Title

Fish Bulletin 131. The Structure, Development, Food Relations, Reproduction, and Life History of the Squid Loligo opalescens Berry

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Publication Date

1964-05-01

STATE OF CALIFORNIA
THE RESOURCES AGENCY
DEPARTMENT OF FISH AND GAME
FISH BULLETIN 131
The Structure, Development, Food Relations, Reproduction, and Life History of the Squid Loligo opalescens Berry

By

W. GORDON FIELDS

1965

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ACKNOWLEDGMENTS

This study ("a dissertation submitted to the Department of Biological Sciences and the Committee on the Graduate Division of Stanford University in partial fulfillment of the requirements for the degree of Doctor of Philosophy") was undertaken at the suggestion, and under the direction, of Tage Skogsberg, Hopkins Marine Station, to whom I am greatly indebted for inspiration and guidance until his untimely death. Thereafter, Rolf L. Bolin was my advisor, and I wish to express my appreciation to him for the help he gave me. In the final part of this investigation and in bringing its results together, Donald P. Abbott, through his enthusiasm, his wide scientific knowledge, his ability and his wisdom, has given encouragement and immeasurable help in many ways: to him I express my deepest appreciation. Lawrence R. Blinks, Director of the Hopkins Marine Station, throughout my work there, arranged suitable laboratory space and conditions for my use and, deftly and to my advantage, resolved all administrative matters referred to him; I am very grateful to him.

Julius B. Phillips, Marine Resources Operations, California Department of Fish and Game, often gave me advice and information from his wide knowledge of fisheries; he and his colleagues collected many squid for me, and he permitted me to use some of his photographs. For help in many ways, I wish to express my appreciation.

I wish to thank Harold N. Arrowsmith, Jr., and DeBoyd L. Smith, who took many of the photographs for me. I wish also to thank many others at the Hopkins Marine Station who helped in many ways.

The men in the fishing industry, whether fishing, canning, or freezing the squid, showed unfailing interest and cooperation in this investigation, and contributed a great deal.

My thanks go also to the California Department of Fish and Game, which cooperated in every way, and also provided a Fellowship to assist with this program. Grants toward expenses of preparing final manuscripts and figures were made from Public Health Service Training Grant GM-647 from the National Institute of General Medical Sciences and from the University of Victoria Faculty Research Fund.

Finally, I wish to express my gratitude to John E. Fitch for his thoughtfulness and unobtrusive aid in preparing this for publication. Only appendices (containing the raw data from which figures were derived) have been omitted; these are given in my thesis which is on file in the Biology Department at Stanford University and at the Hopkins Marine Station. Microfilm copies may be purchased through University Microfilms, Inc., Order N. 63–4599, 313 North First St., Ann Arbor, Michigan (Microfilm $3.60; Xerography $12.60).

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May 1964 Department of Biology, University of Victoria, Victoria, B.C., Canada

1. TAXONOMY

1.1. Introduction

The squid, Loligo opalescens Berry, is abundant along much of the west coast of North America. They often congregate where a light is suspended over the water at night, and at certain seasons, individuals that are spent by spawning may be seen swimming aimlessly near the surface. Great schools spawn in shallow waters like those adjacent to Monterey, California, where they support a valuable fishery. This squid is also important as food for many fishes, sea birds, and marine mammals.

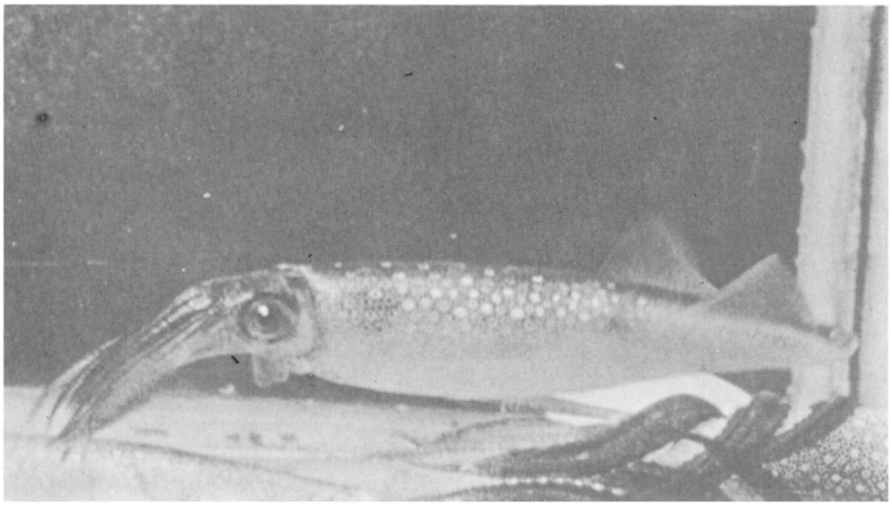

FIGURE 1. Live female squid, *Loligo* opalescens. *Photograph for the author by Harold N. Arrowsmith, Jr.*

FIGURE 1. Live female squid, Loligo opalescens. Photograph for the author by Harold N. Arrowsmith, Jr.

1.2. Classification

The systematic position of L. opalescens can be reviewed, and its general morphology outlined by listing its classification and briefly summarizing the characteristics of each taxon listed.

1.2.1. Phylum Mollusca, Cuvier 1798

Bilaterally symmetrical (except where torsion and coiling modify this in Gastropoda); unsegmented (except in Class Monoplacophora, e.g., Neopilina galatheae described by Lemche and Wingstrand in 1959); generally of three regions: head, foot, and visceral hump, the last being covered by a mantle which may secrete a shell of one, two or eight valves; digestive tract complete and having a radula, except in bivalves; respiration through ctenidia, cerata or wall of mantle cavity.

1.2.2. Class Cephalopoda, Schneider 1784

Head prominent with well-developed eyes; foot transformed into circumoral appendages and temporary or permanent funnel; shell external, internal, or none; mouth with radula and chitinous beak; typical ganglion pairs grouped in head and shielded by cartilaginous cranium; development direct.

1.2.3. Sub-class Coleoidea, E. W. Berry 1928, [Order Dibranchiata, Owen 1836]

Homologous shell, where present, entirely enclosed by mantle, except in Spirula; 8 or 10 circumoral appendages, bearing suckers at least in youth; funnel a permanent tube; eyes with crystalline lens and iris; chromatophores in skin; ink sac and poison glands present; two gills and two kidneys in living groups.

1.2.4. Order Teuthoidea, Naef 1928, [Order Decapoda, Leach 1818]

Eight regular arms and two retractile tentacles with suckers or hooks confined to terminal clubs; suckers pedunculated, bearing horny rings which may be modified as hooks; terminal or lateral fins on mantle; shell present.

1.2.5. Suborder Myopsida, d'Orbigny 1845

Transparent closed cornea with anterior pore; horny rings or suckers never hook-like; oviduct developed on left side only; genital artery arising directly from the heart; mostly littoral in habit; eggs laid singly or in masses fixed to the sea-bottom.

1.2.6. Family Loliginidae, d'Orbigny 1845

Body elongated, more or less tapering posteriorly; fins rhombic to sagittate and terminal, or nearly as long as the mantle; mantle free from head except for sliding cartilaginous articulation at nape; eyes without lid-folds; olfactory crests prominent; suckers usually toothed, in two rows on sessile arms and in four rows in middle of tentacle club; left ventral arm of male hectocotylized, the right arm occasionally modified as well; siphon with dorsal bridle, two sliding cartilaginous articulations with mantle, and internal valve; horny, uncalcified feather-shaped gladius.

1.2.7. Genus Loligo, Schneider 1784, Lamarck 1798

Body elongate, tapering posteriorly. Fins terminal, ordinarily a little longer than half the mantle length, rhomboidal in the young, becoming sagittate in the adult; cartilaginous locking devices with simple longitudinal grooves on siphon, and ridges on mantle; pen as long as the mantle; pupil of eye crescent-shaped, encroached upon dorsally by the iris; buccal membrane with seven elongated points, covered on their inner surfaces with small suckers; below the beak upon this membrane, in the female, is a structure for the storage of spermatozoa.

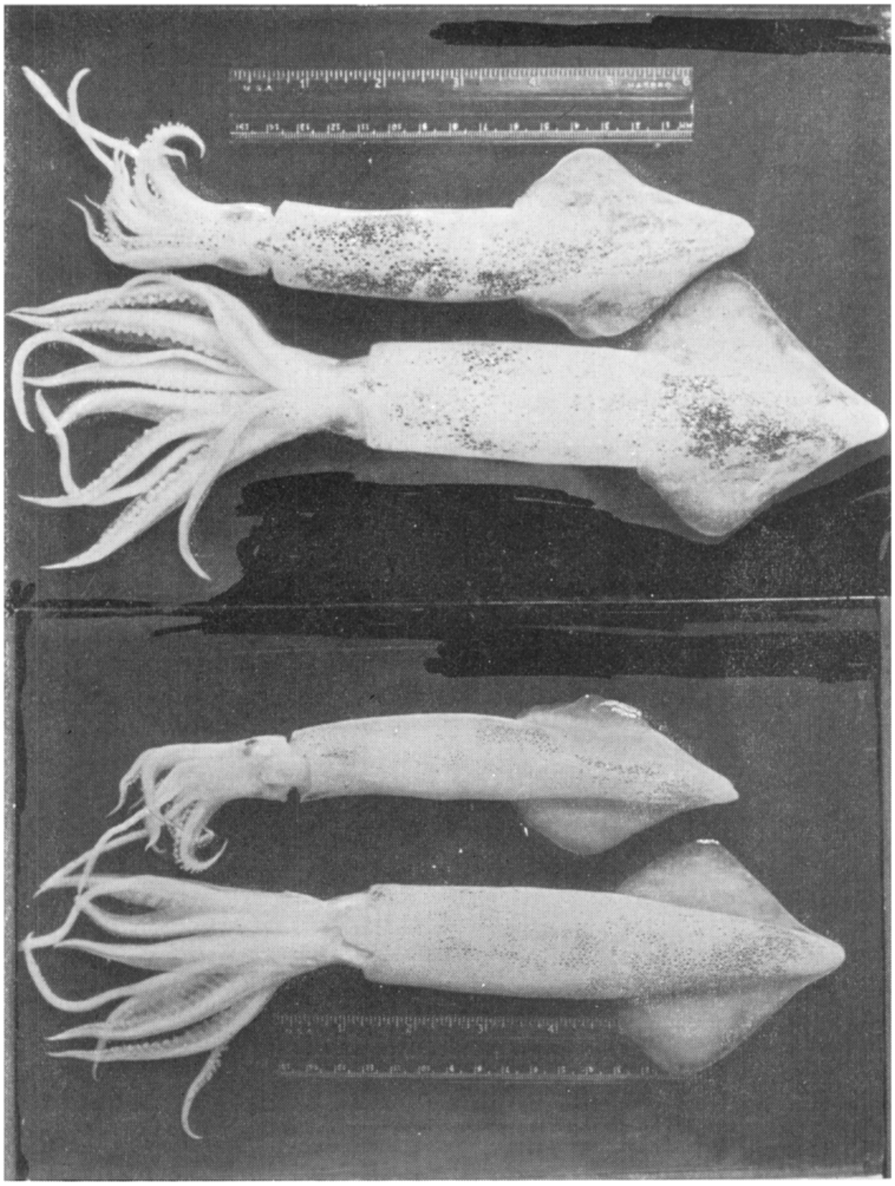

FIGURE 2. **Top:** Dorsal aspects of female (above) and male *Loligo opalescens*. **Bottom:** Ventral aspects of female and male (below) *Loligo opalescens. Photographs for the author by DeBoyd L. Smith.*

FIGURE 2. Top: Dorsal aspects of female (above) and male Loligo opalescens. Bottom: Ventral aspects of female and male (below) Loligo opalescens. Photographs for the author by DeBoyd L. Smith.

1.2.8. Type, Loligo vulgaris Lamarck 1798

Hoyle (1910), Berry (1912), and Sasaki (1929), use "Schneider, 1784" as the authority, concerning which Hoyle says:

"The genus was created by Schneider (1784), but he does not mention any type though his opening sentence ... leaves no doubt that he had the Sepia Loligo of Linné in mind. The difficulty consists in knowing what species this was. I have looked up the various authorities referred to by Linné and find that they include a great variety of forms; in fact they comprise all those with cylindrical body and fins ... Lamarck (1798, 1799) erects a genus Loligo, apparently independent of Schneider, but with the same characters, and names his first species L. vulgaris, with the remark, "*Il est vraisemblable que Linné n'a point connu cette espèce*." Under these circumstances the only reasonable plan occurs to me to be to regard L. vulgaris Lamk. as the type of his genus and therefore of that of Schneider." Thiele (1935), Voss (1956), and Jaeckel (1958) use "Lamarck 1798," Jaeckel adding "(Diagnose bei Naef 1923)."

1.3. Taxonomic Description

1.3.1. Historical

L. opalescens may have been the subject of early references to a Loligo-like squid from the west coast of North America, but none of these included a description sufficient to identify this animal with certainty.

Whiteaves (1887) lists: Ommastrephes sagittatus, *Lamarck*. (Sp.). Three specimens of a squid, which correspond very well with Tryon's description and figures of this species in the first volume of his "Manual of Conchology," were collected at low tide in Victoria Harbour, Vancouver Island." Taylor (1895) adds, "This appears to be the commonest of our Cephalopods" on the Pacific coast of Canada, an observation which in 1962 would apply to L. opalescens, since no Ommastrephes sp. is known from this coast.

Hemphill (1892) stated that a "ten-armed cephalopod" for sale as food in San Francisco markets had been mentioned by a Mr. R. E. C. Stearns in the July 1891 *Nautilus*. Hemphill obtained animals from this source, noted that, "... the arms are not webbed ... it closely resembles Loligo Gahi d'Orbigny, " and proposed the name Loligo stearnsii. Jenkins and Carlson (1903) applied the name of the Atlantic form, L. pealii, to the animals in which they studied nerve physiology at the Hopkins Seaside Laboratory, Pacific Grove, California, and Keep (1904, 1911) spoke of the squid of this area as Ommastrephes tryoni. Lacking an adequate description, each name was at best a *nomen nudum*.

1.3.2. Original Complete Description

Berry (1911) published a brief initial description and a later (1912) full description of a Loligo from the west coast of the United States which he appropriately named L. opalescens. The full description is quoted here in order that it may be widely available again:

"Body of moderate size; firm, cylindrical, narrow, elongate, slightly swollen near the middle, thence tapering acutely to a rather sharp point behind. Fins large, about half as long as the mantle; sagittate; very slightly lobed in front, barely continuous behind, obtusely angled considerably in front of the middle; their margins thin, entire. Mantle margin truncate, deeply emarginate between the prominent lateral angles on either side of the funnel; produced above into a prominent, squarish, rostrum-like process, rounded at the extremity, which is made up chiefly of a continuation of the dorsal connective cartilage of the mantle around the tip of the gladius. Locking apparatus well developed, comprising the just-mentioned cartilage in the nuchal region, besides a prominent elongate cartilaginous groove and ridge on either side of the funnel; the latter simple, with a raised and reflexed margin.

"Head small, narrower than the body, squarish, ornamented above posteriorly by three parallel longitudinal folds of integument, the grooves between which correspond to the cartilaginous ribs of the rostrum. Eyes large, not protruding. Siphon rather large, broad, and plump, with dorsal bridles and a large terminal valve.

"Arms stout and rather short in the male, sometimes a little longer in the female[a] ; unequal, the dorsal arms considerably the shortest, but the proportions of the others somewhat variable, usually 3, 2, 4, 1. Umbrella rudimentary between all the arms except the ventral pair, where it is totally lacking; continued upon the dorsal margins of the dorsal arms as a prominent membranous keel; inner margins of second arms bluntly carinate, third arms obscurely so; outer margins of second and third with a fleshy keel running to their tips; ventral arms provided with a very broad and prominent web along the outer margin, ensheathing the base of the tentacle, and thence gradually narrowing toward the tip; a similar but much less developed keel extends along the inner margins of the ventral arms. Along the sucker-bearing surface of all the arms runs a delicate membranous swimming web, strengthened by numerous slender transverse trabeculae of a muscular nature, occurring in alternation with the sucker pedicels. Save on the ventral pair, where it becomes much reduced, this web is exceedingly prominent on all the arms, but attains its maximum development on the third pair, where its diameter is seen in well-preserved specimens to be as great or greater than that of the arm itself. Suckers small, somewhat kettle-shaped, regularly alternating in two rows, obliquely poised on rather short conical pedicels; margin of cupules hood-like, with a small sinus in the superior margin; horny rings with nine to twelve bluntly rounded, squarish teeth on the upper margin; papillary area wide and very prominent in microscopical preparations.

"Left ventral arm in the male conspicuously hectocotylized; along the proximal two-thirds of the arm the suckers (about twenty pairs) are unmodified, but along the distal third their pedicels become transversely flattened and elongate, the cups showing a simultaneous diminution in size, a condition especially true of the suckers at the extreme distal end of the outer row, where the cups are reduced to mere rudiments. Toward the end of the inner row the pedicels decrease in size and resume their normal shape, the cups decreasing comparatively little, so that the suckers at the extreme distal end of the row are more nearly normal. The outer row is still further unique, in that some six to eight of the more proximal suckers undergoing modification are much more elevated and have broader pedicels than either those opposite or those succeeding or following

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[a] "a Perhaps due to the different preservation of the material."

them; indeed, throughout the modification of each pedicel and sucker in this row is more complete than that of the corresponding sucker of the inner row.

"Tentacles of moderate but variable length, highly contractile; the club but slightly expanded, lanceolate, furnished with a pronounced keel and a narrow swimming membrane. Suckers in four rows, those of the two outermost very small; those of the two median rows much larger, their horny rings armed all around with about thirty-five small, rather elongate, bluntly conical teeth.

"Buccal membrane seven pointed, each point bearing two distinct rows of very minute crowded suckers, seven to nine in a row. The latter have well-developed papillary areas and horny rings with five or six irregularly squarish teeth. There is also an inner buccal membrane like a thickened, radially rugose cushion surrounding the beak.

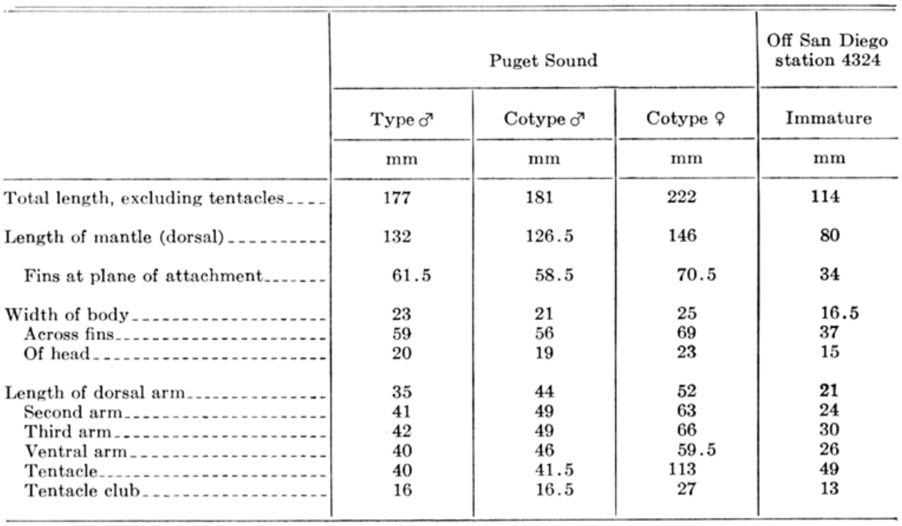
"Gladius thin, broadly lanceolate; midrib slender; slight lateral but no marginal thickenings.

"Color in life not observed; color in alcohol a pale buff, with numerous very distinct and beautiful brownish chromatophores scattered profusely over the whole dorsal surface, and in somewhat less degree over the ventral as well.

"The young are quite different in general appearance, but are not easily confused with any of the other species inhabiting the same region. Besides other features which are in the main obviously due to juvenility, they differ from the adults chiefly in the much shorter, broader, more rounded fins which gradually assume the typical sagittate outline as they increase in size.

"The more important dimensions of the type, two cotypes, and one other specimen, are appended in the annexed table.

Measurements of *Loligo opalescens*



	Puget Sound			Off San Diego station 4324
	Type ♂	Cotype ♂	Cotype ♀	Immature
	mm	mm	mm	mm
Total length, excluding tentacles	177	181	222	114
Length of mantle (dorsal)	132	126.5	146	80
Fins at plane of attachment	61.5	58.5	70.5	34
Width of body	23	21	25	16.5
Across fins	59	56	69	37
Of head	20	19	23	15
Length of dorsal arm	35	44	52	21
Second arm	41	49	63	24
Third arm	42	49	66	30
Ventral arm	40	46	59.5	26
Tentacle	40	41.5	113	49
Tentacle club	16	16.5	27	13

"Type No. 2076 invertebrate series in the collection of Stanford University, a male. Cotypes in the U.S. National Museum and in the author's collection.

"Type locality, Puget Sound, Washington (shrimp fishermen), 3 specimens.

"Distribution: Washington—Puget Sound, near Deception Pass. California—Monterey Bay, San Diego."

1.3.3. Additions and Amendments to Original Description

Color of living animals. The tissues of L. opalescens are quite milky and translucent, with a faintly bluish tone due to the haemocyanin of the blood, which in its oxidized state is blue. Deeply embedded in the skin are iridophores which produce scattered areas of brilliant blue-green opalescence. These iridescent patches are more closely placed on the upper than on the lower surface of the mantle, and form a continuous band above each eye. At most times when undisturbed, a squid has the pale coloration described here, but when excited it exhibits intense and varied color patterns through activity of its chromatophores. These elastic sacs containing red, brown, orange, or yellow pigment lie more superficially in the dermis, and when contracted appear as minute dark dots. The particular chromatophores expanded at one time give their colors to the animal. Waves of coloration run over the whole animal when it is catching its prey; these are followed by general darkening when the animal is eating. During mating, the male's mantle is pale with fleeting clouds of color and some of his arms and his head are dark red, while the female retains her pattern of color. Mottled gold and brown is a common color pattern when the animals are placed in unfamiliar surroundings or appear somewhat excited; if suddenly disturbed the squid becomes very dark, ejects ink, and darts away.

Sexual dimorphism. Differences between male and female animals are not adequately presented in Berry's account. His vague mention of arm lengths and his table of measurements suggest the reverse of the typical relationship, which is that arms and tentacles are distinctly longer in male than in female animals of the same mantle length and of the same sample. Manner of death, conditions shortly thereafter, and earliness and method of preservation apparently affect the degree of contraction of these parts and therefore their stoutness and length relative to mantle length. Similarly-treated animals of any one sample, however, always show that the head, arms, and tentacles of female specimens are smaller than those of males of the same mantle length (Figure 3, Table 1).

It is unfortunate that, after Berry (1912) had inspected more than 330 specimens, he chose three of the latest he saw (according to his register number) to use as "type" and "cotypes," and for generalizations on arm length, because these exhibited the reverse of the normal relative proportions for males and females.

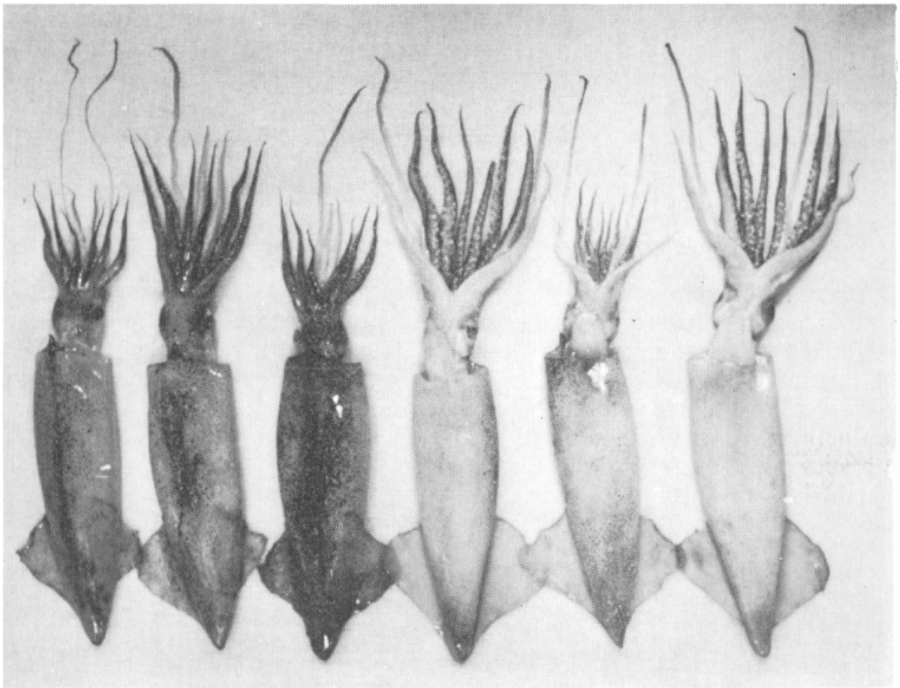


FIGURE 3. Male and female squid showing relative arm lengths. Sexes are alternately placed, starting with a female on the left.

FIGURE 3. Male and female squid showing relative arm lengths. Sexes are alternately placed, starting with a female on the left

TABLE 1

Comparison of Arm Lengths of Female and Male Squid *

	Lengths (mm)						Average	
	F.	M.	F.	M.	F.	M.	F.	M.
Mantle length	155	156	159	160	158	163	157.3 mm (100%)	159.7 mm (100%)
Dorsal arm	32	55	35	55	34	56	21.4%	34.7%
Second arm	36 (37.5)	62	38	59	38	57	23.9%	37.2%
Third arm	42	61	41	59	40	55	26.1%	36.5%
Tentacle	56	66 (88)	58 (55)	55 (65)	52 (64)	65 (69)	36.1%	42.6%
Ventral arm	34	52	37	51	34	51	22.2%	32.2%

* Where arms or tentacles of a pair differ, both lengths are given. Average lengths for each sex (listed as percentages of the average mantle length) are given in the last two columns.

TABLE 1

Comparison of Arm Lengths of Female and Male Squid

Male and female squid differ externally in several ways. The arms of the male, in addition to being longer, are thicker and have wider swimming membranes and keels than do those of the female. The head also is relatively larger in the male, so that head and arms together give a much more massive appearance than in the female, permitting sure and easy recognition of members of each sex. The appearance of the white testis, clearly seen dorsally through the pen and mantle of the male, resembles, but is distinguishable from, that of the whitish apparently glandular region of the skin of the female, covering the same posterior area of the mantle. More detailed examination is required for detecting the hectocotylization of the male or the sperm receptacle in the buccal membrane of the female.

2. DISTRIBUTION AND HABITAT OF L. OPALESCENS

Mere recitation of the geographic boundaries of the area which a creature inhabits contributes little to an understanding of its way of life; only when the dynamic factors impinging upon the individual and the population are known can the observed facts be properly assembled, like the tiles of a mosaic, into a true picture of the animal's life history. For this reason, the recorded limits and the physical oceanography of the habitat of L. opalescens will be described here, and the biological components will be considered in their appropriate places later.

2.1. Distribution

According to Berry (1912) Loligo opalescens ranges from Puget Sound, Washington, to San Diego, California, "... and in its proper season is everywhere abundant, usually occurring in great shoals by the thousand." Steinbeck and Ricketts (1941) reported this squid in the Gulf of California, and mentioned that it was taken in quantity by a shrimp dredger south of Guaymas. If, in fact, they were dealing with L. opalescens, this greatly extends its southern range to below lat. 28° N. and indicates that this pelagic species may frequent the waters to the south of the tip of Baja California (i.e. at least to lat. 22° N.) either continuously or by seasonal migration to provide reproductive continuity with its previously known population to the north.

The northern range must also be extended. Pritchard and Tester (1944) reported L. opalescens was a significant part of the stomach contents of king salmon, Oncorhynchus tshawytscha, caught off the eastern (Gulf Islands) and western (Barkley Sound) coasts of the southern part of Vancouver Island, but did not report them from elsewhere on the British Columbian coast. Gordon C. Pike (1953, pers. commun.) reported finding a single Loligo (in the stomach of a humpback whale, Megaptera nodosa) while examining the stomach contents of whales at the Coal Harbour, British Columbia, whaling station (lat. 50° 36' N., long. 127° 35' W.) during the summer of 1952.

Among the Gulf Islands to the east of southern Vancouver Island this squid is taken in otter trawls in 30–55 fathoms of water fairly frequently in winter; in some summers these animals are seen under the lights of wharves in this area and egg masses are found occasionally. During July and August 1958, this squid was abundant in the harbors of Victoria and Esquimalt, British Columbia, mating and spawning there. In August and September of the next two years, it spawned in great numbers near Victoria in Cadboro Bay, but did not reappear there in 1961.

2.2. Physical Oceanography

A very brief survey of some aspects of the oceanography of the eastern Pacific Ocean will give a general picture of the particular marine environment in which L. opalescens is found. The Monterey Bay region is described in considerable detail because most of my work was done there.

The characteristics of Monterey Bay are well documented, physiographically by Galliher (1932) and by Smith and Gordon (1948), hydrographically by Skogsberg (1936), Skogsberg and Phelps (1946), and with regard to water and plankton characteristics by Bigelow and Leslie (1930), Phelps (1937), and by several reports of the California Cooperative Oceanic Fisheries Investigations. The reports of this series and works by Gislen (1943, 1944), Sverdrup *et al.* (1942), and Dodimead and Hollister (1958) give a broader picture of the coastal waters. Steinbeck and Ricketts (1941) describe some conditions in the Gulf of California, quoting in part from Thorade (1909). Water characteristics in Puget Sound are given by Thompson *et al.* (1928), Johnson and Thompson (1929) and Thompson and Johnson (1930); those of Canadian coastal waters are described by Cameron and Mounce (1922), Barraclough and Waldichuk (1954), Waldichuk (1957) and the Pacific Oceanographic Group (1953).

The warmer oxygen-containing surface water of the Pacific Ocean lies above the deep zone (Gislen 1944) of cold nutrient-rich but oxygen-poor water which has come into the Pacific basin from the Antarctic. Under the influences of the earth's rotation and the prevailing winds the Japan Current (Kuroshio) flows eastward across the northern Pacific. As it approaches North America, this huge shallow stream diverges to form the Alaskan Gyre which turns northward along the Canadian and Alaskan coasts to the Aleutian Islands, and the California Current which flows southward off the coast of the United States to the vicinity of Point Conception where it turns south-westward to join the North Equatorial Current. This offshore trend draws water northward along the Mexican coast, and some of this forms the Southern California Countercurrent, a counter-clockwise eddy in the shelter of Point Conception and the Channel Islands off southern California.

The main clockwise movement of the California Current as a part of the ocean's surface tends by Corioli's force to thicken this layer far offshore, and constant winds at certain times of the year also tend to carry this surface water away from the coast of California. Both of these factors contribute to the upwelling of cold, rich water from intermediate depths along the coast where the continental shelf is narrow. At Monterey, successive pulses of strong upwelling occur from March into August of each year, and the upwelled water moves slowly southward as it mixes with and enriches that at the surface.

According to Reid, Roden and Wyllie (1958), "A deep countercurrent, below 200 meters, flows to the northwest along the coast from Baja California to some point beyond Cape Mendocino. It brings warmer, more saline water great distances northward along the coast," i.e. at least to northern California. Skogsberg (1936) states that some characteristics of the upwelling at Monterey suggest this water is not deflected upward by the coastline itself but by a deep current parallel to the coast.

After the period of upwelling, the California Current apparently slackens and meanders so that its water (typically oceanic in its warmth, reduced phytoplankton, and charactersitic zooplankton) forms the superficial coastal layer during September and October. This is called the oceanic period.

From November to February, the Davidson Current, a strong countercurrent from the south, becomes the dominant feature of the inshore surface water. This carries water from south of Point Conception northward along the whole California coast, and according to Sverdrup *et al.* (1942), "to at least lat. 48° N." In some years, it apparently reaches Canadian waters (Radovich, 1961; Favorite, 1961), for in 1959 the sandcrab Emerita analoga was found on the west coast of Vancouver Island (Butler, 1959), although its northernmost range was reported by Ricketts and Calvin (1952) to be Oregon. An alternative but unlikely possibility is that the Japan Current divergence shifted southward far enough to sweep water from the Oregon coast northward into the Alaskan Gyre.

At Monterey, the upwelling period, oceanic period, and Davidson Current period recur regularly in the general pattern described above, although some variations occur from year to year in the time of onset and termination and in the intensity of the typical conditions associated with each period.

3. HISTORY AND METHODS OF FISHING

3.1. History

The fishery for Loligo opalescens at Monterey began no later than 1863, when a Chinese fishing village was established near Mussel Point, the present site of Hopkins Marine Station. The original fishing method, described by Collins (1892), was to row a skiff with a blazing torch at the bow about the bay at night until a school of squid had been attracted to it, whereupon two accompanying skiffs would set a small purse seine, about 180 feet long and 18 feet deep, around the school. Considerable numbers were taken in this primitive and laborious manner, sun dried, and exported chiefly to China. According to Wilcox (1907) the same fishing methods persisted with little change through 1904. In 1905, lampara nets, capable of taking 20 tons in a single haul, were introduced by Italian fishermen. Using this superior equipment they took complete control of the squid fishing, although Chinese and Japanese continued to dry and market the catch.

3.2. Modern Nets

The lampara net has a central sack or pocket of netting with a small 1¼-inch mesh. This region may be 30 to 40 fathoms wide and the net here is 25 to 30 fathoms deep. From each side of the sack, a wing 40 to 65 fathoms long tapers to a point. Nearest to the sack the wings are of about 4-inch mesh; this soon gives way to 8-inch mesh; and the last 12 fathoms are of 16-inch mesh. The weighted lead line along the bottom of the net is shorter than the buoyant cork line along the top, and as the wings are hauled in simultaneously the lower margin of the sack is drawn beneath the school. Thus when the wings are in, and the lead line has been raised, the squid are entirely enclosed by the fine mesh of the sack. The large mesh of the wings eases hauling of the net, yet retains the squid because they avoid the luminescence induced by its strands. Formerly fishermen hauled these nets entirely by hand, but now power-operated equipment is used to bring in the wings. The lampara net has remained standard equipment on the smaller boats to the present time, but when larger boats have temporarily entered the fishery they have used purse seines.

The purse seine is a rectangular net with floats fastened on one long side, the cork line, so that the net will not sink, and with weights on the opposite margin, the lead line, so that this edge of the net will hang downward. Also along this lower side hang rings through which the purse line extends; when the ends of this line are drawn in, the lower margin of the net is closed or "pursed" below the catch, thus preventing escape downward. These nets are pursed and raised by power winches.

A third type of net, the "half-ring," has been used to some extent for squid fishing. It is power-operated and resembles a purse seine except for being smaller and for having rings along only half its length.

These roundhaul nets and the ways in which they are used are fully described by Scofield (1951).

3.3. Fishing Methods

The southern part of Monterey Bay continues to be the main squid fishing area, and fishing is still done at night when the schools may be located and identified by the luminescence of the unicellular organisms they disturb. Squid schools may be recognized by their more uniform diffuse glow and by their tendency to keep together and maintain original direction, in contrast to the darting, wheeling patterns of fish schools.

When a school if located, a skiff towed by the fishing boat is released, and serves as a floating anchor for one end of the net. Red lights are turned on as warning that the net is down, and the fishing boat travels in a wide circle while the net is paid out over the stern to hang downward about the school. After the two ends of the net have been brought together floodlights illuminate the deck, and the wings and leadline are hauled in until the squid are held in a shallow pocket of net beside the boat. A power-lifted dip net is used to transfer them to the skiff or to the hold of the fishing boat.

Other methods are occasionally used. When squid are abundant, "blind" sets (without surface indications of the schools) may be made in daylight over particular areas where they are known to congregate. Fishing was done in this way, as well as at night, in 1945 and 1946 at Monterey (Figure 4).

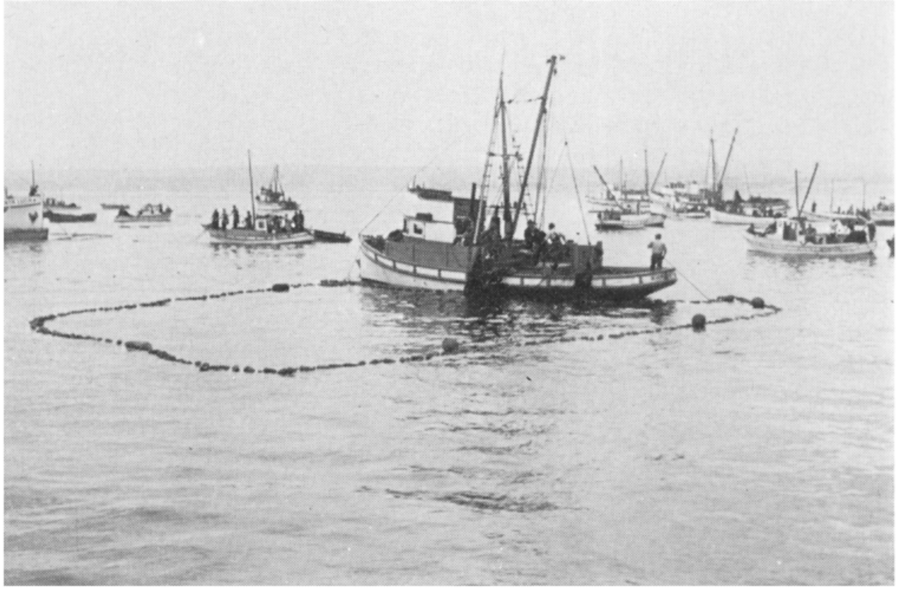


FIGURE 4. Squid fishing at Monterey in May 1946. Lampara nets are being used by the two boats near the center of the picture. *Photograph by J. B. Phillips.*

FIGURE 4. Squid fishing at Monterey in May 1946. Lampara nets are being used by the two boats near the center of the picture. Photograph by J. B. Phillips

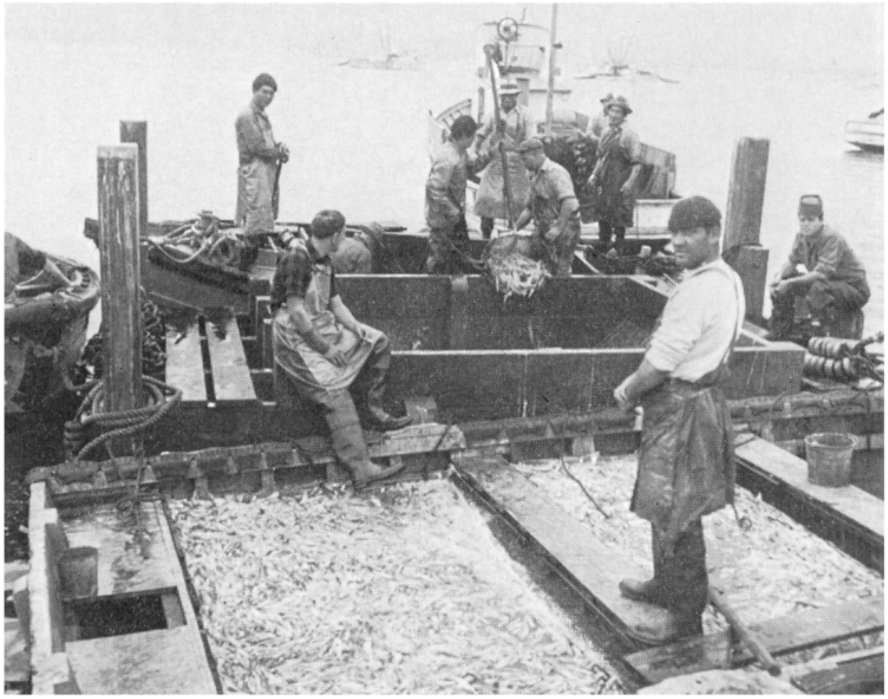


FIGURE 5. Unloading squid from large skiffs into the hopper of a cannery suction pump. Boats in the background are still on the fishing grounds. *Photograph by J. B. Phillips, May 1946.*

FIGURE 5. Unloading squid from large skiffs into the hopper of a cannery suction pump. Boats in the background are still on the fishing grounds. Photograph by J. B. Phillips, May 1946

Tremendous squid concentrations are sometimes encountered off southern California; on one occasion off San Clemente Island no set was made with the net, yet 100 tons were brailed in from beside the vessel (Pacific Fisherman, 1951).

Squid are unloaded from fishing boat or skiff at the wharf or at the hopper of a cannery with power-lifted dip nets. In the past, the smaller boats lacked power for this, and it was done by hand (Figure 5).

4. COMMERCIAL CATCH

4.1. Amount

The squid catch at Monterey in 1904 was about 125 tons, according to Wilcox (1907). Scofield (1924) states that the annual catch varied greatly, but usually was from 100 to 150 tons a year. Since no records were kept prior to 1916, the catch in some years may have greatly exceeded the reported average. For example, Heath (1917) stated, "Five thousand odd tons were taken in a single season," but he gave neither date nor source of information. The California Department of Fish and Game has gathered annual landings data for squid in California since 1916 when the catch was about 140 tons (Figure 6). Until 1932, it fluctuated above this amount, the peak being 5,500 tons in 1930. The average annual catch for the 10 years 1923 to 1932 was 2,100 tons, most of which was dried and shipped to China. Phillips (1937) ascribes the varying catch during this period to the instability of China's silver exchange, and to competition from Japan's squid fishery. Owing to financial conditions, the Oriental market was closed in 1933 and since then virtually no squid has been dried. Canning and freezing of squid for the domestic market (introduced about 1920 and 1926, respectively) maintained the fishery at about 400 tons until 1942. Re-opening of foreign markets combined with a population explosion in Loligo opalescens led to a peak catch in 1946 of 19,000 tons. Since then the annual catch has fluctuated between 1,700 and 10,000 tons, averaging about

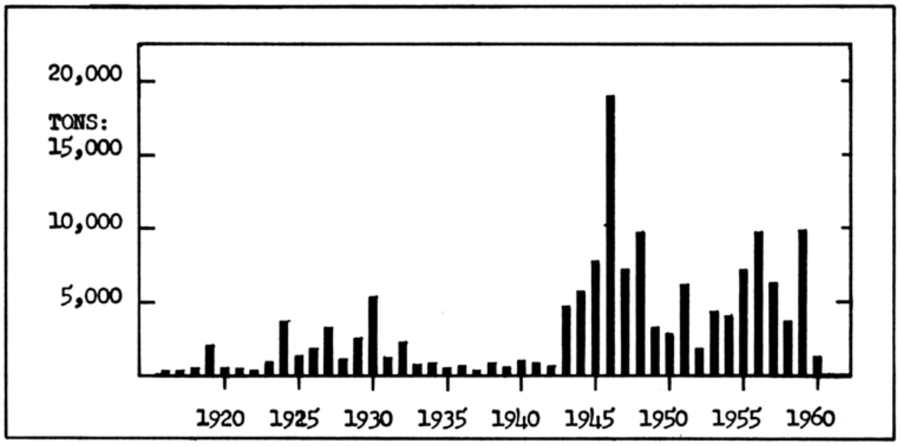


FIGURE 6. California squid landings, 1916-1960. Catch is given in tons.

FIGURE 6. California squid landings, 1916–1960. Catch is given in tons

6,500 tons the past 17 years. These quantities were taken almost exclusively at Monterey except for the years 1953, 1958, and 1959, when the squid catch in the Los Angeles area was 2,682, 1,772, and 2,679 tons, respectively.

4.2. Value

Matters related to disposition of the catch and economics of the fishery are discussed more fully in Phillips (1937), Classic (1929, 1949) and Fields (1950). In the Monterey area, for the years 1944 to 1960 inclusive, the squid fishery had a total value of $5,074,597, with an annual average of $298,506 (Table 2). These values have fluctuated between 3 and 40 percent of the total value of all fish-boat landings at Monterey, averaging 11.9 percent. In order of value among all species (of fish, etc.) landed at this port, squid did not fall below sixth during these 17 years; in 11 years it was third or better, and in 1946 squid was first.

4.3. Fishing Season

Fishing for Loligo opalescens depends upon market demand and upon availability of the animal.

In order to show the fishing season, the average monthly catches during the five, 6-year periods, 1931–1936, 1937–1942, 1943–1948, 1949–1954, and 1955–1960 were compared (Figure 7).

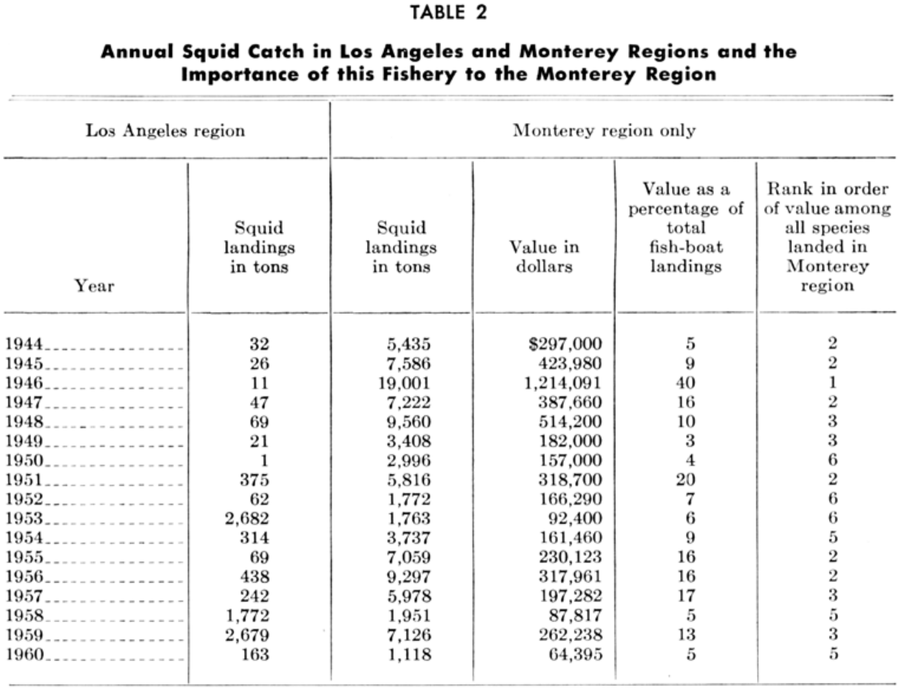


TABLE 2

Annual Squid Catch in Los Angeles and Monterey Regions and the Importance of this Fishery to the Monterey Region

Los Angeles region		Monterey region only			
Year	Squid landings in tons	Squid landings in tons	Value in dollars	Value as a percentage of total fish-boat landings	Rank in order of value among all species landed in Monterey region
1944	32	5,435	$297,000	5	2
1945	26	7,586	423,980	9	2
1946	11	19,001	1,214,091	40	1
1947	47	7,222	387,660	16	2
1948	69	9,560	514,200	10	3
1949	21	3,408	182,000	3	3
1950	1	2,996	157,000	4	6
1951	375	5,816	318,700	20	2
1952	62	1,772	166,290	7	6
1953	2,682	1,763	92,400	6	6
1954	314	3,737	161,460	9	5
1955	69	7,059	230,123	16	2
1956	438	9,297	317,961	16	2
1957	242	5,978	197,282	17	3
1958	1,772	1,951	87,817	5	5
1959	2,679	7,126	262,238	13	3
1960	163	1,118	64,395	5	5

TABLE 2

Annual Squid Catch in Los Angeles and Monterey Regions and the Importance of this Fishery to the Monterey Region

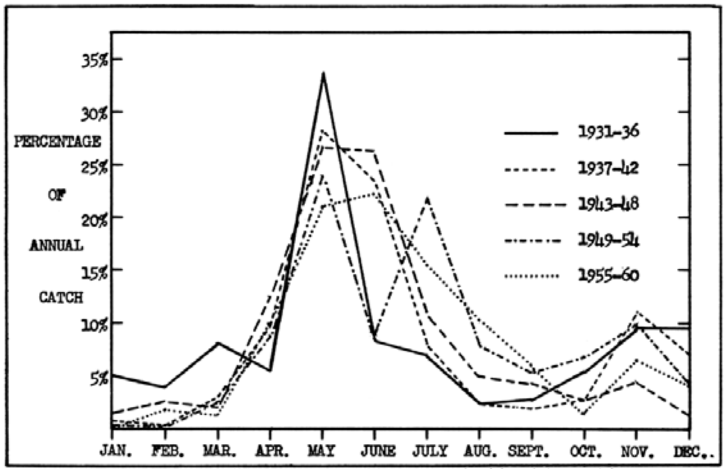


FIGURE 7. Average monthly catch as a percentage of the average annual catch for each six-year period.

FIGURE 7. Average monthly catch as a percentage of the average annual catch for each six-year period

In January, February, and March the catch has been low; normally each of these months produced less than 5 percent of the annual yield. In April, the squid appear in larger numbers and in this and the three ensuing months the great bulk of the year's catch has been taken (for example, 77 percent in 1943–48). The peak has been in May, but the average catch of this month has exceeded that of June only slightly. In August, September, October, and December few squid have been caught; in November they have been found in somewhat greater numbers. In some years, squid were taken in every month; in others none was found for periods of a month or more.

5. FEEDING BEHAVIOR

Because squid are very numerous, active predators which in turn serve as food for many other animals, an attempt was made to assess their place in the food webs of the sea. They were frequently brought alive from fishermen's nets to aquaria at Hopkins Marine Station, where their behavior could be closely observed.

On one occasion, about 200 "broken-back" shrimp (Spirontocaris sp.) were added to a tank (about 12 by 4 by 2 feet deep) in which about 40 L. opalescens had been shuttling back and forth for 3 days. Some of the squid immediately showed excitement: clouds of colour raced over their translucent mantles, the respiratory rate increased, the animal's movements quickened, and in each the sessile arms, hiding the tentacles, formed a sharp cone pointing directly at a swimming shrimp. A squid would make two or three short darts toward and from the prey, coming closer with each approach until, on the last, the tentacles shot out to seize the shrimp and the arms opened for its reception.

The shrimp was immediately held to the mouth and eaten in several bites; some rejected parts appeared laterally between the bases of the arms and were dropped; the arms were individually active but retained the general cone-like arrangement. While eating, a squid would continue to catch more shrimps, and now only the tips of the arms opened to receive each new morsel captured by the darting tentacles. No evidence of poison secretion by the posterior salivary glands was seen; the shrimps enclosed in the arms remained active and in some cases clambered out between them, only to be recaptured by an arm momentarily disengaged from the cone of arms for that purpose.

Thus swimming, finding and catching the prey, holding it in reserve, recapturing escapees, manipulating the prey while eating, and selecting or rejecting portions of the food all occurred together but without mutual interference.

The capacity for such complex behavior, combined with the formidable armament of sucker-bearing arms, powerful jaws and nerve-paralyzing cephalotoxin (Ghiretti, 1959), permit this squid to prey upon animals which might be considered too well armored or too large for attack. When the pistol shrimp, Crago sp., with its heavy exoskeleton was offered as food it was entirely eaten except for the hinge of the heavier chela, which was trimmed to the joint from each side and discarded. A dead sardine, almost as large as the squid in the aquarium tank (and suspended horizontally in the water by string) was seized by a squid, which bit a deep wedge-shaped piece from behind the head, thus removing a section of the spinal cord. The squid did not continue its meal, however, possibly because the sardine had been dead for some hours. Live rockfish (Sebastodes sp.) 2 inches long apparently were ignored when placed in a tank with several squid but stayed cautiously in the corners and in indentations along the sides of the tank.

Squid in aquaria often attack one another. Occasionally, the victim is found dead with a large beak-sculptured hole carved through the ventral mantle wall; in cases where an animal has unaccountably disappeared, its entire consumption by other members of the school has been considered likely.

I have not seen L. opalescens feeding in daylight in natural surroundings, but I have seen them many times beneath wharf lights at night, darting like arrows across the illuminated area and seizing small fishes which were carried off into the darkness.

Methods used by squids for capturing food have been described by several authors. Verrill (1882) recounts observations by Smith and Harger at Provincetown, Massachusetts, of the squid Illex illecebrosus [= Ommastrephes illecebrosus, Verrill 1872] which were feeding among the wharves on young mackerel about 4 or 5 inches long. A squid would become colourless and dart backward among the fish, suddenly turning obliquely to seize one. This would be killed by a bite downward behind the head, removing a triangular piece of flesh and severing the spinal cord. If unsuccessful after several attempts, some of the predators would drop to the bottom, and, matching their colour to that of the sand, would await return of the fish to within close range. Williams (1909) describes a slow zig-zag approach, with a quick turn and dart to reach the prey. The sessile arms are opened widely and the tentacles are suddenly extended forward to seize the fish which is quickly drawn to the mouth and enclosed by the arms. He also speaks of a squid dropping to the bottom and lying in wait, holding to the gravel by means of suckers, until a fish comes into range.

Many writers (Verrill, 1882; Bartsch, 1931; Klingel, 1942; etc.) have described the organized slaughter which occurs when a school of squid attacks a school of fish, and Lane (1957) recounts that a squid attacks a relatively large fish by seizing it from below and cutting into its belly by means of the beak.

Bidder (1950) gives the best description of how a squid eats a fish. When it has been caught and killed, in the manner described above, the head is bitten off and discarded. Then ensheathed by the squid's arms and with tail protruding beyond their tips, the body of the fish is bitten into large angular pieces which are swallowed, apparently without radular action, except that of thrusting the food into the esophagus. The digestive tract of the prey hangs downward as the trunk is being eaten; it is discarded when the rectum is reached and bitten through. The fleshy portion of the tail is stripped of meat and then the posterior fused vertebrae and tail fin are dropped. The meal may take 15 to 20 minutes or more; at its end the stomach of the squid may have expanded to one-third of the mantle length and half its width.

Other feeding methods have been described for other cephalopods. Octopods are bottom-feeding forms, eating littoral crustacea, pelecypods, or gastropods (Isgrove, 1909; Phillips, 1933; MacGinitie, 1938; MacGinitie and MacGinitie, 1949; Lane, 1957). Cuttlefishes may actively stalk the crustacea and fishes which they eat, or lie partly buried awaiting their approach (Tompsett, 1939; Wilson, 1946); Tinbergen (1951) relates Verway's observation of how Sepia officinalis blows jets of water against the sand until buried shrimps reveal their presence and are seized; Wickstead (1956) describes a camouflaged cuttlefish which gently waved its conspicuous white tentacle tips and then attacked the fishes which approached them.

How many of these methods may be used by L. opalescens is not known, but stomach contents suggest this animal feeds chiefly upon actively-swimming organisms and, less frequently, browses upon bottom-living forms.

6. FOOD: KINDS AND QUANTITY

6.1. Stomach Contents

Two series of stomach contents were examined in order to discover the types of food eaten. One series consisted of 83 stomachs from male animals in samples collected from fishermen's catches at Monterey between September 1946 and May 1948. Male squid only were used because in spawning schools their digestive tracts are maintained in potentially active condition, (i.e. the caecum, filled with amber fluid secreted by the digestive glands, extends to the posterior end of the coelom), and the presence of food in their stomachs is not unusual. In contrast, female squid almost always have empty, contracted caeca and empty stomachs. Mantle lengths ranged from 120 to 195 mm; 16 percent were between 135 and 165 mm, 4 percent were smaller and 80 percent were larger.

It was felt, however, that these squid would not show the typical diet because these chiefly large, mature animals, about to spawn, were not representative of the actively feeding, growing members of the general population. Physiological changes with unknown ramifications had directed them from their normal habitat toward the spawning area where, if hunger continued to recur in normal fashion, there would be more chance for cannibalism and less likelihood of finding typical foods in usual proportions.

A second series of stomachs was assembled, therefore, from squid samples collected from sardine, herring, anchovy, or mackerel catches in which squid were a very small minority. Twenty-two of these samples had been taken from July 1948 to November 1949 (representing every month except June and October 1949), five samples from May to September 1950, three in May 1951, and one each in July 1951 and July 1952.

A few full stomachs were sought from each sample for analysis of the food eaten. Squid were cut open and those stomachs, which upon external examination appeared to contain food, were saved; an unrecorded number that appeared empty were discarded. There was no apparent difference between the sexes here with regard to feeding, and full stomachs were taken as they were found, irrespective of sex. Where possible, animals were selected to represent the variety of sizes in each sample, giving a range for the series of 52 to 181 mm mantle length, but fewer than 10 percent were larger than 135 mm. From the 32 samples in this series, 63 stomachs containing food were collected.

A typical full stomach, removed from a male squid with a dorsal mantle length of 151 mm, was 29 mm long and 10 mm in its greatest width. It was filled with fish remains: flesh, bones, scales, skin, and much grease and oil. Many oil droplets were present in the caecum also. After the fluid had been squeezed out of the stomach, the remaining moist solid contents weighed 1.3 grams.

Each stomach of the two series was opened, and its contents placed in a Syracuse dish, covered with water, and examined in reflected and in transmitted light with a stereoscopic microscope. The contents of each stomach were identified and recorded (Tables 3 & 4)

Their food had been bitten into very small pieces before being swallowed. Crustacea were thoroughly dismembered: stalked compound eyes were almost always separate, bodies were in several bits and very rarely was any appendage complete. Other types of food had been treated in similar fashion.

Food in each stomach was commonly of a single type (e.g. consisting only of crustacea, squid, fish, or polycheate worms), but in a few cases, two or even three of these types were found together. In some cases, a stomach contained predominantly one type of crustacean mixed with varying proportions of other species. Four distinct types of stalked compound eyes were noted in one. I attempted to identify the crustaceans to the extent permitted by the fragmentary nature of the material. Euphausiids and mysids, in that order, seemed to provide the

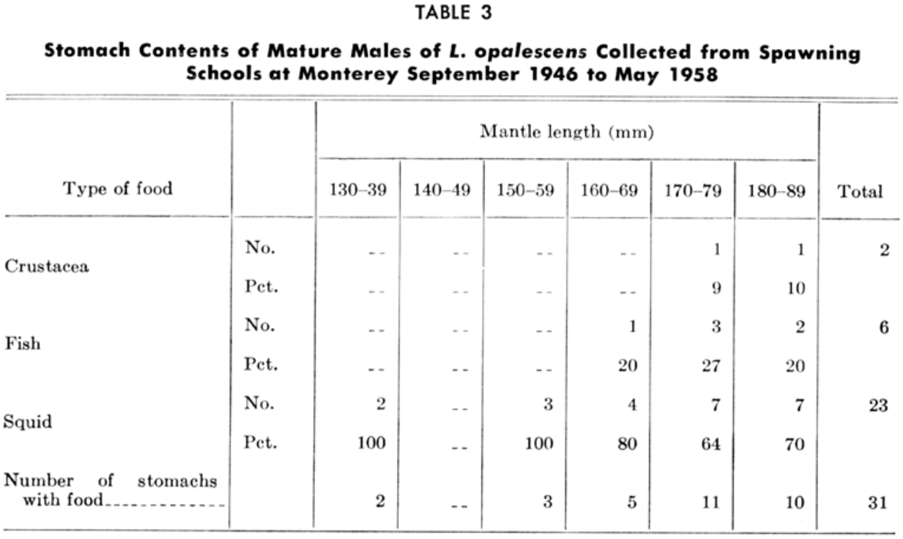


TABLE 3

Stomach Contents of Mature Males of *L. opalescens* Collected from Spawning Schools at Monterey September 1946 to May 1958

Type of food		Mantle length (mm)						Total
		130–39	140–49	150–59	160–69	170–79	180–89	
Crustacea	No.	--	--	--	--	1	1	2
	Pct.	--	--	--	--	9	10	
Fish	No.	--	--	--	1	3	2	6
	Pct.	--	--	--	20	27	20	
Squid	No.	2	--	3	4	7	7	23
	Pct.	100	--	100	80	64	70	
Number of stomachs with food		2	--	3	5	11	10	31

TABLE 3

Stomach Contents of Mature Males of L. opalescens Collected from Spawning Schools at Monterey September 1946 to May 1958

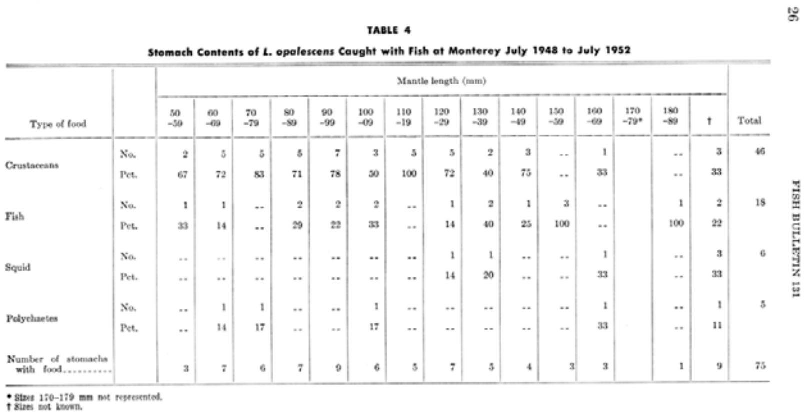


TABLE 4

Stomach Contents of *L. opalescens* Caught with Fish at Monterey July 1948 to July 1952

Type of food		Mantle length (mm)															Total
		50 -59	60 -69	70 -79	80 -89	90 -99	100 -09	110 -19	120 -29	130 -39	140 -49	150 -59	160 -69	170 -79*	180 -89	†	
Crustaceans	No.	2	5	5	5	7	3	5	5	2	3	--	1		--	3	46
	Pct.	67	72	83	71	78	50	100	72	40	75	--	33		--	33	
Fish	No.	1	1	--	2	2	2	--	1	2	1	3	--		1	2	18
	Pct.	33	14	--	29	22	33	--	14	40	25	100	--		100	22	
Squid	No.	--	--	--	--	--	--	--	1	1	--	--	1		--	3	6
	Pct.	--	--	--	--	--	--	--	14	20	--	--	33		--	33	
Polychaetes	No.	--	1	1	--	--	1	--	--	--	--	--	1		--	1	5
	Pct.	--	14	17	--	--	17	--	--	--	--	--	33		--	11	
Number of stomachs with food..........		3	7	6	7	9	6	5	7	5	4	3	3		1	9	75

* Sizes 170–179 mm not represented.
† Sizes not known.

TABLE 4

Stomach Contents of L. opalescens Caught with Fish at Monterey July 1948 to July 1952

bulk of the crustaceans of the squid's diet; other crustaceans (amphipods, megalops larvae, etc.) were present less often and in much smaller proportions.

Fish remains included flesh, bones, scales, and skin, with much oil and grease. Usually the caecal fluid contained a profusion of oil droplets. In most cases, the prey had been of such size that the stomach contained only a fraction of it; less often, parts of several small fishes would be found in a single stomach. For example, one stomach was filled solidly with tiny fish vertebrae, sometimes 12 to 15 still joined, with ribs and flesh, and with remains of at least 50 fish eyes. The species represented were not identified.

Squid remains consisted of pieces of arms with attached suckers, skin with chromatophores, and bits of flesh, pen, crania, radulas, and even beaks. The sucker remains suggested that in a few cases the prey had been the bottom-living sepiolid squid Rossia pacifica Berry; cannibalism was much more common however. The presence of 45 small squid in the digestive tract of one mature female L. opalescens of 141 mm mantle length, showed that large squid of this species may accompany and feed upon schools of young in the manner described by Williams (1909) for L. pealii. Almost all stomachs otherwise empty contained amber, coagulated caecal fluid with star-like silvery flocculence, and in some cases stellate vertebrate pigment cells. often much the same condition was noted in stomachs containing the remains of fish only, or of squid only. In some cases, apparently the same flocculent figures continued throughout the muscular tissue of the stomach wall. These were thought to be artifacts, and the stomachs were regarded as empty unless solid remains were clearly recognizable.

The occurrence of sand grains in several stomachs greatly extended the potential list of animals which might be found as food of the squid. Sand accompanied masses of acicula and, in other cases, fleshy columns bearing jaws and denticles of nereid-type polychaete worms. The relative numbers of jaws and acicula in the latter cases show that the squid must have eaten only the anterior ends of several worms. This, and the presence of sand grains, suggests that these worms were not intercepted while swimming but were seized while in their burrows, and their exposed anterior ends eaten. Considerable sand accompanying remains of crustacea, fish, and squid suggests that these animals, too, may have been bottom inhabitants.

In spawning schools, 75 percent of the meals consisted of fellow squid, but where propinquity does not dictate this pattern, 75 percent of the non-squid meals were of fish and 25 percent of crustacea (Table 5). Squid caught in fish schools had included other squid in only 10 percent of their meals; crustaceans formed the greatest part (73 percent) of their diet, fish contributed to 30 percent of the meals, and polychaetes to 8 percent. Squid of all sizes eat crustaceans, fish, and annelid worms, but only those larger than 120 mm mantle length appear to be cannibals. Also, when this size has been exceeded, the frequency of fish meals appears to increase to 50 percent. Thus the proportion of

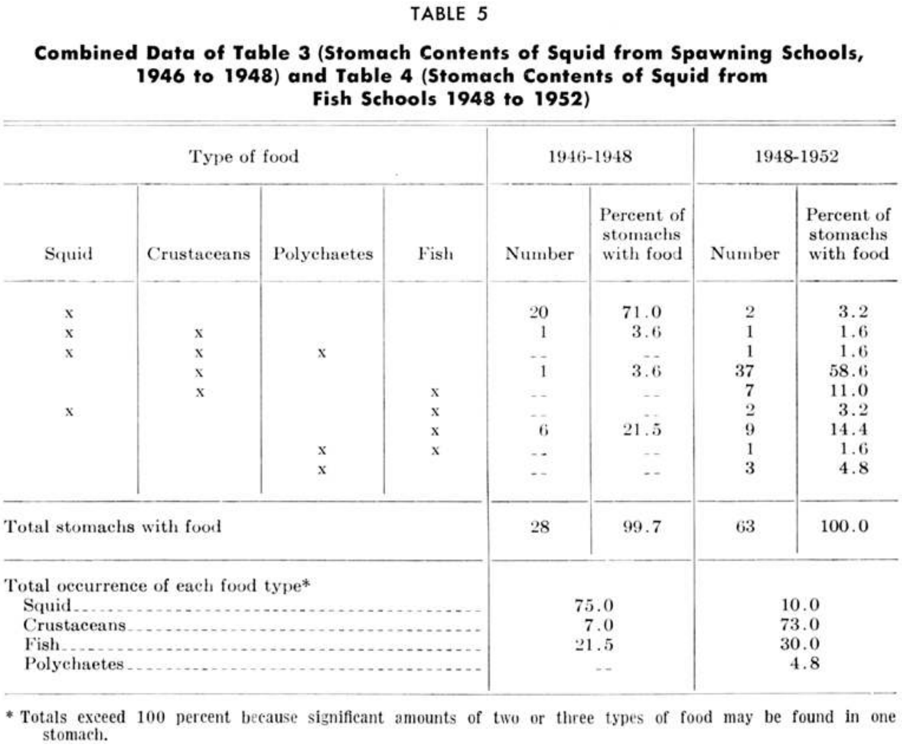


TABLE 5

Combined Data of Table 3 (Stomach Contents of Squid from Spawning Schools, 1946 to 1948) and Table 4 (Stomach Contents of Squid from Fish Schools 1948 to 1952)

Type of food				1946-1948		1948-1952	
Squid	Crustaceans	Polychaetes	Fish	Number	Percent of stomachs with food	Number	Percent of stomachs with food
x				20	71.0	2	3.2
x	x			1	3.6	1	1.6
x	x	x		--	--	1	1.6
	x			1	3.6	37	58.6
	x		x	--	--	7	11.0
x			x	--	--	2	3.2
			x	6	21.5	9	14.4
		x	x	--	--	1	1.6
		x		--	--	3	4.8
Total stomachs with food				28	99.7	63	100.0
Total occurrence of each food type*							
Squid				75.0		10.0	
Crustaceans				7.0		73.0	
Fish				21.5		30.0	
Polychaetes				--		4.8	

* Totals exceed 100 percent because significant amounts of two or three types of food may be found in one stomach.

TABLE 5

Combined Data of Table 3 (Stomach Contents of Squid from Spawning Schools, 1946 to 1948) and Table 4 (Stomach Contents of Squid from Fish Schools 1948 to 1952)

crustacean to fish meals is 3:1 in the diet of young L. opalescens, 1:1 in young-mature animals, and 1:3 in spawning squid, where a large increase in cannibalism occurs.

A very similar feeding pattern is described for the Newfoundland squid Illex illecebrosus (Le Sueur) by Squires (1957). He examined the contents of about 1,500 stomachs, and found fish (capelin, redfish, cod, haddock, small flounders), crustacea (euphausiids, amphipods, mysids, copepods, shrimp), squid, pteropods, whelks, polychaetes, and chaetognaths. In the smallest squid he examined (10 to 12 cm mantle length), euphausiids were the preponderant food, with fish being found in only 12 percent of the food-containing stomachs. In larger squid, the occurrence of crustacea declined to insignificance, but fishes increased in importance rapidly until they became the major component of the diet. This dietary change was concurrent with growth and with migration inshore from Grand Bank. Cannibalism occurred at all sizes; among the largest animals (25 to 27 cm and 28 to 30 cm mantle length) squid remains were found in 16.7 and 25 percent respectively of the food-containing stomachs. The presence in a few stomachs of remains of small flounders, gammarid amphipods, small gastropods, and polychaetes shows that this squid (I. illecebrosus) also occasionally browses upon the sea floor.

Other studies confirm that squids ordinarily eat fish, crustaceans, and young or adults of their fellow squids (Verrill, 1882; Williams, 1909; Bartsch, 1931; Stevenson, 1933; Bidder, 1950; Rao, 1954; Graham, 1955; Soeda, 1956; Squires, 1957; Katoh, 1959). To this list Williams (1909) adds, "pieces of eelgrass (which do not become digested)"; and Yonge (1954), for cephalopods in general, adds, "lamellibranchia," and "may feed on eggs of their own species." Yonge's additions probably apply only to octopods and cuttlefish, and I have no knowledge of eelgrass, bivalve mollusks, or squid eggs forming any part of the diet of L. opalescens.

6.2. Food Consumption

I did not make any studies of the quantity of food consumed. However, some inferences may be drawn, based on general observations and on the work of others.

Squid such as L. opalescens are active, pelagic predators which in captivity swim continuously forward or backward, slowly or with great swiftness, according to the direction and force of the water puffed from the mantle cavity through the funnel. They are greatly specialized with a high metabolic rate and oxygen requirement (Redfield and Goodkind, 1929), and consequently, they need much food to provide the requisite energy. Thorson (1956) states that food consumption by invertebrate predators of the epifauna is four times as high per day and weight unit as that by bottom-dwelling predatory fishes, which consume each day an amount of food equal to five percent of their own weight. That of pelagic forms, such as squids, would be at least as high, and it may be presumed that the average food consumption per day exceeds 20 percent of each squid's weight. Bidder (1950) describes the speed and efficiency with which digestion takes place in Loligo; it is completed in 4 to 6 hours at a rate 10 times as great as that reported by Dawes (1930) for a flatfish. Bidder determined that healthy captive squid will eat once or twice a day, and that they may do so more often when at liberty but do not feed continuously.

Thus L. opalescens probably eats two or more meals each day, foraging from the sea surface to its floor, and any available animals of appropriate size may be its prey. Pelagic crustaceans and fellow squid are important components of its diet; it feeds with, and probably upon, sardines (Sardinops caeruleus) , herring (Clupea pallasi) , mackerel (Scomber diego) , sauries (Cololabis saira) , and anchovies (Engraulis mordax) , and is often found in small numbers with the commercial catches in which these fishes are taken.

7. OTHER FOOD RELATIONSHIPS

Gray (1959) comments that it is unrealistic to study the population of one member of a food chain without reference to those of all the others; having considered the animals from which squid draw their food, this report should also survey those which depend upon squid for some or all of their food.

7.1. Predators

I did not make specific studies of predation on the squid, but a survey of pertinent literature indicates the great importance of squid as intermediates in many food chains. References are not all directly to L. opalescens, but where the predators named are found within this squid's range, it seems likely that they make it a part of their diet.

Squid, as mentioned above, take a considerable toll of their own kind through cannibalism, but fishes are the animals with the greatest potentiality for predation on them. Fishes are present in great numbers (species and individuals) and have an opportunity for continuous contact with squid schools. Clemens and Wilby (1946) state that spiny dogfish (Squalus acanthias) , king salmon, Pacific lancetfish (Alepisaurus richardsoni) , hake (Merluccius productus) , white seabass (Cynoscion nobilis) , Pacific mackerel (Scomber diego) , Pacific bonito (Sarda chiliensis) , albacore (Thunnus alalunga) , lingcod (Ophiodon elongatus) , and halibut (Hippoglossus stenolepis) use squid as food. As qualifying for addition to such a list, the silver salmon (Oncorhynchus kisutch) is named by Pritchard and Tester (1944), the steelhead rainbow trout (Salmo gairdneri gairdneri) by Taylor and LeBrasseure (1957), the bigeye tuna (Thunnus obesus) and yellowfin tuna (Thunnus albacares) by Blunt (1960), the bluefin tuna (Thunnus thynnus) and the swordfish (Xiphias gladius) by Walford (1937), and the billfishes (family Istiophoridae) of the Pacific by Royce (1957). Many ratfishes (Hydrolagus colliei) feed on squid in the spawning areas near Victoria, British Columbia. The extensive use of squid as a bait in commercial and sport fishing also shows its acceptability as a food by these and many other fishes.

The toothed whales and porpoises feed upon squid, as has been described by Robbins et al. (1938) for the sperm whale (Physeter catodon) , by Walford (1958) for the bottlenose whale (Hyperoodon rostrata) , by Scheffer (1953) and Wilke and Nicholson (1958) for porpoises, and by Squires (1957) for the pilot whale (Globicephala scammoni) . In the stomach of a striped dolphin (Lagenorhynchus obliquidens) taken off East Benito Island, Baja California, were remains of more than 20 L. opalescens or a very similar squid (submitted for examination by Lloyd Tevis, Jr.).

Squid are named as a food of sea lions (Eumetopias and Zalophus) by Pike (1958), and of fur seals (Callorhinus alascanus) and harbor seals (Phoca vitulina) by Scheffer (1950, 1958).

Sea birds of several kinds have been observed feeding on squid when the latter are accessible due to their debility following spawning, and at these times great flocks congregate near the spawning grounds. Invertebrate scavengers must also share in the feast as dying squid drift to the sea floor.

7.2. Parasites

A few parasites find harbor and nourishment within L. opalescens, but the frequency of infestation is low. Occasionally plerocercoid larvae of tetraphyllidean cestodes are found in the caecum or elsewhere, and move about very actively if disturbed or if transferred to sea water. Riser (1949) mentions two types, both found in L. opalescens at Monterey, and in the jumbo squid, Dosidicus gigas (d'Orbigny), at Corona del Mar, California, and both, ". . . with leaf-like phyllidia which bear anterior acetabulae, and with an apical sucker. These larvae have a parenchymatous caudal appendage ... behind the zone of growth . . . Some from Loligo were small and slender, while a large robust plerocercoid fitting the description of Pelichnibothrium speciosum Monticelli

1889 was found in Dosidicus, Loligo, and Alepisaurus. " Riser (1956) notes that, "Pelichnibothrium caudatum Zschokke and Heitz, 1914 ... were very similar to Phyllobothrium sp. (Fig. 556) of Joyeux and Baer (1936) . . . (Similar larvae were present in the cecum of the cephalopods Dosidicus gigas (d'Orbigny) . . . and Loligo opalescens ..." In L. opalescens, other active plerocercoids have been found which have a body form and caudal appendage similar to those described above, but the bothridia in living specimens appear to lack the anterior acetabula and are instead biloculate, with the margin and septum of each bothridium smooth, of uniform breadth, and completely without folds. The bothridia closely resemble some figured by Joyeux and Baer (1936, Fig. 569B) except that the inner four loculi are somewhat smaller in diameter than the outer four.

Occasionally plerocercoids closely resembling some illustrated by Joyeux and Baer (1936, Fig. 559) and Wardle and McLeod (1952, Fig. 105) are found encapsulated in the muscular wall of the stomach or esophagus. These also are ascribed to Phyllobothrium sp. by Riser (pers. commun.).

Phyllobothrium sp. lives in Loligo loligo at Arcachon, France, and in Todaropsis eblanae at Concarneau, France; P. dohrni occurs in Todarodes [Ommatostrephes] sagittatus at Naples (Dollfus, 1936). Stevenson (1933) found P. loliginis in the digestive tracts of L. pealii at St. Andrews, New Brunswick; Linton (1922) believed the adult of this cestode to be P. tumidum which is found in some sharks. Squires (1957) found in Illex illecebrosus the tapeworms Dinobothrium (*sensu lato*) sp. as plerocercoids in the digestive system walls and Phyllobothrium sp. as plerocercoids moving freely between stomach, caecum, and rectum.

Any consideration of other hosts of these cestode parasites of L. opalescens can only be speculation, but what was apparently a larval cestode was observed in a crustacean appendage in one of the squid stomachs examined; Marshall and Orr (1955) state that, "a few hundred" tetraphyllid larvae may be present in a single copepod. Adults of Phyllobothrium spp. are found in many selachians (Dollfus, 1936; Riser, 1949). Wardle (1932) found larval stages in all species of the salmon, Oncorhynchus spp., and noted that the adult form was found by Canavan (1928) in O. keta; Yamaguti, 1934 (*fide* Wardle and McLeod, 1952) moved these forms into the genus Pelichnibothrium Monticelli 1889, the description of which lists, "Adults in selachians. Larva tailed, in teleostean fishes and cephalopod molluscs," but the appropriateness of this has been questioned (Riser, 1956). No adult Phyllobothrium spp. are listed for birds, cetaceans, or pinnipeds by Joyeux and Baer (1936), and Margolis (1956) found them absent from the Stellar sea lion (Eumetopias jubata) and the harbor seal of the Canadian Pacific coast.

Solitary nematode worms have been seen in L. opalescens on a few occasions.

Mesozoans have been found in some cephalopods on this coast, but there is no certain record of their presence in L. opalescens. McConnaughey (1949) reported their absence from all of the squid of this species that he had examined, but stated that, "A very few dicyemids were present on some smear preparations kindly sent to the author by Mr. N. Riser of the Hopkins Marine Station, made from a specimen of Loligo opalescens taken in Monterey Bay in September, 1947. . . . This is the first record of infection of squid from the Pacific coast by mesozoa." However, there is a possibility that the smears actually involved Octopus instead of Loligo. At any rate, I have repeatedly examined the kidneys of L. opalescens specifically for mesozoans with negative results.

8. ANATOMY OF REPRODUCTIVE STRUCTURES

Although the life cycle of any animal begins with the zygote, this beginning is seen in better perspective if the reproductive systems and behavior of the parents, through which the gametes have their origins and their union, are first considered. This is particularly true of the

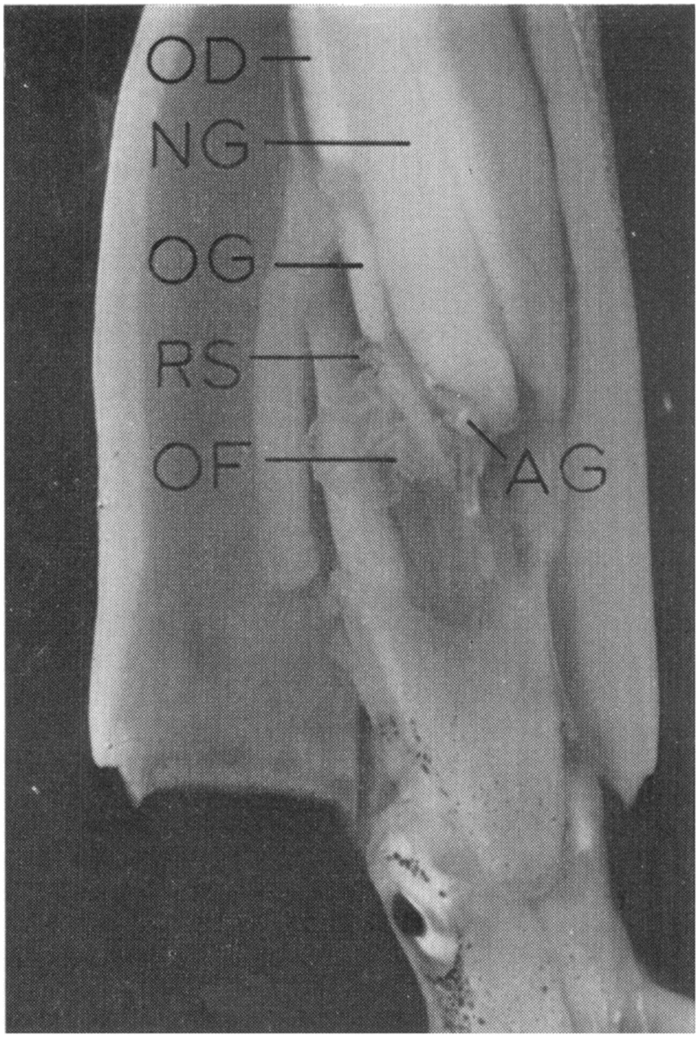


FIGURE 8. Mantle cavity of female squid showing nidamental gland (NG), accessory nidamental gland (AG), oviducal gland (OD), external glandular oviduct (OG), and expanded lace-like oviducal funnel (OF). Photograph for the author by DeBoyd L. Smith.

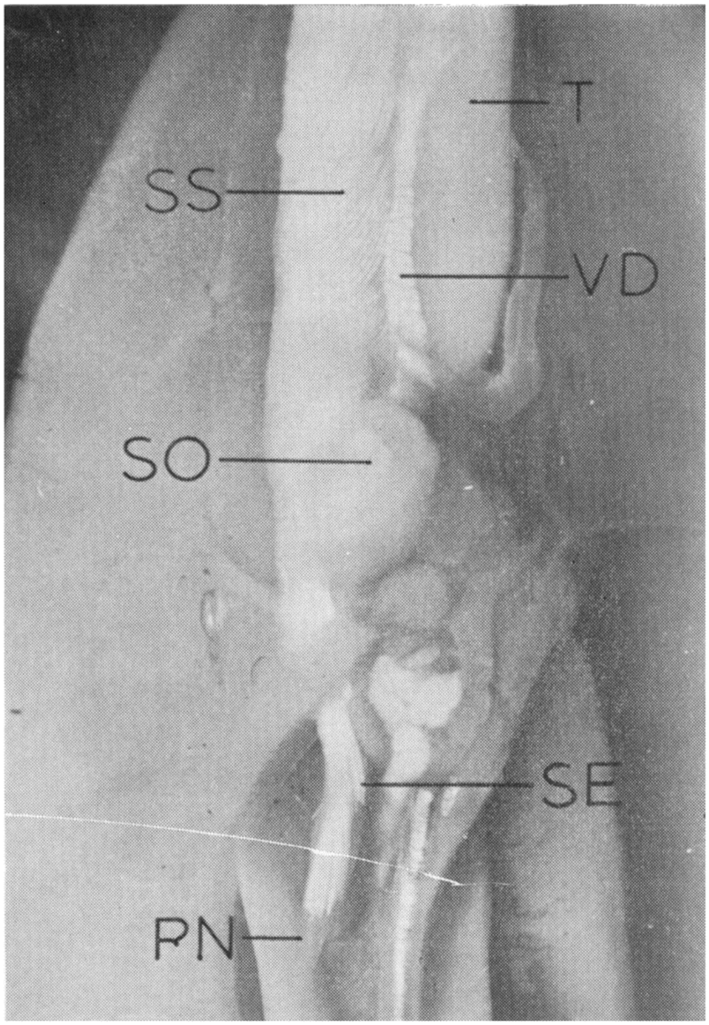
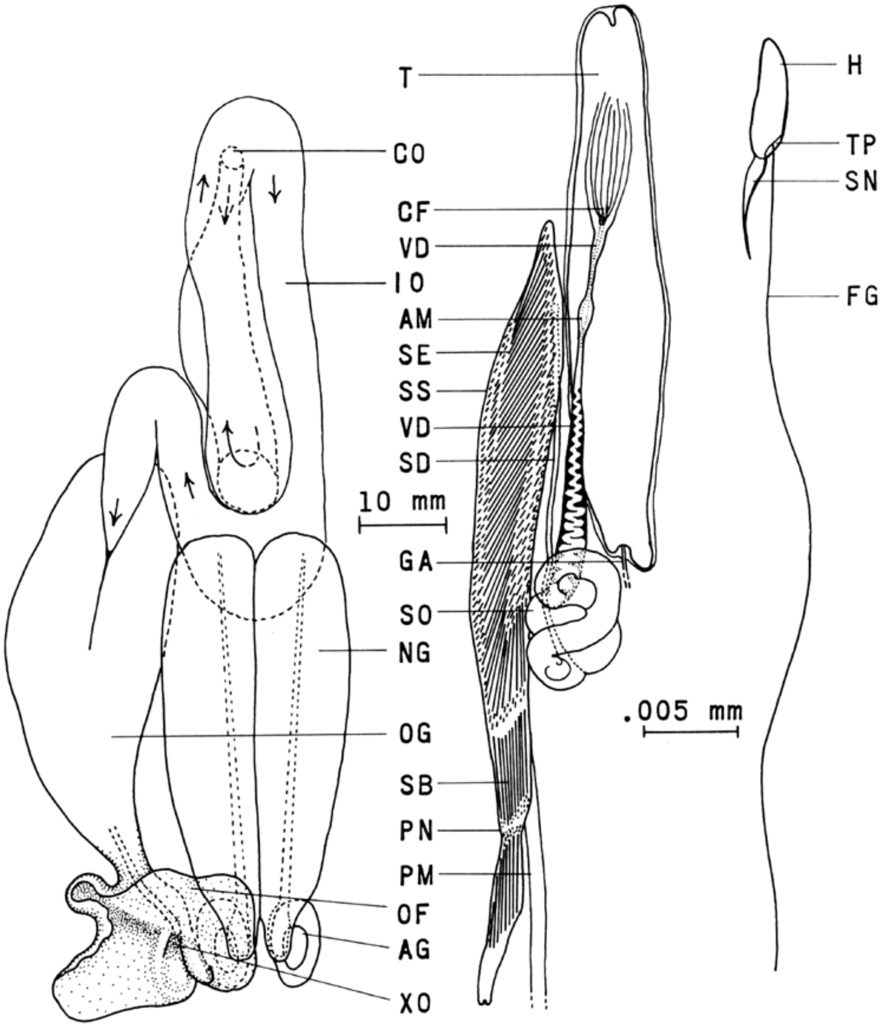


FIGURE 9. Mantle cavity of male squid showing testis (T), vas deferens (VD), spermatophoric organ (SO), and spermatophores (SE) in spermatophoric sac (SS) and penis (PN). Photograph for the author by DeBoyd L. Smith.

squid, in which complex structures and elaborate behavior are involved. Here eggs are fertilized before the egg capsule is deposited, although neither the penis nor the oviduct can be extended beyond the mantle cavity. Internal fertilization is effected by the male's use of its hectocotylized left ventral arm to transfer sperm packets or spermatophores from its penis to the mantle cavity of the female beside the mouth of the oviduct.

In L. opalescens the visceral mass, of which the reproductive system is a part, lies along the upper wall of the mantle cavity; the gills and the oviduct (penis in males) are suspended in this cavity by mesenteries. In general plan, the reproductive system consists of a long gonad, lying in the coelomic space behind the pericardial cavity and supplied by the genital aorta from the systemic heart, and a duct on the left side providing egress for the gametes (Figures 8 and 9).



FIGURES 10–12 (left to right). 10) Female reproductive system; 11) male reproductive system; 12) a sperm.

FIGURES 10-12 (left to right). 10) Female reproductive system; 11) male reproductive system; 12) a sperm

8.1. Female Reproductive System

The female reproductive system consists of the ovary, a single oviduct, the paired nidamental and accessory nidamental glands, and the sperm receptacle (Figures 8 and 10).

The ovary arises from the upper wall of the coelomic space behind the precardial cavity. Buds grow downward, branch and re-branch, and at the tip of each twig an ovum is formed within a mass of follicle cells. While developing, each ovum is translucent and its surface is greatly folded, with blood vessels lying in the channels upon its surface; when mature, it is transparent and has a glass-smooth surface within its chorion of follicular origin.

When the chorion separates from its ovarian twig, the ovum is carried through a ciliated opening into the membranous internal portion of the single oviduct. This is a broad, thin-walled tube which runs forward, backward, and then forward again in the posterior two-fifths of the visceral mass, and the mature ova are stored in it until spawning. This tube narrows abruptly where it enters one side of the heart-shaped oviducal gland; this and the remainder of the external oviduct to its ostium are heavy and glandular.

Anteriorly, the glandular portion opens into an oval spoon-shaped depression, which has a shallowly convex structure hinged to the proximal portion of its medial margin. The latter could act like a close-fitting lid which would become more firmly seated when pressure increases in the mantle cavity; anything the oviduct extrudes between the lips of these firm, curved structures would tend to be wound spirally, as is the egg-enfolding mucilaginous core of the egg capsule. The outer margins of the lips are continuous with a thin membrane which expands broadly to form a thin-walled funnel; lateral to the oviduct's mouth this encloses a pouch with a hooded lateral opening. In spawning females, this funnel is often intricately folded about the juxtaposed openings of the nidamental and accessory nidamental glands, and within it during spawning, the jelly coats are added while the egg capsule is being formed.

The soft, white nidamental glands lie in front of the membranous internal oviduct, ventral to the middle one-third of the visceral mass. Each is about one-quarter as wide as long, is rounded posteriorly and laterally, and is flattened medially where the two are in contact. Each narrows anteriorly and ends in a spoon-shaped protrusion into which the gland's lumen opens.

Apposed to these openings are those of the boat-shaped accessory nidamental glands which lie beside the intestine. Each consists of scores of flask-shaped vesicles; the apertures at the narrow ends of these face the oval, shallow crater of the gland's lumen. Ordinarily whitish, the vesicles independently become yellow, orange, then red as the time of spawning approaches; the whole range of colors may be present together.

The openings of the oviduct, and of these four glands, lie just behind the funnel.

The sperm receptacle lies in the buccal membrane below the mouth. It is a rounded protrusion with a central opening, and invariably is distended with inactive spermatozoa when the squid come to the spawning grounds. In L. pealii, Drew (1911) found sperm reservoirs from spermatophores lodged nearby, and narrow streams of apparently inactive spermatozoa being transported into the receptacle.

Female reproductive systems of several myopsid squids are described by Doring (1908) and Williams (1909); these differ in varying degrees from the proportions found in L. opalescens.

8.2. Male Reproductive System

The male reproductive system consists of the testis, a vas deferens, a spermatophoric organ, duct and sac, and a penis. Except for the median testis, these parts lie on the left side (Figures 9 and 11).

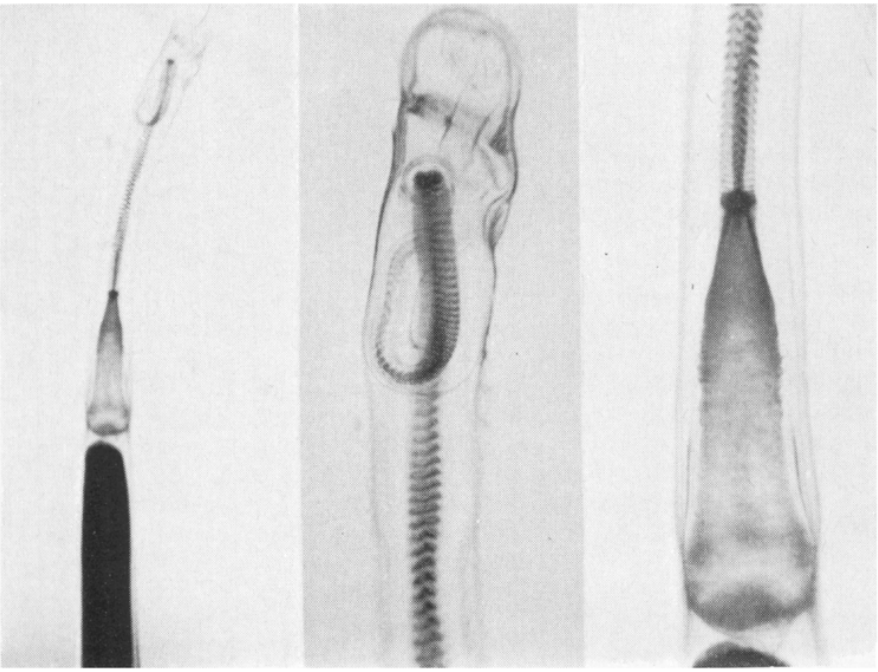
The testis is a long, flattened, white organ enclosed and supported by a medial mesenteric fold from the upper wall of the coelomic space behind the heart. Its longitudinal lumen opens into the surrounding capsule from which, posteriorly, a ciliated funnel draws sperm into the vas deferens. This tube bears an enlargement, the ampulla, then narrows and becomes gradually more folded until it enters the ovoid spermatophoric organ in which the spermatophores are formed (Drew, 1919). Each emerges thread end foremost, and passes along the spermmatophoric duct to enter the spermatophoric sac one spermatophore's length from its posterior end. Thrust into this end, it displaces its predecessor, which is pushed forward and laterally parallel to the many spermatophores already stored obliquely in the sac. This thin-walled storage region is continuous with the muscular penis, which is capable of extension through the funnel to its outer opening, where it delivers bundles of spermatophores to the hectocotylized arm during copulation.

Marchand (1907) made a comparative study of the male reproductive systems of several dibranchiate cephalopods; Williams (1909) describes that of L. pealii, which L. opalescens closely resembles.

8.3. Spermatozoa

Spermatozoa are .05 mm long and rather bizarre in shape (Figure 12). The head, about .0065 by .0018 mm, is somewhat ovoid, with the anterior end bent slightly to one side and more pointed than the posterior. The tail is six times as long as the head. It appears to arise subterminally from the center of an oval thickening which is set obliquely upon the posterior part of the head's more curved side. Beside this plate and apparently continuous with its margin, a curved spine, as long as the head, extends backward from the posterior end of the latter. The shape of this at its base is difficult to determine, but it appears to be either flattened or trough-shaped with its concavity toward the tail plate; wide through the proximal one-third of its length, it narrows swiftly and then tapers to a long, sharp point; in its length it twists spirally through about 180 degrees. Near its tip, this spine may lie close to the flagellum or stand at a considerable angle from it. This is the appearance, under phase-contrast, of the typical, active spermatozoa that are released from a spermatophore.

The parts separate in a few cases. Heads alone lie immobile, as do most head-tail-only combinations; in a few cases the latter, apparently without the spine, have been observed swimming. Combinations of spine-and-tail-only appear to be just as active as whole sperm. In these, the sharp angle between the parts remained; the spine was never seen to turn so that its point was directed forward, which would give much the same shape that Thesing (1903) has shown for cephalopod spermatozoa, with heads approximately the shape of the spine in L. opalescens.



FIGURES 13–15 (left to right). 13) Internal ejaculatory apparatus of spermatophore (thread is not visible); 14) oral end of spermatophore showing looping of ejaculatory apparatus; 15) aboral region of ejaculatory apparatus showing tunics, membranes, spiral filament, cement body, and connecting cylinder to sperm mass. *Photographs for the author by DeBoyd L. Smith.*

FIGURES 13-15 (left to right). 13) Internal ejaculatory apparatus of spermatophore (thread is not visible); 14) oral end of spermatophore showing looping of ejaculatory apparatus; 15) aboral region of ejaculatory apparatus showing tunics, membranes, spiral filament, cement body, and connecting cylinder to sperm mass. Photographs for the author by DeBoyd L. Smith.

8.4. Spermatophores

Each spermatophore is a slender, slightly curved cylinder with rounded ends; the elaborate ejaculatory mechanism is housed in one end (Figures 13, 14, 15, 16).

A spermatophore's outer sheath consists of a thin inner tunic (IT), a hygroscopic, granular middle tunic (MT) and an elastic outer tunic (OT) which is continuous about one end, but is closed at the other end by being fused to the periphery of the thread-bearing terminal cap. In its final formative stage, the whole spermatophore shrinks, becoming turgid, and tension arises in the elastic outer tunic.

The bulk of the spermatophore is occupied by a cylindrical sperm mass (SM) containing a vast number of inactive spermatozoa laid down as a ribbon wound spirally (with one edge forming the core and the other edge the periphery) within a mucilaginous matrix. This is enclosed by the delicate inner membrane (IM). In the cap-bearing oral end of the spermatophore lies an intricate mechanism which, together with the action of the tunics, effects the release of the sperm mass and has been called the ejaculatory apparatus. Here is found a cylindrical sac, consisting of the outer membrane (OM) and the oral portion of the inner tunic, with its open end toward the oral end of the spermatophore and its closed end, containing a mass of cement (CB), joined by a connecting cylinder (CC) of inner tunic to the sperm mass. A middle membrane (MM), continuous at the cap (C) with the outer tunic, has a flared, open aboral end which encloses the oral end of the cement body. This part of the cement-body sac consists of the thin inner membrane only, which continues orally through the point of rupture (PR) to the cap end as a slender cylinder supported internally by fluid and by a spiral filament (SF). The space (SL) between inner and middle tunics also contains liquid. Because the ejaculatory apparatus is longer than its enclosing space, it lies in loops at its oral end (Figure 14).

Drew (1919) ascribes a supportive function to the spiral filament and speaks of its fragmentation during ejaculation. In L. opalescens the fragments are bristle-like and oriented transversely to the filament's length; in the intact spermatophore the spiral filament appears pleated with the folds interlocking in successive turns (Figure 15). This support of an eversible tube against external pressure by the interlocking of a spiral of internal bristles may be analogous to the arrangement in the threads of some coelenterate nematocysts.

The spermatophores produced by one animal are usually quite uniform in size but may vary by as much as 10 percent. Lengths are roughly proportional to the mantle length of the animal (Table 6), but in animals of the same size there are considerable differences.

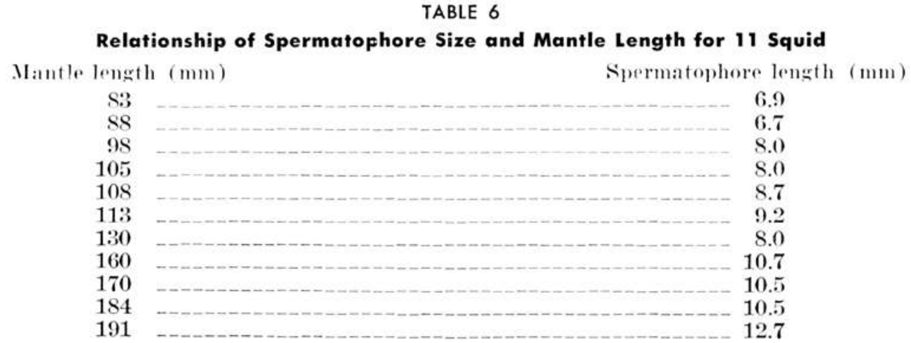


TABLE 6

Relationship of Spermatophore Size and Mantle Length for 11 Squid

Mantle length (mm)	Spermatophore length (mm)
83	6.9
88	6.7
98	8.0
105	8.0
108	8.7
113	9.2
130	8.0
160	10.7
170	10.5
184	10.5
191	12.7

TABLE 6

Relationship of Spermatophore Size and Mantle Length for 11 Squid

The proportion of the spermatophore occupied by the sperm mass varies irregularly from less than 60 percent to more than 75 percent in animals smaller than approximately 105 mm mantle length; in those larger than this, the proportion more consistently lies between 75 and 85 percent, with the larger squid tending to have relatively larger sperm masses.

Ejaculation of most spermatophores takes place if they are simply transferred into sea water, and pulling on the thread (CT) will set off the remainder. Both types of stimulation occur during mating; the cap is loosened and the middle tunic thickens quickly due to taking up sea water by osmosis. The swelling of this tunic and the elastic shrinking of the outer tunic supply the force which splits the cap and causes ejaculation. Thus, as the space in which they lie becomes constricted, the fluid and the sperm mass are squeezed swiftly toward the thread end of the spermatophore, broken open by the cap's removal. Mounting fluid pressure causes the double-walled tube of inner membrane and middle membrane to roll outward through itself so it becomes completely everted. This action draws the cement body and (by the connecting cylinder) the proximal end of the sperm mass through this tube toward its opening. At the same time, the outer membrane and the inner tunic are turned inside out, thereby enclosing the advancing sperm mass. As the cement body emerges, the inner membrane tears loose from it at the point of rupture. When that portion of the cement body covered only by the inner membrane has emerged, the spermatophore is as fully everted as the pressure of liquid within accomplishes alone.

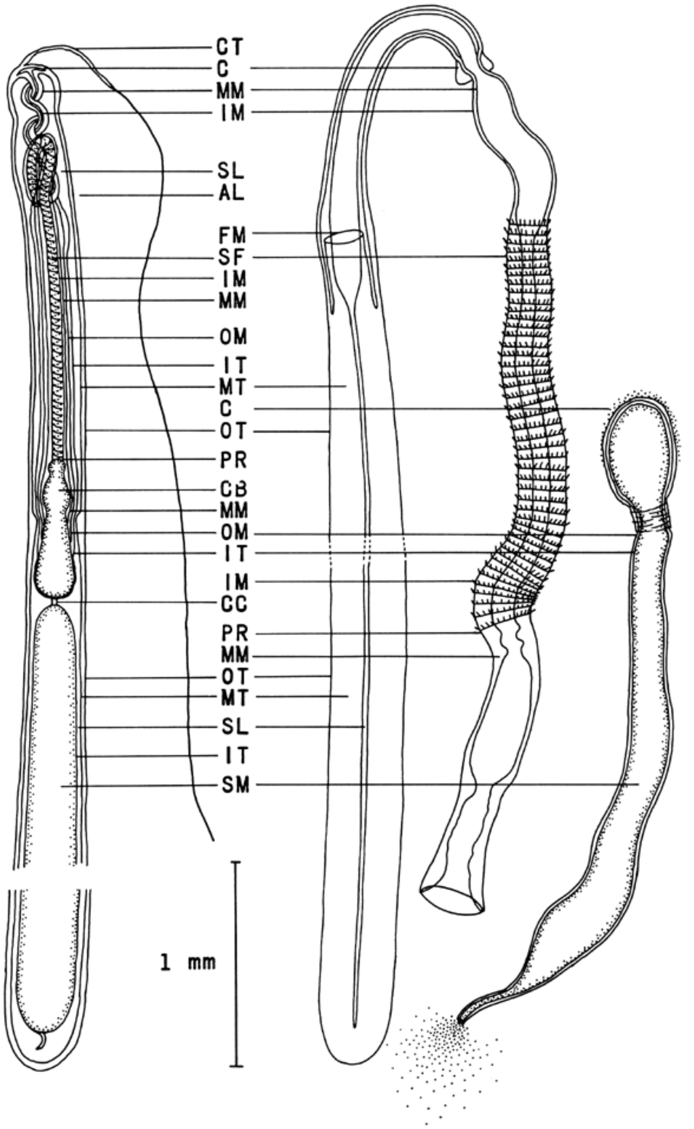
Drew (1919) notes that at this stage movement stops briefly until pressure behind the sperm mass (due to thickening of the middle tunic) becomes sufficient to burst the thin inner membrane covering that portion of the cement body already protruding. The head of the sperm mass then advances, everting the remainder of the cement sac about the sperm mass with the cement (CM) now upon the exterior. With this everting of the cement sac, the free margin of the middle membrane, which until this time has closely surrounded the cement body, everts also to become the terminal collar of the spermatophore husk. Through it the remainder of the sperm reservoir, consisting of the outer membrane and inner tunic, and containing the sperm mass, is thrust out swiftly. The leading end of the reservoir (the everted cement sac) becomes anchored firmly by means of the cement to any surface it touches; the male holds the spermatophore in such fashion that the site of attachment is usually on the oviduct or on the mantle nearby. When its open end emerges from the collar, the reservoir loses all connection with the spermatophore's husk which is carried away by the female's respiratory current (Figures 17 and 18).

The matrix in which the sperm are embedded takes up water, thereby actively releasing the sperm; water entering swiftly through the wall of this sac causes great turmoil within so that the reservoir appears almost peristaltic, and clouds of sperm are ejected from its small opening. In some cases, the force of ejaculation is so great that the first-emerged part of the reservoir bursts; in other cases, it apparently becomes so greatly stretched that sperm escape directly through its whole surface.

Spermatophores of L. opalescens in their structure and ejaculation closely resemble those of L. pealii as described by Drew (1919); his description of spermatophore formation, which was not studied here, is probably applicable to L. opalescens.

9. MATING BEHAVIOR

When transferred alive from fishermen's nets into suitable aquaria, groups of L. opalescens continue to mate and spawn. These activities usually occur sporadically during the daytime but much more intensively at night, and once engaged in mating the animals are not dissuaded even by brilliant illumination. In 1946, movies were taken for analyzing these processes (Figure 19); these have been studied and squid reproduction has been closely observed a great many times since then.



FIGURES 16–18 (left to right). 16) A spermatophore; 17) husk of spermatophore; 18) sperm reservoir.

FIGURES 16-18 (left to right). 16) A spermatophore; 17) husk of spermatophore; 18) sperm reservoir

Female squid seem to differ in their ability to attract males, for several males may single out one or two females from a group and mate several times with them, ignoring the other females present. Later, as mating activity increases, there is general participation, but again certain females are in greater demand than others. Tompsett (1939) notes that males of *Sepia* are attracted from great distances if a ripe

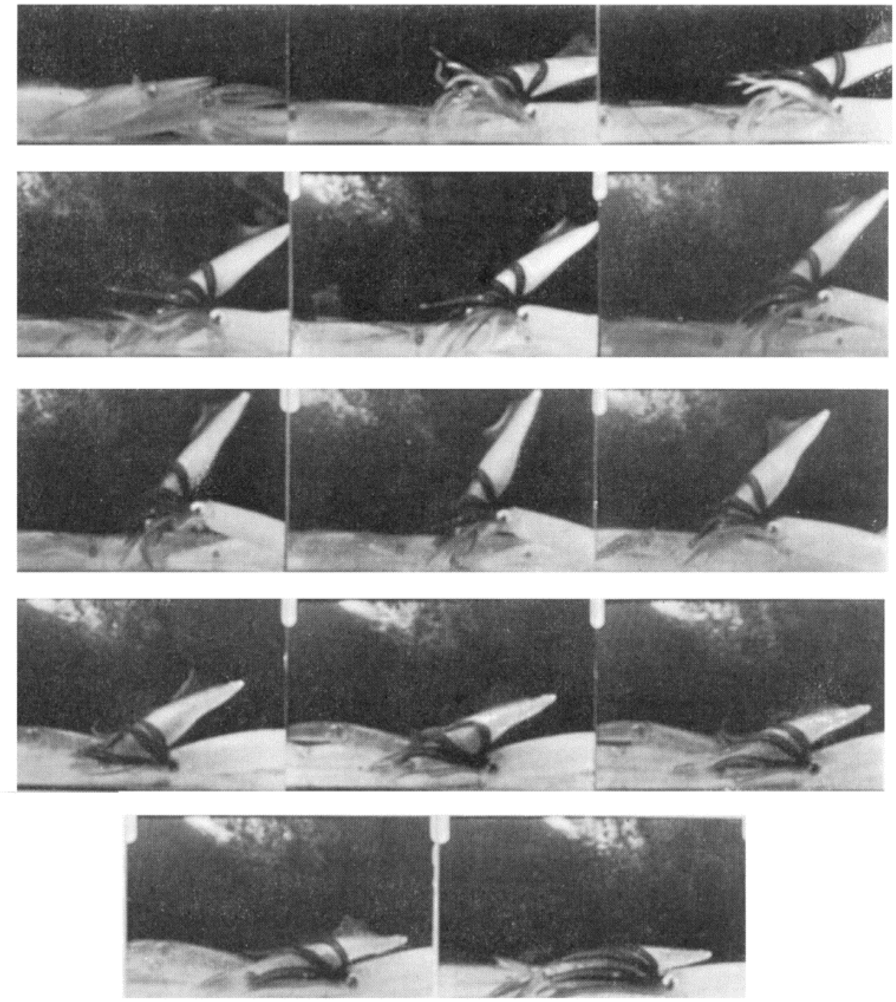


FIGURE 19. Mating behavior (left to right, top to bottom): a) female and male squid swim beside each other; b & c) male, with three pairs of arms darkened, has seized the female and has inserted his right ventral arm (not visible from this view) into her mantle cavity; d-f) left ventral arm of male moves downward and backward to funnel; g & h) hectocotylus curls about spermatophores and carries them forward for placing in mantle cavity of female; i) male holds spermatophores while sperm reservoirs become attached near oviduct of female; i-m) ventral arm being withdrawn while other arms of male "walk" backward along mantle of female; n) male holding female while they swim together prior to spawning. Photographs from a motion picture made for the author by Harold N. Arrowsmith, Jr.

female is attached to a fixed line and left in shallow water. These observations suggest that females ready to mate produce a diffusible material that attracts the males.

When a male Loligo becomes "excited," waves of expanding red chromatophores run over his head and arms; when he seizes the female these parts become dark maroon and remain that color until the female has been released. The male usually darts sideways to seize the female from below about the front half of her mantle, turning her so that her midventral line lies above the mid-dorsal line of his head. His arms on left and right sides are spread about their respective sides of her mantle, and extend forward and upward. She may reach ventrally with her arms to repulse him before this position is attained; in this case he usually swims about for a few minutes, begins to blush, and tries again.

If the female has been acquiescent, the male quickly shuffles his clasp farther forward about her mantle, at the same time thrusting his right ventral arm beside her funnel into her mantle cavity. After approximately 5 seconds, the left ventral arm of the male sweeps back to the opening of his funnel and the terminal portion—bearing special hectocotylized suckers—curls about a bundle of 20 to 40 spermatophores which appear at that instant. As the left arm bearing the spermatophores approaches the mantle edge of the female, the right arm is withdrawn from the mantle cavity and the left arm is inserted in its place. For 15 to 20 seconds the male holds the spermatophores close to the female's oviduct, while the sperm sacs are ejaculated and become anchored to the oviduct or more often to the adjacent part of the viscera or mantle.

The male then withdraws his arm and shuffles back into his original position so that the tips of his arms (except the short mid-dorsal pair) just reach the anterior edge of the female's mantle. Almost at the same time, the husks of the spermatophores are blown with the respiratory stream of water from the female's siphon.

The male may retain this hold for a considerable time, swimming with the female while eggs are laid, and further copulation may occur. Each may subsequently mate with other animals.

I do not know of any account of a cephalopod using its ventral arms in succession in this manner during mating. Robson, 1926 (*fide* Sasaki, 1929, p. 105), "... assumes that the function of the hectocotylized arm of Decapoda is not same with that of Octopoda, namely, is that of insemination, but rather that it serves for the purpose of tactile stimulation during coitus; he therefore suggests a new term "nuptial arm" for the arm in question in Decapoda." In L. opalescens the unmodified right ventral arm apparently serves this function and the hectocotylized left ventral arm transfers the spermatophores.

There is a considerable contrast between the normal pedicels and suckers of the right ventral arm and the tall, glandular pedicels with minute suckers in both rows of the hectocotylized region of the left ventral arm (Figure 20). Distally, pedicels and suckers of the medial row become more normal in their proportions, but much larger than those on the right arm, while in the lateral row, pedicels and suckers

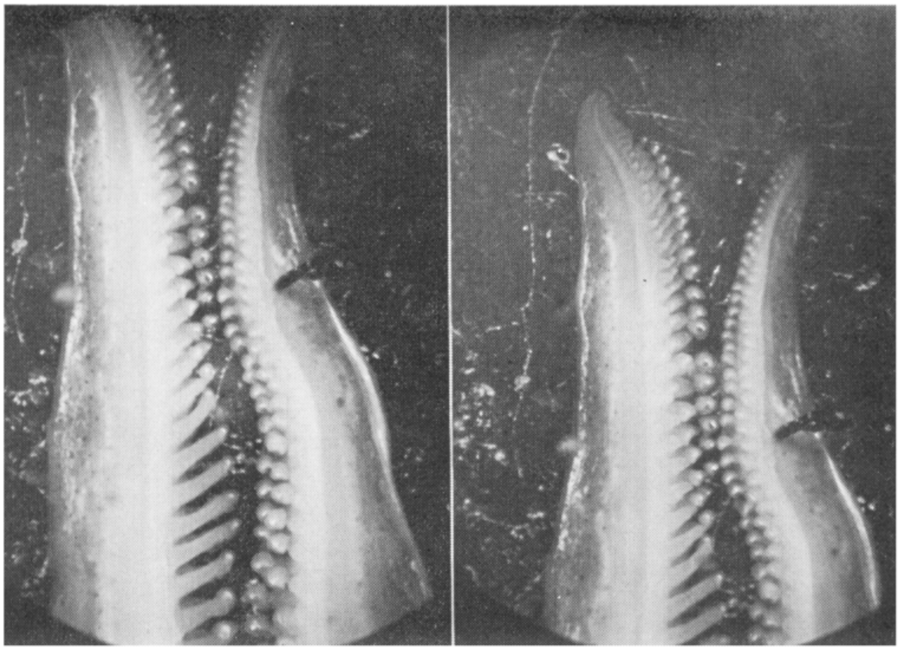


FIGURE 20. Ventral arms showing modified pedicels and suckers of the hectocotylized left arm.

FIGURE 20. Ventral arms showing modified pedicels and suckers of the hectocotylized left arm

become minute and terminally some suckers disappear. The left arm is heavier and broader distally than the right arm.

A second type of copulation is reported in the eastern squid Loligo peallii. In this, the animals meet head-on, and spermatophores are placed in the bursa copulatrix in the peristomial membrane of the female. A similar structure is found in Loligo opalescens, and dormant sperm are stored in it in spawning females, yet in scores of encounters I have observed, only once (between a small male and a large female) might there have been copulation of this type.

Drew (1911) states that in Loligo pealii, "Without exception every adult female that had not spawned had the sperm receptacle filled more or less completely with sperm, although in many cases the eggs were far from mature." Soeda (1950, 1956), in discussing Ommastrephes sloani pacificus shows that the female receives sperm in her seminal receptacles of the buccal membrane, "previous to her maturation." Planting the spermatophores in this manner, "takes place chiefly from Autumn to Winter, at the Tsugaru Straits ...," in northern Japan, whereas, "the spawning occurs generally in the west-southern seas of Japan." McGowan (1954) thinks it probable that this type of sperm transfer in L. opalescens occurs after a population which is ready to spawn moves from offshore into a relatively shallow area near shore. My own impression is that this procedure occurs considerably earlier, probably soon after the first few ova or spermatophores mature while the bulk of the gonad products are still unripe, and that spermatophore placement near the oviduct becomes the only pattern when the bulk of the eggs ripen, the nidamental glands expand,

and the sacs within the accessory nidamental glands become distended and bright yellow and orange in color. (Fox and Crane, 1942, found traces of carotenoids in accessory nidamental glands of this squid, but no record is given whether it was in spawning condition.) Drew (1911), who studied both methods of mating exhibited by L. pealii, found that wherever spermatophores were inserted in the mantle chamber the accessory nidamental glands were highly colored with bright red.

10. SPAWNING

10.1. Spawning Areas

The spawning grounds at the southern part of Monterey Bay, where most of this investigation has been done, have been described by divers familiar with the area and by Galliher (1932). The gently sloping sea floor is of muddy greenish sand, traces of which adhere to the anchor portions of dislodged egg masses. Eggs are laid in great numbers off the Monterey harbor mouth and breakwater, and wherever the substrate is suitable along the whole waterfront in the southern part of Monterey Bay.

L. opalescens is known to spawn in a number of other localities from British Columbia to southern California in depths of 10 to more than 115 feet, frequently in partly sheltered bays, where the sea floor is of mud or sand. Cadboro Bay, at the southeastern tip of Vancouver Island, where heavy spawning occurred in 1959 and 1960, is a sheltered bay with a muddy sand floor sloping gently to a depth of 50 feet. A squid spawning area of unknown extent was located off Santa Catalina Island at a depth of 70 feet when, on February 14, 1949, the research vessel *Orca* of the Sefton Foundation obtained about 350 pounds of squid eggs in two dredge hauls made about 1.5 miles southeast of Catalina Harbor. McGowan (1954) and Limbaugh and Shepard (1957) have recounted their direct observations and made movies of such areas off La Jolla, where spawning takes place each year on a sandy bottom chiefly about the rims of submarine canyons, with some on gentler slopes and shelves within the canyons themselves.

10.2. Spawning Season

Various types of evidence were useful in defining the squid's spawning season. The best evidence is the presence of egg masses; these show not only that spawning has taken place but, by the degree of embryo development, tell when it occurred. At Monterey, eggs were found at every time of the year when squid were available over the spawning grounds. In addition, the prevalence of eggs has been proportional to the number of squid present.

Another evidence is the readiness of the animals to spawn when they come to this vicinity. The commercial catch consists entirely of mature squid, most of them gravid. At every time of the year when live squid have been brought from fishermen's nets to aquaria at the Hopkins Marine Station, they have spawned there.

These evidences strongly suggest that the squid fishery is based entirely upon schools of spawning animals, and that the seasons of availability are, therefore, spawning times. The fishing records (Figure

6) and fishery observations indicate the season of most intense spawning at Monterey is April to July, followed by a minor peak in November. In some years, squid are present and spawn in every month, but in other years they may be absent for periods of 2 months or more.

If it could be shown that all of the squid arrive at Monterey solely to spawn, the validity and usefulness of catch records as indicators of spawning would be strengthened; samples were taken and observations made with regard to this point and will be described later.

Records of spawning times of L. opalescens in other areas are scanty. Nothing is known to me about spawning in the Gulf of California. Taylor (1949), aboard the *Orca*, collected squid eggs which had been laid in January off Catalina Harbor, and collected spawning squid off South Coronado Island. Bickford (1957) saw squid spawning in Avalon Harbor in February 1954. McGowan (1954) describes spawning during February and March 1953, at La Jolla. Garth (*fide* Lane, 1957) reports that L. opalescens was mating and that egg capsules were found in July 1951 at Emerald Cove, Santa Catalina Island. These records from southern California suggest a main spawning season there from January to March, with some spawning in summer.

After a reported absence from Puget Sound of about 10 years, immature L. opalescens were available at Friday Harbor, Washington, in August 1958. Mature squid were present in August 1959, and spawned in the University of Washington Biological Station aquaria. In late July and in August 1958, L. opalescens spawned in considerable numbers in bays around southern Vancouver Island. No spawning of comparable magnitude had been observed there for about 10 years. In August of 1959 and 1960, large numbers appeared in Cadboro Bay near Victoria, British Columbia, and by early September huge shoals of these animals filled the bay and squid egg-masses were reported by skindivers to carpet the entire floor of the bay from the low-tide line downward. Squid did not return in 1961.

Thus L. opalescens spawns mainly in winter in the southern portion of its range, and in the late summer in the northern portion. off central California, the patterns overlap, but the chief reproductive activity is in months other than the spawning times to the south and north.

10.3. The Process of Spawning

Squid brought to aquaria at the Hopkins Marine Station continued their spawning activities, which were studied closely and recorded (Figure 21).

Spawning may take place at any time, but occurs chiefly at night. While the first eggs are being laid, the male may continue his post-copulatory embrace, but he soon departs and the female swims alone while spawning most of her eggs. From 180 to 300 (estimated by counting the eggs in measured parts of egg capsules and then calculating total content) of these are laid at one time, enclosed in a flexible, jelly-like capsule. The eggs lie in a central transparent homogeneous matrix secreted by the oviducal gland; this is enclosed by firm outer translucent layers which apparently arise from the combined secretions

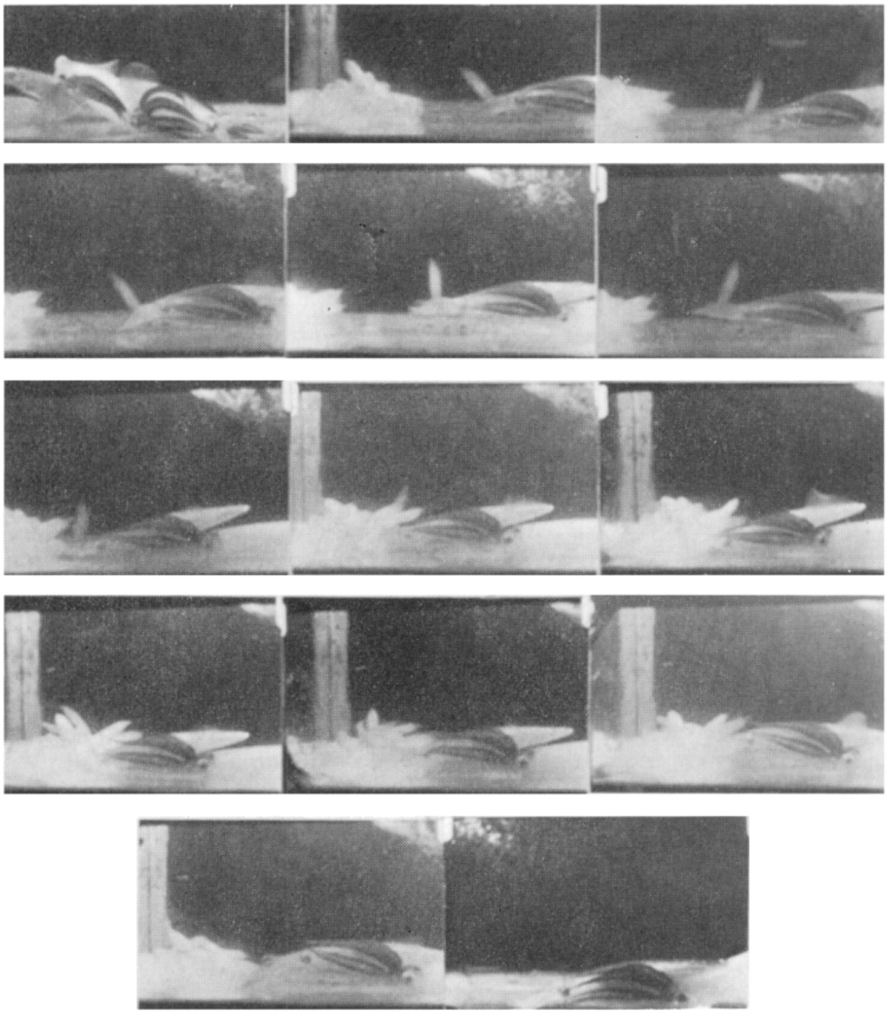


FIGURE 21. Spawning (left to right, top to bottom): a) male holds a female while egg capsule is formed; stalk portion with globular tip extends beyond female's arms (lower right-hand corner); b-e) animals approach and retreat from cluster of capsules several times while female holds globular anchor portion of new capsule between her arms; f-h) female finally darts into egg cluster; i-k) sinuous writhing of arms accompanies anchoring of egg capsule; l & m) animals ''bound'' back from egg cluster; n) animals are inactive between laying of capsules. *Photographs from motion picture made for the author by Harold N. Arrowsmith, Jr.*

FIGURE 21. Spawning (left to right, top to bottom): a) male holds a female while egg capsule is formed; stalk portion with globular tip extends beyond female's arms (lower right-hand corner); b-e) animals approach and retreat from cluster of capsules several times while female holds globular anchor portion of new capsule between her arms; f-h) female finally darts into egg cluster; i-k) sinuous writhing of arms accompanies anchoring of egg capsule; I & m) animals "bound" back from egg cluster; n) animals are inactive between laying of capsules. Photographs from motion picture made for the author by Harold N. Arrowsmith, Jr.

of the nidamental and accessory nidamental glands. Capsules (egg fingers) are spindle-shaped, with one end drawn out forming a tapered stalk on which a slight terminal enlargement serves for attachment to the ocean floor. Sizes vary, but average capsules are about 8 cm long and 1.2 cm in diameter (Figure 22).

While the egg capsule is being formed, the siphon of the female is extended far forward to within 3 or 4 mm of the cleft between her ventral arms, and the capsule is extruded from the funnel through

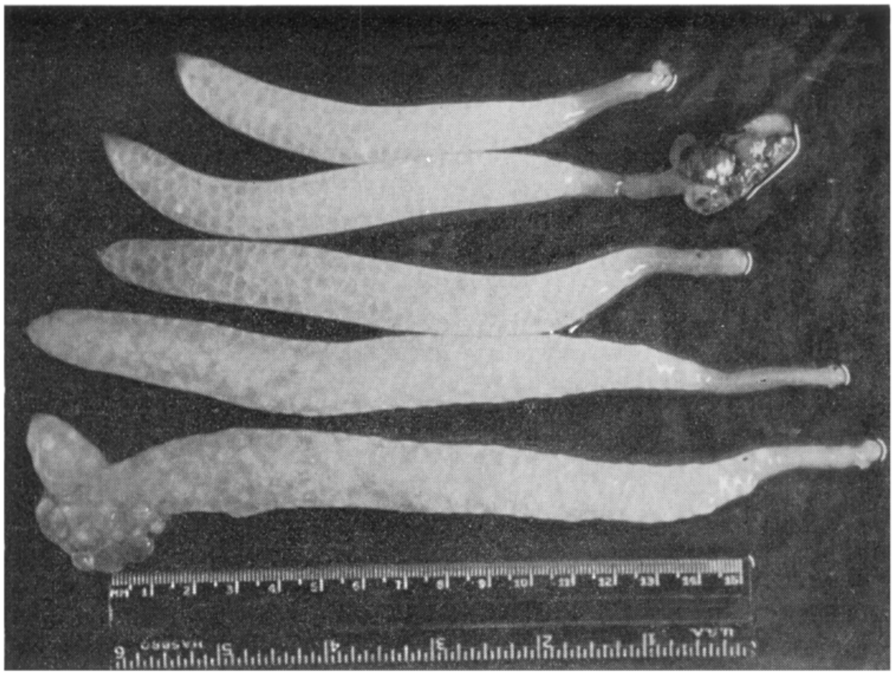


FIGURE 22. Egg capsules of *L. opalescens* showing changes in size with time. Lowermost was cut into in order that spherical chorions might be seen more clearly. Newly-laid capsules are slightly smaller and taper more gradually than smallest (uppermost) capsule in this picture.

FIGURE 22. Egg capsules of L. opalescens showing changes in size with time. Lowermost was cut into in order that spherical chorions might be seen more clearly. Newly-laid capsules are slightly smaller and taper more gradually than smallest (uppermost) capsule in this picture

that cleft into the space between the arms. This is done slowly and, apparently, with much exertion, as evidenced by the working of the mantle and by the force with which the water ultimately escapes. With successive mantle contractions, the eggs may be seen to flow forward from the funnel as though in a transparent tube; with intervening brief relaxations, the eggs move somewhat backward. When the capsule has finally wholly entered the arms, the water in the mantle cavity is forcibly expelled and the respiratory contractions of the mantle, in abeyance while the eggs are laid, become quite rapid for a short time.

The end of the egg capsule, which will become the anchor, emerges from the siphon first. The capsule is longer than the space between the arms of the female, thus before the last of it leaves the funnel, the anchor portion has come to extend 2 or 3 cm beyond the tips of the arms. The stalk portion may extend more than twice that distance when the whole mass is finally enclosed by the arms. Now the capsule is moved backward until the anchor tip is between the tips of the arms and the conical opposite end extends upward about 5 cm between the bases of the mid-dorsal arms, then forward again into its original position. This occurs several times. The capsule membranes are still penetrable by sperm which are released from the bursa copulatrix beneath the mouth, and this manipulation may assure ferilization of all of the eggs; hardening of the jelly may begin at this time before the capsule is deposited.

Drew (1911) describes how egg capsules were taken from a female L. pealii before they were drawn between the arms. Although she was found later to have no sperm reservoirs in the mantle cavity, 50 percent of the eggs were fertilized, presumably by sperm in the water from matings of the other squid present, and very few sperm were found upon the egg capsule. Those egg strings which she was permitted to lay in normal fashion showed more than 99 percent fertilization and sperm swarmed over the surface, freely entering the soft jelly. To other sperm applied later, it was impenetrable.

During this period of manipulation, the female squid cruises about as though examining various places for fastening the eggs. If other eggs are already present, those newly-laid are almost always added to the cluster. With anchor tip between ends of her arms and the other end of the egg string extending upward between the bases of the dorsal arms, the female finally darts into the egg cluster, where she rapidly manipulates the very tips of her arms, and then backs away leaving the egg string anchored to the united stalks of the egg cluster.

Many animals will contribute to the same cluster until, divers at Monterey report, it may become a pillar 5 feet high, broader above than below. Such huge clusters may be widely scattered over the sea bottom or in places so closely grouped that a diver may have trouble thrusting his way through between them. McGowan (1954) describes egg masses 40 feet in diameter on the slopes of La Jolla submarine canyon. Portions of large egg masses scooped from shallow water near Victoria, British Columbia, were interconnected by anastomosing, continuous tough jelly cords, irregularly 1 to 2 inches in diameter and many feet in length with egg capsules attached everywhere over them.

Squid in aquaria frequently anchor their egg clusters about an aerated water inlet pipe. In one case where an inlet pipe was above the water surface, a female made 25 to 30 attempts to fasten eggs in the foam area caused by water pouring in. She would cruise across this area, about 12 inches in diameter, with arm tips extended about three-quarters of an inch above the water making grasping movements.

One other type of behavior occasionally observed might be mentioned. A female, with male holding her, moved backward and forward continually for 30 minutes over a small egg cluster. Her arms would lie limply as the animals moved away from the cluster, but would extend vertically to the bottom in a line, resembling teeth of a comb, as brushing movements were made toward the center of the cluster. The stroke was about 6 inches. Possibly this type of action in natural conditions might heap sand onto the anchored part of a huge cluster, making it more secure, or it might maintain for a short time a high sperm concentration about the egg mass through continued emptying of spermatophores previously placed in the female's mantle cavity. Except for this activity by a few squid, no post-spawning care of, or reaction to, egg masses has been observed in L. opalescens. This is in marked contrast to the brooding habits of octopi, well-known through the observations of Fisher (1923), Fox (1938), MacGinitie and MacGinitie (1949) and others.

Possibly the mating and spawning behavior of L. opalescens in natural surroundings should not be inferred from that in captivity, but I believe it is safe to do so in this case. Here the patterns are unchanged whether the animals are newly-captured or the last survivors of their group, whether they are in small glass or in very large cement aquaria, whether they have been fed or starved, and whether the lighting is intense or faint. All steps are corroborated by my own observations in the field, and many steps by reports of McGowan (1954), Limbaugh and Shepard (1957), and Garth (*fide* Lane, 1957). Drew (1911) gives details of the reproductive activities of the Atlantic Loligo pealii, which in some aspects are distinctly different from those of L. opalescens. However, the fixity of behavior in a squid is illustrated by Drew's observation that a female squid, from which he took each egg finger as it emerged from the funnel, continued all steps of the egg-laying ritual as though she still held each egg string, and never interrupted the orderly sequence of her activities because she had lost a string of eggs.

10.4. Number of Eggs Produced

On one occasion, four females laid overnight approximately 17,000 eggs in 85 capsules which weighed 446 grams. The total weight of the four animals afterward was only 245 grams. Because the ova prior to laying are only a fraction of the squid's total weight, water must be taken up rapidly while the egg-enclosing materials are being secreted.

11. DEVELOPMENT TO THE TIME OF HATCHING

Squids (Loligo spp.) have been widely used for embryological studies and the developmental stages of several species have been described, *e.g.*, L. pealii (Brooks, 1880), L. vulgaris (Naef, 1928), and L. bleekeri (Hamabe, 1960), but Loligo from the eastern Pacific Ocean have never been studied in this manner. (The squid embryos described by Harman and Gardner (1927), because of the commonly spherical shape and other aspects of the illustrations, do not appear to be identifiable with L. opalescens.) To remedy this lack, I have included here a series of illustrations and a brief description of the gross embryology of L. opalescens. No histological preparations were made; where intimate details discernible only with those techniques are included for continuity, they have been derived from standard works dealing with cephalopod embryology to which references are given in the text.

11.1. Study Methods

The embryology of Loligo opalescens was studied from living material. For the earlier stages, I cut open the mantles of live males and females and placed a few spermatophores from the male and several glassy ova from the membranous part of the female's oviduct in separate watch glasses of fresh sea water. A few drops of the sperm suspension, formed by ejaculation of the spermatophores, were added to the dish containing the ova and were mixed by swirling. With a hair loop, eggs were transferred either to a depression slide to observe sperm penetration and polar body formation, or to a large dish of fresh sea water for later observation of cleavage stages. At intervals, a minute cup of Vaseline (petroleum jelly) was fashioned in a dry depression slide or Syracuse dish which was then filled with sea water; into this cup, an egg was set on end so the germinal disc was uppermost. Its details were then clearly visible, due to the transparency of the egg and chorion.

To study later stages, I kept a number of egg fingers, laid at a known time, in an aquarium of running sea water. When embryos were to be examined, the jelly coatings were cut open, two or three of the intact chorions were transferred to a dish of sea water, and their inhabitants were examined for uniformity. Usually, the embryos would slide into the same position no matter how the chorion was rotated, and to study other views, it was often necessary to discard the chorion and set the embryo into a Vaseline cup. Removing some embryos from an egg finger did not affect those remaining, because each is isolated within its own chorion. This was confirmed by comparing with undisturbed egg fingers in which the young were clearly visible through the faint translucence of the jelly coats.

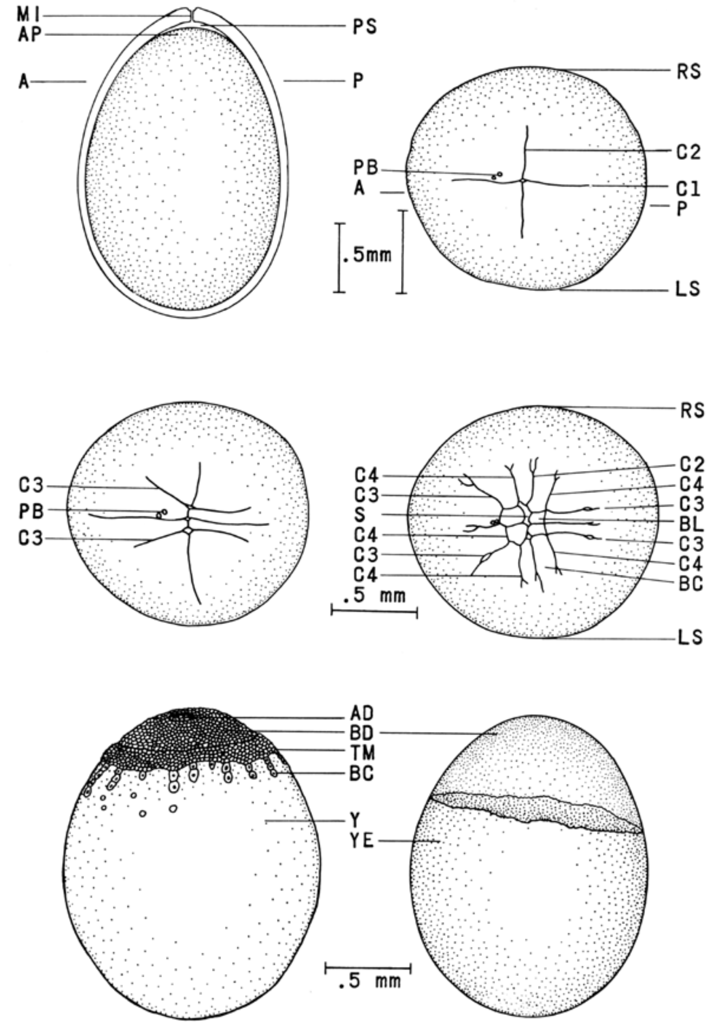
11.2. Incubation Period

Embryonic development takes 3 to 4 weeks in aquaria at approximately 16° C. Usually, hatching begins on the 22nd or 23rd day, when numerous young appear, and continues for about a week. Occasionally, a few emerge after 18 or 19 days. Under cooler natural conditions, the time is probably at least a week longer. MacGinitie and MacGinitie (1949) found that eggs of L. opalescens hatch in about 29 or 30 days; McGowan (1954) found that 30 to 35 days are required at an average temperature of 13.6° C. In the warmer waters at Woods Hole, Mass., L. pealii emerges after only 11 or 12 days of incubation (Costello *et al.*, 1957). Hamabe (1960) cited incubation times of 46 days at 10° to 12° C., and 36 to 43 days at 13 to 17° C. for Loligo bleekeri Keferstein.

In the score of L. opalescens egg capsules, laid at the same time and observed while I recorded their development, hatching began on the 24th day, was heaviest during the 28th and 29th, and decreased for several days thereafter. I have given the approximate time that elapsed between laying of the eggs and the attainment of each stage; however, individuals progress at somewhat different rates (as shown by the range in hatching times) and all would be influenced by lower or higher temperatures, so these times should be interpreted accordingly.

11.3. The Ovum

The egg of Loligo opalescens (Figure 23) is large and telolecithal; a thin cytoplasmic layer invests the massive yolk and thickens at the animal pole to form the blastodisc in which the nucleus lies. The egg is bilaterally symmetrical; its median plane will become the mid-sagittal plane of the adult. In this plane, the initial cleavage occurs; the second, at right angles to it, separates anterior from posterior. The egg's least dimension is from left to right; its greatest is from blunt vegetal to more-pointed animal pole. The posterior margin is straighter, the anterior margin more curved. The center of the blastodisc does not coincide with the apex of the egg, but lies anterior to it.



FIGURES 23–28 (left to right, top to bottom). 23) An ovum; 24) Day 1, second cleavage; 25) Day 1, third cleavage; 26) Day 1, fourth cleavage; 27) Day 2, gastrula; 28) Day 4, growth of blastoderm.

FIGURES 23-28 (left to right, top to bottom). 23) An ovum; 24) Day 1, second cleavage; 25) Day 1, third cleavage; 26) Day 1, fourth cleavage; 27) Day 2, gastrula; 28) Day 4, growth of blastoderm

The egg is enclosed by a thick chorion of follicular origin. From the bottom of a cup-like depression in its outer surface, the micropyle leads to the narrow perivitelline space above the blastodisc.

Eggs range in length from approximately 2.0 to 2.5 mm, and in width from approximately 1.3 to 1.6 mm. Inclusion of the chorion adds about 0.1 and 0.075 mm, respectively. Egg sizes are usually, but not always, proportional to the sizes of the animals in which they are found. Eggs of an individual often vary in length by about 5 percent.

11.4. Fertilization

Transparency of chorion and egg permits one to observe clearly the passage of the sperm through the micropyle and its entry into the egg. Soon after this, the egg shrinks, widening the perivitelline space between itself and the chorion, and two polar bodies are cut off. These arise in the median plane considerably in front of the plane of the initial transverse (second) cleavage, and typically remain in this position through at least the first six divisions of the blastoderm.

11.5. Cleavage

Cleavage in L. opalescens is meroblastic (Figures 24, 25, 26). The first cleavage furrow (C1) is in the median sagittal plane, and the second (C2) is at right angles to this. Third cleavage produces a pair of furrows (C3) which, behind the transverse furrow, are almost parallel to the first cleavage plane, but which diverge anteriorly, separating each anterior quadrant into almost equal parts. All eight cells at this stage are continuous peripherally with the surrounding cytoplasm.

Fourth cleavage again produces two furrows (C4) which extend laterally almost parallel to the transverse (second) cleavage furrow. Centrally, these cut off and give complete boundaries to tips of anterior and posterior pairs of medial cells, thereby producing the first equatorial (Korschelt and Heider, 1900) or circumferential (MacBride, 1914) cleavage. By further cleavages of this and of radial types, more blastomeres (BL) with complete boundaries are cut off to form a blastoderm or discoblastula (Raven, 1958) of which the marginal cells (blastocones, BC) remain continuous with the peripheral cytoplasm.

The chorion, by a closing of the micropyle soon after fertilization, becomes a private aquarium within which the developing embryo maintains an environment suitable to itself. Presumably, metabolic wastes, remaining within, create a continuous inward flow of water due to osmosis; the chorion remains turgid and continues to expand more rapidly than its inhabitant throughout the embryo's growth.

11.6. Gastrulation

Gastrulation (Figure 27) is a complex process which begins when blastomeres cease forming from the blastocones (BC). These latter, no longer appearing to have continuity with the surrounding cytoplasm, proliferate outward in several regions about the blastoderm (BD). In some cases, a single cell moves outward from the blastodisc margin, but retains continuity with it by a slender cytoplasmic bridge which may be seen until, in some cases, it is more than 10 times as long as its cell body. However derived, cells of peripheral origin rapidly become scattered over and embedded in the yolk (Y) surface, and from them is derived a layer of squamous cells, the yolk epithelium (Lankester, 1875) or perivitelline membrane (YE). This grows centrally between yolk and blastodisc and outward and downward about the cytoplasm-enclosed yolk mass.

At the same time, the margin of the blastoderm becomes two-layered by delamination of an internal cell layer. This entomesoderm also grows centrally toward the animal pole together with (but more slowly than) the perivitelline membrane, and later separates into mesodermal and gut-forming endodermal components (Naef, 1928; Sacarrao, 1952, 1953, *fide* Raven, 1958). The center of the blastoderm, marked by a shallow depression (AD), remains a single cell layer for a considerable time but eventually becomes underlain by mesoderm. Concomitant with the initiation of delamination of the margin of the blastodisc, an ectodermal sheath, later invaded by mesoderm, begins to grow outward and downward from it over the perivitelline membrane to form the external yolk sac (YX); this will close about the eighth day (Figures 28, 29, 30).

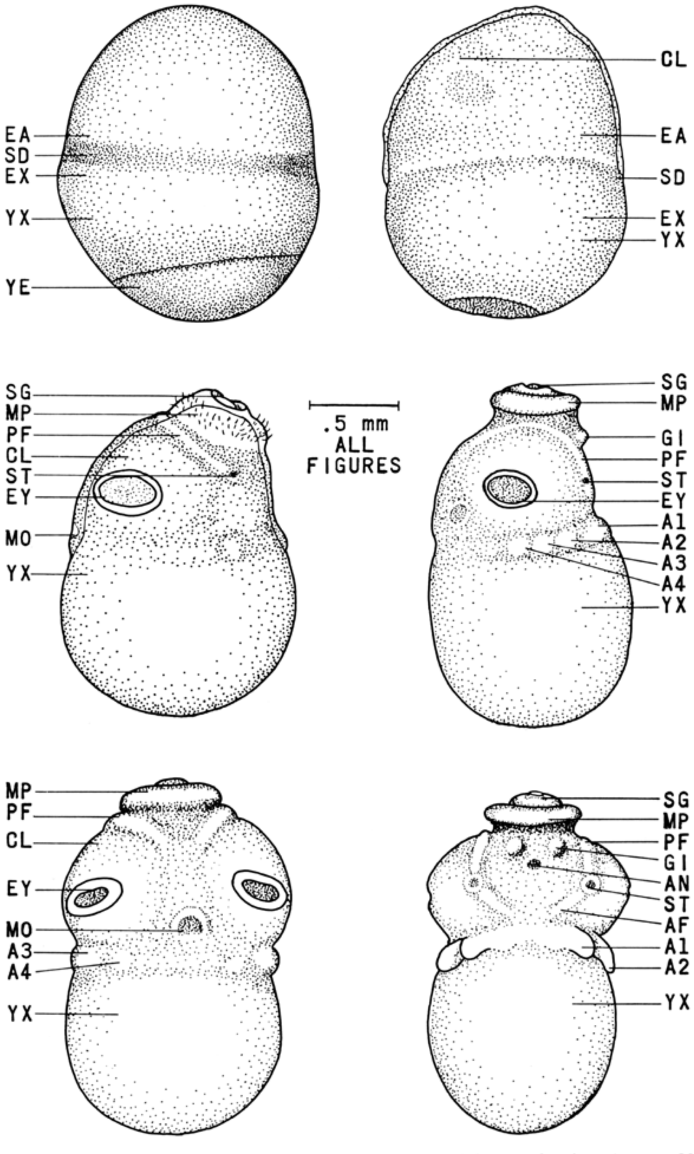
The perivitelline membrane is considered endoderm, although it arises separately from that which forms the lining of the gut. It becomes a syncytium which contributes to digestion and absorption of the yolk (Portmann and Bidder, 1928).

11.7. Organogenesis

Late in the sixth day (Figure 29), a shallow girdling depression (SQ) appears about the equator, marking the boundary between external yolk sac (YX) and embryo (EA), and on the seventh (Figure 30), the wisp-like fertilization membrane separates from the entire surface and disintegrates, permitting one to observe the ciliary activity of all of the cells wafting dark particles to the vegetal pole, where they disperse like smoke.

During and following the eighth day (Figure 31), organ formation progresses swiftly. The apex shifts backward and increases in prominence, and paired antero-lateral cephalic lobes (CL) begin to protrude. These arise by massive proliferations of ectodermal cells, from which the nervous system and eyes will be derived (Faussek, 1900). A shallow ring-like depression, the shell gland (SG), indents the new apex; below and about its rim a concentric ridge, the mantle primordium (MP), rises. Broad, shallow depressions, lying antero-laterally upon the cephalic lobes, form the eye primordia (EY). Anteriorly, the stomodeum (MO) appears, but considerably above its final site.

During the ninth day (Figures 32, 33, 34), the mantle ridge thickens and the eyes grow more prominent. Anteriorly, ridges which will become the posterior funnel folds (PF) extend over the eyestalks onto the posterior surface, where they end at the open statocyst pits (ST). Directly below the latter, at the margin of the external yolk sac, the first-forming ventral arms (A1) appear. At about this stage, Faussek (1900) shows, as a common primordium for the cerebral ganglion and optic ganglion on each side, a band curving across the



FIGURES 29–34 (left to right, top to bottom). 29) Day 6, definition of embryonic area; 30) Day 7, shaping of embryonic rudiments; 31) Day 8, embryogenesis; 32) Day 9, lateral view; 33) Day 9, oral view; 34) Day 9, aboral view.

FIGURES 29-34 (left to right, top to bottom). 29) Day 6, definition of embryonic area; 30) Day 7, shaping of embryonic rudiments; 31) Day 8, embryogenesis; 32) Day 9, lateral view; 33) Day 9, oral view; 34) Day 9, aboral view

lower surface of the eyestalk from near the mouth almost to the statocyst; he also shows separate primordia for pedal and visceral ganglia extending from the region of the statocyst obliquely forward onto the eyestalk and backward near the posterior funnel fold, respectively. By the end of this ninth day, the shell gland is closing, lenses are forming in the eyes, gill primordia (GI) and anus (AN) have appeared, and four pairs of arm (and tentacle) buds (A1, A2, A3, A4) line the sides of the constricting embryonic "waist." The mantle fold, eye bulbs, and yolk sac are covered with cilia, all of which beat downward actively so that the embryo tends to ride up the slope within the now greatly expanded chorion.

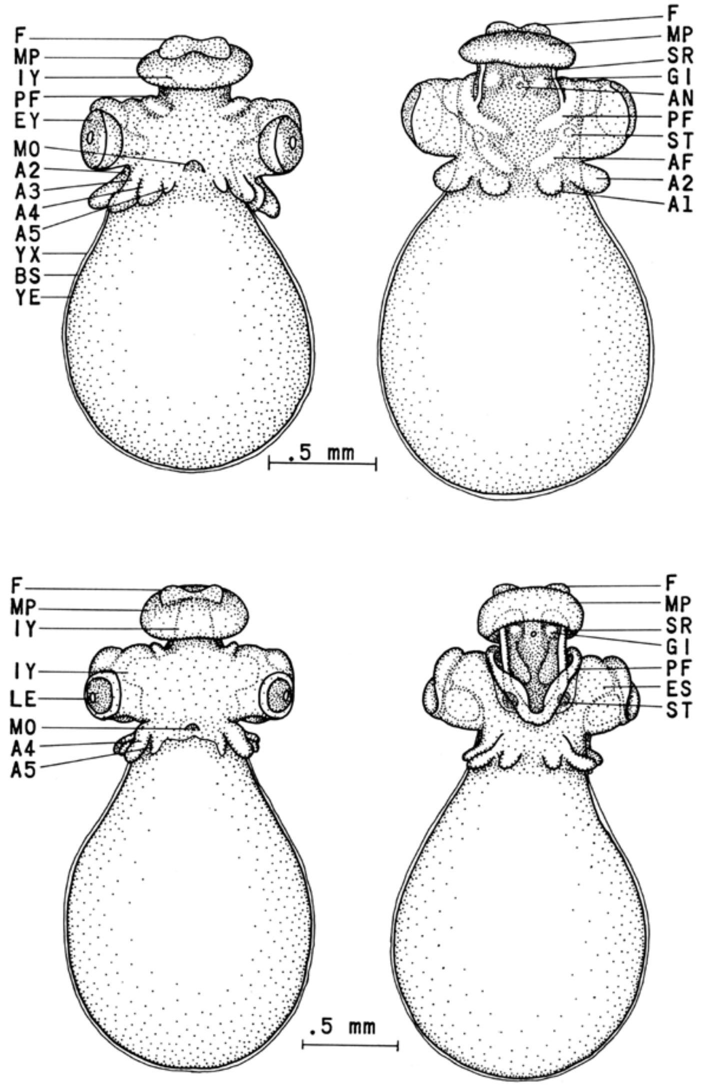
On the 10th day (Figures 35, 36), the shell gland cup closes and transverse fin folds (F) develop upon the broadening mantle. Posterior (PF) and anterior (AF) funnel folds extend toward the midline, and the funnel retractor muscles (SR) appear. The most anterior pair of arms (A5) becomes recognizable. Peristaltic action of the yolk sac begins circulating food-laden blood from the blood sinus (BS) of the external yolk sac to sinuses within the embryo (Portmann and Bidder, 1928).

During this and ensuing days (Figures 37 to 45), the eye bulbs continue to increase in proportion as eyes and ganglia develop. The mantle curves downward, saucer-like, the gills lengthen, at first appearing serrated, and the funnel primordia unite in the midline. The yolk stalk narrows greatly, due to contraction of the circumoral muscles, and there is an actual movement toward each other of paired structures such as statocysts and arm primordia. During this time the fins, mantle, gills, branchial hearts (BR), funnel (FF, FL), eyes, some ganglia, and arms are developing, and the embryo rapidy expands as the contents of the external yolk sac are transferred within.

11.8. Development of Specific Organ Systems

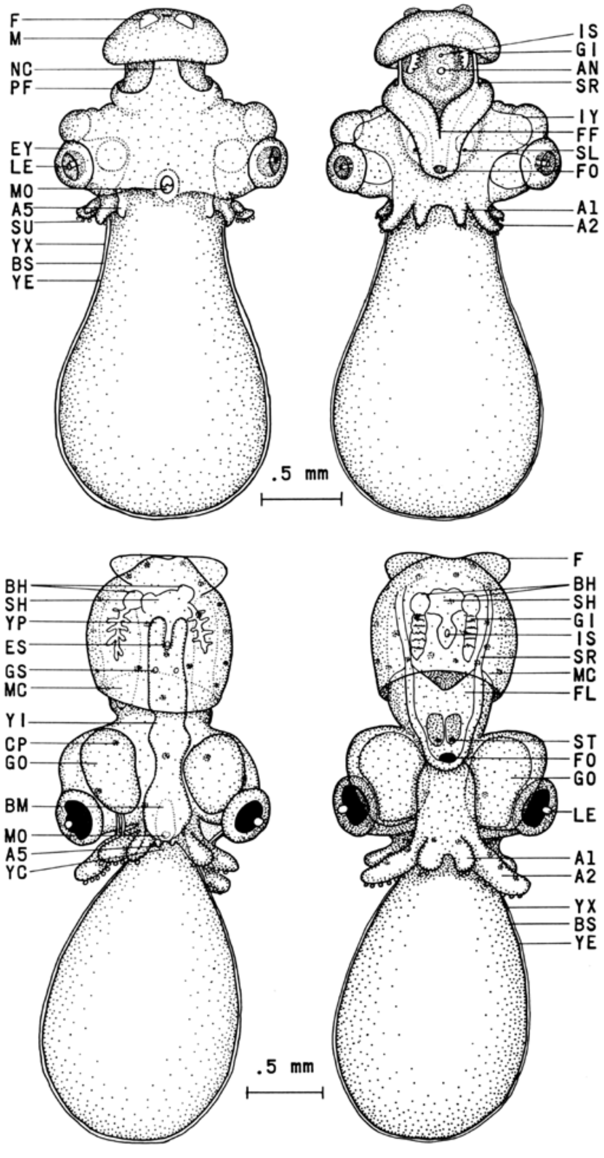
11.8.1. Digestive System

The first visible sign of the developing digestive tract (Figures 34 *et seq.*) in L. opalescens is the elevation posteriorly of a rounded projection bearing an ectodermal invagination which will become the anus. When this appears, a narrow ridge extending posteriorly rises beneath it and then widens. Lankester (1875) says of the cavity formed within, "The whole of the alimentary canal, with the exception of pharynx and esophagus, develops by the growth of this primitive chamber of the anal tubercle." This chamber and its walls develop from a plate of endodermal cells which, by delamination of a common primordium, becomes separate from the residual mesoderm (Naef, 1928; Sacarrao, 1952, 1953, *fide* Raven 1958). Raven (1958) describes how the central region of this plate bends away from the vitelline membrane to form a tall chamber which will become the intestine, and a diverticulum from it, the ink sac (IS). Posteriorly, the plate extends itself toward the apex of the yolk sac, where expansions form a caecum (CE) and stomach (S), into which the elongating stomodaeum (MO) soon opens. The margins of the plate curve inward, beginning the closure of the gut tube. From the region which will become the caecum, two hepato-pancreatic



FIGURES 35–38 (left to right, top to bottom). 35) Day 10, oral view; 36) Day 10, aboral view; 37) Day 12, oral view; 38) Day 12, aboral view.

FIGURES 35-38 (left to right, top to bottom). 35) Day 10, oral view; 36) Day 10, aboral view; 37) Day 12, oral view; 38) Day 12, aboral view



FIGURES 39–42 (left to right, top to bottom). 39) Day 15, oral view; 40) Day 15, aboral view; 41) Day 18, oral view; 42) Day 18, aboral view.

FIGURES 39-42 (left to right, top to bottom). 39) Day 15, oral view; 40) Day 15, aboral view; 41) Day 18, oral view; 42) Day 18, aboral view diverticula (LL) grow forward laterally within the perivitelline sinus. The early stages here were not seen because no histological preparations were made but, once formed, the organs, labelled in the figures, could be followed through the remainder of their development in L. opalescens.

The detailed description of yolk-embryo relationships in two species of Loligo by Portmann and Bidder (1929) appears directly applicable to L. opalescens. Four periods are noted: of these, the first extends through the development of the external yolk sac to the beginning of its contractions. In the second period, the entire perivitelline membrane digests and absorbs yolk, passing its products into the blood in the surrounding sinus space. Rhythmic contractions of the outer integument of the yolk sac maintain a constant circulation of food-laden blood into the sinus spaces within the embryo. This ends when communication between outer and inner sinuses ceases, due to constriction by the circumoral musculature.

During the third period, peristaltic action by the circumoral muscles pumps the undigested yolk from the external yolk sac into the internal yolk sac within the expanding embryo. Most of the yolk remains anterior to the hearts, caecum, and stomach, but two lobes (YP) extend about the esophagus, becoming contiguous posteriorly. The internal blood sinus disappears, except for a small part which persists to form the abdominal vein. The anterior portion of each hepato-pancreas becomes leaf-shaped, as long and deep as the anterior yolk sac, and closely applied to its lateral surface. These anterior parts (LL) become the liver; the more posterior portions expand to form the pancreas. Hatching occurs at or near the end of this period, by which time the external yolk sac has almost or entirely disappeared.

During the fourth period, the liver becomes very active, absorbing the yolk and growing thereby until, as Lankester (1875) says, its lobes, "come to occupy exactly the same space once filled by all ... the inner yolk."

The buccal mass (BM) with the beak-guarded mouth (MO), the posterior salivary gland (PG), the ink sac and the anal valves (AV) all arise well before hatching and are easily identified.

11.8.2. Circulation

The systemic and branchial hearts (Figures 41 *et seq.*) begin to beat very early, and many blood vessels are easily traced by their pulsations. The anterior aorta (AO) parallels the course of the esophagus (OE) between the posterior lobes of yolk, and runs forward dorsally to branch widely in the head. The broad, contractile vena cava (VC) collects blood from the head and runs posteriorly ventral to the internal yolk mass (IY) to divide about the intestine. Its two branches become invested by renal tissue; the resulting double walls become greatly folded (Raven, 1958), and are the sites of excretion into the surrounding renal sacs (K). The paired venae cavae lead to the branchial hearts; after traveling through the branchial circulation (BV), blood returns to the systemic heart. Except for the folded nature of the renal-vena-caval walls, these parts are all clearly observable in L. opalescens.

11.8.3. Nervous System

The nervous system develops from the primordia, described for day 9, which by continuing proliferation and delamination become massive thickenings of ectoderm underlain by others of mesoderm (Faussek, 1900). Because of the number and developmental complexity of the parts derived from these, their growth was not followed, but I have shown some of their derivatives (Figures 41 to 47). These cerebral, optic, visceral, and stellate ganglia are all readily recognizable, and many of their nerves can be seen in a young squid. The pedal ganglion is more obscure; its position only has been shown. No attempt was made to trace the remainder of the nervous system; the following summary of Raven's (1958) description of the development of this system will serve to bridge the gap.

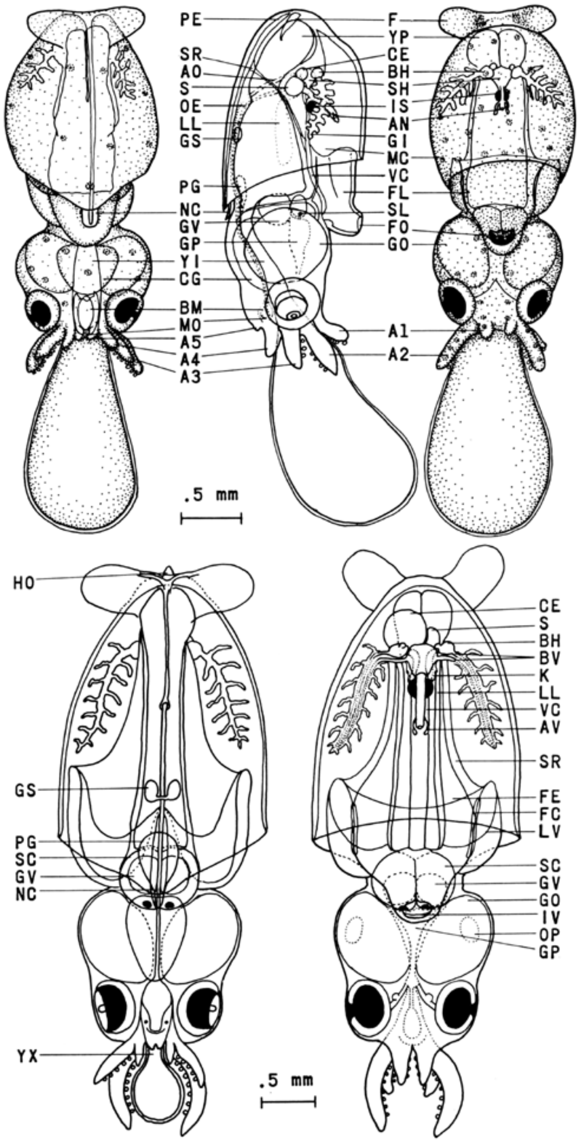
of the three pairs of nerve-tissue primordia described for day 9, the common primordium on each side separates into an optic ganglion (GO) and a cerebral ganglion (CG); the former grows in bulk from additional sites of proliferation behind the eyes (Faussek, 1900). The two cerebral ganglia become joined by a commissure and then fuse after approaching each other, due to constriction of the circumoral musculature. The paired primordia of visceral (GV) and pedal (GP) ganglia unite medially behind and in front of the statocysts (SC), and then form a single subesophageal ganglion (Raven, 1958). Other smaller ganglia and the white bodies develop in the head, and the paired stellate (GS) and branchial ganglia, and the single splanchnic ganglion, arise in the mantle, in the gills, and on the gut, respectively. Connectives, commissures, giant fibres, and nerves arise from the ganglia.

11.8.4. Sensory Structures

Prior to hatching, the primordia of the olfactory organs (OP) appear as oval thickenings of the epidermis ventrally on the head; statocysts, with their anteriorly-placed statoliths (SI), have enlarged and show finger-like inward foldings of their anterior and lateral walls; the eyes and their muscles are fully developed and mobile. Upper and lower surfaces of the eyes show a strong red and geeen metallic iridescence.

11.8.5. Funnel

The funnel (Figures 36 *et seq.*) develops mainly from the anterior funnel folds (AF) which fuse medially (FF) leaving a broad internal opening (FE) and a small external opening (FO). The latter can be tightly closed by the small animal by pressing the sides together, beginning posteriorly. A transverse internal valve (IV) and paired lateral valves (LV) develop, and control the entry of water into, and its egress from, the mantle cavity. Funnel retractor muscles (SR) extend posteriorly and dorsally about the internal yolk to origins beside the pen (PE). Funnel cartilages (FC) interlock with others in the mantle, and the nuchal cartilage (NC) with the anterior end of the pen; together they form guides for the piston-like movement of the head. The development of all of these parts can be followed in L. opalescens.



FIGURES 43–47 (left to right, top to bottom). 43) Day 21, dorsal view; 44) Day 21, lateral view; 45) Day 21, ventral view; 46) Day 24, hatched: dorsal view; 47) Day 24, hatched: ventral view.

FIGURES 43-47 (left to right, top to bottom). 43) Day 21, dorsal view; 44) Day 21, lateral view; 45) Day 21, ventral view; 46) Day 24, hatched: dorsal view; 47) Day 24, hatched: ventral view

11.8.6. Mantle and External Features

The mantle is thin, muscular, and swiftly contractile. It is transparent, as are all of the young animal's tissues, except the pigment-containing eyes, ink sac, and chromatophores; the skin here, as elsewhere, has a rough, mosaic-like texture. Iridocytes appear in the skin of the mantle shortly before hatching. The anterior edge of the mantle, supported dorsally by the pen, forms an obtuse angle behind the head. Posteriorly in the mid-dorsal line is a ridge which divides so that its parts extend onto the posterior roots of the fins. In this region, the hatching organ (Hoyle's organ, HO) forms.

Three pairs of arms and the tentacles are obvious, but the last-formed dorsal arms remain very small and are difficult to see, particularly when the buccal mass is protruded.

11.9. Changes in the Egg Capsules

While the embryo develops, considerable change takes place in the protecting capsule also. The increasing volume of each chorion due to absorption of water has been mentioned, and a series of capsules illustrated (Figure 22). The outer coatings stretch, but do not break; the largest capsule was cut into to show the spherical, expanded chorions more clearly and, by their extrusion, to show the elasticity of the outer coatings. Normally water continues to be taken in until, when hatching begins, the volume and weight of each capsule has reached about five times its original value (Table 7).

11.10. Survival of Egg Capsules Until Hatching

Embryonic squid are very vulnerable if the egg masses are attractive to bottom-feeding predators. To test whether they are eaten, set lines were put out near but not on the spawning areas, and successive hooks were baited with a piece of fish, a piece of squid flesh, and a piece of a squid egg-finger. These were left out until every hook that had borne fish or squid flesh was eaten clean; every hook bearing squid egg-finger

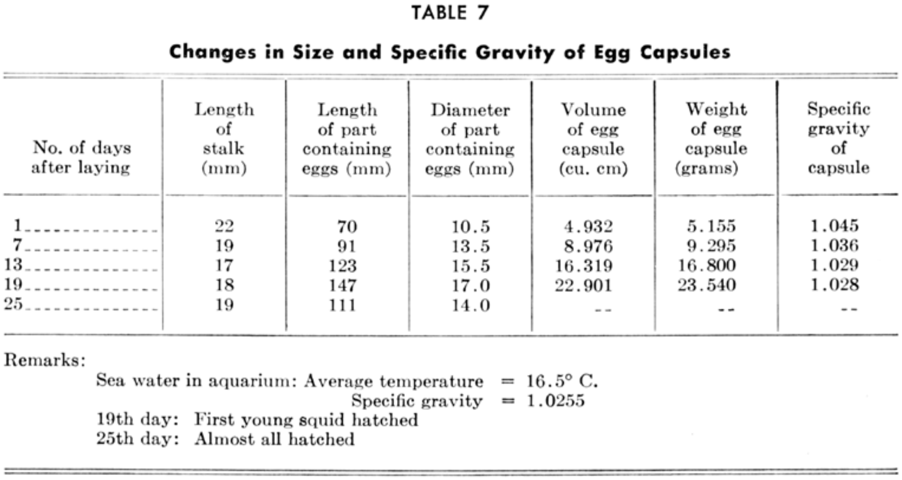


TABLE 7

Changes in Size and Specific Gravity of Egg Capsules

No. of days after laying	Length of stalk (mm)	Length of part containing eggs (mm)	Diameter of part containing eggs (mm)	Volume of egg capsule (cu. cm)	Weight of egg capsule (grams)	Specific gravity of capsule
1	22	70	10.5	4.932	5.155	1.045
7	19	91	13.5	8.976	9.295	1.036
13	17	123	15.5	16.319	16.800	1.029
19	18	147	17.0	22.901	23.540	1.028
25	19	111	14.0	--	--	--

Remarks:

Sea water in aquarium: Average temperature = 16.5° C.
Specific gravity = 1.0255
19th day: First young squid hatched
25th day: Almost all hatched

TABLE 7

Changes in Size and Specific Gravity of Egg Capsules

had remained untouched. Squid eggs left in the same aquaria with them have been ignored by the starfishes Pisaster ochraceus, Pateria miniata, and Pycnopodia helianthoides, by several kinds of crabs, by hermit crabs, by the isopod Cirolana harfordi, by the moon snail Polinices sp., and by various large anemones. When an egg capsule was slid between the arms of a P. helianthoides that had been without food for weeks, it was drawn toward the mouth by the tube feet and the animal humped up into feeding position but later abandoned the undamaged capsule. MacGinitie (1938) reports feeding squid eggs to a sea anemone and having them returned unaffected 2 hours later, and that a starving starfish, Pateria miniata, enclosed a squid egg-finger with its stomach for more than 3 days before maceration began, and required another full day before digestion was completed.

A polychaete worm, Capitella ovincola, is frequently found in the capsules, but it inhabits the intermediate jelly coatings without in any way interfering with successful development and hatching. It is probable, therefore, that embryonic squid suffer little predation while within the egg capsules.

11.11. Hatching

When a juvenile squid is ready to hatch, a Y-shaped area extending along the mid-dorsal line posteriorly and out onto the fins becomes glandular and slightly elevated to form the hatching gland (Hoyle's organ). This area adheres to the chorion where it is closest to the surface of the egg finger, and chorion and enclosing jelly coats are digested through to produce a round hole (Hibbard, 1937). In L. opalescens Hoyle's organ or part of the region posterior to it (Figure 46, HO) can be quickly everted or retracted by muscular action; when extended it is a considerable conical protrusion at the posterior end between the fins; its shape may change from that of a pointed to that of a truncated cone by withdrawal of the tip, or to that of a stout spindle by dilation midway along its length. This apparently contributes mechanically to breaching the chorion and capsule membranes (Hamabe, 1960, describes how a young L. bleekeri repeats drilling at a particular spot with the "tooth process" it has at the end of the mantle until it comes out through a perforation made in this way); when a young L. opalescens has made the opening large enough it escapes by strong mantle contractions and becomes free-swimming. In laboratory aquaria with continuously running aerated sea water, almost 100 percent of the eggs develop and hatch successfully.

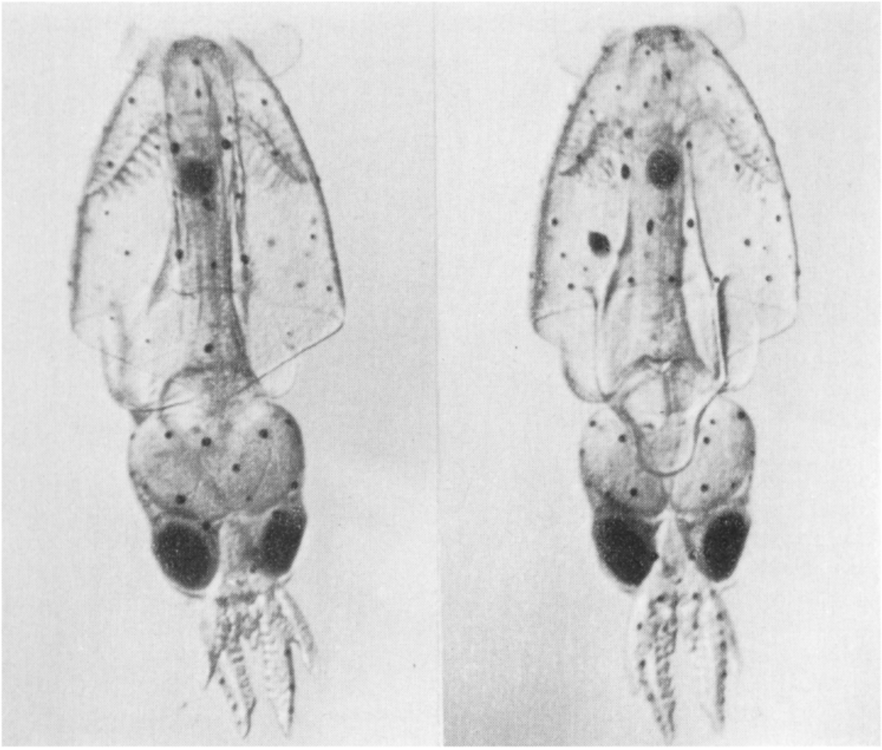
Squid rarely hatched during hours of daylight from egg capsules kept in laboratory aquaria. They usually hatched profusely at night while the laboratory was in darkness. Experiments were conducted to discover whether this was linked to some innate rhythm or to the different light intensities. These tests showed that (i) light was the factor involved, (ii) young squid hatched much more readily in the dark, and (iii), where several hours of darkness follow several hours of light, more than half of the hatching occurred during the first 4 hours of darkness. If the same mechanisms operate in the subdued illumination of the spawning areas, presumably most of the young emerge in darkness in the early part of the night and, by swimming upward and by tidal drift, are clear of the spawning areas before light returns sight to any predators, including adult squid, prowling the spawning grounds.

12. YOUNG SQUID AFTER HATCHING

12.1. Characteristics

When hatched, a young squid has a dorsal mantle length of about 3mm and a total length of about 5mm. A small external yolk sac may still persist; internally, a considerable volume of yolk remains. Physical features of the young animal can be shown in diagrams and black-and-white photographs, but these lack the colors of the chromatophores and of the iridescent eyes and skin which give the transparent animal a jewel-like appearance (Figures 46, 47, 48, 49).

A newly-hatched squid is immediately active and agile. When swimming gently to maintain its position in the water, a young squid keeps its fins upward and its head obliquely downward so the long axis of the body is about 45 degrees from the horizontal. The arms are carried flexibly in a loose cone which may be spread laterally; occasionally, they are swept upward and held briefly pointing somewhat backward above the head in a posture often exhibited by adults. The fins wave gently and the mantle contracts regularly 90 to 125 times per minute.



FIGURES 48 & 49 (left to right). 48) Dorsal view of newly-hatched *L. opalescens*; 49) Ventral view of newly-hatched *L. opalescens*.

FIGURES 48 & 49 (left to right). 48) Dorsal view of newly-hatched L. opalescens; 49) Ventral view of newly-hatched L. opalescens

The repeated jets of water from this respiratory circulation make the squid appear to bounce and tilt in the water. It is heavier than sea water and sinks downward about one mantle length (3 mm), with the head turning more downward, between successive exhalations; each exhalation restores the distance sunk, and lifts the head so the body axis is closer to horizontal than 45 degrees. Occasionally, the contractions are checked for 20 to 30 beats and the animal sinks downward head-foremost at a somewhat accelerated rate. Increases in strength or tempo of mantle contractions lift the animal through the water.

When the small squid reaches the surface it may continue bobbing in the same posture just beneath the surface film, or it may swing into a horizontal position and move short distances forward and backward. This more horizontal pose is usually assumed when the animal is more active, e.g., when it hunts tiny crustacea in the aquarium. Occasionally when the prey is on the side of the aquarium the squid's suckers become locked onto the glass for a short time before they are able to be released.

The most common avoiding reaction of a small squid, when a large object is brought close to it, is simple cessation of swimming so that the colorless animal sinks inertly downward. Less often one will dart straight, or by a zig-zag path, away from an approaching object; if pursued or repeatedly approached by the object the small animal may turn dark by means of its chromatophores and ink may be ejected. often when being watched under a microscope, a small squid with mantle contracting normally will suddenly beat its fins swiftly in unison prior to strong mantle contractions by which it darts swiftly about. If much of the water is removed from the watch glass or depression slide in which the squid is being observed, the latter may bend strongly from side to side so that the arms almost touch the fins.

12.2. Feeding Experiments

Several attempts were made to raise young squid in 1947–52 and again in 1962. Newly-hatched individuals were kept in aquaria made of well-seasoned redwood and glass, and supplied with continuously running aerated sea water, or in glass dishes in which the sea water was changed daily. Food offered included newly-hatched larvae of the copepod Tigriopus fulvus and of the phyllopod Artemia salina, motile cells of the volvocaline alga Platymonas subcordiformis, the alga Dunaliella viridis, zoospores of the filamentous alga Cladophora, the diatom Nitzschia closterium minutissima, and on some occasions fine planktonic material.

The squid, particularly when a few days old, would approach and apparently inspect small motile objects. Where these were crustaceans, some of the squid, by their actions and chromatophore activity, seemed to become excited, and some of these went through the pattern of food capturing seen in adults. In the encounters that I watched, the squid appeared to fail in, or seemed not to attempt, the final capture of the prey. Although none was seen to eat, it was believed that some, not under direct observation, did so because they retained their dark color for an unusually long time; adult squid remain dark while eating and digesting their food.

These aquarium specimens always died by about 10 days after hatching. Other workers (Budd, 1940; Orcutt, 1950) experienced similar results when attempting to raise marine fishes using methods very like these. The squid deaths had always been ascribed to starvation due to unsuitability of the food offered, but when I examined some in greater detail in 1962 I found that the internal yolk did not appear to be exhausted. Fungal infection, not lack of food, apparently caused death; the posterior end of the animal, which had been repeatedly pushed against the glass walls and wooden ends of the aquarium, became encrusted by a mycelium from which hyphae sprouted. The fins often withered and the gills shortened and stiffened; the animals became sluggish and died.

These squid had not reached the stage at which they were dependent on the food they captured; under conditions regulated to avoid infection, Artemia might yet prove suitable for feeding the young.

Williams (1909) and Wilson (1947) name copepods and other smaller larval crustacea as the food of very young squid and cuttlefish, respectively; Wells (1958) states that, after absorption of their yolk, young *Sepia* will always attack and eat *Mysis*, and as this food becomes more familiar the *Sepia* will more readily attack other moving objects which previously were ignored.

12.3. Dispersal in the Sea

After hatching, young L. opalescens swim upward and toward light, which brings them to the surface. When not swimming actively they sink slowly, darting occasionally at small moving objects; sustained swimming always carries them back toward the surface. Bigelow and Leslie (1930) describe the upper 15 meters in July 1928 in Monterey Bay as a nursery area. Two-thirds of the diatom population and many dinoflagellates are concentrated here, as are larvae and juveniles of copepods, euphausiids, and decapod crustacea. Adults of microcopepods and appendicularians are present in large numbers. The chief predators are ctenophores, arrow worms, and siphonophores. The young squid join this surface assemblage, probably feeding upon larvae and juvenile crustaceans, and following them to deeper levels as prey and predators grow.

Young squid, together with other plankters, are transported and dispersed by the coastal currents. Squid which hatch in Monterey Bay during the period of upwelling from May to August will be carried chiefly southward, although eddies in the shelter of promontories may slow their progress. During September and October, slackening of the California Current flow, and meandering of the coastal waters would scatter them widely. Many squid from the north would join those spawned locally in the circulation off southern California and Baja California, in which Johnson (1939) has shown Emerita analoga larvae may be found up to 130 miles from the mainland. This shore-living sand crab and L. opalescens have very similar North American ranges, both have their periods of most intensive spawning (insofar as squid at Monterey are concerned) in May and June, and the young squid and the larval sand crabs would become planktonic in the same months in the same coastal waters. Therefore the drift pattern of Emerita may be considered indicative of the pattern for young of L. opalescens while they are planktonic or while they are following and feeding upon planktonic crustacea near the surface. Some would be swept offshore into the North Equatorial Current, but many would be carried northward again by the surface Davidson Current of November to February or, if they sought their prey at greater depth, by the deep California Counter Current which flows northward throughout the year.

Squid spawned at Monterey during the winter, would, upon hatching, be carried northward until upwelling began and their direction thereby reversed, or until they passed offshore into the influence of the California Current. Some possibility that young squid may move to considerable depths is suggested by the samples of March and July 1931 taken in plankton hauls during which the net was believed to have fished chiefly at 200 meters and 70 fathoms, respectively. In each case, however, the net was open from the surface to the fishing depth and back to the surface again, and there is no way of knowing at what depth the squid were taken. If small squid were to seek depths below 200 meters, they would come within the influence of the deep California Counter Current which flows northward.

That some squid (smaller than 40 mm) may remain in, or return to feed in, sheltered bays in the vicinity of the spawning grounds is suggested by the capture on one occasion of thousands of individuals 20 to 30 mm in mantle length in a shrimp trawl haul taken at 5 to 10 fathoms in Soquel Cove in the northern part of Monterey Bay. However, most of the juveniles, ranging from 40 mm upward, examined during this study were taken in commercial catches of fish from areas subject to the water movements mentioned above. This suggests that distribution is of a coastwise nature, and that few individuals remain as local inhabitants in Monterey Bay.

13. PROCEDURES AND DATA FOR POPULATION STUDIES

13.1. Factors Determining Procedures in Population Sampling and Analysis

Several factors controlled my choice of procedures for population sampling and analysis. The first of these was the fact that the commercial squid catch in Monterey Bay consists of spawning animals only, without any other stages of the life history represented in it.

It was assumed initially that squid of all ages, living in Monterey Bay and its vicinity, ranged through the southern part of the bay for feeding, as well as for spawning. It was thought, as a consequence, that squid caught there would be representative of the whole population of the area. However, qualitative examination of a great many squid in the commercial catch from May to September 1946, showed that all were mature, although there were great variations in the condition of the reproductive system and in the thickness of the mantle. Accordingly, a quantitative study was begun in the hope that consistent trends in body proportions or in the condition of organs or sex products would outline periods of spawning and its cessation and, possibly, show the relative numbers of animals reproducing at different times of the year.

A series of 29 samples was collected from commercial squid catches between September 1946 and July 1947. The length, weight, and mantle thickness of each animal were measured, the reproductive systems were dissected, and each part was weighed (Fields, 1949). Six additional samples extended this series to May 1948, but fewer measurements were taken. These 35 samples included 287 squid.

The reproductive systems of the squid in these samples showed clearly that the stores of ova and spermatophores, the condition of the accessory reproductive structures, and the reserves in the mantle did not vary in seasonal fashion, but were large in individuals coming to the spawning grounds at all times of the year. Squid arrive there in condition to spawn, and the deterioration that takes place is due to spending their sex products and reserves in this process. Thus the fishery is not based upon the general population, but exclusively upon spawning schools (Fields, 1949).

The second factor determining what procedures I should use in sampling and analyzing the population involved recognizing that catch records are acceptable criteria of spawning intensity and these showed that one major and one minor peak of this activity occurred in Monterey Bay each year. I have previously discussed this seasonal fluctuation in availability in considering the fishing season, and demonstrated it in the monthly catch averages for a series of 6-year periods (Figure 7). Where a general pattern is repeated through so many years, catch becomes acceptable as a criterion of availability, because variations in demand will tend to cancel out. The records for 1943 to 1948 are most valid, because throughout those years there was constant demand and very intensive fishing over the small area into which the schools migrate to spawn. These figures should reflect quite accurately the fluctuations in the squid numbers temporarily inhabiting the spawning grounds, and show also the variations in the intensity of spawning during these years. Although the annual variations are considerable within each year-class, the curves for all year-classes show the same general pattern, and justify our acceptance of this as the pattern of availability, and therefore of spawning and fishing seasons also.

All of the year-classes conform generally to this pattern but, beginning in the 1943–1948 period, the proportion of the catch taken in spring and early summer decreased, while that of the later summer and fall increased greatly. Formerly, spawning was finished for most squid by June or July, but now increased numbers apparently do not attain spawning readiness this early, and these animals extend the season of active spawning into September. The period of most intense spawning is, however, usually from April to July, with a minor peak often occurring in November; the fishing season coincides with the availability of these spawning animals.

These conclusions supply information about the spawning adult and, equally important, provide a starting point for the life cycle. Young animals enter the population throughout the year, but in greatest numbers from the spring spawning; this, and possibly the November peak, should make obvious crests in any population profiles studied for age and growth rates.

A third factor in determining procedures in this investigation was that only one of the three possible methods for measuring growth rates could be used here. The methods employed for determining mollusc ages have been grouped by Haskin (1954) into the three categories of size-frequency study, interpreting growth interruption lines on hard parts of the animals, and experimental methods involving release and recovery of marked individuals. He considers age determinations to be somewhat doubtful when based on either of the former two alone, unless confirmed by evidence from one of the other methods.

Growth lines are valuable as age indicators if their causes can be identified with certainty, as in the Pismo clam, Tivela stultorum, studied by Weymouth (1923), where they were demonstrably winter checks. Mason (1957) describes growth rings related to two spawning periods, one in spring, one in autumn, of the scallop, Pecten maximus. Haskin (1954) relates personal communications from Posgay (1954) stating that growth interruption lines in the sea scallop, Pecten grandis, may be caused by dredging disturbance or by summer heat, as well as by winter cold (producing two or more checks per year), and from Turner (1954) who tells how growth in the moon snail, Polynices duplicata, is determined by food supply, thus making shell-growth checks completely unreliable as indicators of age.

The pens of L. opalescens show a great many fine lines which may be due to periods of growth interruption, but no significant pattern is discernible—in fact, if a recognizable pattern had been found, there would be few known data regarding fluctuations in the squid's environment with which the pattern could be coordinated. It was assumed that the same factors of unidentifiable frequency and nature would affect statolith deposition, and that any markings there similarly would be impossible to interpret.

Releasing and recovering tagged animals provides reliable growth information where the marking is of a type which does not affect normal activities and where a good recovery of marked animals may be expected. This method has been used very successfully for a number of molluscan types, and also is common practice in fisheries work.

Successful tagging of the squid Ommastrephes sloani pacificus (Steenstrup) during a study of its migrations in the coastal waters of Japan is reported by Soeda (1950, 1956) and by Machinaka (1959). A small, broad strap-tag was used, clipped onto a fin. The longest time elapsing between release and recapture of an animal by Soeda (1950) was 108 days; tag recoveries ranged from 0.43 percent to 2.324 percent. The catch consists mainly of migrating animals, distant from the spawning grounds, which are taken chiefly by jigging with hand lines.

Tagging experiments with L. opalescens were carried out in the laboratory in 1948. Strap opercular tags, measuring 3 by 17 mm when attached, of the type used and illustrated by Fry and Roedel (1949), were tried in various ways. The best position for attaching them appeared to be transversely on the posterior part of the fin, and longitudinally about the anterior, lateral margin of the mantle behind the eye. The tag did not appear to impede the animal's movements, but in some cases muscular action enlarged the hole where the tag was clamped through the fin or mantle. Average survival time in the aquaria apparently was shorter for tagged than for untagged members of a sample. No program of releasing marked squid was undertaken because I doubted that they would live sufficiently long and normally to yield useful data if recaptured, and because of the small tag return likely where such large numbers are taken by wholesale methods without being individually handled, but mainly because of increasing certainty that a mature squid comes to Monterey only once to spawn, and then dies.

Thus, the only method remaining by which age, growth rate, and related questions could be answered for L. opalescens was by collecting and interpreting population data.

A fourth major factor determining procedures in sampling for a population analysis was that the Hopkins Marine Station did not have a suitable boat and nets which would permit direct collecting by the investigator. For obtaining samples of the squid population, I was completely dependent upon commercial catches, wherever and at whatever seasons they were available. Since this was the case, there arises a question as to the degree to which the samples I finally obtained could be considered representative of the bay's squid population. On one hand, the adequacy of the material obtained from commercial samples of various sorts was related to the place and method of capture, and to the procedures used by fishermen and cannery workers in handling the catch prior to the time when samples could be taken for study.

On the other hand, the degree to which the samples obtained from catches of various sorts could be considered representative of the squid in the bay has been an important factor in determining the methods used in analyzing the resulting data.

No doubts exist as to the adequacy of the large random samples taken from the commercial squid catch. These squid were caught as described earlier, and large random samples were obtained by dipping specimens out of the catch with a bucket. Samples taken in this way could be considered quite representative of the catch. However, the catch itself represented almost excusively the reproductively mature spawning element of the squid population, and did not contain proportional representation of the earlier parts of the life history.

Real doubts do exist as to the adequacy of the samples on which an interpretation of the earlier free-swimming stages of the life history have had to be based. Occasional small squid are taken in commercial catches of reproductively mature adults; these are so few that an adequate number could be obtained only by highly selective removal of small animals, which immediately introduces a statistical bias. Most of the other small squid obtained were those accidentally or incidentally taken by fishermen along with schools of fish. Here, the fishermen, searching Monterey Bay and adjacent waters for fish schools, would usually need to set their nets a number of times about different schools to complete the night's catch. In most cases, no squid were among the fish, occasionally there were a few, but rarely were there many. Thus if admixture of squid occurred only occasionally, it was unlikely to be widely representative.

Fish handling gave chances for loss of smaller animals. Some might be lost through the mesh of the net, or through those of the dipnet with which the catch was loaded and unloaded. Several boats would unload in sucession at a cannery, brailing the fish into a hopper from which a rotary pump drew them through a water-filled pipe into the cannery. Here the fish were lifted by an elevator consisting of a swiftly-moving endless belt of open-wire mesh with projecting crosspieces; the heavy stream of water would pour through the net carrying small objects with it while the fishes and any squid that had been retained were lifted, weighed, and carried in flumes to temporary storage tanks. As needed, the fishes were moved from these by flume and elevators, to cutting tables, where they were cut to suitable size and packed in cans. Many squid were discarded with the fish residues; some would accumulate in unused areas upon and beneath the work space, and in some cases workers would toss them aside for their own use.

If any squid were among fish being unloaded, I would pick out as many as possible from the moving, loaded elevator, and these probably were good samples of any schools taken where the boat had fished. When the canneries had been operating for some time, I would collect all of the squid that were available along the cutting or packing tables. These parts of the sample probably differed from the initial proportions taken in any one school, but they may have been more widely representative, being drawn, as they were, from the catches of many boats. These admittedly were haphazard collection methods, but they were the only methods by which I could obtain sufficient numbers to derive a picture of juvenile squid growth. While these methods of sampling the juvenile squid population do provide some information on squid growth to maturity, they do not provide the sort of data which lend themselves to critical statistical analysis.

13.2. Body Measurements

The data presented here are based mainly upon length, but in some cases upon weight also, of a squid or its parts.

The dorsal mantle length was taken as the basic measurement for comparative purposes because it is one of the few dimensions of the animal which is stable regardless of the animal's condition, the cause of death, or subsequent treatment. The skeletal pen prevents any significant change in the mantle's length. Measurements were made from the tip of the rostrum above the head to the posterior end of the mantle between the fins. This is the dimension meant when I use the term length.

When mantle thickness was to be measured, the whole ventral midline of the mantle was slit open at right angles to the surface with a sharp blade so that its thickness was not affected. In adults the mantle reached maximum thickness, usually about 25 mm behind its anterior margin, so at this point the thickness at the cut edge was measured with dividers which were then applied to a fine scale.

Where whole animals were to be weighed, they were first arranged so that any water in the mantle cavity could drain out completely, but they were not dried in any other way. Where small dissected parts were to be weighed, they were touched briefly to or rolled upon a towel to remove excess water. Thus where weights are given they are of moist animals or of moist parts.

13.3. Population Samples and Data

13.3.1. Samples from Spawning Schools September 1946 to May 1948

Thirty-five samples were collected to study the reproductive systems described in the preceding section; mantle lengths were recorded on all of these. Mantle length of the largest male was 191 mm; that of the largest female was 180 mm. Samples taken from January 1947 until the end of this series each contained only a few animals selected according to sex; those of September to December 1946 were random samples totaling 20 to 50 squids per month. These have proven very valuable, because they are the only known samples of this nature showing squid which grew to maturity while sardines were still a major component in the fauna of the waters off central and northern California.

13.3.2. Random Samples from Spawning Schools June 1948 to July 1962

Between June 1948 and July 1962, large random samples were collected from commercial squid catches from Monterey Bay. Some samples were taken from the nets, some were taken aboard the fishing boats or as the catch was being unloaded, and a few were obtained from wholesale dealers before any selection had occurred. The only sample not obtained from commercial squid catches was that of February 28, 1949, obtained aboard a drag boat (trawler) when no regular catches had been available for several weeks.

I recorded the weights and mantle lengths of all specimens in the samples collected from June 1948 to September 1950, except for the sample of May 10, 1949, of which the 12 males and 75 of the females, taken at random were measured and the remaining 76 females were discarded.

In addition, mantle thickness, and weights of the dissected parts of the reproductive systems were measured for four representative samples taken in September and December 1948, and February and May 1949. For the samples later than September 1950, only the mantle length and general condition (e.g. gravid, spent, etc.) of each animal were recorded.

The mantle lengths of all males and females taken in random samples from spawning schools, June 1948 to July 1962, were recorded separately. Samples collected in any one month were grouped. Size groups were set up for each 5 mm range of mantle length; each was identified by the multiple of five which was its class center. I listed the number of animals in each group, and the percentage which this number represented of the whole number in the samples of that month. I also recorded the number of samples and the number of animals taken in each month. These 79 samples included 3,897 males and 3,763 females. Monthly population profiles were drawn from these data (Figures 50 and 51) for spawning males and females.

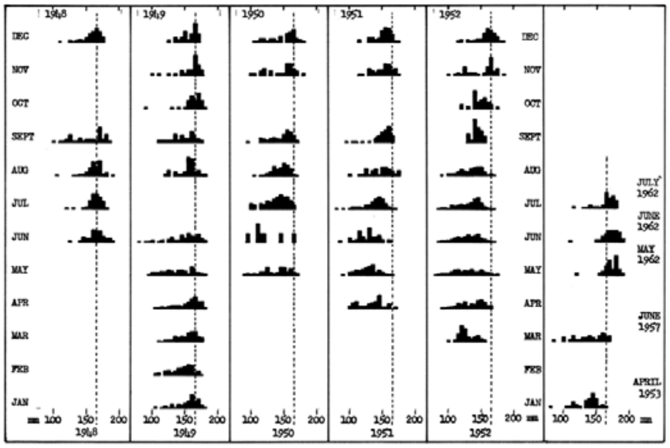


FIGURE 50. Length distribution of male squid in spawning schools, June 1948 to July 1962. Numbers of animals in each size group are shown as percentages of the total number of male animals in normal random samples collected from spawning schools in each month. Broken lines at 165 mm permit comparison of profiles to show seasonal and long-term fluctuations in size.

FIGURE 50. Length distribution of male squid in spawning schools, June 1948 to July 1962. Numbers of animals in each size group are shown as percentages of the total number of male animals in normal random samples collected from spawning schools in each month. Broken lines at 165 mm permit comparison of profiles to show seasonal and long-term fluctuations in size

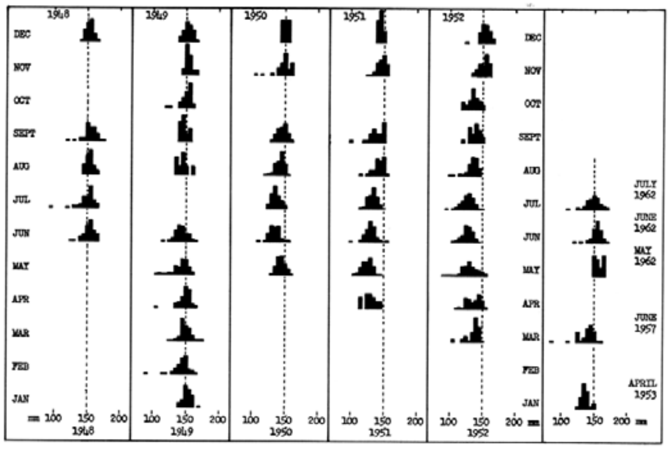


FIGURE 51. Length distribution of female squid in spawning schools, June 1948 to July 1962. Numbers of animals in each size group are shown as percentages of the total number of female animals in normal random samples collected from spawning schools in each month. Broken lines at 150 mm permit comparison of profiles to show seasonal and long-term fluctuations in size.

FIGURE 51. Length distribution of female squid in spawning schools, June 1948 to July 1962. Numbers of animals in each size group are shown as percentages of the total number of female animals in normal random samples collected from spawning schools in each month. Broken lines at 150 mm permit comparison of profiles to show seasonal and long-term fluctuations in size

Similar data were summed by month for the 1,016 males and 1,142 females of the 25 samples collected from June 1948 to December 1949. All of the animals caught in the same month of both years (1948–1949) were grouped, and the numerical and percentage frequencies of various size groups were noted, as were the number of samples and the number of animals taken in each month.

I recorded separately the mean mantle lengths of the male and of the female squid taken in each month in the random samples from spawning schools, June 1948 to July 1962.

13.3.3. Selected Samples from Squid Schools June 1948 to September 1950

Because the mature small animals were a minority of the spawning schools, they appeared erratically and in very small numbers in the normal samples taken. In order to have significant numbers for determining their size frequencies, sex ratio, and condition, a series of samples selected for smallness was collected—that is, all of the animals which seemed below some approximately set limit were taken as they appeared. Such samples were taken in March, April, and May 1949, and in May 1950, and three animals were obtained from a catch in December 1948.

It was recognized that the upper ends of such samples would have no significance because they would normally be continuous with increasingly larger numbers of larger animals, and because the location and abruptness of the separation from larger forms differed considerably, due to variations in collection. These data are useful, however, because they show the relative frequencies of all of the small animals from below this area of overlap downward, and because they show much more clearly than the random samples can, the lower limits of sizes and relative frequency by sexes of small squid entering the spawning schools. Each sample was collected on a single day, and represents from one to several squid catches, each usually of 10 tons or more; through sampling in this way, as many small animals, in their normal ratio within the limited size range, were obtained for study as would have been taken in an average sample if the entire catch had consisted of small individuals. In a few cases, some larger squid were picked out for other purposes; these were listed with the samples, but the numbers shown for them have no relationship to the relative frequencies of animals of these sizes.

Separate listings were made for numerical and percentage frequencies of the mantle lengths of male and female animals, their mean mantle lengths, the number of samples, and the number of animals taken in each month. Samples were taken in May 1949 and May 1950; for these figures are both separate and combined.

Although the same selective process applied to both sexes in collecting these samples from the spawning population, the males greatly outnumbered the females in the smaller sizes, while the females were more numerous as their normal spawning size was approached. For calculating the means, only animals smaller than an arbitrarily set limit of 132.5 mm were used.

13.3.4. Samples from Fish Schools April 1947 to July 1952

Immature animals were not normally found in the commercial squid catch, but sometimes were found in small numbers among sardine, anchovy, or mackerel catches taken in Monterey Bay. Two small samples were taken in April and May 1947; from July 1948 until July 1952, larger samples were taken whenever possible. Samples collected in 1948 were chiefly from the cutting tables of the canneries. Occasionally, squid were found in large numbers, but frequently several canneries were visited to obtain the animals used in a single sample. At times, no squid would be found along the whole of "Cannery Row" in Monterey. Starting in 1948, samples were taken whenever possible from cannery elevators or scales while the catch was being unloaded. This gave a better picture of where the young were found in Monterey Bay, because the fisherman could be questioned when a catch included any squid.

The numerical and percentage frequencies of the size-groups (based on mantle lengths) of males and females, the number of samples, and the number of animals taken in each month from among fish schools were recorded. Some of these animals were mature but most were not. If spermatophores were present in the spermatophoric sac or penis, and if there were glassy, mature eggs in the oviduct, they were judged mature.

These 44 samples representing minor populations in fish schools included 1,319 males and 1,302 females. Mantle length of the smallest male was 39 mm, that of the smallest female was 38 mm.

I also made summations by month of similar data for both males and females which were caught in the same month of various years from 1947 to 1952.

13.3.5. Samples of Smaller Animals from Various Sources

Except for newly-hatched squid, which appeared frequently in plankton hauls, very few animals having mantle lengths of less than 50 mm were examined.

In October 1930, Tage Skogsberg recorded the occurrence of "thousands of small squid in a shrimp trawl haul" taken in Soquel Cove at the northeast corner of Monterey Bay in 11 meters. Twenty specimens were preserved. The smallest of these had a mantle 21 mm long, the largest was 32 mm long. It was not possible to separate the sexes in these animals. Their size distribution was recorded according to mantle length.

In July 1931, Dr. Skogsberg found seven squid ranging in mantle length from 4 to 9 mm in a plankton haul taken from 200 meters 6 miles northwest of Pt. Pinos, Monterey Bay.

In March 1931, G. E. MacGinitie collected 11 L. opalescens of about 50 mm mantle length from a depth of 70 fms., but I have no record of where in Monterey Bay these were taken.

I did not dissect the specimens in these three samples so their sexes were not distinguished. Numbers, and size-distribution of males and females have been very similar in samples of small squid where such determinations have been made. The size range within each of the three samples was very small, so I assumed that little error would be introduced if all of the specimens in each sample were used as though they represent males only, and again as females only, in deriving growth curves, etc.

In February and March 1953, R. W. Morris and D. J. Miller collected samples of small squid with a dipnet under a light at Moss Landing. Sexes of these were separated and data on them recorded.

13.3.6. Samples from South of Monterey Bay

A few squid samples from off the coast south of Monterey Bay were also examined.

1) From October 1946 to February 1947, California State Fisheries Laboratory personnel collected seven samples, a total of 46 squid, from among sardine catches delivered to San Pedro. Data regarding maturity, mantle length, and mean mantle length in each month were recorded, although the mean mantle length has little significance, due to the small numbers concerned.

2) In January and February 1949, some squid were taken aboard the research vessel *Orca*. A 116 mm long female was caught in January in a beach seine in Santa Barbara Harbor; the other animals of the January samples were taken off Santa Cruz Island. Those of the February samples were collected off San Clemente and South Coronado Islands. They were collected chiefly by means of a light and dipnet.

3) In September 1950, a squid sample was obtained from among sardines caught off Salmon Cove near Piedras Blancas. Data regarding mantle lengths of these animals were recorded for both males and females; however, this sample was not included in my summations of samples and animals, nor in my calculations of mean mantle lengths for that month.

14. SEX RATIO

The equality of numbers of male and female animals in the population of L. opalescens became clear very early in my study. Single samples, or in some cases, a succession of samples might show much variation, but the cumulative totals of the two sexes remained very similar to each other.

Between April 1947 and September 1950, 32 samples of small squid were collected from fish catches. In them were 1,280 animals, 654 or 51.1 percent males and 626 or 48.9 percent females.

From September 1950 to July 1952, 12 additional samples were collected from fish catches. In them were 665 males and 676 females, bringing the cumulative totals for samples from this source to 1,319 males and 1,302 females.

From June 1948 to September 1950, 35 samples were taken from catches of adult spawning animals in Monterey Bay. of the 3,041 specimens in them, 1,443 or 47.4 percent were males and 1,598 or 52.5 percent were females.

Between September 1950 and July 1962, 44 additional random samples were obtained from the spawning population, and these contained 2,454 males and 2,165 females; giving totals of 3,897 (or 50.9 percent) males and 3,763 (or 49.1 percent) females from this source. Thus, it may be concluded that approximately equal numbers of the two sexes are found both in the spawning population and among smaller squid feeding with fish schools.

15. GROWTH AND MATURATION

The problems of growth rate, age at maturity, number of seasons of spawning, and life span were most tantalizing. Spawning adult animals alone comprise the commercial catch; animals of intermediate size could be obtained with difficulty and during part of the year only; smaller animals were comparatively inaccessible. Spawning occurs throughout the year, thus intergrading of sizes tends to conceal successive year-classes.

15.1. Spring Spawning Peak

Fortunately, the intensity of spawning varied during the year. The bulk of the squid catch during each of my arbitrary 6-year periods (Figure 7) was taken between April and July, with the peak in May, and a minor peak in November. From studying squid reproductive systems from the 1946–48 period, I had concluded that catch records are indicative of both availability and spawning intensity over the spawning grounds; thus, the May–June peak of spawning should produce a recognizable population crest. Enough data were accumulated so that their analysis permits tracing of this crest to reveal the growth rate. May was taken as the typical spawning month from which any population crest would originate, and regular progressions in size were sought in succeeding months. Because peak spawning recurred constantly in the spring (although the exact months varied somewhat from year to year), it was assumed that most of the animals spawning then had been spawned in the spring, 1, 2, or more years before.

15.2. Composite Population Profiles

In order to picture annual changes, a composite figure was prepared for each sex which included the data from all of the random samples from squid catches in Monterey Bay between June 1948 and December 1949, inclusive, and from all of the small animals available through 1952. The percentage frequencies of size-groups (based on mantle length) shown for each type of sample are summations of all the animals taken in the same month of the years represented. For each type of sample, a scale convenient to it has been chosen; these are not inter-related, and do not express the proportions of these animals from different sources in the general squid population.

The percentage frequencies of size groups for each month's samples of each type are represented by histograms for males (Figure 52) and females (Figure 53).

All of the specimens in each of the samples taken by Skogsberg in 1930 and 1931, and by MacGinitie in 1931, are included in each figure, because it was not possible to separate the sexes in these animals. The sexes are shown separately for all other samples.

15.3. Growth Rate

Data permitting derivation of growth rates accumulated slowly. The typical mantle length of the male adult was about 165 mm; the bulk of spawning in May and June gave an origin for any advancing major population crest. As profiles of spawning schools were drawn, a pattern emerged which appeared to be repeated. Modes, or size groups which

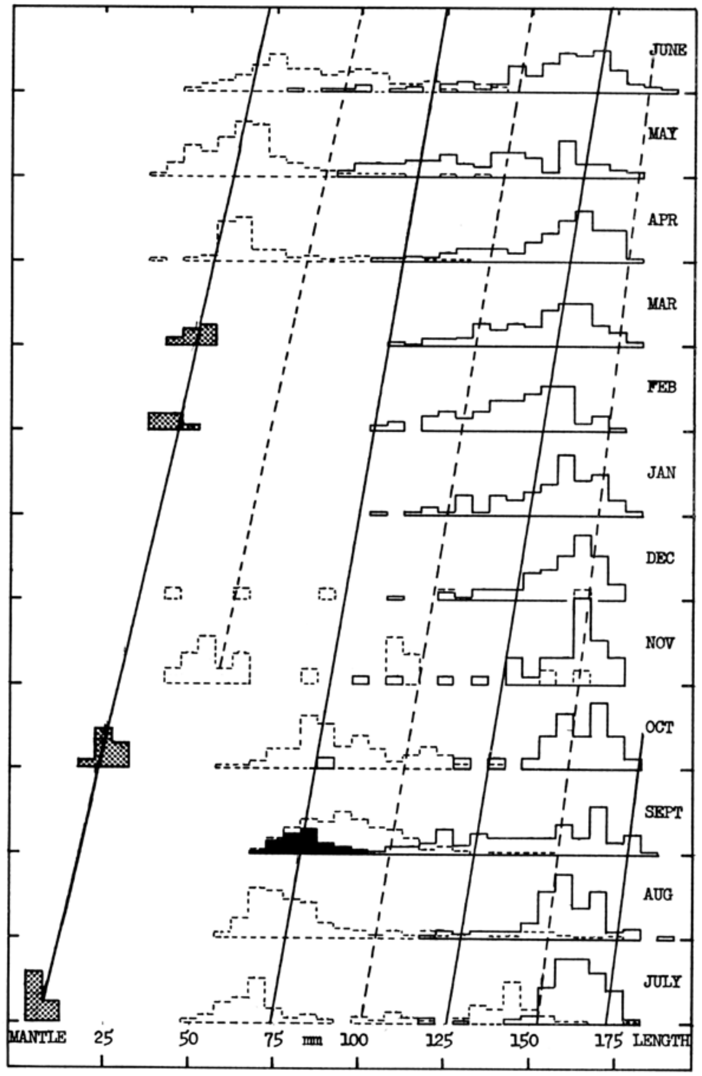


FIGURE 52. Composite population profiles of male squid showing growth rate. Polygons represent samples from fish schools (broken lines), from spawning schools (solid lines), young from various sources (stippled centers), and September 1950 samples from fish schools (solid centers). Diagonal lines indicate growth curves of spring-spawned stock (solid) and fall-spawned stock (broken).

FIGURE 52. Composite population profiles of male squid showing growth rate. Polygons represent samples from fish schools (broken lines), from spawning schools (solid lines), young from various sources (stippled centers), and September 1950 samples from fish schools (solid centers). Diagonal lines indicate growth curves of spring-spawned stock (solid) and fall-spawned stock (broken)

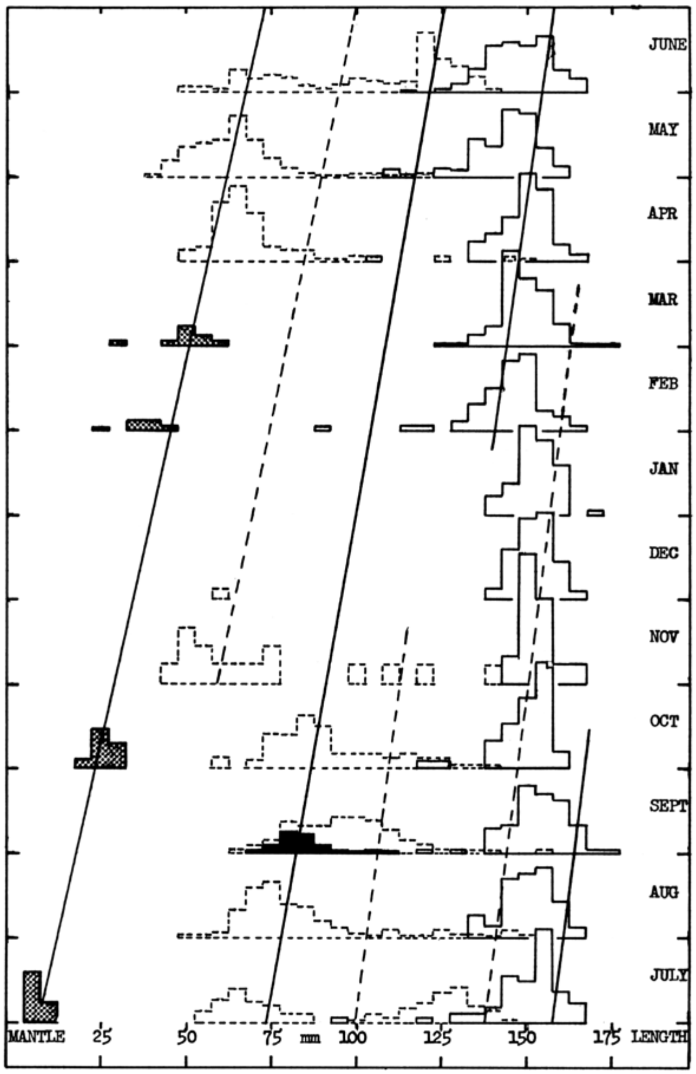


FIGURE 53. Composite population profiles of female squid showing growth rate (for explanation of symbols see caption of Figure 52).

FIGURE 53. Composite population profiles of female squid showing growth rate (for explanation of symbols see caption of Figure 52)

were taken to represent schools derived from the same season of spawning, appeared to advance in size through successive months at a rate of approximately 4 mm per month. Apparently the main February 1949 population (with mode 155 and 160 mm) advanced in size through March (mode 160–165 mm) and April (mode 165 mm), was not dominant in May, then advanced in size but was represented only by small numbers in June (mode 170 mm) and August (Figure 50). Another half-year-class first seen in may apparently contributed the bulk of the June and August-to-December line. In 1950, a group seen in May (mode 145–150 mm) seems to be followed by others from the same spawning which supplied most individuals of the July, August, and September schools.

Many other examples, sometimes more clearly seen in separate samples than in data combined by the month, reiterated this size advance of approximately 4 mm per month for modes of the spawning animals of both sexes.

When extended downward from 165 mm, a line of this slope needed to be deflected very little to find an origin 35 months earlier in the 3 mm mantle length of a newly-hatched squid (Figure 52). Initially this provided a hypothetical growth curve and the hypothetical age of 3 years for the typical adult.

Samples of small squid, collected over many years (Figure 52), appear to confirm that this curve shows correctly the squid's growth pattern through its first 10 months of life.

Documenting the next 7 months of the squid's growth was much more difficult. Data were obtained by studying squid from fish catches. The extent to which these samples were likely to conform with or differ from the natural population was considered in deciding how the data should be treated.

The first factor I considered was whether the squid population of all sizes was uniformly distributed throughout Monterey Bay (in which case every fish catch should bring in a representative sample), or whether squid congregate in schools; if the latter, does a school include a wide range of sizes, only animals of a half-year-class (i.e., from May–June or from November spawning peaks) or a range even smaller than this?

Data already studied left little doubt that young squid go in schools of narrow size range. In July 1931, Skosberg took seven individuals of 4 to 9 mm mantle length from a depth of 200 meters more than 7 miles from the spawning grounds. In October 1930, he found, "thousands of small squid in a shrimp trawl haul" in Soquel Cove (in the northern part of Monterey Bay); 20 specimens he saved were 21 to 32 mm in length. In a plankton haul in March 1931, MacGinitie took 11 squid with lengths ranging from 48 to 57 mm. Young L. opalescens are found only occasionally in plankton hauls, and the measurements of individuals from single hauls indicate they are not uniformly distributed, but are in schools containing a narrow size range of individuals.

Data from many squid samples taken in fish schools confirm this. In July 1948, 30 of 35 male squid in three samples were between 53 mm and 72 mm (range 20 mm); in November 1948, out of 18 in two samples, 9 were between 42 and 67 mm (range 25 mm), and 5 between 108 and

117 mm (range 10 mm); in April 1949, out of 14 in two samples, 7 were between 48 and 72 mm (range 25 mm), and 5 between 92 and 102 mm (range 10 mm); in August 1949, out of 34 squid, all 22 of the immature animals were between 72 and 102 mm (range 30 mm); in September 1950, out of 71 squid in two samples, 69 were between 67 and 97 mm (range 30 mm); and in May 1951, all 63 in a sample were between 57 and 92 mm (range 35 mm); each of these groups is separated by a size gap from other animals of the sample and presumably represents a school.

Taken together, this information and the hypothetical growth rate I have proposed strongly suggest the pattern that exists in the hierarchy of squid schools. If a typical male squid returns to spawn when 3 years old and 165 mm long, it has had a growth rate, after a month in the egg capsule and 2 or 3 months when very small, averaging 55 mm per year (i.e., slightly less than 5 mm per month). If this is the squid's growth rate, then the size ranges of the schools cited above represent approximately one-half or less than one-half of a year's growth. Thus, each school is typically composed of animals spawned within a half-year period (i.e., from the May–June peak or from the November–December peak but not from both, with animals spawned in the intervening periods joining one group or the other). This implies that, at any time, there is a series of squid schools stemming from each of these peaks; each follows its own growth path parallel to, but separated from, the paths of those series in which the animals average younger or older.

If squid spawned only in May and November, there would be at all times three size groups of squid 18 months old or less, and the range in each group would average 30 mm, ideally with no overlap. However, each spawning period extends for several months, overlapping with the next, with the result that the modes from the spawning peaks are not sharply separated and distinct. Furthermore, the analysis of catches shows that the range within a school frequently may be considerably less than 30 mm; this means that individuals derived from a given peak spawning period are further subdivided into schools representing smaller size groups and that, therefore, several size-groups of squid, younger than 18 months and schooling separately, are present in the Monterey Bay area at all times.

Under these circumstances, it would be necessary to combine a great many samples to produce figures completely representative of the population. The sampling methods I used do not appear to have drawn from schools in proportion to their actual frequency in some months, and small samples apparently typical of the modes corresponding to peak spawning periods were submerged, e.g. the solid black areas in Figures 52 and 53, representing the two samples of September 1950. Also in some months, for the same reason, the growth series derived from the November spawning appears more prominent than its minority numbers warrant. Such data may represent two successive year-classes of fall-spawned animals alone, or an overlapping of spring- and fall-spawned populations.

It is noteworthy here that September typically brings the so-called Oceanic Period in the cycle of water masses at Monterey; cessation of up-welling and incursion of warmer surface water produce variable conditions in September and October, and conditions may not be repeated in successive years. By November, the surface Davidson Current from the south has become established. Adult squid participating in the November spawning peak dominate in these fall months; they appear to be accompanied by young animals of the same fall-spawning cycle. These young squid as they approach 1 year old in November and December are 45 to 65 mm long, and approaching 2 years old in September they are 95 to 115 mm (Figures 52 and 53); male animals continue to be obvious until the spring when, at an age of 2½ years, males and females appear with older animals in the spawning schools. The disappearance of essentially all the spring-spawned animals and the sudden relative abundance of 1- and 2-year-old animals of November origin (Figure 52, November) immediately prior to and during the Davidson Current period appears to be related to the seasonal change in hydrographic climate in the Bay.

Other complicating factors are the seasonal and long-term fluctuations in growth rate associated with changes in amounts and types of food available. In the much larger (adult male mantle length 640 mm) squid Ommatostrephes todarus in Icelandic waters, Fridriksson (1943) observed growth increases per 30 days of 7.6 cm in July, 5.2 cm in August, and 2.8 cm in October in juveniles, and 2.2 cm during winter in adults. It seems likely that seasonal fluctuations in growth rate occur in L. opalescens also.

Finally, squid larger than 85 mm (roughly 17 months old) are virtually absent from the fish catches brought into Monterey; they appear again in the catches only as adults in spawning schools. However, if the 4 mm per month adult growth rate has continued during the intervening 19 months, a male squid 3 years old would have a mantle length of 165 mm, which is the typical size for male spawning animals.

In summary, then, the best interpretation of all data concerning the growth rate of male squid seems to be that animals spawned in the spring (i.e. May) would have mantle lengths of approximately 65, 120, and 165 mm when 1, 2, and 3 years old (Figure 52). This spring-spawned stock apparently contributes the majority of the male squid found in spawning schools from January to June.

An intervening series of minor peaks provides a second growth curve (Figure 52, broken line). Its inclination corresponds to that of the curve for the spring-spawned animals, and if November, the month when fishing records indicate a minor spawning peak, is accepted as the typical month in which these animals were spawned, then their mantle lengths at ages 1, 2, and 3 years are the same as those of spring-spawned animals at the same ages. These fall-spawned animals dominate the spawning schools from July to December, and are prominent in January.

The females show the same general growth pattern as males (Figures 51 and 53). Two distinct growth series enter the spawning grounds during the year. One is dominant from January to June, the other from July to December. In each, modes or size groups taken to be derived from the same season of spawning advance in size through successive months at a rate similar to that shown by males.

Young squid of both sexes show the same growth rate, for their size distribution in samples from fish schools is essentially the same, at least up to 90 mm; definite crests shown by females at 120 to 125 mm in June and 125 to 130 mm in July (Figure 53), suggest that a common rate continues until these sizes are reached. Thus, at ages 1 and 2 years, the sizes for both sexes would be approximately 65 and 120 mm, respectively. However, when 3 years old, a typical spawning female has a mantle length of approximately 150 mm, whereas that of a male of the same age is about 165 mm. This discrepancy cannot be ascribed to a difference in age. If the females were a whole year younger than the males, they would show a greater early growth rate than they do; if they were half a year younger, the annual spawning pattern would not repeat. The retarded progression of sizes of females observed in the spawning schools suggests that the beginning of maturity of the ova is accompanied by reduction or cessation of body growth.

Tinbergen and Verwey (1945) find that males of Loligo vulgaris with ventral mantle lengths of 130 to 140 mm and 210 mm seem to be 1 year and 2 years old, respectively, and that any older than this are rare. Females are reported to have the same growth rate to 120 mm (at an estimated age of 6 to 9 months), thereafter growing more slowly to a size of 170 mm at what seems 2 years of age. These patterns of growth of the two sexes of L. vulgaris relative to each other are very similar to those found in L. opalescens; the growth rate of L. vulgaris, however, seems to be as accelerated as is the embryonic development of another Atlantic squid, L. pealii, relative to similar processes in L. opalescens.

Rao (1954) finds a somewhat similar size disparity between the sexes of the Palk-Bay squid, Sepioteuthis arctipinnis Gould on the east coast of South India. He concludes that the females do not live beyond the second vear of their lives and that males live a year longer. Persistence of a constant sex ratio in juvenile and spawning populations of L. opalescens prevents my considering that explanation here, because an extra year of predation upon one sex would materially decrease its numbers.

15.4. Age Composition of Spawning Schools

The bulk of the male animals in spawning schools appear to be approximately 3 years old. A few males 6 months older appear with them, and in August, a very few a whole year older. Males 6 months younger than the modal age are fairly numerous, while others a year or even 18 months younger than the mode are found in small numbers.

Most of the females in spawning schools are approximately 3 years old. Very few differ from that modal age by more than 6 months. They are never more than 6 months older, except possibly a very few in March and September, but may be up to 18 months younger than the mode, especially during the spring. However, the number of females differing from the mode is insignificant compared to the vastly greater number of males which do so.

15.5. Size and Age at Maturity

The criteria of sexual maturity which I chose were the presence of any spermatophores in the spermatophoric sac of the male, or of any mature, glassy ova in the oviduct of the female. Hectocotylization of the left ventral arm of the male develops concomitantly with the maturation of the reproductive system. This modification may be recognized in late April in males 65 mm long in which the testis has reached about half adult proportion, and in which the spermatophoric organ is small, but apparently complete, although there are no spermatophores.

Small male squid are more frequently precocious in their maturity and association with spawning schools than are the small females. Small mature males, 105 mm or less in length, and presumably somewhat less than 2 years old, were found in normal samples taken in every month of the year. In May, June, and July their size range often was continuous down to 80 mm. Males in spawning condition as small as 72 mm long have been obtained from catches based on spawning schools. Such animals would be little more than 1 year old. These smallest mature animals have been found in the spring, when the proportion of small animals is highest (Figure 54).

Small mature females 105 mm long or less have been found with the spawning schools from February until November. Their numbers are far fewer than those of the males of like size. Female animals as small as 81 mm have been found in spawning condition. The minimum size for spawning females appears to increase somewhat from October to January, but fewer animals have been examined from these than from other months (Figure 55).

The sizes of the smallest mature males found in fish schools were much like those of the smallest males found spawning, i. e. 70 to 90 mm from April to July and 90 to 110 mm from August to November. The length of the largest immature males found in fish schools was 100 mm in the spring, but gradually increased until in the fall these animals sometimes exceeded 130 mm. These sizes declined quickly through November and December. One male taken in December was 144 mm long, but appeared barely mature. Its testis was huge, its spermatophoric sac was very small, and contained only six spermatophores. Its general proportions were much like those of the smallest mature males of April.

The smallest mature females in spawning schools vary between 85 and 105 mm from April to November; those in fish schools showed similar sizes from April until July, after which sharp increases raised their minimum sizes to 125 mm in August and 135 mm in November. Sizes of the largest immature females in fish schools increased regularly from 100 mm in April to 140 mm in September and October, then decreased more swiftly through November and December. Thus, through November and December, there was an abrupt decline in maximum size of immature squid of both sexes found in fish schools, as though some factor contributing to maturity becomes intensified during this time.

Consideration of these data (Figures 54 and 55) leads to some observations with regard to the onset of maturity. By April and through July some 80 mm male squid become mature, join the schools of larger animals, and spawn. From August through November, the minimum size at which this occurs increases appreciably, then falls again in December. The maximum size to which these animals grow before becoming mature stands at 100 mm in May and June, rises by 10 mm per month from July to September, then decreases considerably in November and December.

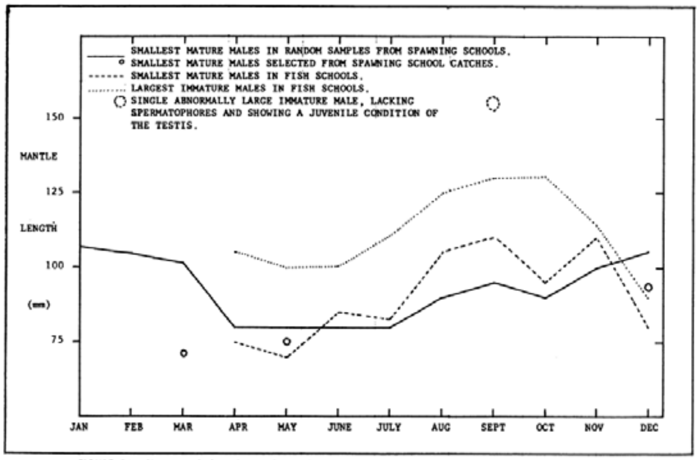


FIGURE 54. Sizes at which male squid may become mature, and size to which they may remain immature.

FIGURE 54. Sizes at which male squid may become mature, and size to which they may remain immature

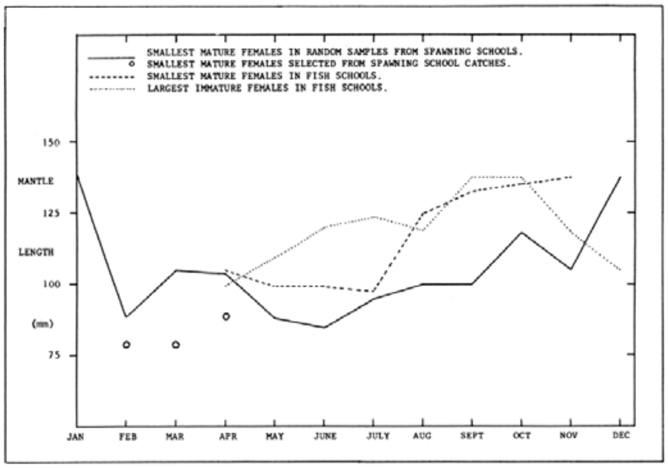


FIGURE 55. Sizes at which female squid may become mature, and size to which they may remain immature.

FIGURE 55. Sizes at which female squid may become mature, and size to which they may remain immature

The same general pattern is shown by females but at larger sizes. From April through July, mature animals about 100 mm long are found in schools of fish or spawning with larger squid, in the latter case, minima of 90 and 85 mm are found in May and June, and sizes increase above 100 mm in October to December. The minimum size of mature individuals in fish schools steps upward sharply from about 100 mm in July to 135 mm in September. The maximum size to which these animals grow before becoming mature is 100 mm in April, increases almost continuously to 140 mm in September and October, then falls sharply in November and December.

16. COMPOSITION OF THE SPAWNING POPULATION

16.1. Length Frequencies

The spawning population of L. opalescens is a dynamic association of which some characteristics have been discussed already in tracing the development of the individual; its collective aspects, however, have not been considered. One of these is an analysis of annual length frequencies (Figures 50 and 51), with a comparison of the sexes in this regard. To do this I combined data for 23 large random samples, representing the year 1952, and arranged size frequencies by each 5 mm of mantle length as a percentage of the total number of individuals for each sex (Figure 56).

Similar data for June 1948 to May 1949, (Fields, 1950) were included. The two pairs of curves represent separate summations of the random samples for the two periods; these were not weighted in any way to make them proportional to the seasonal numbers of spawning squid; this may contribute slightly to the size reductions shown, but the major cause was an actual decrease in the average sizes of individuals in the squid population.

More than half of the individuals of each sex in each group of samples fell within a size range of 30 mm. The females were much more uniform in size than the males, where the range was greatly extended by many small animals. The modal size of males exceeded that of females by 10 to 15 mm; there was less difference between the means, again because of the many small males. Average sizes of the squid in the 1952 samples were considerably below those in 1948–49; the averages of the means of mantle length for all random samples from spawning schools from June 1948 to July 1962 are 146.7 mm for males and 143.0 mm for females.

Interpretation of population data given earlier indicates that the modal spawning age for both sexes is 3 years. Animals either 6 months older or younger than this are fairly common, and a few apparently 4-year-old males occur. The minimal age at which maturity occurs, in a very minute percentage of each sex, is 1 year. Very few females mature below the modal age and size, but many small males are found in spawning schools; greatest numbers of small animals are present in the spring.

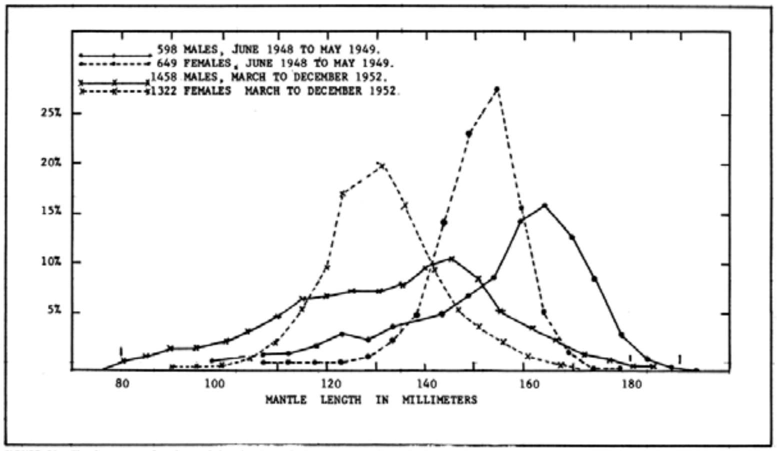


FIGURE 56. The frequency of males and females in each 5 mm range of mantle length, shown as a percentage of the total number of individuals of the respective sex.

FIGURE 56. The frequency of males and females in each 5 mm range of mantle length, shown as a percentage of the total number of individuals of the respective sex

16.2. Weight-Length Relationship

Weight-length relationships were determined from scatter diagrams representing 495 males and 536 females. Groups were set up for each 5 mm range of mantle length, and the average weight in each group was found for each sex (Figure 57). The weight differences are small between male and female animals less than 120 mm long. In larger specimens, the average weight of the male is greater than that of the female of comparable length. This difference increases regularly with increasing mantle length.

In general, the weights of the males were closer to their group averages than the weights of the females were to theirs (Table 8).

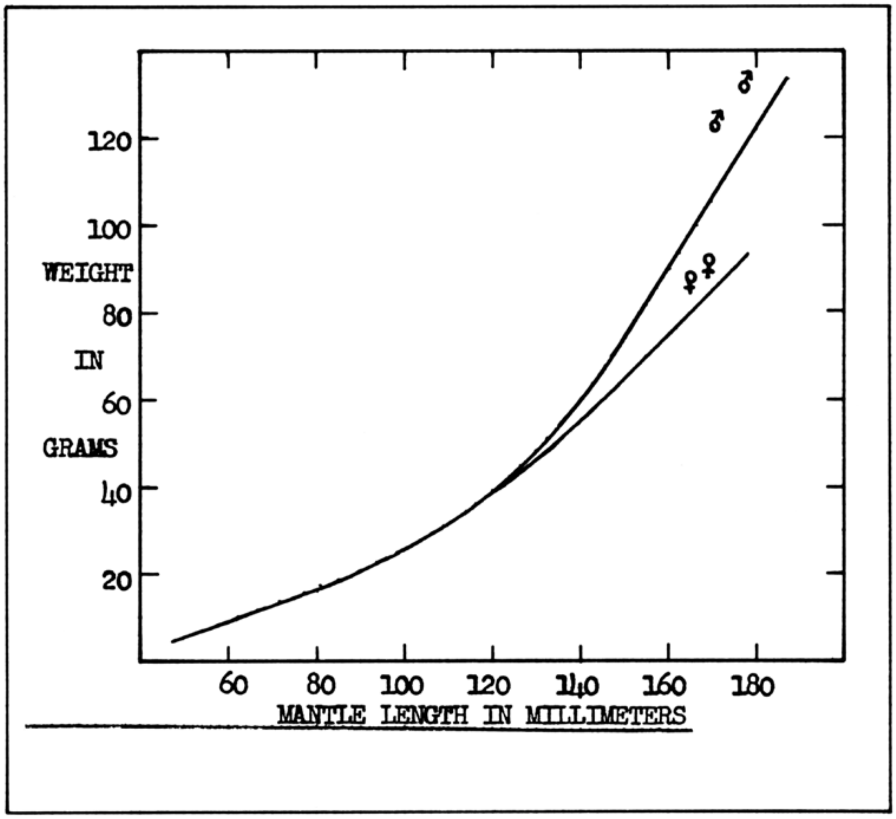


FIGURE 57. Weight-length relationship.

FIGURE 57. Weight-length relationship

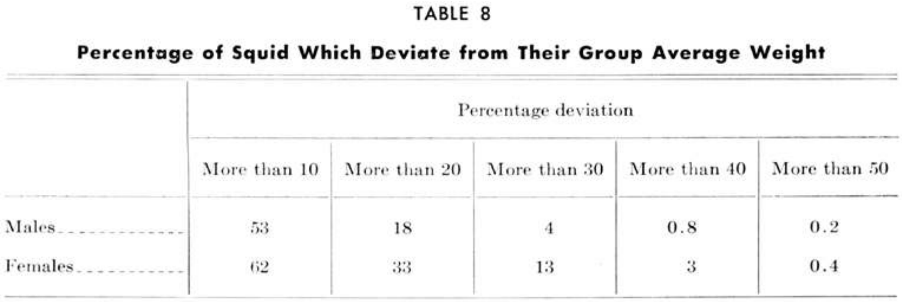


TABLE 8

Percentage of Squid Which Deviate from Their Group Average Weight

	Percentage deviation				
	More than 10	More than 20	More than 30	More than 40	More than 50
Males	53	18	4	0.8	0.2
Females	62	33	13	3	0.4

TABLE 8

Percentage of Squid Which Deviate from Their Group Average Weight

Among females, the greatest degree of variation from average weight was in animals 135 to 165 mm long, that is, within the average size-range of mature animals. Among males, the greatest variation was not within the common spawning size-range, but among the precocious small animals 95 to 140 mm long.

16.3. Average Size and Weight

The approximate average mantle lengths in the commercial catch were 150 mm for males and 140 mm for females. The average weights for animals of these sizes are approximately 70 and 50 grams, respectively (Figure 57). The sex ratio is 1:1. Consequently, the commercial catch averages about 7.5 squid per pound or 15,000 squid per ton.

16.4. Condition of Animals Before Spawning

The squid in spawning schools are in excellent condition when they enter the spawning area. Each animal is fat and heavy, its skin is glossy and unmarked. The mantle is large in circumference, and thick and firm. In most cases the stomach is empty.

In females, the ovary and the egg filled oviduct are very large and completely fill the posterior third of the mantle cavity. The gland of the oviduct and the nidamental glands are large, firm, and white. The accessory nidamental glands are orange-red in color, and may be seen clearly through the translucent mantle. In mature specimens 80 to 110 mm long, the whole reproductive system, including ova, may make up more than 25 percent of each animal's weight; in animals of average spawning size, this system may account for 30 to 50 percent of the total weight (Table 9).

In male animals, the testis is of medium size, the spermatophoric organ is large and firm, and the spermatophoric sac, filled with neatly-stored spermatophores, extends almost to the posterior end of the mantle cavity. Once a male becomes mature, spermatophores are present in this sac during all seasons and throughout the animal's life. In mature males 80 to 110 mm long, the reproductive system may represent 10 to 12 percent of the total body weight. When the animal reaches average spawning size, this system makes up only 4½ to 7 percent of the total weight (Table 10).

Small mature squid in the spawning schools have reproductive systems which, in proportion to the animals' weights, compare favorably with those of larger animals. When the averages of four typical females

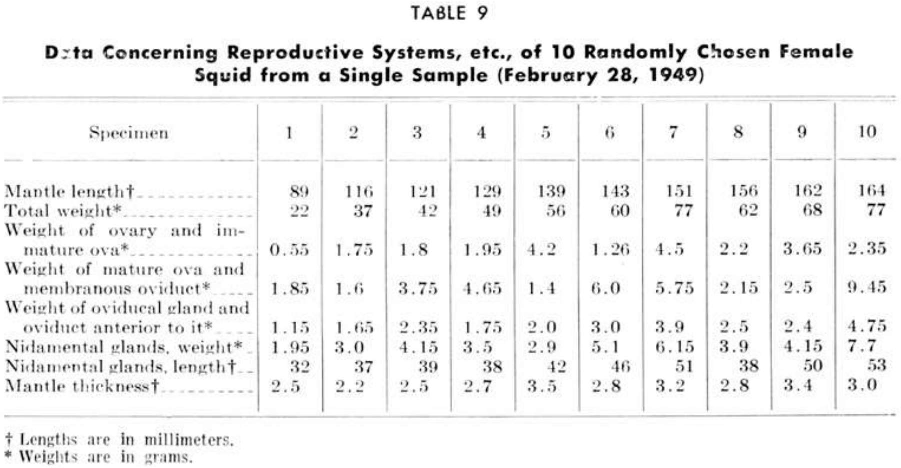


TABLE 9

Data Concerning Reproductive Systems, etc., of 10 Randomly Chosen Female Squid from a Single Sample (February 28, 1949)

Specimen	1	2	3	4	5	6	7	8	9	10
Mantle length†	89	116	121	129	139	143	151	156	162	164
Total weight*	22	37	42	49	56	60	77	62	68	77
Weight of ovary and immature ova*	0.55	1.75	1.8	1.95	4.2	1.26	4.5	2.2	3.65	2.35
Weight of mature ova and membranous oviduct*	1.85	1.6	3.75	4.65	1.4	6.0	5.75	2.15	2.5	9.45
Weight of oviducal gland and oviduct anterior to it*	1.15	1.65	2.35	1.75	2.0	3.0	3.9	2.5	2.4	4.75
Nidamental glands, weight*	1.95	3.0	4.15	3.5	2.9	5.1	6.15	3.9	4.15	7.7
Nidamental glands, length†	32	37	39	38	42	46	51	38	50	53
Mantle thickness†	2.5	2.2	2.5	2.7	3.5	2.8	3.2	2.8	3.4	3.0

† Lengths are in millimeters.
* Weights are in grams.

TABLE 9

Data Concerning Reproductive Systems, etc., of 10 Randomly Chosen Female Squid from a Single Sample (February 28, 1949)

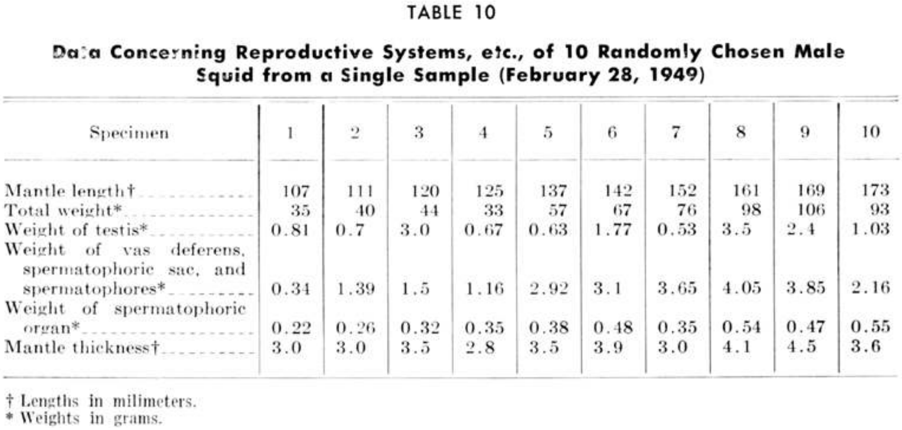


TABLE 10

Data Concerning Reproductive Systems, etc., of 10 Randomly Chosen Male Squid from a Single Sample (February 28, 1949)

Specimen	1	2	3	4	5	6	7	8	9	10
Mantle length†	107	111	120	125	137	142	152	161	169	173
Total weight*	35	40	44	33	57	67	76	98	106	93
Weight of testis*	0.81	0.7	3.0	0.67	0.63	1.77	0.53	3.5	2.4	1.03
Weight of vas deferens, spermatophoric sac, and spermatophores*	0.34	1.39	1.5	1.16	2.92	3.1	3.65	4.05	3.85	2.16
Weight of spermatophoric organ*	0.22	0.26	0.32	0.35	0.38	0.48	0.35	0.54	0.47	0.55
Mantle thickness†	3.0	3.0	3.5	2.8	3.5	3.9	3.0	4.1	4.5	3.6

† Lengths in milimeters.
* Weights in grams.

TABLE 10

Data Concerning Reproductive Systems, etc., of 10 Randomly Chosen Male Squid from a Single Sample (February 28, 1949)

were compared to small mature and immature females, the total weights of the reproductive systems were 24.1, 20.7, and 1.5 percent, respectively, of the animals' weights (Table 11).

The testis of a precocious male squid is disproportionately large (Table 12), and when the averages of four typical males were compared to small mature and immature individuals, the reproductive systems were 6.0, 12.8, 0.34 percent, respectively, of the total body weights.

16.5. Changes Due to Spawning

Spawning brings about profound changes in a squid. A spent female is small in diameter and the mantle is thin and limp. Few eggs in the ovary are approaching maturity; few or no mature eggs remain in the membranous oviduct. The gland of the oviduct and the nidamental glands are small and flaccid; the accessory nidamental glands are faintly pink. The oviduct, and an area on the mantle adjacent to it. bristle with spent spermatophores. In the female, more than 50 percent of the original weight may be lost.

When two animals of the same size from the same school were compared (Table 13), they appeared to be typical of the gravid and the spent females on the spawning grounds. The differences between them closely resembled the changes which take place in a single animal during the spawning process. If the two sets of data are used as though

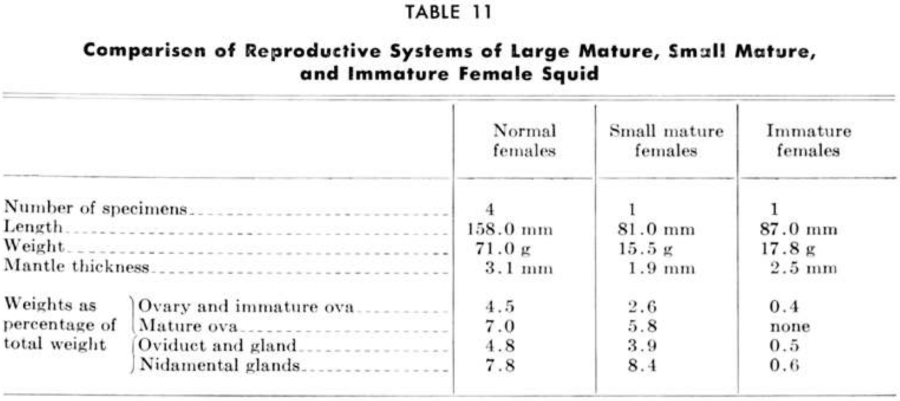


TABLE 11

Comparison of Reproductive Systems of Large Mature, Small Mature, and Immature Female Squid

		Normal females	Small mature females	Immature females
Number of specimens		4	1	1
Length		158.0 mm	81.0 mm	87.0 mm
Weight		71.0 g	15.5 g	17.8 g
Mantle thickness		3.1 mm	1.9 mm	2.5 mm
Weights as percentage of total weight	Ovary and immature ova	4.5	2.6	0.4
	Mature ova	7.0	5.8	none
	Oviduct and gland	4.8	3.9	0.5
	Nidamental glands	7.8	8.4	0.6

TABLE 11

Comparison of Reproductive Systems of Large Mature, Small Mature, and Immature Female Squid

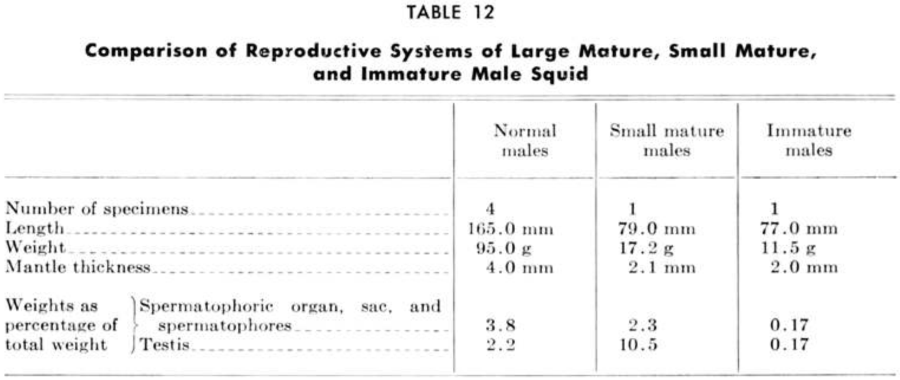


TABLE 12

Comparison of Reproductive Systems of Large Mature, Small Mature, and Immature Male Squid

		Normal males	Small mature males	Immature males
Number of specimens		4	1	1
Length		165.0 mm	79.0 mm	77.0 mm
Weight		95.0 g	17.2 g	11.5 g
Mantle thickness		4.0 mm	2.1 mm	2.0 mm
Weights as percentage of total weight	Spermatophoric organ, sac, and spermatophores	3.8	2.3	0.17
	Testis	2.2	10.5	0.17

TABLE 12

Comparison of Reproductive Systems of Large Mature, Small Mature, and Immature Male Squid

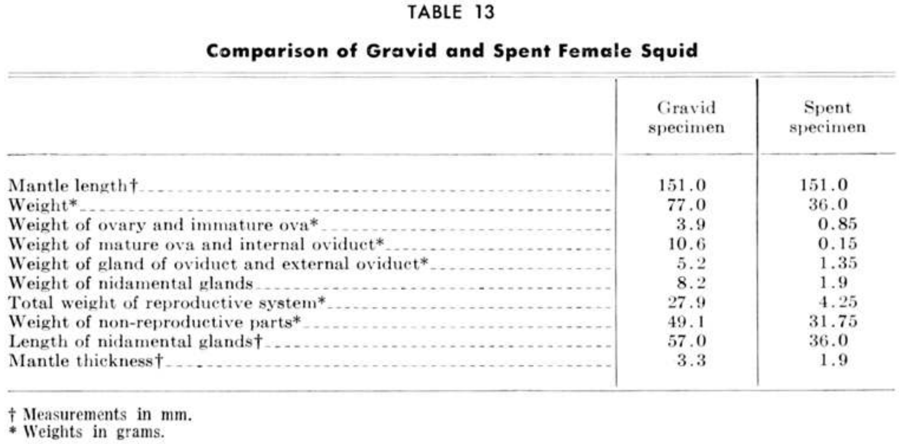


TABLE 13

Comparison of Gravid and Spent Female Squid

	Gravid specimen	Spent specimen
Mantle length†	151.0	151.0
Weight*	77.0	36.0
Weight of ovary and immature ova*	3.9	0.85
Weight of mature ova and internal oviduct*	10.6	0.15
Weight of gland of oviduct and external oviduct*	5.2	1.35
Weight of nidamental glands	8.2	1.9
Total weight of reproductive system*	27.9	4.25
Weight of non-reproductive parts*	49.1	31.75
Length of nidamental glands†	57.0	36.0
Mantle thickness†	3.3	1.9

† Measurements in mm.
* Weights in grams.

TABLE 13

Comparison of Gravid and Spent Female Squid

they were measurements of the same animal before and after spawning, they show:

Total weight loss:	41 grams	(53 percent)
Weight loss by the reproductive system:	23.6 grams	(85 percent)
Weight loss by the non-reproductive parts:	17.4 grams	(35 percent)

Arms, head, and pen showed no diminution, but the mantle decreased in thickness from 3.3 to 1.9 mm, and in girth from 71 to 54 mm. Thus it appears that the mantle is the chief site for storing food reserves consumed during this period.

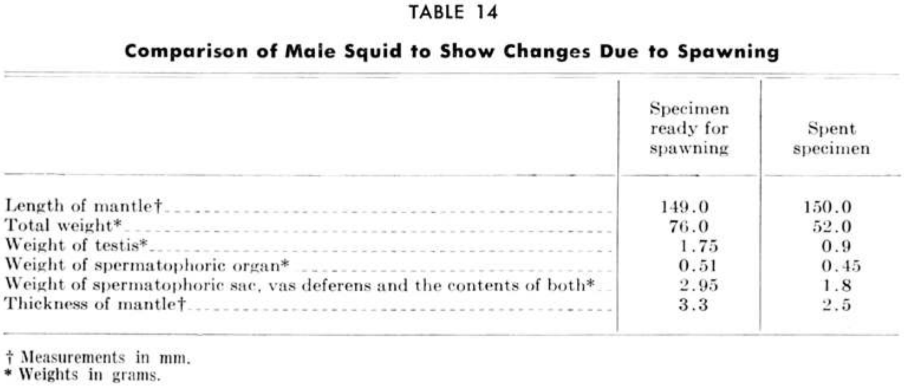
Males show similar changes during spawning, but the proportion of weight lost is smaller than in females. The testis and spermatophoric sac become small and the spermatophores are reduced in number, but the chief weight loss is from reserves in the mantle tissues. Typical changes were illustrated by comparing two males from a single sample, one specimen ready for spawning, the other spent (Table 14).

The same type of depletion occurs in the spawning of small mature squid. In a single sample, males 100 and 101 mm long weighed 32 and 22 grams respectively, and females 101 and 100 mm long weighed 35 and 21 grams respectively. All of these were in comparatively good condition; animals of this same size showing more severe depletion often weigh less than 16 grams.

These changes which occur during spawning make the squid less acceptable to the fishing industry, and when the proportion of spent animals in the catch becomes too great, squid packing ceases until fresh schools appear.

17. FATE OF SPAWNING ANIMALS

In addition to changes in proportions, degenerative changes also occur in both sexes during and after spawning. On some occasions, live squid brought to aquaria at the Hopkins Marine Station differed greatly within the sample, and have shown in varying degrees the changes that occur in nature during spawning. Although mechanical damage occurred because of the artificial surroundings, this did not appear to upset the sequence of natural changes. The animals continued to mate and spawn, but as depletion became more severe, the males



	Specimen ready for spawning	Spent specimen
Length of mantle†	149.0	150.0
Total weight*	76.0	52.0
Weight of testis*	1.75	0.9
Weight of spermatophoric organ*	0.51	0.45
Weight of spermatophoric sac, vas deferens and the contents of both*	2.95	1.8
Thickness of mantle†	3.3	2.5

† Measurements in mm.
* Weights in grams.

TABLE 14

Comparison of Male Squid to Show Changes Due to Spawning

ceased to single out receptive females and attempted to seize any animal of either sex. The arms of such an attacker often became mutilated as a result of repeated repulses by stronger animals. When a weaker animal was seized, spermatophores might be placed in its mantle cavity; it was often held for a long time and its mantle edge or funnel might be gnawed or its mantle might be bitten through. Continual rasping by suckers would often strip the skin from large parts of the arms, head, and anterior half of the mantle, and sometimes would expose the pen of the grasped squid.

This death hold of one squid upon another is illustrated by Lane (1957) in his plate 32, wrongly labeled, "A male grasps a female with his arms." Here is shown a degenerating male with tattered arms stiffened and no longer sinuous, which has, during its continued embrace, damaged the mantle of what is unquestionably another male squid. In all squid injured in such activities, a necrotic whiteness replaced the normal translucence of damaged parts, and loss of chromatophore control left the posterior half of the mantle permanently dark-colored. Motor control of the arms decreased until they became stiffly intertwined. Swimming became erratic and feeble, and the squid sank to the bottom and died.

Changes similar to those observed in aquaria occur naturally over the spawning grounds and have been noted on many occasions at Monterey. From late June until the middle of August 1951, hundreds of squid usually could be seen swimming aimlessly in the water about the Coast Guard dock (Monterey breakwater). Many had no chromatophore control (some had no skin) on the anterior part of the mantle and arms. Arms were tattered and stiffly intertwined much as in animals found dead after spawning in aquaria. Some were seen bobbing vertically up to the surface; swimming was abnormal in many. Several were lying dead on rocks inside the breakwater.

The following laboratory notes of two specimens typify the animals swimming about: "Male, 144 mm, 43 grams. Skin missing from most of anterior inch of mantle; torn elsewhere. Shallow pits present on inner surface of mantle near margin and on ventral arm. Much of arm tissue missing so that some arms are mere cores. Tentacles and part of funnel missing. Tip of pen exposed. Spermatophoric sac, stomach and caecum empty." "Female, 139 mm, 24 grams. Arms and fins tattered. Skin stripped from whole mantle in front of fins; pen exposed. Oviduct empty; no mature eggs in ovary; glands reduced; a few spermatophores remain near oviduct."

It seems impossible that any animals in this condition could recover or that any potential survivors would escape the varied and numerous predators which congregate on the spawning grounds at this time. For example for two months (July and August 1951) a huge flock of shearwaters (Puffinus sp.) and gulls (Larus sp.) fed so voraciously on squid that they could not fly out of a boat's path until each had regurgitated some food. Rolf Bolin, who passed through the flock at the southern end of Monterey Bay on several occasions, estimated that the number of birds exceeded 1 million (i.e. the flock occupied an area of roughly a square mile, with a bird every 5 feet in each direction). If each bird ate only five squid a day, such a flock in that time could have consumed 300 million aimlessly swimming squid.

Direct observations confirm that death typically occurs after spawning. In 1946, a commercial diver at Monterey described to me how he had, on some occasions, seen large masses of disintegrating squid near the spawning areas. In the spring of 1952, Keith Cox, California Department of Fish and Game, found the sea floor off the Monterey breakwater strewn with dead squid every few feet. Salmon fishermen in the area commonly snag dead squid or their pens from the bottom. McGowan (1954) and Limbaugh and Shepard (1957) describe their observations off La Jolla, California, where they found the bottom in the vicinity of egg masses completely covered with the dead and dying of both sexes.

Tompsett (1939) reports that at certain times of the year the water and shores along some parts of the Irish Sea are so covered by buoyant cuttlefish pens that these are given the name of "sea foam." Such tremendous numbers could well be accounted for by cuttlefish dying also at the completion of their spawning.

From the foregoing, it appears certain that squid die after a single spawning at full adult size and typical spawning age. Additional consideration is required to resolve whether death after a single spawning comes to animals that mature precociously and reproduce before the modal spawning age, or whether they survive to spawn again. Evidence, both direct and indirect, indicates that they also spawn once and then die. Direct observation of the catch from the spawning schools shows that these young animals receive the same type and severity of damage as do the older animals. In older animals, this degree of damage precedes death. Their smaller sizes make the young even more susceptible to seizure and destruction than their larger fellows.

Indirect evidence derived from several sources confirms the observations that squid die after spawning once. First, except for exceedingly small numbers of sexually precocious individuals, or a few scattered large squid in which the breeding urge has evidently been delayed a year beyond normal, the females spawning at Monterey are very uniform in size, lying well within the range of one year's growth. Animals of the same age seem to dominate the spawning schools for periods of about half a year. Ova probably require several months to mature when the animal is in excellent condition. After spawning, females are extremely emaciated, frequently having lost more than 50 percent of their weight. Many carry grave wounds, some certainly mortal. It seems very unlikely that a female squid could recover from one spawning, produce an egg crop and the needed tissue reserves, and participate in another spawning before animals of that age group disappear.

Second, cephalopods are said to have great powers of regeneration, and this appears to be the case in L. opalescens. In one animal, half of the arms had been lost and small arms had begun to develop from the stumps. However, it seems very unlikely that the severe damage often occurring during spawning would heal so completely that no trace would remain. Yet among the thousands of female animals measured. only one had the type of scar which might result from the healing of major spawning damage.

Third, in spawning schools the males are widely distributed in size and age, while the females form a much more compact group, with a very small percentage of their numbers differing from this modal size and age. If survival permitted successive spawnings of males, the proportion of males to females in spawning schools would be increased by a large percentage. Thus a change in the sex ratios would occur between young and spawning populations, and the increased ratio of males in the latter would be proportional to the number of males spawning more than once. However, my studies show no such change in the sex ratio.

Fourth, if male squid which spawn when 2 years old were to survive after spawning, as many 3-year-old males as females could be expected in the spawning schools. Instead of this, the number of 3-year-old males is far below the number of 3-year-old females, and just enough younger males are in the spawning population to give equality of numbers with the females. Thus the number of 3-year-old males lacking is equal to the number of younger animals present. Presumably none of these returns to spawn again.

It might be suggested that the very constant ratio could be accounted for if squid were monogamous and approached the spawning grounds in pairs. This is not borne out by observed behavior in aquaria, where squid appear completely promiscuous. Disruption of the school and abnormal conditions in the aquarium could easily upset their normal behavior; in the cuttlefish Sepia, Grimpe (1926) reports, "a certain amount of monogamy was observed," but Tompsett (1939) states that males will flock from great distances to a gravid female confined in shallow water. In L. opalescens a considerable disparity of the sexes in successive random samples occurs frequently and suggests an unbalanced ratio may persist for some time over the spawning grounds. Each of the five large samples taken from January 4, 1949 to March 14, 1949 contained at least 50 percent more males than females; at other times the balance is in the other direction. This frequent disparity, and all observations of behavior, show that this squid is not at all monogamous. Thus the 1:1 ratio is not artificial, but correctly records equal numbers of the two sexes.

These deductions from population data confirm that female L. opalescens spawn once only and, since the sex ratio is 1:1 both among immature animals and in spawning schools, that males, irrespective of age, also die after one mating season.

18. CHANGING SIZES OF SQUID IN SPAWNING POPULATIONS

During the course of my investigation, the chief question asked by those associated with the squid fishery has been, "Why are the squid so much smaller now than they used to be?" This question is evoked, not by fishermen's nostalgia, but by a real reduction in the sizes of spawning animals. In the years 1946, 1947, and 1948, the squid catch at Monterey was 19,001 tons, 7,222 tons, and 9,560 tons, respectively. Only a few random samples for the year 1946 were measured. When I first began regular sampling in 1948, squid were distinctly smaller. This decline continued through 1952, and small sizes persisted in the bulk of the spawning population for many years; larger sizes apparently

ently became re-established for the first time in the May to July spawning population in 1962.

The nature of these changes was followed by plotting monthly means and modes of mantle lengths for males and females, taken in random samples from commercial squid catches (Figures 58 and 59). For May to July, the mean mantle lengths of males fell from above 160 mm to about 130 mm. These smaller sizes became typical of more months each year from 1949 through 1952. The same pattern was apparent in females spawning at the same time. Their mean length was approximately 152 mm in 1948, 143 mm in 1949 and below 140 mm for increasing numbers of months in 1950, 1951, and 1952. The decrease was greatest for animals spawning in spring and summer and least for those spawning in fall and winter. These very unequal changes imply that two populations are involved, and that one of these is more exposed, or more susceptible to whatever condition has caused the departure from the normal pattern.

The changes are not merely in the relative numbers of smaller and larger animals such as one might expect prior to the advent of the modal spawning age of a very large year-class; instead they represent a general size reduction and disappearance of larger animals, particularly from the spring-spawning population. For example, in 1948, 15 percent of the males in normal samples exceeded 172 mm in length; in 1949, only 7 percent did so; less than 1 percent of the male animals in the 1950 samples were this large.

Overfishing for squid could not be the cause of their decreased sizes because they spawn only once, and the commercial catch consists of spawning animals which would die after spawning in any event. However, the decrease in size closely followed the virtual disappearance of the sardine from the coastal waters of central and northern California, thereby inviting consideration of possible relationships between these two events.

The sardine must have provided a considerable part of the diet of many predators. In its absence, these predators might have drawn much more of their food from squid, and the life expectancy of the individual would decrease. The larger, older animals would become a smaller fraction of the squid population, and might even be eliminated by intensified hunting. The average size would decrease gradually, but the modal size of spawning animals of mixed ages could be expected to step down abruptly from one year-mode to the next as the older age groups were successively decimated. Changed modes of this nature were not shown by these squid, indicating that predation was not a major factor in the decline.

Another significant factor is availability of squid food. Fishes make up a part of their diet, and possibly made up a much greater proportion when sardines abounded. Formerly present in huge numbers, sardines would spawn chiefly off Baja California and southern California, and would migrate northward, feeding on the abundant zooplankton. Older sardines would travel as far as Canadian coastal waters, but would return southward to spawn. Smaller sardines migrated shorter distances. Ranging through the same waters, young squid competed with sardines for the same planktonic copepods and euphausiids; when

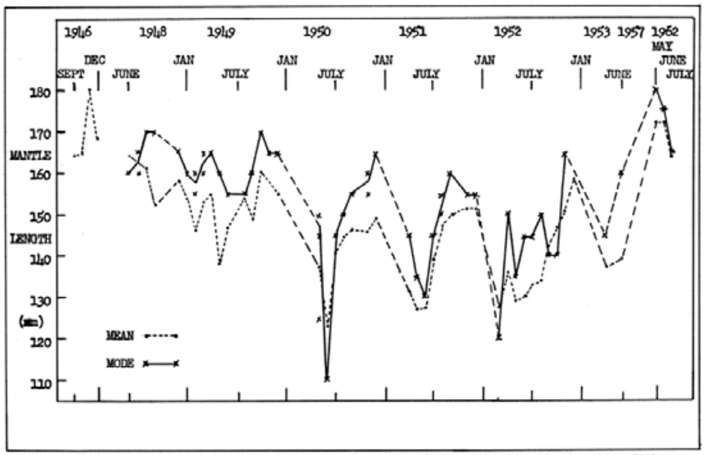


FIGURE 58. Mean mantle lengths and modes of male squid in random samples from commercial squid catches, 1946 to 1962.

FIGURE 58. Mean mantle lengths and modes of male squid in random samples from commercial squid catches, 1946 to 1962

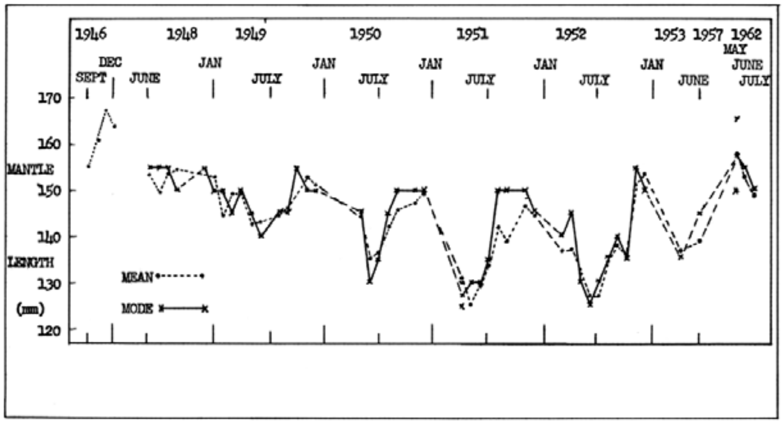


FIGURE 59. Mean mantle lengths and modes of female squid in random samples from commercial squid catches, 1946 to 1962.

FIGURE 59. Mean mantle lengths and modes of female squid in random samples from commercial squid catches, 1946 to 1962

large enough, they may have attacked even the sardines as food, and grown quickly to a large size before spawning. Now, to the north of Point Conception, sardines are no longer available as food for squid, which must complete their adult growth and maturity upon a continuation of their juvenile diet of crustaceans, supplemented with presumably less useful fishes as substitutes for the sardine.

Kinds of food and quantity available have both been shown to control the growth rate and final size of animals by Bruce, Knight, and Parks (1940) for oysters, and by Digby (1954) for copepods. Prakash and Milne (1958) have shown that a much greater growth rate in the silver salmon results if the diet contains fishes plus crustaceans instead of crustaceans only. Thus the observed squid size decreases might be ascribed to the disappearance from part of its environment of a major important food source, possibly the sardine. Such a loss would slow the growth rate and reduce the average size at spawning age, and cause gradually decreasing size-modes such as are found here.

As previously noted, the decline in normal spawning size (Figures 50, 51, 58, and 59) showed distinct seasonal differences: the animals spawning in November showed less growth retardation than did those spawning in the spring. This suggests that the autumn-spawning animals finished their growth where some sardines were found, i.e., south of Point Conception, and that those spawning in the spring matured in the waters to the north of that point. This is consistent with a migratory pattern for L. opalescens which I outlined earlier, and which may be summed up briefly here.

Squid from south of Point Conception are still able to "top off" their growth with sardines of the diminished population there; these squid spawn chiefly during the Davidson Current period (November to February) from La Jolla to Monterey, migrating northward with the Davidson Current or in some years during the Oceanic period; these southern animals form the August to February population at Monterey. Squid from north of Point Conception have abundant juvenile food in the absence of sardine competition, and there is greater survival because of reduced cannibalism; they work longer and harder, feeding chiefly on crustacea, to accumulate the food reserves and other factors necessary for maturity and spawning; they do not grow as large, nor is the bulk of the population ready to spawn as early in the year as formerly; these animals come to Monterey to spawn during the time of upwelling from March to July.

A predominance of small squid through the spring and summer, according to fishermen and fisheries biologists, continued until the reappearance of large animals in 1962. Samples taken in May, June, and July (Figures 50, 51, 58, and 59) showed females as large as, and males larger than, the animals of the 1948 spring-spawning population, which had not been approached in size, in this season of the year, since that time. The causes of this resurgence of size are not known. Possibly anchovies, present in great numbers in 1961 and 1962, provided a satisfactory substitute for sardines in the maturing squid's diet. Possibly conditions leading to the flourishing of the anchovies were equally favorable to squid; or possibly this size restoration presaged an undetected repopulation of northern waters by sardines.

19. SUMMARY

1. Loligo opalescens Berry, 1911, is the common squid along the west coast of North America from Baja California, Mexico, to British Columbia, Canada. My studies on this animal were conducted at Monterey Bay, California.

2. I have amended the description of L. opalescens to note that arms of the male are approximately 50 percent longer than those of the female, and supplemented it by describing the colors of living animals.

3. The oceanographic seasons affecting a squid's life at Monterey, California, include a period of upwelling from March to August, an oceanic period during September and October when offshore water approaches the coast, and a Davidson Current period from November to February when an inshore current flows northward along the coast.

4. The fishery for L. opalescens is centered at Monterey, where lampara nets are used. The average catch 1944–1960 was 6,500 tons per year. The bulk of this was taken from April to July, with a small peak in November; in some years squid were available in every month.

5. Squid feeding behavior is described. While eating one crustacean (e.g., Spirontocaris sp.) L. opalescens continued capturing others with its tentacles, building up a reserve of active prey within a loosely-held cone of arms. I saw no evidence of cephalotoxin being used.

6. Studies of squid stomach contents showed that crustaceans, fishes, and polychaete worms were commonly eaten, with the proportion of crustacean meals decreasing and fish meals increasing in larger animals. Squid larger than 120 mm mantle length exhibited some cannibalism, but squid remains were not seen in stomachs of animals smaller than this. Plerocercoid stages of tapeworms were occasionally found in the gut.

7. Reproductive systems, spermatophores, gametes, and the processes of mating and spawning are described and illustrated.

8. L. opalescens spawns in winter in the southern portion of its range, and in late summer in the northern portion. At Monterey, some spawning may occur in every month of the year; major spawning takes place from May to July, and a minor peak occurs in November.

9. Gross embryology is described and illustrated. The incubation period is 3 to 4 weeks at 16° C. Hatching takes place mainly at night.

10. The sex ratio was 1:1 among immature animals and in spawning schools.

11. Population data indicated that at ages of 1, 2, and 3 years, dorsal mantle lengths were approximately 65, 120, and 165 mm for males and 65, 120, and 150 mm for females.

12. Two distinct populations entered the spawning grounds during the year. One was dominant from January to June, the other from July to December. Each population was associated with different oceanographic conditions at Monterey; the November spawning group

apparently migrated from south of Point Conception with the Davidson Current.

13. Males may be mature at 72 mm or remain immature to 130 mm. Comparable sizes for females are 81 and 140 mm, respectively.

14. Almost all females spawn at the age of 3 years; this is the modal age for spawning males, but a few older and many younger individuals greatly extend the size-range of males in spawning schools. All squid die after one season of spawning.

15. A severe reduction in average size of the spring-spawning stock occurred 1947–1952 and persisted through 1961; sizes in 1962 were equal to or larger than those of 1948.

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GLOSSARY OF ABBREVIATIONS USED IN FIGURES

A: anterior
AD: apical depression
AF: anterior funnel fold
AG: accessory nidamental gland
A1–5: arms in order of appearance (ventral first, dorsal last)
AL: oral limit of inner tunic and outer membrane
AM: ampulla of vas deferens
AN: anus
AO: aorta
AP: animal pole
AV: anal valve
BC: blastocone
BD: blastoderm
BH: branchial heart
BL: blastomere
BM: buccal mass
BS: blood sinus
BV: branchial vessels
C: cap
CB: cement body
CC: connecting cylinder
CE: caecum
CF: ciliated funnel
CG: cerebral ganglion
CH: chorion
CL: cephalic lobe
CM: cement
CO: ciliated opening into oviduct
CP: chromatophore
CT: cap thread
C1–4: cleavage planes in order of their appearance
E: primordium of embryo
ER: embryonic region
ES: eye stalk
EX: extraembyronic region
EY: eye
F: fin
FC: funnel cartilage
FE: funnel entrance
FF: fusion of funnel folds
FG: tail
FL: funnel
FM: free margin
FO: funnel opening
GA: genital aorta
GI: gill
GO: optic ganglion
GP: position of pedal ganglion
GS: stellate ganglion
GV: visceral ganglion
H: head
HO: hatching (Hoyle's) organ
IM: inner membrane
IN: intestine
IS: ink sac
IT: inner tunic
IV: inner valve of funnel
IY: internal yolk sac
K: kidney
L: left side
LE: lens
LI: liver
LL: liver lobes
LV: lateral valve of funnel
MA: mantle
MC: mantle cavity
MI: micropyle
MM: middle membrane
MO: mouth
MP: mantle primordium
MR: marginal thickening
MT: middle tunic
NC: nuchal cartilage
NG: nidamental gland
OD: oviducal gland
OE: esophagus
OF: oviducal funnel
OG: external glandular oviduct
OI: internal membranous oviduct
OM: outer membrane
OO: ovary not shown
OP: olfactory plate
OT: outer tunic
P: posterior
PB: polar bodies
PE: pen
PF: posterior funnel fold
PM: protractor muscle of penis
PN: penis
PR: point of rupture
PS: perivitelline space
R: right side
RS: sperm reservoir
S: stomach
SB: bundle of spermatophores
SC: statocyst
SD: spermatophoric duct
SE: spermatophore
SF: spiral filament
SG: shell gland
SH: systemic heart
SI: statolith
SL: liquid-filled space
SM: sperm mass
SN: spine
SO: spermatophoric organ
SP: space
SQ: shallow depression
SR: funnel retractor muscle
SS: spermatophoric (Needham's) sac
ST: statocyst primordium
SU: sucker
T: testis
TM: thickened margin due to delamination
TP: tail plate
VC: vena cava
VD: vas deferens
VP: vegetal pole
XO: external opening of oviduct
Y: yolk
YC: yolk constricted by contraction of musculature at arm bases
YE: yolk epithelium (perivitelline membrane)
YP: posterior lobes of internal yolk sac
YX: external yolk sac