of the Enoploteuthinae other than *W. scintillans*.

We are aware of only two other records of net-caught eggs. Allan (1945), working off the eastern coast of Australia, found a single, unidentified egg with a well-developed embryo, and Nesis (1972, 1973) found eight eggs in the upper 300 m off the coast of Peru and Ecuador which he thought might belong to the enoploteuthid *Abraliopsis affinis*. The latter eggs were nearly spherical (1.10 × 1.15 mm) and were coated with a sticky, buoyant, transparent jelly.

The waters around the Hawaiian Islands are occupied by 49 species of oegopsid squids, most of which probably spawn in the area. On several occasions over the past 14 years, we have found large egg masses of *Thysanoteuthis rhombus* floating at the sea surface. We have not encountered any other egg masses despite extensive trawling from the surface to depths greater than 1000 m using 3-m midwater trawls equipped with 1-m cod ends made of 333-μm or 505-μm mesh. Egg masses, therefore, have eluded us as they have eluded most other researchers. The scarcity of records of oegopsid eggs has been perplexing. Clarke (1966) suggested that squids may spawn on the continental slope at depths greater than 1000 m, where sampling is difficult.

In November 1983, while examining near-surface plankton tows for squid larvae aboard the Japanese fishery training vessel *Hokusei Maru*, we found an egg containing a well-developed squid embryo. On subsequent tows, similar but undeveloped eggs were found. These eggs were placed in vials with filtered seawater that was frequently changed. All the eggs developed into squid. Subsequent trawling, reported in this paper, demonstrated that oegopsid eggs of a variety of species are abundant in the near-surface plankton around Hawaii and are easily reared through hatching and for several days after hatching.

MATERIALS AND METHODS

Plankton tows were taken in Hawaiian waters during a cruise from 16 November to 3 December 1983 aboard the FTS *Hokusei Maru* and during five subsequent cruises (19–22 December 1983, 9–12 March 1984, 6–15 April 1984, 8–11 August 1984, and 19–24 October 1984) aboard the R/V *Kana Keoki* and the R/V *Kila*. Data on the vertical distribution of eggs were obtained from a series of stratified oblique tows to a depth of 300 m with paired, opening-closing, 70-cm bongo nets with 505-μm mesh. Each tow was designed to uniformly sample a 50-m depth stratum in the upper 200 m and a 100-m stratum from 200 to 300 m. Our only method of determining the depth of the nets during the tow was a calculation based on wire angle and wire out. A time-depth recorder attached to the nets gave an accurate record, after the tow,

of the actual depth fished. Forty-four tows were successful, and our accuracy in placing the nets at appropriate depths was adequate. In the upper 150 m, the strata sampled averaged 43 m (SD = 7.2 m) in range and at depths over 150 m they averaged 80 m (SD = 33 m) in range. Distributional data were compiled by apportioning the catch for each tow equally into 5-m depth increments. The catch rate for a given depth increment was taken as the average for all rates at that depth. Subsequently, the increments were combined into 25-m depth zones.

Oblique tows (75 or 150 m to the surface) for live eggs were taken with 1-m nets of 505-μm mesh. These samples were sorted on board ship using stereomicroscopes. Squid eggs removed from these samples were placed in 0.045-μm filtered seawater within the wells of tissue culture trays and were kept in an air-conditioned room (22–24°C) with constant light. For identification purposes, photographs of the eggs and embryos were taken every 6 hr, at which time the filtered seawater was changed. After hatching, the larvae were transferred to $\frac{1}{2}$ or 1-liter bottles containing 0.045-μm filtered seawater. The bottles were placed on rotators to prevent the young squids from contacting the sides of the bottles. Some of the larvae were given one or a combination of the following as a food source: (1) mixed plankton, (2) rotifers, (3) copepods, (4) rotifers and/or copepods in combination with three types of phytoplankters.

RESULTS

Oegopsid eggs were found in a variety of shapes and sizes (see Figure 1) and colors. The eggs found were always single rather than clumped in a common layer of jelly. Most of the eggs were about the same size as most fish eggs (usually about 1 mm in diameter). Prior to the appearance of distinctive embryos, however, squid eggs were easily distinguished from fish eggs in the following manner: fish eggs generally possess an oil globule whereas squid eggs do not; fish eggs generally have a noticeable perivitelline space whereas squid eggs lack a detectable perivitelline space except occasionally at the animal pole or at the animal and vegetal poles; squid eggs are usually ovoid whereas fish eggs are usually spherical; squid eggs are usually surrounded by a sticky gelatinous layer or have a sticky film (remnant of the gelatinous layer) on the chorion whereas most fish eggs lack a gelatinous layer. (For a characterization of fish eggs, see Ahlstrom and Moser 1980.) The large size, homogeneous appearance of the yolk, and presence of a jelly layer distinguish squid eggs from most free-floating crustacean eggs. Of the first 59 plankton samples from the 1-m net, 54 (92%) contained squid eggs. This high success rate has been approximately the same on subsequent cruises, which have now covered all seasons.

The vertical distribution of the eggs is shown in Figure 2. The data indicate that about 90% of the eggs were in the upper 100 m, with 55% above 50 m. Since the bottom of the mixed layer during this cruise was at about 70 m (Figure 2), most of the eggs were taken within this layer. Of the 17 tows with upper depth limits deeper than 100 m, only three captured eggs. One tow, however, captured seven eggs between 150 and 200 m. The integrated catch through the water column was 0.25 egg/m^2 of sea-surface area. This is about half the abundance that was estimated from oblique tows taken from 150–0 m with a 1-m net during the December cruise (0.56 egg/m^2).

During the April cruise, we attempted to raise 148 of the eggs captured. Of these, 81% survived to hatching. All larvae died by 7 days after hatching while kept at 22–24°C, presumably due to starvation. At the time the eggs were removed from the plankton sample, approximately 90% were either involved in germ-layer formation or in the earliest stages of organogenesis. These eggs, therefore, were unrecognizable as cephalopods to the untrained eye. A sample of 11 developing embryos had a mean development time of 34 hr from capture, approximately Stage V of Naef (1923), to a stage where the embryos were easily recognized as squids (approximately Stage XIII of Naef) at 22–24°C. The same embryos took another 16 hr (average) before hatching. These data are in general agreement with the relative

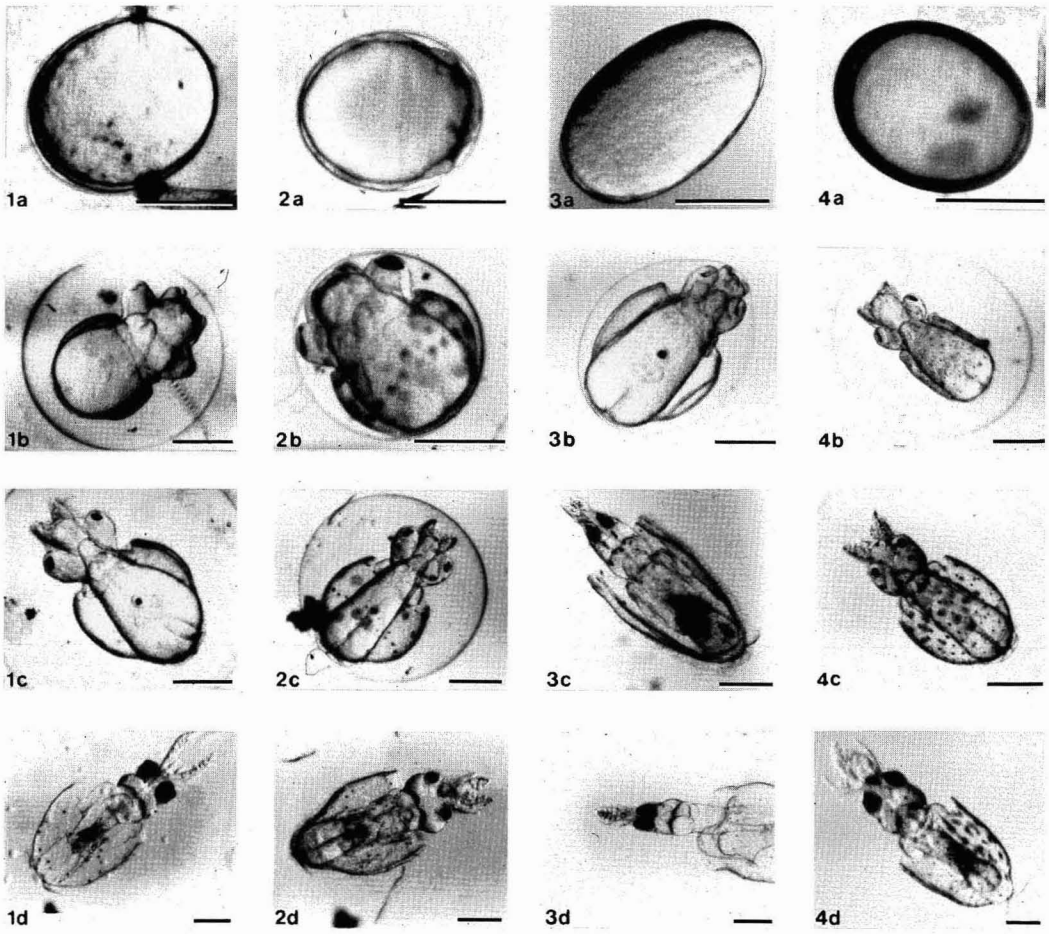

FIGURE 1. Early life-history stages of oegopsid squids taken from near-surface plankton. Times indicate age since capture. Scale bar represents 0.5 mm. *1.* Species 1: $a = 1$ hr, $b = 29$ hr, $c = 41$ hr, $d = 6$ days. *2.* Species 2: $a = 1$ hr, $b = 20$ hr, $c = 39$ hr, $d = 6$ days. *3.* Species 3: $a = 1$ hr, $b = 33$ hr, c and $d = 6$ days. *4.* Species 4: $a = 1$ hr, $b = 41$ hr, $c = 59$ hr, $d = 3$ days.

rate of development of *Illex illecebrosus* raised in the laboratory (O'Dor et al. 1982), which indicate that the time spent in early development (up to Stage XIII) is about 66–75% of the total time to hatching.

If we assume that the 16 hr from Stage XIII to hatching in the Hawaiian eggs represents 25–34% of the total embryonic life, we can estimate that the time from spawning to hatching in these eggs was 2.0 to 2.7 days. (Water temperature in the lab was 1–3°C cooler than the mixed layer.) The development rates also suggest a capture ratio of unrecognizable embryos (younger than Stage XIII) to easily recognizable embryos (older than Stage XIII) of 2 : 1 to 3 : 1, well below the 9 : 1 actually taken. During the rearing experiments, premature hatching was often induced by trauma. Premature hatching in the trawls, combined with natural mortality, presumably is responsible for this discrepancy. At the time of hatching, the young squids possess a large internal yolk supply and appear, on morphological grounds (no apparent mouth, suckers without acetabulae, and so forth), to be incapable of feeding. The squid hatchlings were easily raised until the internal yolk was fully absorbed. The feeding experiments, which

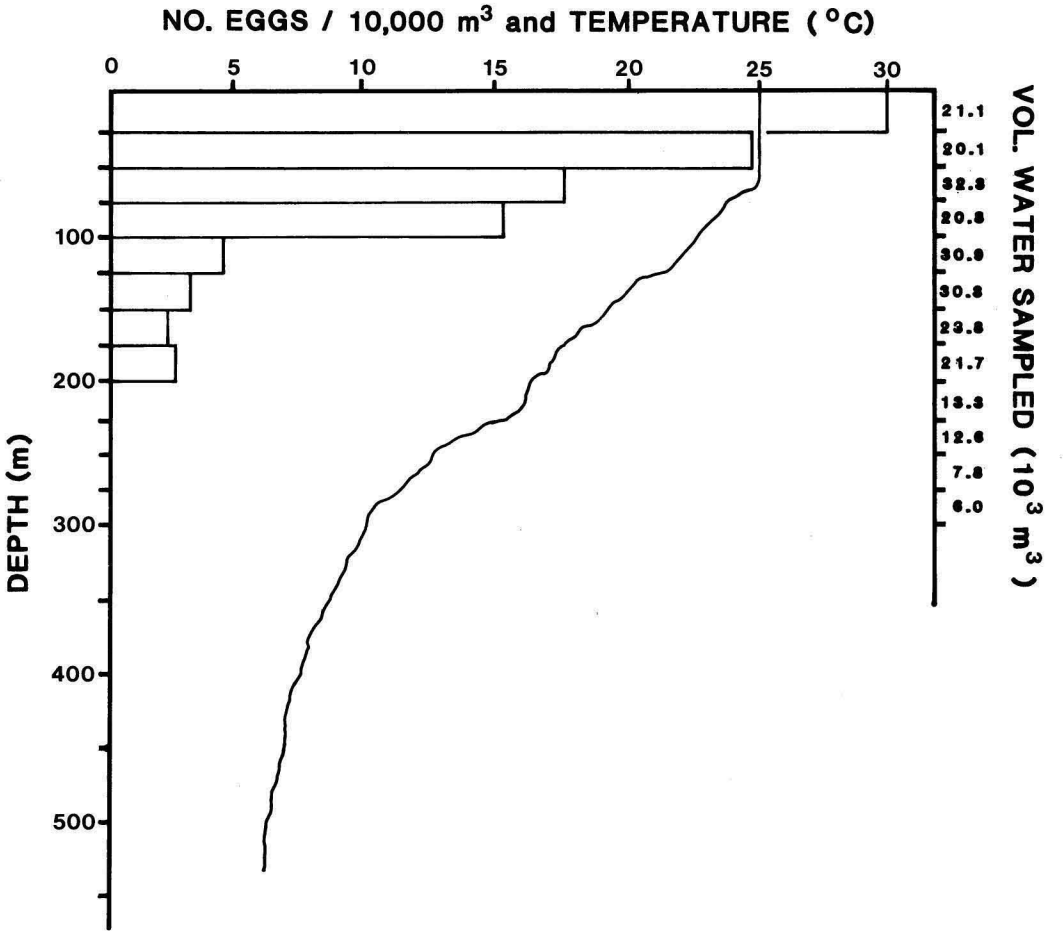

FIGURE 2. Vertical distribution of eggs in upper 300 m; sampling effort; vertical temperature profile. Histograms (0–300 m) indicate number of eggs. Curve represents temperature. Egg abundance and temperature scales are identical.

commenced two days after hatching, were unsuccessful. We were unable to confirm that any feeding occurred.

Many of the eggs, embryos, and hatchlings have distinctive features which should eventually allow identification at a very early stage. Of the four species illustrated in Figure 1, for example, two had distinctive egg shapes (Species 3 and 4). One had a distinctive sculptured chorion (Species 4). One had a distinctive green tint (Species 2). The early embryo of Species 3 was distinguished by the weak development of the arms. The late embryo of Species 4 was distinguished by its large number of chromatophores. The early embryo of Species 2 was distinguished by the relatively early appearance of very large pigmented areas. Species 1 embryos were distinguished by the relatively early development of the ink sac. All of the hatchling types had distinctive chromatophore patterns. We could identify two of the species reared. Our Species 3 hatchling, with its long neck and distinctive chromatophore pattern, could be matched with larvae taken from plankton tows. This species is our common species of *Brachioteuthis*. (The systematics of this genus are confused and most species cannot be identified.) Our Species 4, with a distinctive sculptured chorion, could be identified as

Enoploteuthis reticulata. A large female of this species in our collections carried these distinctive eggs, whereas related species had unsculptured eggs.

Although identification of other species must await the difficult process of tracing the identity of captured specimens through a decreasing size series to the smallest larvae, we can narrow the possibilities. The characteristics of the hatchlings do not match those of many of the common larvae collected during our sampling periods. Among these were larvae of the Onychoteuthidae, Ommastrephidae, Ctenopterygidae, and the enoploteuthid subfamily Pyroteuthinae. The larvae from these groups comprised 60% of all larvae captured. The two types of eggs identified belong to species that were represented by 7% of the net-captured larvae. Another nine families, representing 16 species, made up only 9% of the net-captured larvae. The remaining 24% of the larvae belonged to the enoploteuthid subfamily Enoploteuthinae. We have tentatively recognized between 7 and 11 species from the hatchlings obtained thus far.

DISCUSSION

The eggs sampled represent only a portion of the species that were spawning during the cruise periods. Judging from the relative abundance of net-captured larvae, most of the unidentified eggs probably belong to the enoploteuthid subfamily Enoploteuthinae. Around Hawaii, there are eight species in this subfamily (two *Abralia*, three *Abraliopsis*, and three *Enoploteuthis*). Since we could be sampling eggs of as few as seven species, the numbers are compatible with this hypothesis.

Members of this subfamily lack nidamental glands and are thought to lay single pelagic eggs (Okiyama and Kasahara 1975). One of our eggs, however, belongs to the family Brachioteuthidae. Nidamental glands, which are responsible for egg mass formation, occur in species of the Brachioteuthidae (M. Sweeney, U.S. Mus. Nat. Hist., pers. comm.). Presumably, *Brachioteuthis* spp. either spawns single eggs using a different mechanism than in the Enoploteuthinae or it spawns fragile egg masses that fragment shortly after spawning.

The absence of eggs from the other common families suggests that these species are laying eggs in masses. Abundance figures for the captured eggs provide a method for estimating the probability of capturing a pelagic egg mass. Assuming that a squid, such as one of the smaller ommastrephids, produces an egg mass of 10,000 eggs (a small egg mass), and that egg abundance in this population is about the same as that of the eggs of the most common species found in this study (about 1.3 eggs/1000 m^3, or approximately 10,000 eggs/7,700,000 m^3 of water), and that the egg masses are randomly distributed in the upper 100 m, then with a 1-m net, which samples 1400 m^3 per tow, we would have only a 63% chance of capturing an egg mass with about 5500 net tows that sample the appropriate depth stratum. (About 5500 tows would be needed to filter 7,700,000 m^3.)[4] This exercise suggests that the chance of encountering an egg mass of any appreciable size with a plankton net is small. These odds are compounded by the fact that a captured egg mass may not have easily recognizable eggs. Therefore, the scarcity of reports of squid egg masses from plankton tows is not surprising. Clearly, quantitative sampling is impractical if the eggs remain in masses until hatching. Eggs laid individually or in fragile egg masses can be easily sampled, and their availability opens exciting new avenues of research.

ACKNOWLEDGMENTS

We thank the officers and crews of the FTS *Hokusei Maru*, the R/V *Kana Keoki*, and the R/V *Kila* for their help and cooperation and B. Burch for her assistance in sorting and raising eggs on one cruise. We also thank S. von Boletzky, T. Okutani, and C.F.E. Roper

[4] The probability of encounter is determined by terms in the expansion of $(p + q)^n$, where q is the probability of not encountering an egg mass in a single tow (that is, 5499/5500), p is the probability of encountering an egg mass in a single tow, and $n = 5500$. The probability of encountering an egg mass in 5500 tows is $1 - q^{5500}$ (Mendenhall 1971).

for reviewing the manuscript and M. Pace for advice on probability determinations.

LITERATURE CITED

AHLSTROM, E. H., and H. G. MOSER. 1980. Characters useful in identification of pelagic marine fish eggs. Rep. CalCOFI. 21:121–131.

AKIMUSHKIN, I. I. 1963. Cepalopods of the seas of the U.S.S.R. [transl. from Russian by A. Mercado]. Israel Prog. for Sci. Transl., Jerusalem.

ALLAN, J. 1945. Planktonic cephalopod larvae from the eastern Australian coast. Rec. Austral. Mus. 21(6):317–350.

BERRILL, N. J. 1966. The life of the ocean. McGraw-Hill, New York.

BOLETZKY, S. V., L. ROWE, and L. AROLES. 1973. Spawning and the development of the eggs, in the laboratory, of *Illex coindetii* (Mollusca: Cephalopoda). Veliger 15:257–258.

CLARKE, M. R. 1966. A review of the systematics and ecology of oceanic squids. Pages 91–300 *in* F. S. Russell, ed., Advances in marine biology. Vol. 4. Academic Press, London.

COLLINGWOOD, C. 1873. On a new form of cephalopodous ova. J. Linn. Soc. Zool. 11:90–94.

D'ORBIGNY, A., and A. FERUSSAC. 1839. Histoire generale et particulaire des cephalopodes acetabuliferes, vivantes et fossile. Paris.

GRENACHER, H. 1874. Zur Entwicklungsgesichte der Cephalopoden. Z. Wiss. Zool. 24:419–498.

HAMABE, M. 1961. Environmental studies on breeding habit and development of the squid, *Ommastrephes sloani pacificus* Steenstrup, pt. II: Spawning behavior. Zool. Mag. Tokyo 70:385–394.

———.1963. Spawning experiments of the common squid, *Ommastrephes sloani pacificus* Steenstrup, in an indoor aquarium. Bull. Jap. Soc. Sci. Fish. 29(10):930–934.

JATTA, G. 1896. I cephalopodi viventi nel Golfo Napoli (Sistematica). Fauna Flora Golf. Neapel 23:1–268.

JECKLIN, L. 1934. Beitrag zur Kenntnis der Laichgallerten und Biologie der Embryonen decapoder Cephalopoden. Rev. Suisse Zool. 41:593–693.

MANGOLD-WIRZ, K. 1963. Biologie des Cephalopodes benthiques et nectoniques de la Mer Catalane. Vie Milieu 13 (suppl.): 1–285.

MCGOWAN, J. A. 1954. Observation on the sexual behavior and spawning of the squid *Loligo opalescens* at La Jolla. Calif. Fish & Game 40:47–54.

MENDENHALL, W. 1971. Introduction to probability and statistics. 3rd ed. Duxbury, Mass.

MISAKI, H., and T. OKUTANI. 1976. Studies on the early life history of decapodan molluscs—VI. An evidence of spawning of an oceanic squid, *Thysanoteuthis rhombus* Troschel, in Japanese waters. Jap. J. Malac. 35(4):211–213.

NAEF, A. 1923. Die Cephalopoden. Fauna Flora Golf. Neapel 35:1–863.

NESIS, K. N. 1972. Oceanic cephalopods of the Peru Current: Horizontal and vertical distribution. Okeanol. 12(3):426–442.

———.1973. Cephalopods of the eastern equatorial and southeastern Pacific Ocean. Trud. Inst. Okeanol. 94:188–242.

———.1975. Cephalopods of the American Mediterranean Sea. Trud. Inst. Okeanol. 100:259–288.

NISHIKAWA, T. 1906. On a pelagic cephalopod egg. Zool. Mag. Tokyo 18:310–314.

O'DOR, R. K., N. BALCH, E. A. FOY, R.W.M. HIRTLE, D. A. JOHNSTON, and T. AMARATUNGA. 1982. Embryonic development of the squid, *Illex illecebrosus*, and effect of temperature on development rates. J. Northw. Atl. Fish. Sci. 3:41–45.

OKIYAMA, M. 1965. Some considerations on the eggs and larvae of the common squid *Todarodes pacificus* Steenstrup. Bull. Jap. Sea Reg. Fish. Res. Lab. 15:39–53.

OKIYAMA, M., and S. KASAHARA. 1975. Identification of the so-called "common squid eggs" collected in the Japan Sea and adjacent waters. Bull. Jap. Sea Reg. Fish. Res. Lab. 26:35–40.

PRICE, P. W. 1974. Strategies for egg production. Evolution 28:76–84.

SANZO, L. 1929. Nidamento pelagico, uova a larve di *Thysanoteuthis rhombus* Troschel. Memorie R. Comm. talassogr. ital. 161: 1–10.

SASAKI, M. 1914. Observations on Hotaru-ika *Watasenia scintillans*. J. Coll. Agric. Tohoku Imp. Univ., Sapporo 4(4):75–107.

SHIMOMURA, T., and H. FUKUTAKI. 1957. On the year-round occurrence and ecology of eggs and larvae of the principal fishes in the Japan Sea. Bull. Jap. Sea Reg. Fish. Res. Lab. 6:155–290.

SHOJIMA, Y. 1970. Cephalopod larvae and eggs taken at the surface in the northern South China Sea—I. Bull. Seikai Reg. Fish. Res. Lab. 38:61–77.

———.1972. The common squid, *Todarodes pacificus*, in the East China Sea—II. Bull. Seikai Reg. Fish. Res. Lab. 42:25–58.

STAUFFER, G. D., and S. J. PICQUELLE. 1980. Estimate of the spawning biomass of the central subpopulation of northern anchovy. SWFC Admin. Rep. LF-80-09.

STEARNS, S. C. 1976. Life history tactics: A review of the ideas. Q. Rev. Biol. 51: 3–47.

SUZUKI, S., H. MISAKI, and T. OKUTANI. 1979. Studies on early life history of decapodan molluscs—VIII. A supplementary note on floating egg mass of *Thysanoteuthis rhombus* Troschel in Japan—the first underwater photography. Jap. J. Malac. 38(2): 153–155.

WALLER, R. A., and R. I. WICKLUND. 1968. Observations from a research submersible: Mating and spawning of the squid *Doryteuthis plei*. Biosci. 18:110–111.

YAMADA, T. 1937. On the spawning of the squid, *Watasenia scintillans*, in the waters of the east coast of Tyosen. Bull. Jap. Soc. Sci. Fish. 6(2):75–78.

YAMAMOTO, T. 1943. Squids and octopus. Kaiyo no Kagaku 3(10) [via Shimomura and Fukutaki 1957].

———.1946. On the eggs and larvae of *Ommastrephes sloani pacificus* collected from Korean waters. Jap. J. Malac. 14(4):228–240.