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Reproduction, Life History, and Ecology of the Round Stingray, Urolophus Halleri Cooper

by
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ABSTRACT

This is the first comprehensive study of the reproduction, growth, habits, food, and environment of the round stingray. Gametogenesis is described in both sexes. Previously unreported testicular appendages and a corpus luteum of unique origin are revealed. Sperm storage is demonstrated for the first time in a male batoidean. Gestation is described and illustrated. The relationship between certain of the ray's reproductive adaptations and its high biotic potential is discussed; these adaptations include rapid embryonic development, birth of large well-protected young, and a specialized pattern of oogenesis which permits annual ovulation.

Male embryos outnumber female embryos, but the sex ratio approaches parity in newborn rays due to a higher male mortality. The sex ratio remains nearly balanced until maturity, after which males become progressively more numerous at depths of less than 7.5 fathoms. Conversely, mature females are more numerous beyond this depth, apparently segregating themselves from the males.

The growth rate of U. halleri was determined by four separate means: (i) the Petersen method of width frequencies, (ii) a captivity study, (iii) tagging and recapture, and (iv) double sampling. The species is unique among elasmobranchs for which there are growth data; both sexes attain sexual maturity relatively early in life and at about the same size and age. The significance of early sexual maturation lies in the short time span between generations and the relatively longer reproductive life of the individual. Both factors contribute to a high biotic potential.

Movements of U. halleri were traced by tagging and recapture, and from analysis of trawling and seining records. These rays are normally nonmigratory, tending to remain in or return to the same locale. No recaptured individual moved more than 4.75 miles. The most rapid movement was 1 or 2 miles in 4 days. Distances traveled increase with animal size. Young rays remain close to shore and gradually move seaward with growth. Mature females move farthest offshore and return shoreward in June for mating and again in September to bear young. Adults prefer the warmer coastal waters in winter, only entering inlets to forage. Many rays populate the warm inlets, however, during summer.

Over 94 percent of the ray's food volume is supplied by the three invertebrate classes—Pelecypoda, Polychaeta, and Crustacea, which are listed in order of importance. Mature rays eat a relatively larger volume of polecypods than do young rays. Urolophus halleri burrows in the substratum for food and concealment. Captive rays locate food by scent as well as by sight.

Water temperature appears to limit the depth-distribution of U. halleri. Most rays reside within a narrow coastal zone, at depths of 10 fathoms or less, where temperatures generally remain above 10°C. Latitudinal distribution also seems controlled mainly by water temperature.

Local population densities are greatest where a soft substratum exists just offshore and where suitable inlets are available for mating and for bearing young. Inshore dredging and the erection of coastal breakwaters and jetties are improving the ray's environment and may be contributing to a population increase in some locales.

The relative abundance of associated fish species was determined from trawling catches. Urolophus halleri ranks fourth among benthic fishes taken in the study area. Little is known of the feeding relationships which exist between U. halleri and other associated fishes; however, the ray is believed to compete with some of the valuable flatfishes. Trawling catches do not accurately reflect the relative abundance of small invertebrates used as food by U. halleri; some of these invertebrates lie beneath the surface of the substratum, while others pass through the net.

ACKNOWLEDGMENTS

I wish to express my gratitude to my doctoral committee at the University of Southern California for their expert guidance in this study and for the effort given by them in reviewing this paper; namely I wish to thank my committee chairman Robert M. Chew, the late Norman T. Mattox, Walter E. Martin, Jay M. Savage, and Orville L. Bandy.

Use of facilities of the Biology Department and Allan Hancock Foundation, University of Southern California, is appreciated. Several of the Allan Hancock Foundation staff generously contributed time to the food study. Olga Hartman was particularly helpful in identifying polychaete worms, J. Laurens Barnard helped with the amphipods, John C. Yaldwyn with decapod crustaceans, and Robert J. Menzies with isopods. Assistance rendered by librarian Dorothy M. Halmos is also acknowledged.

Rays were collected and tagged offshore, using the California Department of Fish and Game trawling boat. John G. Carlisle, Jr., Parke H. Young, Jack W. Schott, and John L. Baxter, California State Fisheries Laboratory, Terminal Island, actively helped with this work. John E. Fitch aided in identification of mollusks for the food study, and Norman J. Abramson assisted with statistical problems. I wish to convey my thanks to other Terminal Island personnel who have lent a helping hand.

The administration at Marineland of the Pacific provided aquarium space and laboratory facilities, thereby making possible a study of Urolophus halleri in captivity. I wish to acknowledge the assistance given by curators Kenneth S. Norris and John H. Prescott during the study, and the efforts of Jerry Goldsmith who cared for the animals.

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Orange County Harbor Department and Kerckhoff Marine Laboratory at Balboa made their skiffs available on several occasions.

Moving pictures of the round stingray were taken by Robert R. Given, and V. L. Gregory gave technical advice for still photography.

I am grateful to the National Science Foundation for financial support during the last 2 years of this study, provided under Research Grant No. 8704.

John Stanley Babel
June, 1966

1. INTRODUCTION AND HISTORICAL ACCOUNT

The stingray was known to the ancients, for according to Coupin (1899), Ulysses of Greek mythology was said to have been slain by the spine of a large stingray. The natural history of Pliny, as translated by Bostock and Riley (1890), recounts the awesome power of the ray Pastinaca which supposedly withered a tree with its sting.

Relatively little attention has been given the round stingray, Urolophus halleri, since its description by Cooper (1863). Some observations have been made concerning its range, habits, abundance, and undesirable qualities. Three workers have done limited morphological studies on the animal, and since 1950, several papers dealing with the physiological effect of its venom on other vertebrates have been published.

It was the purpose of this doctoral dissertation to set forth the more important details concerning the reproduction, growth, food, and environment of the round stingray. Such a study seemed to have merit not only from a purely scientific standpoint, but also from a practical one. The abundance and habits of this fish make it increasingly important to the many people who now use southern California beaches. It will be of interest to fishermen to learn that the round stingray is not a scavenger as suggested by Starks (1907) but apparently competes for food with some sport fishes.

J. G. Cooper, M.D., while at San Diego Bay in 1862, attended the small son of Major G. O. Haller, U.S.A., who was wounded in the foot while wading along the muddy shore. Cooper believed the wound to have been inflicted by one of the small abundant round stingrays. After examining some of these rays, he published the first description of the species (Cooper, 1863).

Jordan and Gilbert (1882) said Urolophus halleri was the smallest of North American rays, noting that it was exceedingly abundant in sheltered bays from Point Conception southward. They believed it was closely related, if not identical, to the Australian Urolophus cruciatus. Jordan and Evermann (1896), gave the range of U. halleri as Point Conception to northern Mexico.

Starks (1907) observed that this animal was so common in San Diego Bay as to be a pest to fishermen, fouling and cutting their nets, but suggested it might have considerable value as a scavenger. He noted the great variation in color pattern and described two uterine embryos taken from a single female. He gave the range as Santa Barbara, south, probably to Panama.

A new genus Urobatis was created by Garman (1913), for the urolophids of the West Indies and eastern Pacific. He restricted the genus Urolophus to several species found in the western Pacific. Garman's division was based mainly on relative length of tail and body, the tail being shorter than the body in Urolophus and the same length as the body in Urobatis. He examined over 100 specimens taken at San Diego, California, noting considerable color variation. He described a large animal in the collection that was 20.5 inches long and 12.25

inches wide, but did not give its sex. A new species, Urobatis maculatus, also was described by Garman from a specimen taken in the Gulf of California. He believed it was closely related to Urobatis halleri, differing mainly in color.

Breder (1928) reported a single specimen of the round stingray, captured by the Bingham Oceangraphic Expedition at San Francisquito Bay near the head of the Gulf of California. He adopted the generic name Urobatis, suggested by Garman, as did most subsequent writers.

An excellent anatomical study of elasmobranchs was made by Daniel (1934). He found that in early development the round stingray was very similar to the typical shark. In comparing the adult skeletal structure of sharks and rays, however, he discovered notable differences. In U. halleri the upper segment of hyoid arch supports the mandibular in the regular manner, but the lower segment of the arch is united with the posterior cranium. Another unusual feature in this fish is the union of the left and right pectoral fin propterygii at the tip of the ethmoid region.

Barnhart (1932) made some brief observations on the spawning season, feeding habits, gestation period, size of eggs, and numbers of young of the round stingray. His observations, though helpful, were incomplete and in some cases in error.

Holmgren (1940) made a comparative study of embryonic development of the selachian skull and later extended his work to the adult selachian cranium (1941). U. halleri was included in both investigations, and he concluded from his work that rays and sharks had developed independently over a long period of time.

Herald (1953) reported the capture of two round stingrays at Elkhorn Slough, Monterey Bay, California, thereby extending the known range about 170 miles northward.

Motor innervation for the pectoral fins and tail of the round stingray were studied by Campbell (1951). Using spinal transections at various levels in living rays, he was able to demonstrate that the nerve centers which control pectoral fin and tail movements are in the spinal cord posterior to the brain. Severing of the cord just behind the brain did not inhibit swimming or striking movements.

There has been a general return to the generic name Urolophus, since Bigelow and Schroeder (1953) published an authoritative book on sharks and rays. They believe the minor difference used by Garman to separate Urobatis was only of specific significance.

Increased recreational use of southern California beaches in recent years has resulted in a considerable number of stingray injuries. Russell (1953), in reviewing the treatment of such injuries, reported 474 attended cases in 1952. between April and November. He assumed that additional unattended cases occurred during that period. He attributed the preponderance of such wounds to U. halleri, whose habits and abundance make it by far the most dangerous ray to man.

Holloway, Bunker, and Halstad (1953) determined that the venom of the round stingray was concentrated in the epithelium which lined the two ventrolateral grooves of the sting. Extracts of the venom produced convulsions, respiratory arrest, and death in white mice.

The cardiovascular effect of this ray's venom upon rabbits, frogs, and mice was investigated by Russell and van Harreveld (1954). In small dosages, the venom had a variable effect, either causing immediate vasoconstriction or vasodilatation followed by vasoconstriction. Larger amounts of venom caused vasoconstriction and cardiac standstill followed by slow shallow heartbeats evoked from a source outside the sino-auricular node. They believed it unlikely that a single injury could seriously endanger human circulation.

Russell (1955) in a paper on the incidence of multiple caudal spines in the round stingray, reported that about 25 percent of 1,196 animals examined, possessed two or more caudal spines. Multiple spines occurred more often in larger individuals, and a significant correlation existed between length of an animal and length of its primary caudal spine. A record of Russell's catches over a 12-month period showed that September yielded the largest number of animals at four of the five localities sampled. The one open-beach site yielded a slightly greater catch in August. An unusual sex ratio of 2.4 males to each female was reported for the 1,196 individuals examined.

Herald, Schneebeli, Green, and Innes (1960) compiled a table of all elasmobranchs taken at Elkhorn Slough, Monterey Bay, California, in 17 shark derbies since 1951. Ten round stingrays were recorded, eight being mature males, while the sex of the other two animals was unknown. The unbalanced sex ratio led these authors to suggest a sexual segregation for the species.

Until recently, Monterey Bay was the northern limit for the round stingray. However, a specimen has now been taken at Eureka, California, by the California Department of Fish and Game (Best 1961), thereby extending the known range northward some 295 air miles.

2. MATERIALS AND METHODS

All round stingrays used in my study, were measured, sexes determined, and an identifying number given at time of capture. Total length and disc width were determined to the nearest millimeter. Notes on the condition of each animal, the time and place of capture, and certain environmental details were also recorded.

Rays were taken near shore with beach seines of 40- to 100-foot length and of 1- to 0.25-inch mesh size. Most seines had center bags for trapping fishes, and all were heavily weighted to ride along the ocean bottom. Nets were laid about 250 feet offshore and parallel to it, by means of a skiff. Crews on shore then hauled in the nets with ropes.

offshore collecting was done from a trawling boat of the California Department of Fish and Game, employing a commercial otter trawl to take California halibut, Paralichthys californicus, for tagging and other biologic studies. After each 20-minute trawl, the net was reeled in and emptied on deck. Trawls of longer duration caused excessive injury to animals. Round stingrays were placed in a holding tank until tagged or preserved. Other fishes and invertebrates were rapidly identified, counted, and returned to the ocean, or utilized in tagging or biologic studies.

The tag used for U. halleri consisted of a short length of vinyl plastic tubing 2 mm in diameter, upon which was threaded a thin plastic disc 9 mm in diameter. The disc was inscribed with a number and a

request that fish and tag be returned to the California State Fisheries Laboratory. The vinyl tubing was threaded through the left pelvic fin of the animal and tied in a loop which trailed about 1 cm behind the posterior margin of the fin.

Small stingrays were frequently preserved entirely in 10 percent formalin after first opening the abdominal cavity. Only the gonads, digestive tract, and in some cases the reproductive tracts of large rays were saved. These parts were wrapped in gauze, numbered, and placed in formalin. Stomachs were removed from formalin after 3 days and placed in 40 percent isopropyl alcohol to prevent disintegration of mollusk shells. All other material was kept in formalin.

Each stomach to be examined for food was opened in the laboratory and emptied into a small dish containing 40 percent isopropyl alcohol. This material was sorted into major taxonomic groups, and each group placed in a separate watch glass for further study. Identification was carried to species level when condition of the material permitted. Each minor taxonomic group was then dried on paper toweling for a few minutes. Small animals such as amphipods were placed in a short section of vertically-held pipette that had been filled to a known level with water. The displaced water volume was then estimated to the nearest 0.01 ml. Larger animals were placed in a 10 ml graduated cylinder and the displaced water volume estimated to the nearest 0.025 ml.

Photomicrographs were made with a 35 mm Contaflex camera, Leitz Wetzlar adapter, and Leitz Wetzlar binocular microscope equipped with illuminator and transformer. A 12.5X ocular lens, and objective lenses of 3.5, 10, 45 and 100 magnifications were employed. Panatomic X film was selected for is fine grain and printing was done on number 3 paper for strong contrast.

All still photographs were made with the Contaflex using Panatomic X film, a series 5 adapter ring and 2 + lens. The camera was mounted on a copy stand with flood lights attached.

Moving pictures of rays in aquaria were taken with 16 mm Bell and Howell 70-DL camera with Egleet Golden Navitar, 12 mm, wide angle, F 1.2 lens, using black and white negative type, Plus X film. Flood lights were mounted above the aquarium. Exposures were made in slow motion at 80 frames per second to reduce blur, and selected frames were printed on number 3 paper at a considerable enlargement.

Marineland of the Pacific furnished aquarium space, food, and care for the young rays studied in captivity. Thirty-three animals ranging from 73 to 109 mm in disc width were captured at Upper Newport Bay in October. They were placed in an aquarium with sand bottom into which filtered sea water was piped continuously at a temperature of about 19° C. The water was kept well aerated and occasionally a 2 percent copper sulphate solution was admitted for short periods to control ectoparasites and bacteria.

Captive animals were tagged with a 12 mm length of vinyl plastic tubing, 2 mm in diameter. Each piece of tubing was numbered with vinyl ink, dilated slightly and slipped over the caudal spine, where it was held firmly in place by the barbs. The elastic sleeve allowed for subsequent spine growth, permitted safe handling of rays, and provided a means of identification during the 10 months of captivity.

Frozen brine shrimp, Artemia, was the main diet, supplemented by finely chopped Mytilus and fresh shrimp, Penaeus. Length and width measurements were recorded for each animal at monthly intervals. Remarks on condition and behavior were also recorded at the time of measurement. Additional observations were made at irregular intervals throughout the study.

Stingrays were collected from coastal waters between Ventura and San Diego, but some sites were sampled more heavily than others (Figure 1). Very limited trawling was also carried out north and south of the coastal region shown.

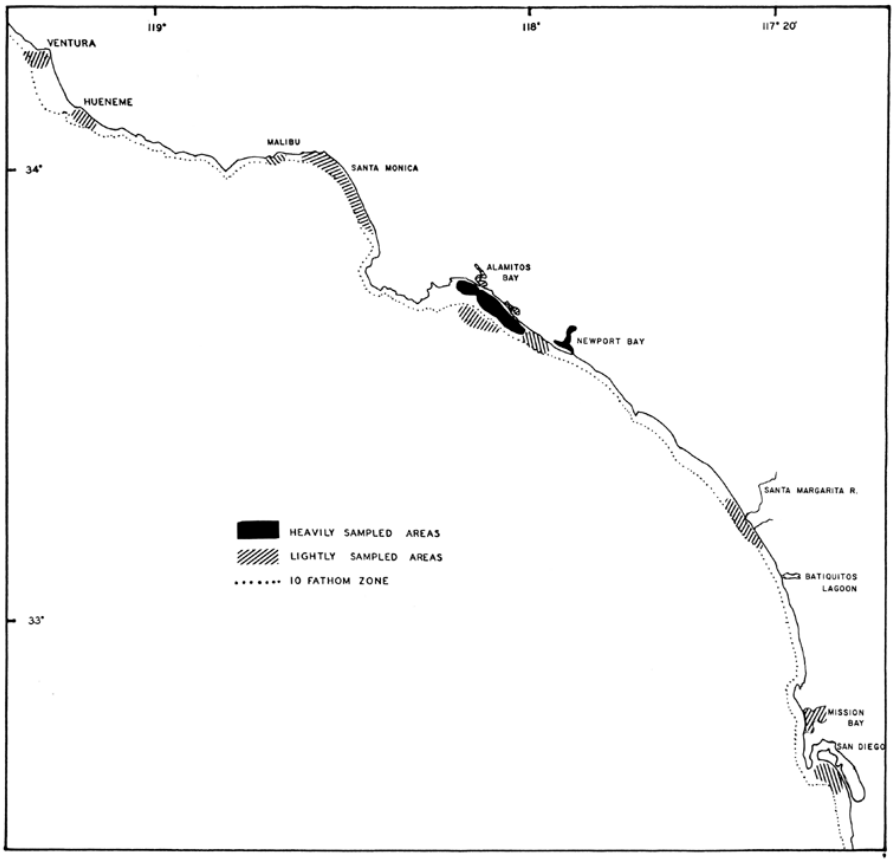
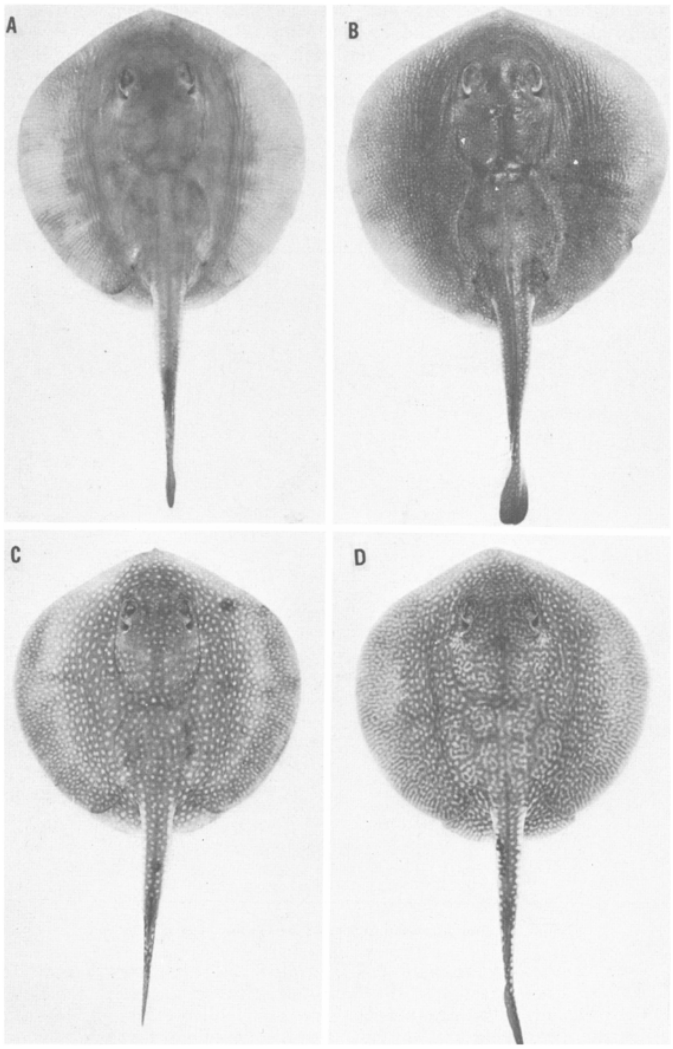


FIGURE 1. Map of coastal region included in this study of *U. halleri*.

FIGURE 1. ***Map of coastal region included in this study of U. halleri.***

Four methods were used to determine age and growth rate for U. halleri, since no single method yielded sufficient data : (i) the Petersen method of width frequencies (Petersen, 1891); (ii) double sampling and comparing the two resultant frequency curves; (iii) tagging and recapture (Perlmutter, 1954); and (iv) rearing in captivity.



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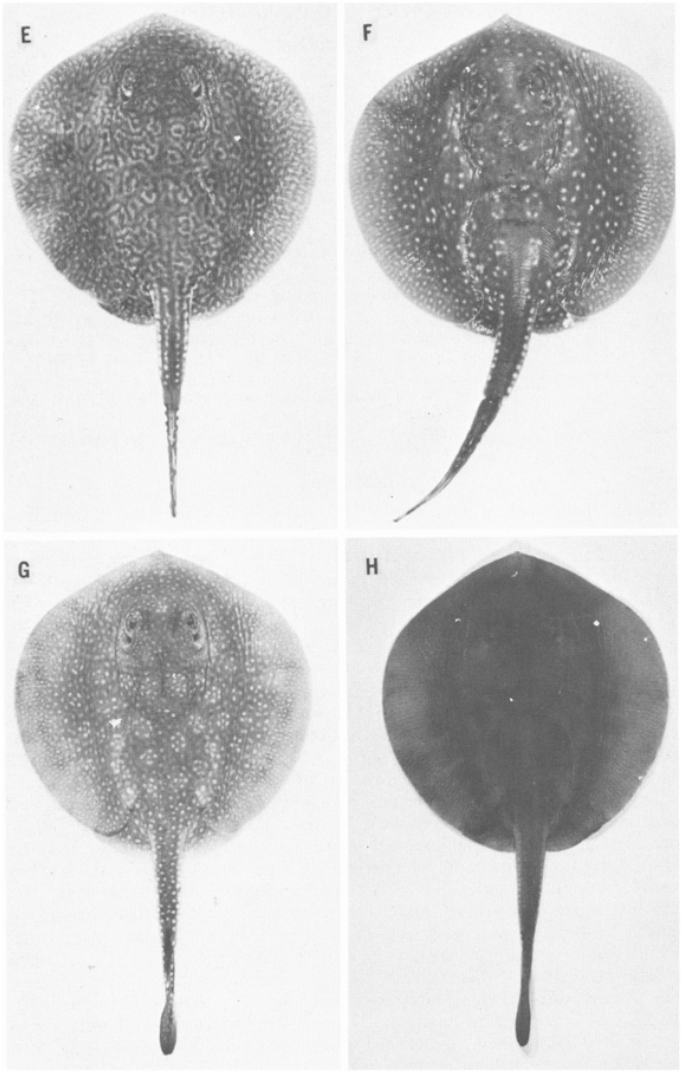


FIGURE 2. Variations in dorsal markings of *U. halleri*. (A-H)

FIGURE 2. ***Variations in dorsal markings of U. halleri. (A-H)***

3. DESCRIPTION OF UROLOPHUS HALLERI

3.1. Classification

Phylum		CHORDATA
Subphylum	VERTEBRATA	(CRANIATA)
Superclass		GNATHOSTOMATA
Class		CHONDRICTHYES
Subclass		ELASMOBRANCHII
Order		Batoidea
Family		Dasyatidae

Urolophus halleri Cooper 1863

3.2. Partial Synonomy

Urolophus halleri	Cooper, 1863, Proc. Cal. Acad. Sci., Vol. 3, p. 96; Jordan and Gilbert, 1882, Bull. 16, U.S. Nat. Mus., p. 46; Jordan and Evermann, 1896, Bull. 47, U.S. Nat. Mus., p. 80.
Urolophus umbrifer	Jordan and Starks, 1895, Proc. Cal. Acad. Sci., Ser. 2, Vol. 5, p. 285; Jordan and Evermann, 1900, Bull. 47, U.S. Nat. Mus., p. 2,752.
Urobatis halleri	Garman, 1913, Mem. Mus. Comp. Zool., Harvard, Vol. 36, p. 403.

3.3. Description

Body dorso-ventrally compressed; pectoral fins forming a rounded disc which is obtusely pointed in front; disc ranges from slightly longer than wide to 1.07 wider than long. Skin smooth. Spiracles posterior to orbits and farther apart than orbits. Distance between tip of snout and a line tangent to anterior margin of both orbits, is greater than distance between orbits. Distance from tip of tail to center of cloaca less than from center of cloaca to tip of snout. Pelvic fins extend posterior to disc and are slightly longer in females. Basipterygium of pelvic fin in males extends posterior to fin as a clasper. Tail cylindrical and tapering from base to origin of caudal spine, becoming laterally compressed more distally and terminating in a spatulate caudal fin. Base of caudal spine becomes free from tail at 0.55 of distance from center of cloaca to tip of tail.

Ventral surface white. Dorsum with gray or brown background, becoming lighter around periphery of disc. Variable pattern of yellow markings generally superimposed on background but markings may be completely absent in some (Figure 2A). Very small yellow dots often evenly distributed over entire back (Figure 2B). In some rays, the dots are large and widely spaced over central part of disc, becoming smaller and more closely spaced around periphery (Figure 2C). Individual dots may merge into vermiculate markings which form large rosettes on center of disc and radial lines around its periphery (Figure 2D). Entire dorsum is sometimes covered by vermiculate pattern (Figure 2E). A few animals have small widely spaced rosettes of only three to five large dots each, over center of disc; dots become closely and evenly spaced peripherally (Figure 2F). A common pattern is one of closely spaced rosettes, each consisting of five to seven small dots (Figure 2G). The entire dorsum of about 1 in 800 specimens is black (Figure 2H).

4. REPRODUCTION

4.1. Female Urogenital System

4.1.1. Morphology of the mature ovary

The ovaries of the round stingray are dorsoventrally compressed and elongate; their medial edges are attached along either side of the vertebral column by a mesorchium. The dorsal surface of each ovary is slightly convex, conforming to the inner surface of the dorsal body wall. The right ovary is noticeably smaller than the left, even in young animals. Small ova can be found in the right ovary, but none develops beyond 0.3 mm. Such a condition is not unusual in elasmobranchs, for similar cases can be cited among both sharks and rays (Giacomini, 1896; Daniel, 1934).

Islands of light-staining tissue with a glandular appearance are present in the atrophied right ovary of U. halleri (Figure 3). Thin connective tissue septa divide this cell mass into a number of roundish lobules. Possibly secretions from these cells help prepare the uteri to receive ova, for the cells are prominent at the time of ovulation. Both uteri of one ray examined, contained a newly ovulated egg, and the islands in the right ovary were quite sharply defined (Figure 3). Any glandular function possessed by this tissue does not seem critically involved with egg development, for large ova were found in one ray in which the right ovary was completely absent.

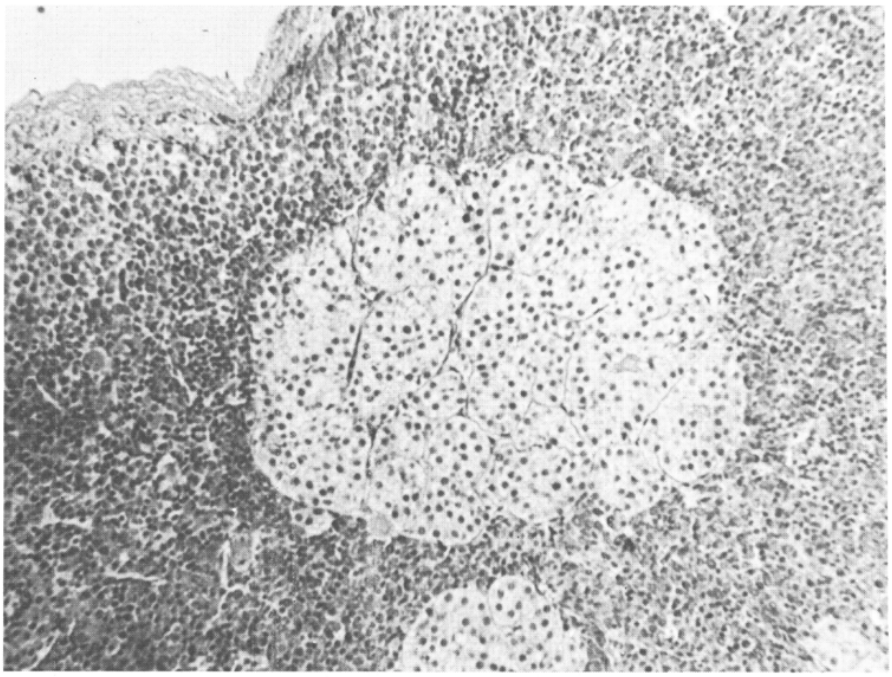


FIGURE 3. Islands of light-staining tissue in right ovary of *U. halleri*. 125x

FIGURE 3. ***Islands of light-staining tissue in right ovary of U. halleri. 125x***

4.1.2. Reproductive and urinary tracts

Ripe ova are released from the functional left ovary of U. halleri into the abdominal cavity; they must pass anteriorly to the two ostia situated on both sides of the esophagus and close to the transverse septum. Both oviducts are functional in the round stingray, but the left ostium receives more ova, probably due in part to the fact that the route between left ovary and left funnel is more direct and with less obstruction. The tendency for slower development of the right oviduct and uterus, no doubt, also limits their use in young animals.

The thin-walled oviduct can be traced from its anterior opening, caudad, alongside the vertebral column, beneath the peritoneum of the dorsal coelomic wall. A few centimeters from the ostium the oviduct expands into the small oviducal gland which has two distinguishable zones. The "albumin-secreting zone" which occupies the anterior one-third of the gland is flesh-colored externally; the more posterior "shell-secreting zone" is a cream color. The shell-secreting function has been lost, with acquisition of viviparity. A stained cross section through the posterior zone (Figure 4) reveals a slit-like lumen. Radiating out from the lumen are many long tubules, each lined with a single layer of tall columnar cells. These tubules extend out to the smooth muscle layer of the gland's wall.

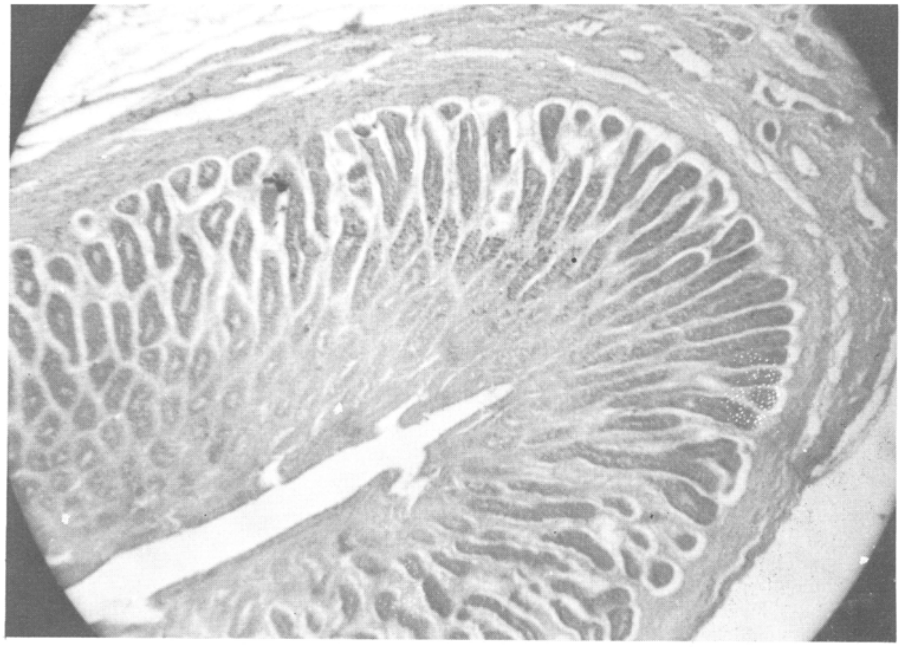


FIGURE 4. Cross section through shell-secreting zone of oviducal gland of *U. halleri*. 44x

FIGURE 4. ***Cross section through shell-secreting zone of oviducal gland of U. halleri. 44x***

The females of two elasmobranch species have been reported to store sperm in their oviducal glands; in one species the storage site is the gland's shell-secreting zone (Metten, 1939). The oviducal glands of four adult round stingrays, captured in September, were examined, but no sperm were found. A broader sampling of mature females should

be made, however, before ruling out the possibility of sperm storage in this sex.

Posterior to the shell gland, the oviduct narrows slightly before again enlarging into an elongate, spindle-shaped uterus. Near the posterior end of the coelom the two uteri constrict and each gives rise to a vagina. The two vaginas are separated by a septum that terminates just anterior to the urinary papilla, and they empty into the cloaca immediately dorsal to the rectal opening. The cloaca is covered by two folds which meet along the midline, forming a cloacal slit.

In females, the anterior portion of the kidney is a slender strip of tissue while the posterior portion is broad and flat. The posterior portion is drained by a branched duct whose main stem enters the urinary sinus. The sinus functions only as a part of the urinary tract, and after receiving the two opisthonephric ducts as its broad anterior end, it narrows rapidly, penetrates the posterior coelomic wall and protrudes from the cloaca roof as a small urinary papilla.

4.2. Male Urogenital System

4.2.1. Morphology of the mature testis

Both testes are well developed and functional in males of U. halleri. The medial edges of these elongate, dorsoventrally-flattened testes, are attached along either side of the vertebral column by a mesorchium. Twelve to 18 slightly raised, circular areas are spaced over the dorsal surface of the testis (Figure 5A). These are the testicular lobules in which spermatogenesis occurs.

A transverse cut through a nearly ripe testis shows the internal structure of these lobules and the ducts which drain them (Figure 5). I have called the central portion of each lobule a primary lobule, because it forms first and is a permanent structure; extending from its center is a small testicular appendage whose core contains large germ cells. The large, temporary, peripheral portion of each lobule, I have called a secondary lobule; it forms periodically, sheds ripe sperm, then degenerates completely. The secondary lobules (Figure 5B) are about two-thirds maximum size, relative to the pictured testis size.

Several ducts pass lengthwise through the testis (Figure 5B); branches from them penetrate the primary and secondary lobules; in the secondary lobule these branches lie within connective tissue septa which subdivide each secondary lobule into wedge-shaped segments (Figure 5C).

In a cross section of a longitudinal duct the single row of epithelial cells around its lumen are seen to possess cilia that probably move the sperm along toward the vas efferens (Figure 6); an outer sheath of connective tissue surrounds the duct. Smaller branches from a longitudinal duct have a similar structure (Figure 7). The longitudinal ducts join the coiled vas efferens which lies adjacent to several testicular lobules at the anterior end of the testis. The vas efferens is seen adjacent to two anterior lobules (Figure 8); its irregular lumen is lined with highly folded, pseudostratified epithelium (Figure 9).

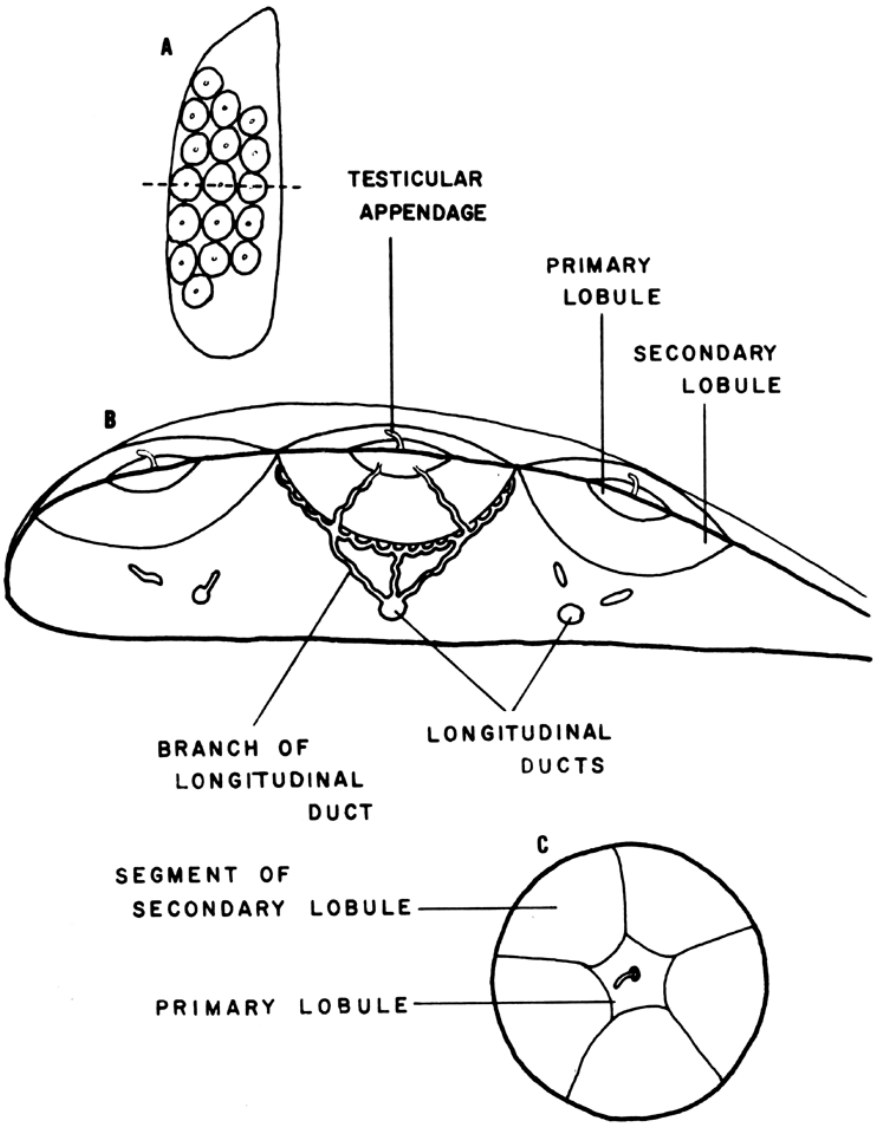


FIGURE 5A. Dorsal view of testis with ripe testicular lobules.

B. Section through testicular lobules and ducts which drain them.

C. Dorsal view of primary and secondary lobules.

FIGURE 5A. ***Dorsal view of testis with ripe testicular lobules.***
B. Section through testicular lobules and ducts which drain them.
C. Dorsal view of primary and secondary lobules.

4.2.2. Reproductive and urinary tracts

The single vas efferens extends from the gonad's anterior end, across the mesorchium in which it is embedded, and joins the epididymis. This latter structure lies ventral to the slender, anterior part of the kidney and conceals it. The left testis has been moved to the animal's right side to expose the epididymis (Figure 10).

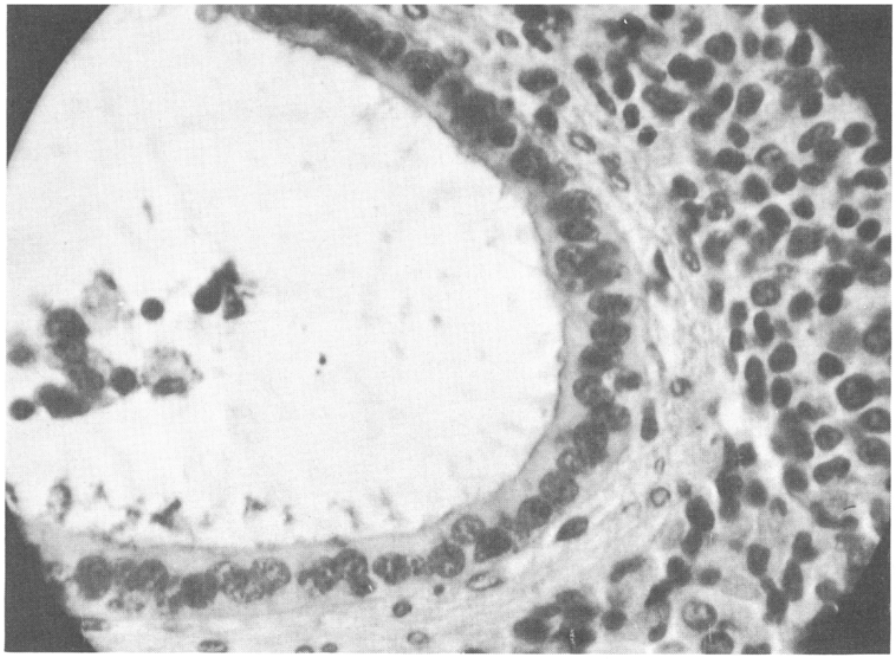


FIGURE 6. Longitudinal duct of testis, seen in cross section. 562x

FIGURE 6. ***Longitudinal duct of testis, seen in cross section. 562x***

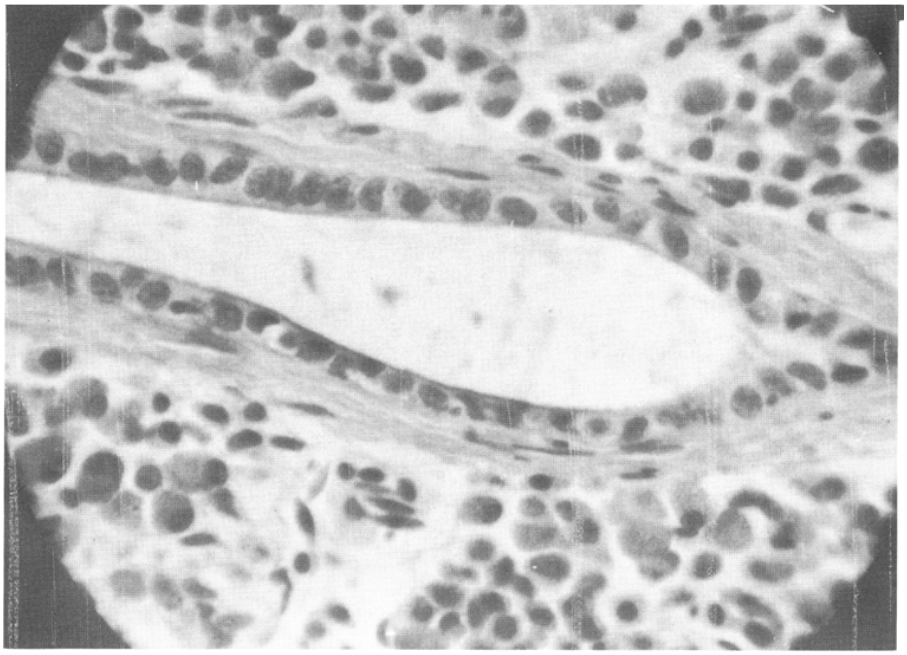


FIGURE 7. Branch of a longitudinal duct of the testis, seen in longitudinal section. 562x

FIGURE 7. ***Branch of a longitudinal duct of the testis, seen in longitudinal section. 562x***

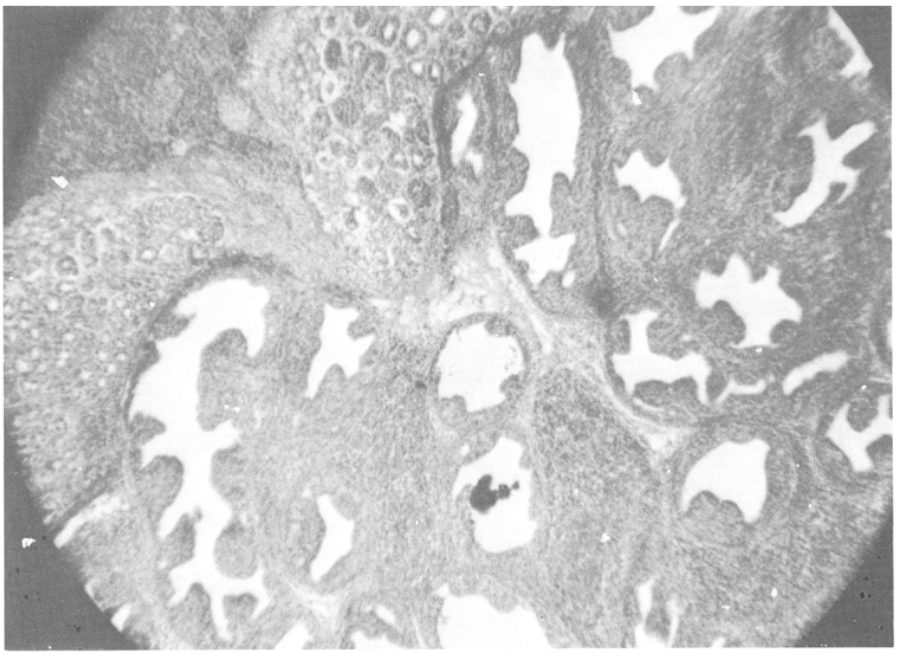


FIGURE 8. Coiled vas efferens at anterior end of testis. Two adjacent testicular lobules (left). 44x

FIGURE 8. ***Coiled vas efferens at anterior end of testis. Two adjacent testicular lobules (left). 44x***

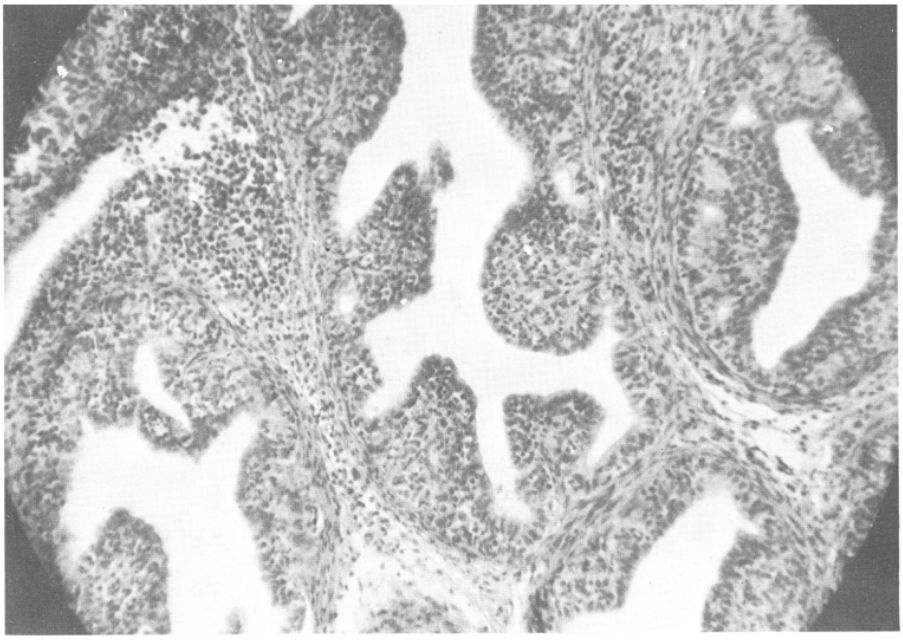


FIGURE 9. Magnification of vas efferens showing epithelium. 125x

FIGURE 9. ***Magnification of vas efferens showing epithelium. 125x***

The anterior strip of kidney has lost its urinary function and the secretory tubules are collectively called the gland of Leydig (Borcea, 1906). These tubules lie against the dorsal coelomic wall and are somewhat intermingled with the coils of the more ventral epididymis. Both structures extend caudad, just lateral to the vertebral column as a narrow, flattened strip of tissue. The loops of epididymis can be seen through the peritoneum (Figure 10).

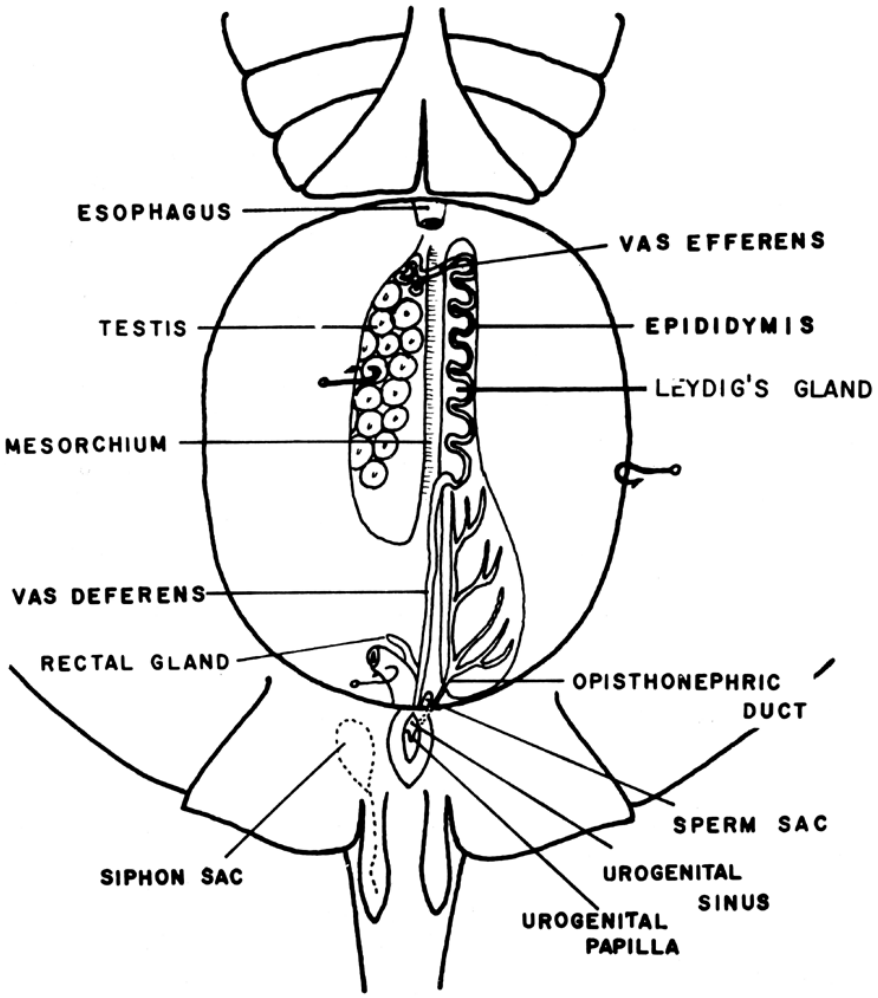


FIGURE 10. Urogenital system of male round stingray. Rectum and left testis moved to animal's side.

FIGURE 10. ***Urogenital system of male round stingray. Rectum and left testis moved to animal's side.***

The epididymis is readily distinguished histologically from the smaller tubules of Leydig's gland. Although both are lined with an epithelium of ciliated, columnar cells, the tubules of Leydig's gland have a small, regular lumen while the inner walls of the epididymis

are highly folded, producing a large irregular lumen. Leydig's gland contains no sperm and is believed to be primarily secretory. Glomeruli are absent from this part of the kidney.

The kidney begins to broaden at about the midpoint of its length; the more ventral epididymis straightens out at this point to become the enlarged vas deferens, which then receives the gland of Leydig. Posterior to this, the vas deferens extends along the medial edge of the broad, functional part of the kidney (Figure 10).

At its anterior end, the vas deferens has a round lumen; the folds on its inner walls are lower and less numerous than in the epididymis and the epithelium is of cuboidal cells. The posterior two-thirds of the vas deferens has high folds projecting into its lumen and some of these form compartments in the duct. Sperm are typically shed from the testis in February (Figure 43), and stored in the vas deferens until mating in June. During this time the duct is distended with milky seminal fluid; many of the sperm in this fluid remain arranged in clumps, as they were in the testicular follicles.

Near the posterior abdominal wall, the vas deferens opens into the broad anterior end of the urogenital sinus. The sperm sac also enters the sinus just lateral to this point. Slightly more caudad, the urogenital sinus becomes narrower and receives an opisthonephric duct from each kidney, then constricting still more it passes through the dorsal cloaca wall as the urogenital papilla. The papilla is just dorsal to the rectal opening. The rectal gland extends anteriorly, from its attachment to the dorsal surface of the rectum.

From the urogenital sinus, the opisthonephric duct extends anteriorly along the medial edge of the broad mesenephros, and is embedded in its ventral surface. This main duct sends off several branches to the posterior portion of the kidney. The coiled kidney tubules in this region superficially resemble the more anterior tubules of Leydig's gland; the kidney tubules, however, connect to glomeruli; also, their ciliated columnar cells are lower.

4.2.3. Male secondary sex organs

Certain highly-developed secondary sex characters are found in elasmobranchs and Holocephali, namely the claspers and siphon sac. The more specialized batoideans have in addition evolved a gland on the dorsal wall of the siphon sac called the siphon gland.

Males of U. halleri do not differ significantly from other batoideans with regard to anatomy of the clasper, siphon gland, and siphon sac. The cartilaginous basipterygium supports the medial margin of the pelvic fin and in mature males it becomes extended beyond the posterior margin of the fin as a stout rod. The clasper is not a solid mass, but is a part of the fin rolled up to form a tube whose edges overlap. Following the nomenclature of Leigh-Sharpe (1920), the proximal opening of the clasper tube is the apopyle, and the distal opening the hypopyle (Figure 11). The apopyle is on the dorsal surface of the clasper near its base, and about 5 mm posterior to the lower end of the cloacal slit. The folds of the clasper tube extend from that point, caudad along the dorsal side of the clasper, and end at the terminally-situated hypopyle.

The siphon sac lies near the ventral surface of the pelvic fin, a short distance anterior to the clasper's base (Figure 11). The sac has a narrow duct from its posterior end which empties into the clasper tube near the apopyle. On the dorsal wall of the siphon sac of U. halleri, there is a gland whose papillae pour milky, semi-viscous fluid into the sac. About 36 papillae lie along a median longitudinal groove in the dorsal wall of each siphon sac. The groove is darkly-pigmented making the round white papillae quite conspicuous; they resemble a single string of pearls that graduate to a small diameter posteriorly (Figure 11). Contractions of the muscular sac force the secretion through the siphon duct and into the clasper tube.

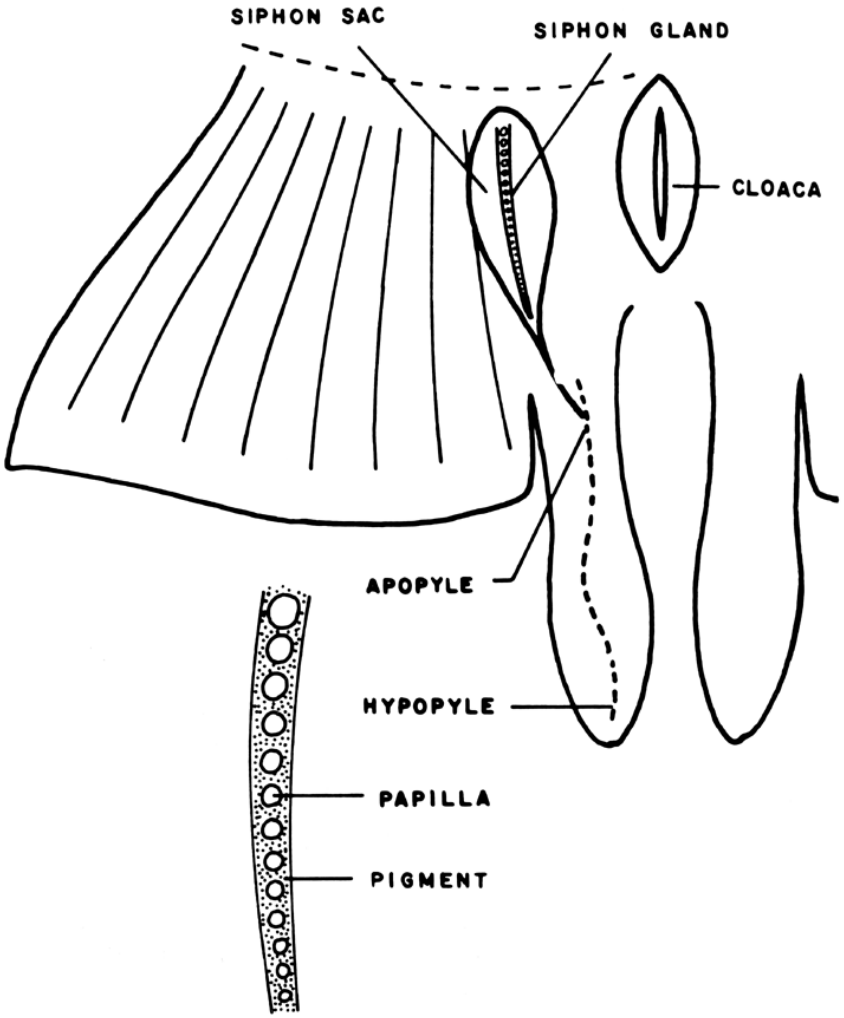


FIGURE 11. Male secondary sex organs of *U. halleri*. Siphon gland shown below, enlarged.

FIGURE 11. ***Male secondary sex organs of U. halleri. Siphon gland shown below, enlarged.***

Muscular adduction and the suffusion of blood into the tissue of the clasper, cause it to erect. In so doing, it bends forward at its base to lie along the animal's belly. At the same time it rotates so that the dorsally-located apopyle contacts the cloaca. During erection, the apopyle widens allowing sperm to pass from the urogenital papilla, through the cloaca and into the clasper tube. Contraction of the siphon sac then forces fluid through the clasper tube, which carries the sperm out the distal end of the tube.

4.3. Egg Development

Oogenesis begins in females of the round stingray when they are still embryos. Histological examinations show that shortly after birth many small ova are already present in both ovaries. Only those of the left ovary, however, attain maturity. The eggs in that organ begin to enlarge about 7 months after birth and six or eight of them soon surpass all others in size. Growth of the six to eight dominant ova is slow, and after 6 months the largest of the group has attained a diameter of only 0.7 mm (Figure 12).

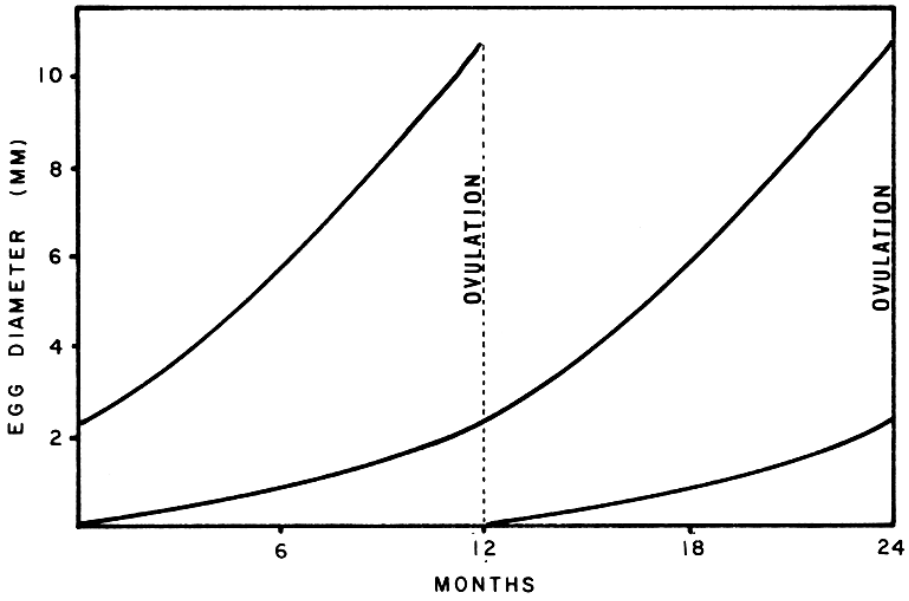


FIGURE 12. Growth rate curves for three different groups of ova developing in *U. halleri*, based on 312 individuals.

FIGURE 12. ***Growth rate curves for three different groups of ova developing in U. halleri, based on 312 individuals.***

By the 12th month, one ovum has definitely outgrown the others, reaching a diameter of over 2.0 mm. Meanwhile the smaller ova begin to degenerate. The dominant egg now grows more rapidly, soon forming a slight bulge on the ovary surface; accumulating yolk can be seen through the follicle wall. By the 18th month, the single ovum has reached 5.5 mm and ova in a second group have begun to enlarge. The last 6 months of egg growth are marked by a nearly constant and maximum rate of diameter increase (Figure 12). In young females,

the single egg ripens and is ovulated at a diameter of about 9.5 mm. By this time, ova of the second group have reached 2 mm, and one or more of these will ripen about 12 months later. In mature rays, two dominant egg groups are usually present, as well as many uniformly small ova of about 0.1 mm. At about the time of ovulation, some of these small eggs begin to enlarge (Figure 12). Oogenesis is therefore a continuous process throughout an animal's reproductive life.

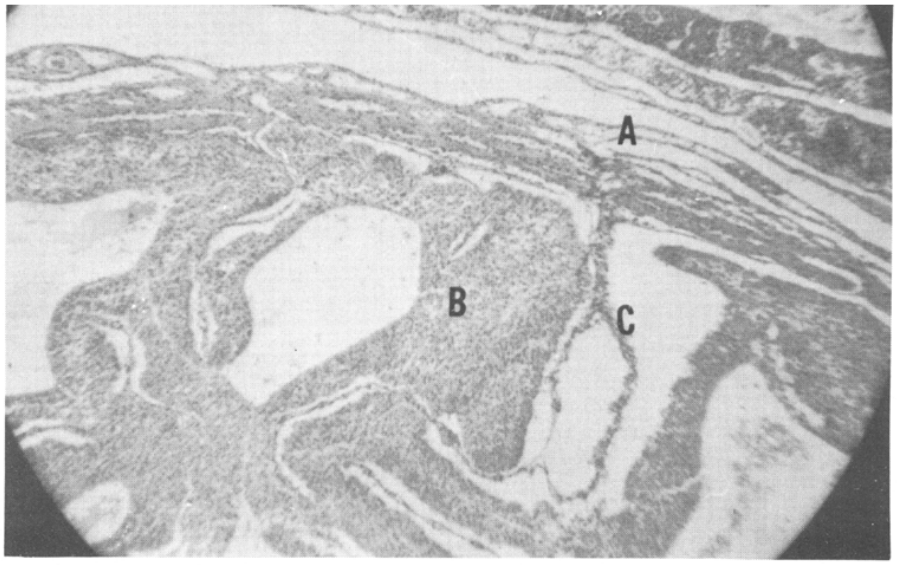


FIGURE 13. Ovum of 4.5 mm diameter, in advanced stage of degeneration. Outer theca, A; thickened follicular epithelium, B; inner theca extending into follicular fold, C. 44x

FIGURE 13. ***Ovum of 4.5 mm diameter, in advanced stage of degeneration. Outer theca, A; thickened follicular epithelium, B; inner theca extending into follicular fold, C. 44x***

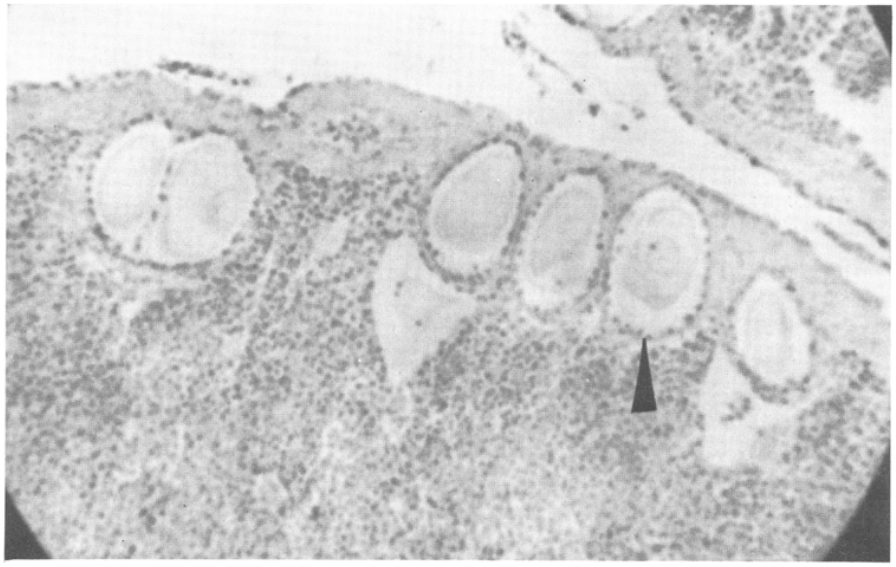


FIGURE 14. Early ova of 0.1 mm diameter, surrounded by a single row of epithelial cells (arrow). 125x

FIGURE 14. ***Early ova of 0.1 mm diameter, surrounded by a single row of epithelial cells (arrow). 125x***

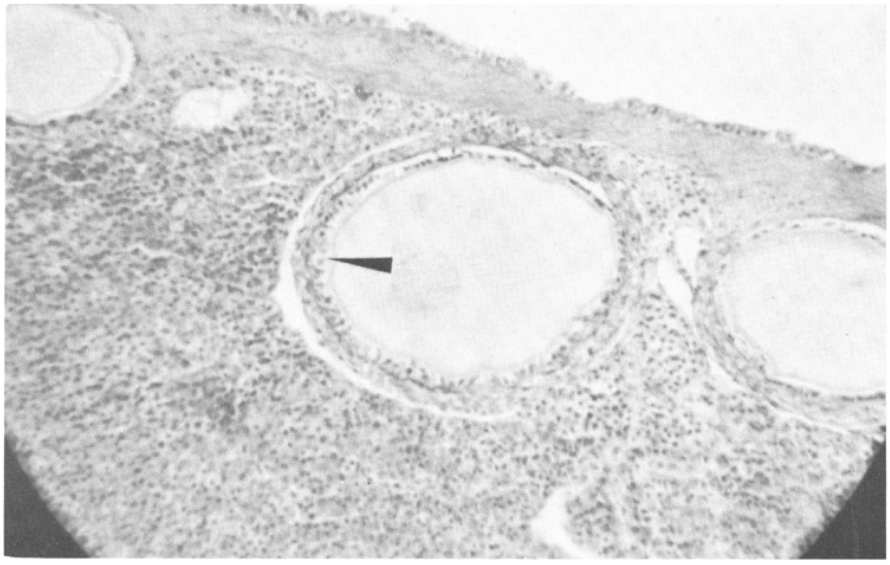


FIGURE 15. Ovum of 0.3 mm, with enlarging nutritive cells in the follicular epithelium (arrow). 125x

FIGURE 15. ***Ovum of 0.3 mm, with enlarging nutritive cells in the follicular epithelium (arrow). 125x***

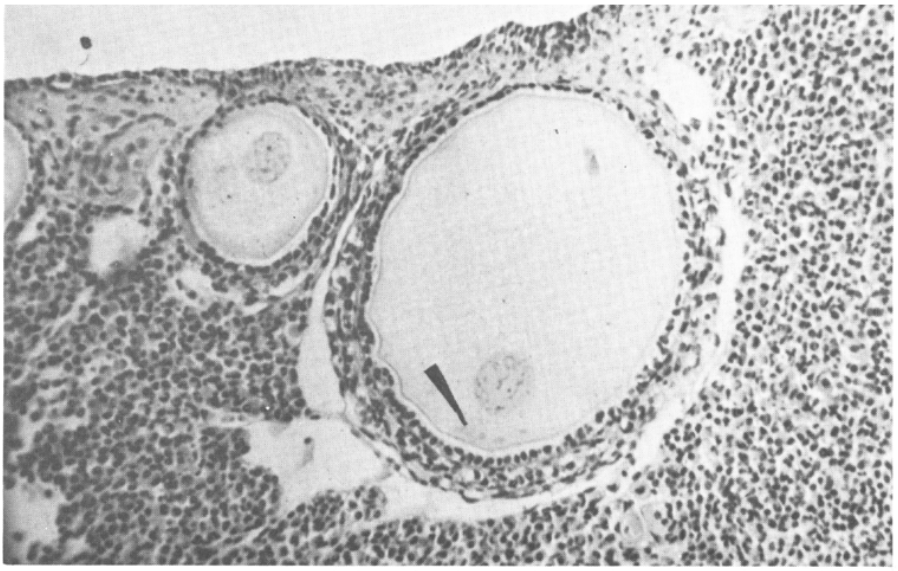


FIGURE 16. Ovum of 0.4 mm in which the nucleus lies close to the germinal disc (arrow). 125x

FIGURE 16. ***Ovum of 0.4 mm in which the nucleus lies close to the germinal disc (arrow). 125x***

There is a definite relationship between animal size and number of eggs ovulated, and some correlation also exists between animal size and mature egg size. Thus, when a female first reaches sexual maturity, she will normally ovulate one egg of about 9.5 mm diameter. In the second season, two slightly larger eggs are generally produced, while a very large animal may ovulate eight eggs ranging from 10 to 12 mm.

In each group of enlarging eggs, some will degenerate. Usually the degenerative process begins before a diameter of 2 mm is reached, but may occur in ova of 4.5 mm (Figure 13). Large degenerate eggs are sometimes mistaken for corpora lutea, and for this reason may be called false or spurious corpora lutea (Giacomini, 1896).

The early ova of U. halleri are similar to those of other elasmobranchs, at first being surrounded by a single row of follicular cells whose nuclei stain more darkly than those of cells in the surrounding ovarian stroma (Figure 14). Just peripheral to the follicular epithelium is the fibrous, sparsely-nucleated theca, forming an outer envelope for the follicle. Immediately inside the epithelial layer and directly against the yolk is a single egg membrane with radial striations, called the zona radiata. According to Balfour (1878) and Giacomini (1896), this membrane is always present in elasmobranchs.

Certain cells of the follicular epithelium begin to enlarge when the ovum has reached a diameter of about 0.3 mm (Figure 15). Consequently, that layer soon consists of a single row of large cells spaced at more or less regular intervals around the ovum, between which are interposed small undifferentiated cells. In an ovum of slightly larger diameter, the nucleus tends to have moved toward the germinal disc which is usually most distant from the ovary surface (Figure 16).

When an egg of U. halleri has attained a diameter of 1.5 mm, the follicular epithelium begins to proliferate inward at a number of points (Figure 17). In an ovum of 4.5 mm the proliferation has produced extensive epithelial folds (Figure 18), which project far in toward the center of the egg, carrying with them some inner layers of theca and small blood vessels.

In an ovum of 7 mm, the germinal disc, now containing the nucleus, lies close to one side of the large follicle as in an avian egg (Figure 19). There are no epithelial folds in the vicinity of the disc and it is bounded along its free side by a thin limiting membrane. In the germinal disc of a 9.6 mm ovum, the nucleus lies quite close to the egg membrane and follicular epithelium through which the sperm makes its entry (Figure 20). Following fertilization, cleavage commences in the disc of the meroblastic egg, much as it does in the ovum of birds.

It has been fairly well established by Wallace (1903) and others that the large cells of the follicular epithelium produce yolk material or a precursor substance. In some manner, this nutrient material passes through the zona radiata, into the egg. The large cells in the follicular epithelium of a rapidly growing 7 mm ovum, contain globules which closely resemble the yolk globules within the egg (Figure 21). Multiplication of the yolk-producing cells which accompanies the inward folding of the follicular epithelium, probably accounts for the rapid egg growth from a diameter of about 2.5 mm onward.

Shortly before ovulation, the large nutritive cells of the follicular epithelium begin to degenerate, reducing that layer to about one-half its former thickness. Uniformly fine-grained yolk granules now appear throughout the ovum, indicating ripeness (Figure 22).

An ovary was obtained from which a ripe ovum was escaping (Figure 23). The ovulating egg was sectioned and found to still contain the folded follicular epithelium (Figure 24). The theca within each epithelial fold was flattened, and its small blood vessels were collapsed.

At the base of each fold, the theca was wrinkled, perhaps due to shrinkage of the theca surrounding the egg. The cavity in the ovary contained

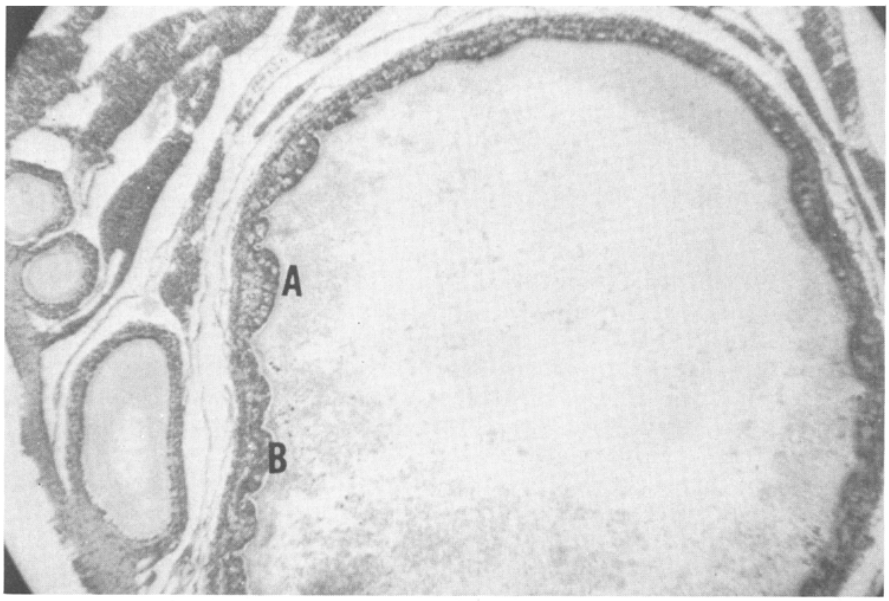


FIGURE 17. Ovum of 1.5 mm with follicular epithelium beginning to fold inward at A and B. 44x

FIGURE 17. ***Ovum of 1.5 mm with follicular epithelium beginning to fold inward at A and B. 44x***

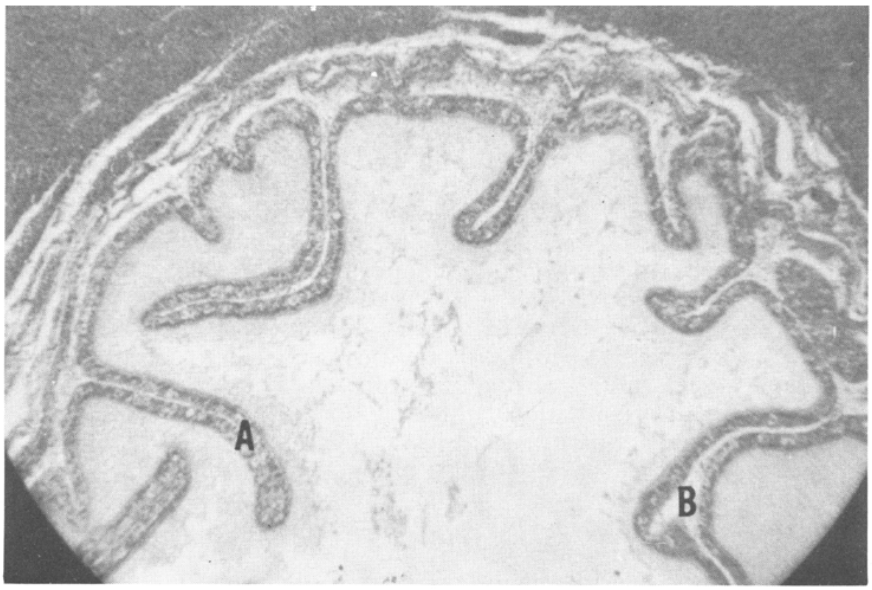


FIGURE 18. Ovum of 4.5 mm with large epithelial folds extending inward at A and B. 44x

FIGURE 18. ***Ovum of 4.5 mm with large epithelial folds extending inward at A and B. 44x***

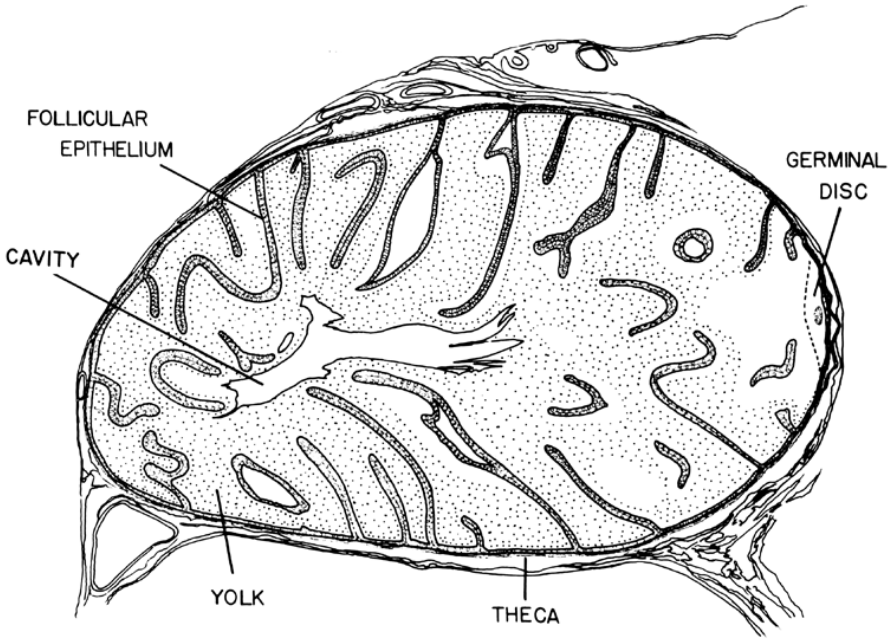


FIGURE 19. Ovum of 7 mm showing germinal disc with egg nucleus

FIGURE 19. ***Ovum of 7 mm showing germinal disc with egg nucleus***

only some outer layers of theca (Figure 25). It must be concluded, therefore, that the corpus luteum in this species is not derived from the follicular epithelium as in a number of elasmobranchs, some viviparous reptiles, and in mammals. It appears, instead, to arise from the outer envelope of theca which remains in the ovary.

In the round stingray, corpora lutea are bright-yellow structures just beneath the surface of the ovary. They typically are flattened, ovoid bodies of granular texture measuring about 7 x 4 x 2 mm. They form rapidly after ovulation and persist throughout pregnancy. Females captured a few days after parturition still possessed corpora lutea that were very little diminished in size (Figure 26). A thick, connective tissue capsule surrounds the structure. Fibrous trabeculae extend inward giving the mass of light-staining luteal cells a lobular appearance. After parturition, the corpora lutea begin to degenerate, eventually being reduced to small fibrous masses.

When the temporal distribution of ovulation is plotted, two peaks of ovulation occur, spaced 6 months apart, and it can be seen that the June peak is by far the greatest (Figure 27). Since an individual ovulates at intervals of about 1 year the small December peak must represent a segment of the female population that is 6 months out of phase with the rest.

4.4. Sperm Development

4.4.1. Development of the immature testis

A previously undescribed structure, which I have named a testicular appendage, is present in male U. halleri. One of these small fingers

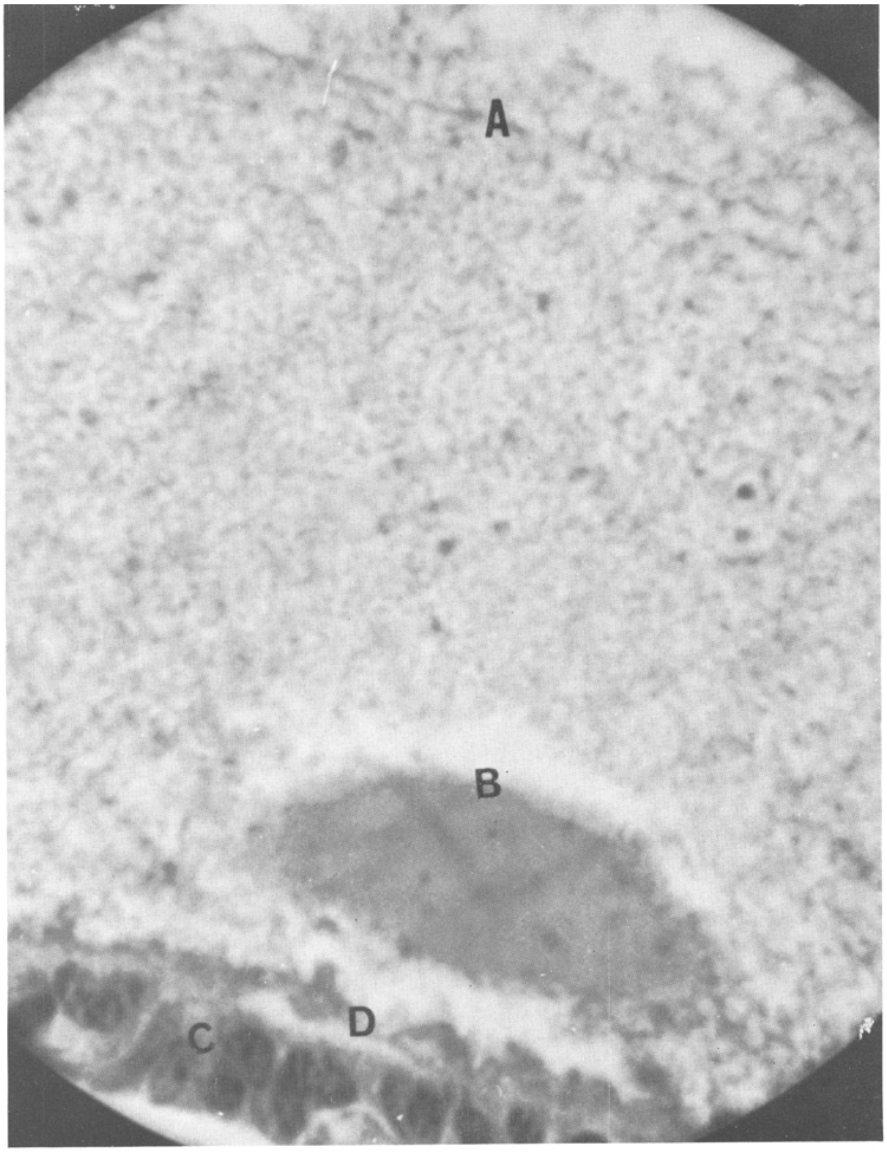


FIGURE 20. Germinal disc of 9.6 mm ovum. Limiting membrane, A; egg nucleus, B; follicular epithelium, C; egg membrane, D. 560x

FIGURE 20. ***Germinal disc of 9.6 mm ovum. Limiting membrane, A; egg nucleus, B; follicular epithelium, C; egg membrane, D. 560x***

of tissue extends from the center of each primary lobule (Figure 5B). In newborn rays, the appendages are about 0.2 mm in diameter and 1 mm long; they are slightly larger in adults. An appendage usually extends freely from a small pit in the gonad surface (Figure 28). Some appendages, however, lie entirely beneath the surface of the testis, and are covered by folds of gonadal tissue (Figures 29, 30, 31).

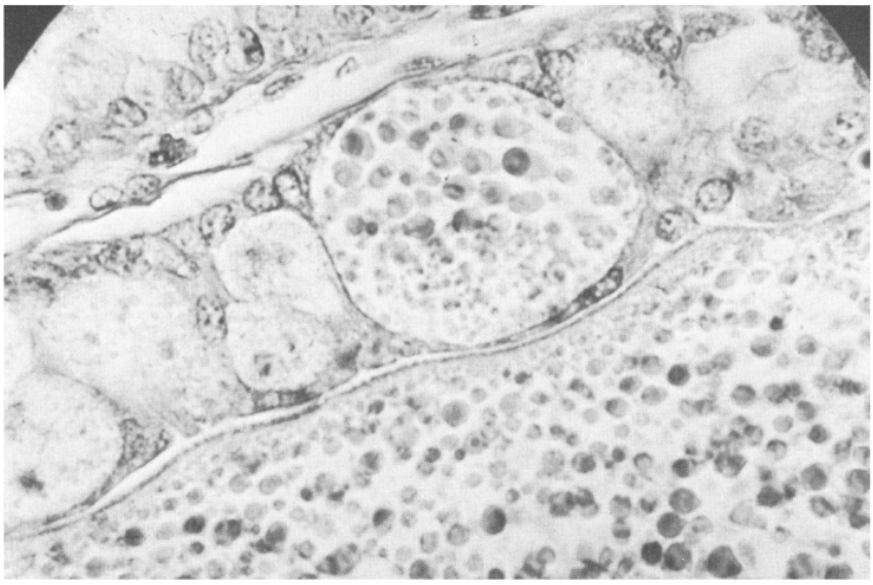


FIGURE 21. Globules in the nutritive cells and in the yolk of a 7 mm ovum. 792x

FIGURE 21. ***Globules in the nutritive cells and in the yolk of a 7 mm ovum. 792x***

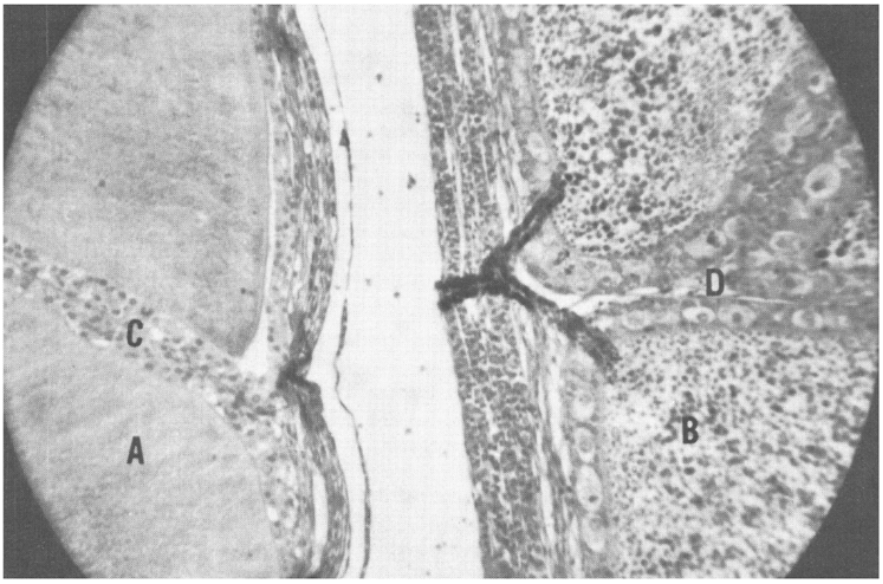


FIGURE 22. Comparison of ripe and nearly ripe ova. Fine yolk granules in ripe egg, A; coarse granules in unripe egg, B; degenerated nutritive cells, C; large nutritive cells, D. 125x

FIGURE 22. ***Comparison of ripe and nearly ripe ova. Fine yolk granules in ripe egg, A; coarse granules in unripe egg, B; degenerated nutritive cells, C; large nutritive cells, D. 125x***

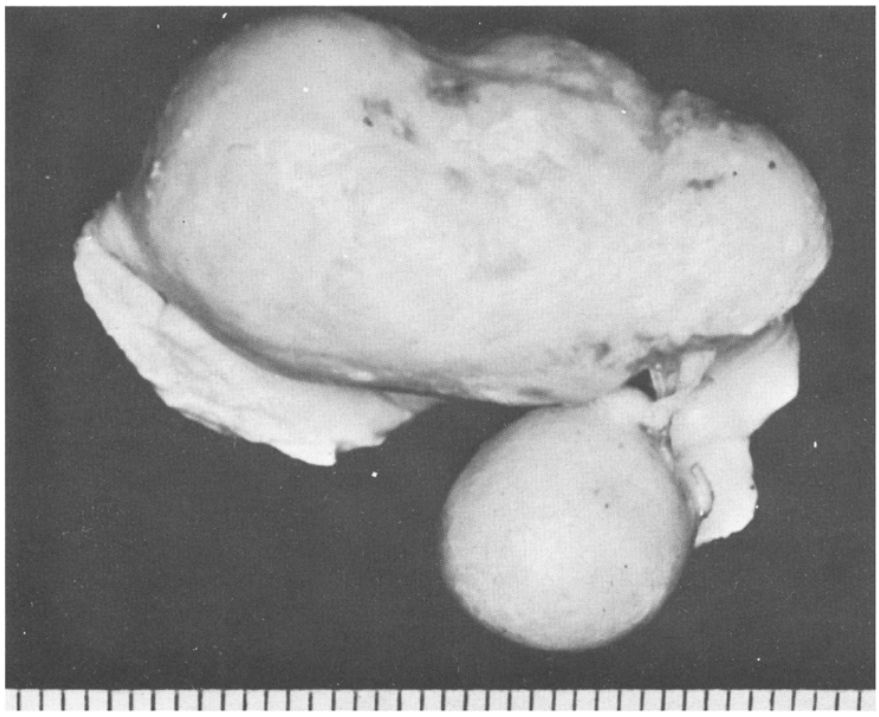


FIGURE 23. Ovulating egg.

FIGURE 23. ***Ovulating egg.***

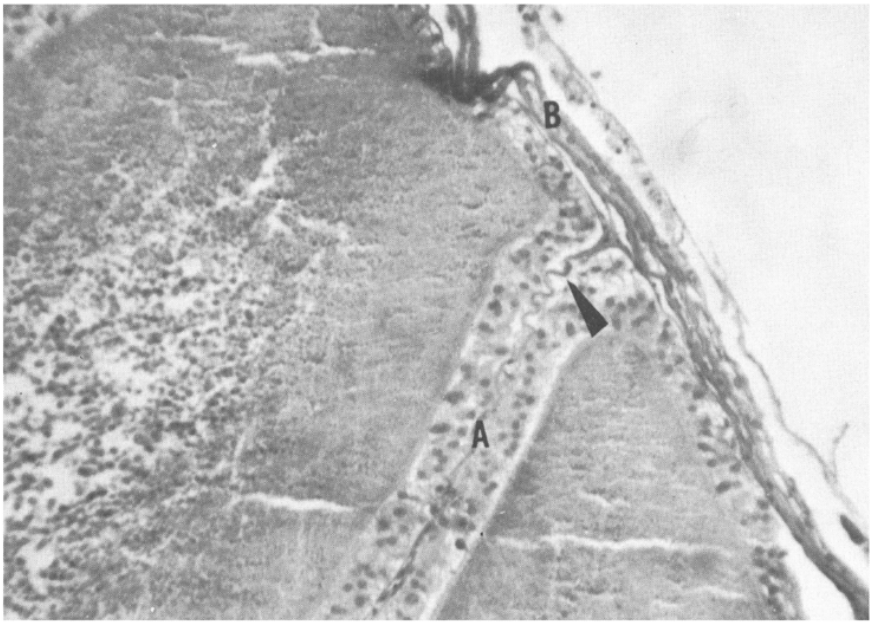


FIGURE 24. Section through ovulating egg of Figure 23. Epithelial folds still present, A; theca surrounding ovum, B; wrinkled theca in epithelial folds (arrow). 560x

FIGURE 24. ***Section through ovulating egg of Figure 23. Epithelial folds still present, A; theca surrounding ovum, B; wrinkled theca in epithelial folds (arrow). 560x***

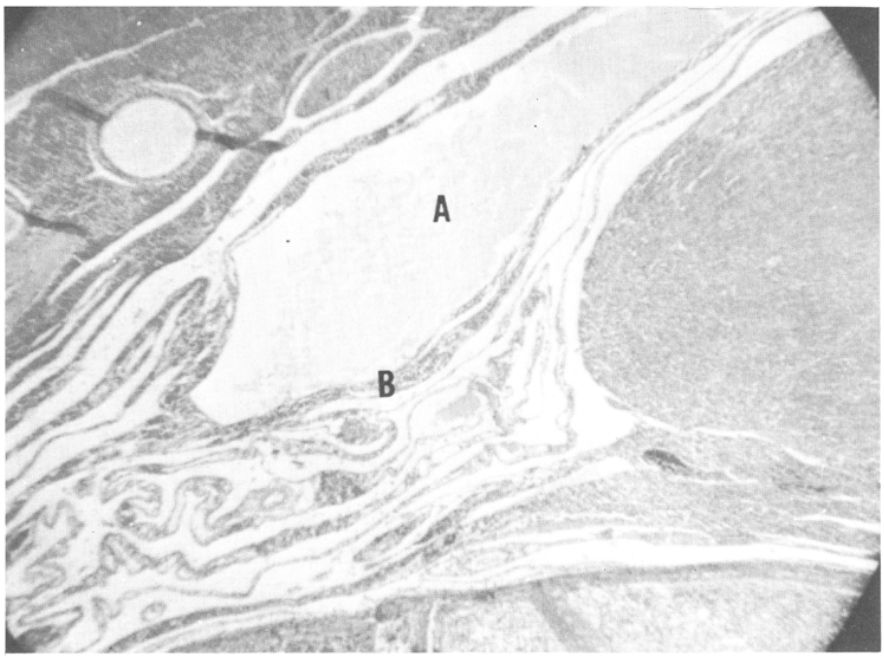


FIGURE 25. Cavity in ovary, after ovulation, A; outer theca remaining in ovary B. 125x

FIGURE 25. ***Cavity in ovary, after ovulation, A; outer theca remaining in ovary B. 125x***

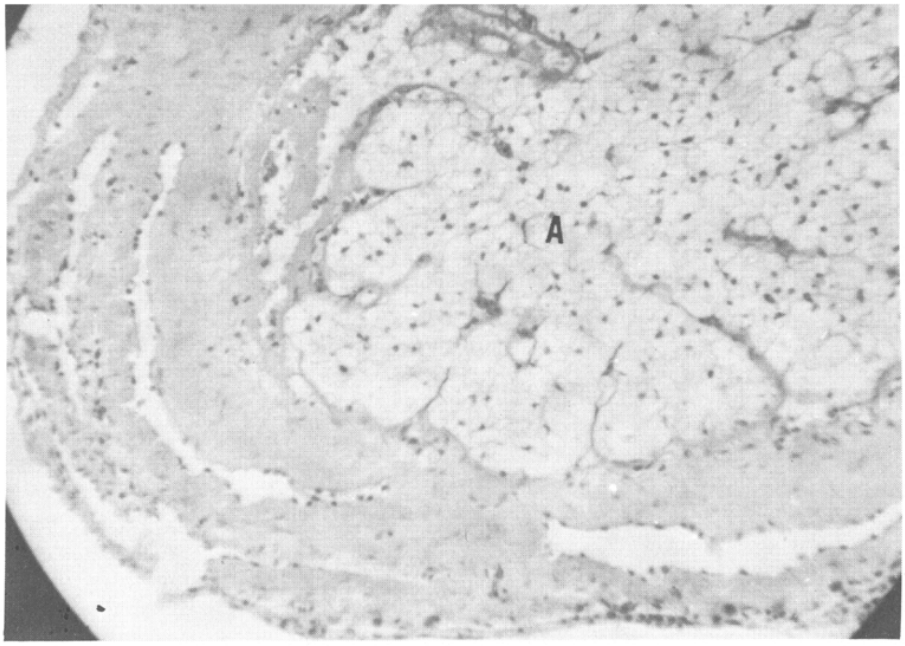


FIGURE 26. Corpus luteum in left ovary of postpartum ray. Luteal cells, A. 125x

FIGURE 26. ***Corpus luteum in left ovary of postpartum ray. Luteal cells, A. 125x***

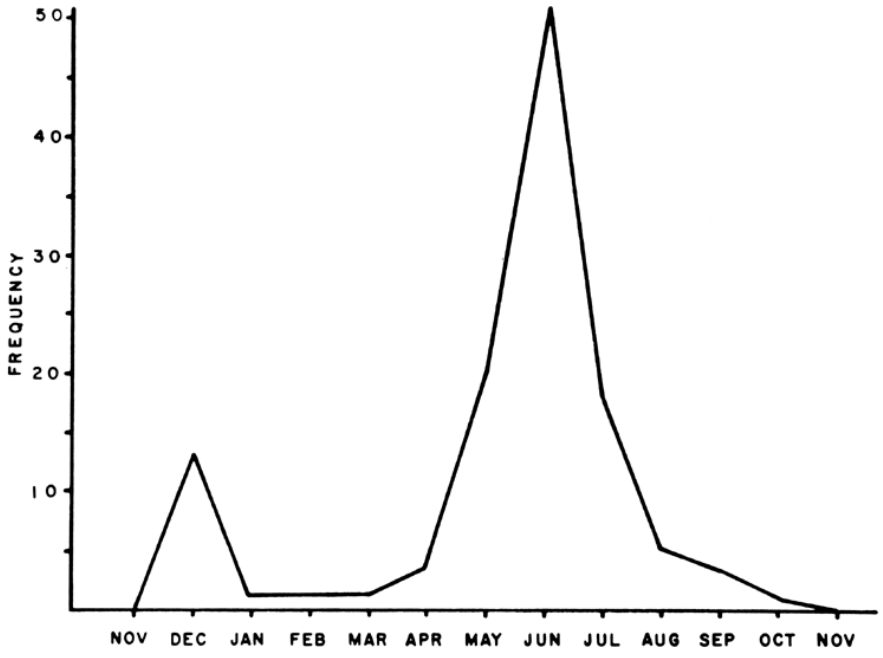


FIGURE 27. Temporal distribution of ovulation for *U. halleri,* based on 119 individuals. All rays had either just ovulated or contained large ova.

FIGURE 27. ***Temporal distribution of ovulation for U. halleri, based on 119 individuals. All rays had either just ovulated or contained large ova.***

An appendage, when viewed in cross-section, contains large, light-staining cells near its center. I have not studied the embryonic origin of these cells; they may be primordeal germ cells which have migrated from the yolk sac wall or from elsewhere, to the genital ridge to be incorporated into the testis. In this study I will refer to them simply as large germ cells.

The large germ cells begin to migrate from the appendages into the testis when a ray is about 12 months old. At the base of each appendage these cells gather into hollow balls called follicles, and this initiates development of the primary lobules which then continue to enlarge by addition of follicles. In the appendages of an immature 18-month-old animal, the large germ cells appear to be arranged in cords, and at this age a limited number of follicles is present in the rather small, adjacent primary lobule (Figure 32). A primary lobule in the testis of a 21-month-old ray is larger and contains a greater number of follicles; many large ducts now penetrate the lobule and these in turn, join a system of longitudinal ducts deep in the testis (Figure 33).

As follicles form in an immature primary lobule, they move away from their point of origin near the base of the testicular appendage and at the same time they enlarge by cell divisions. The central cavity of a follicle enlarges as the follicle migrates and adds new cells (Figures 34, 35). Primary lobules are fully formed and contain many follicles in a 23-month-old male. Once formed, these lobules serve as permanent reservoirs of spermatogonia and primary spermatocytes.

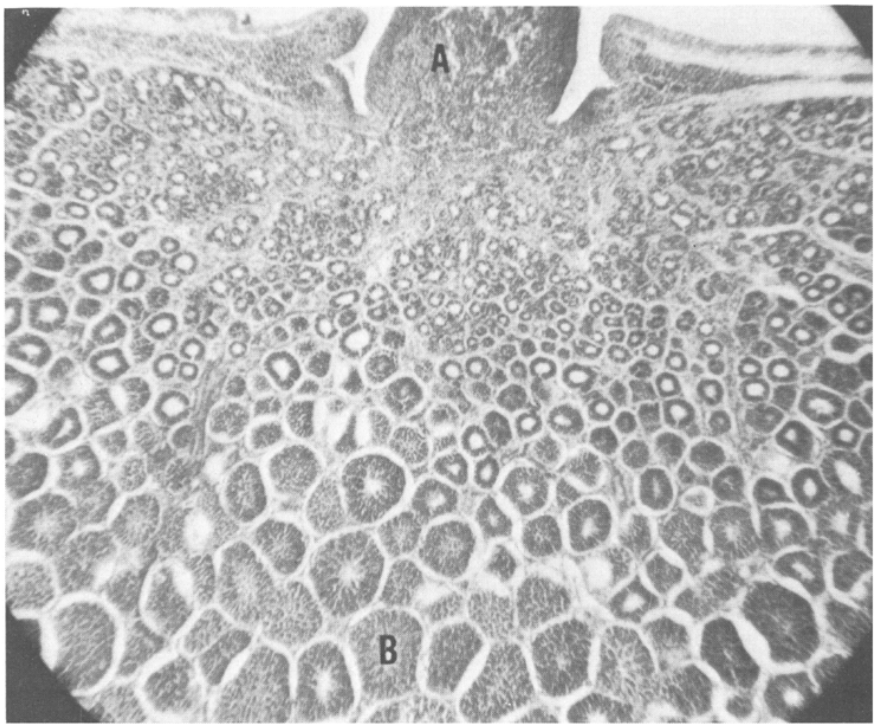


FIGURE 28. Testicular appendage extending from dorsal gonad surface, in oblique section, A; large follicle filled with secondary spermatocytes, B. 44x

FIGURE 28. ***Testicular appendage extending from dorsal gonad surface, in oblique section, A; large follicle filled with secondary spermatocytes, B. 44x***

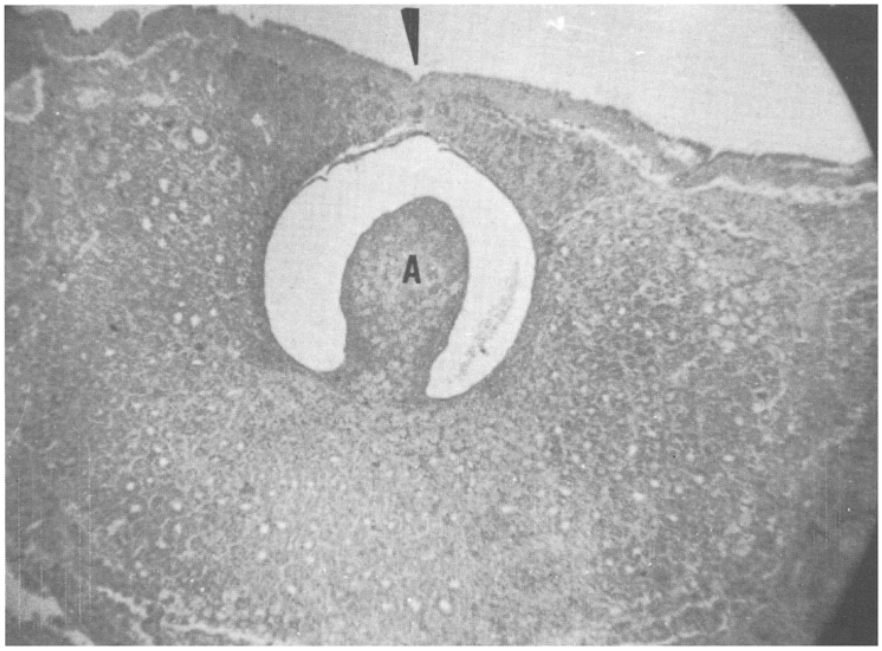


FIGURE 29. Testicular appendage beneath gonad surface, in transverse section, A. Folds of testis meet above the appendage (arrow). 44x

FIGURE 29. ***Testicular appendage beneath gonad surface, in transverse section, A. Folds of testis meet above the appendage (arrow). 44x***

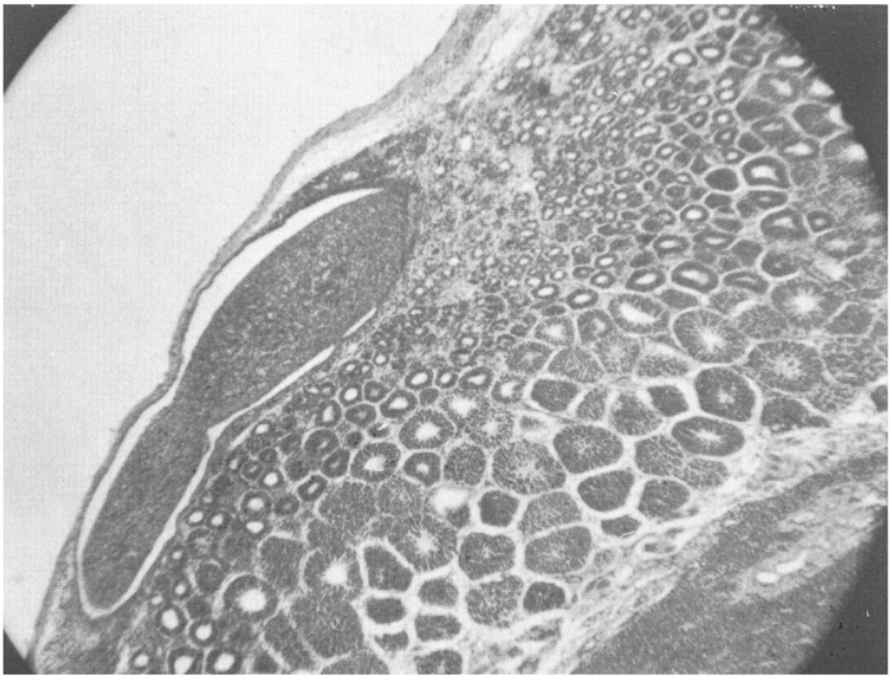


FIGURE 30. Testicular appendage beneath gonad surface, in longitudinal section. 44x

FIGURE 30. ***Testicular appendage beneath gonad surface, in longitudinal section. 44x***

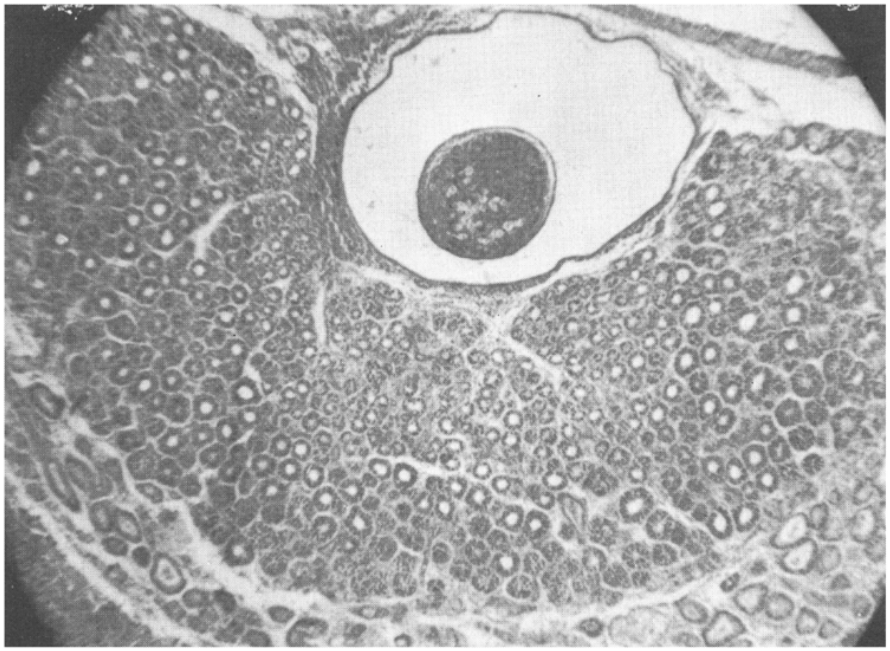


FIGURE 31. Transverse section through distal end of enclosed testicular appendage. 44x

FIGURE 31. ***Transverse section through distal end of enclosed testicular appendage. 44x***

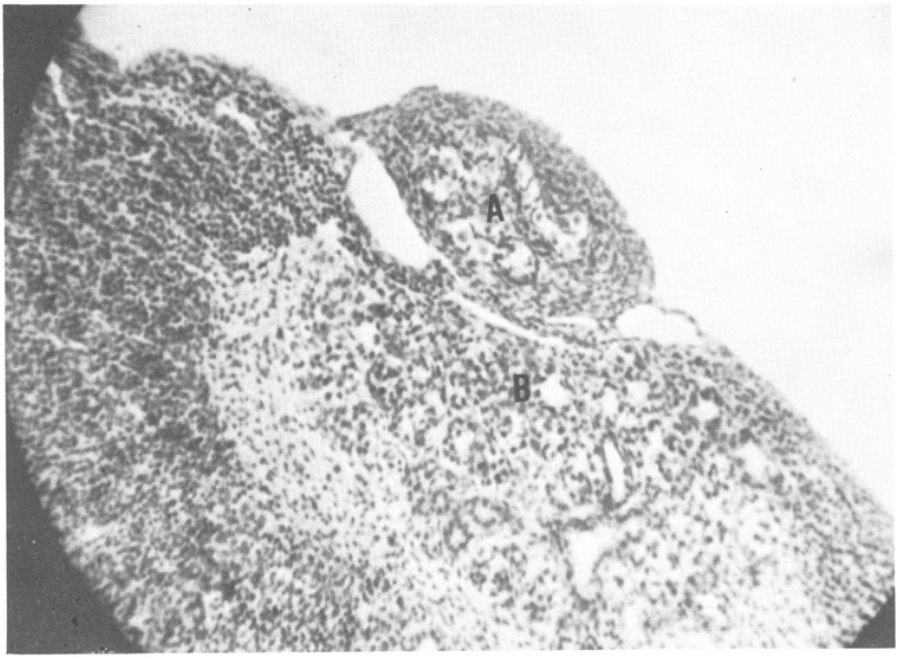


FIGURE 32. Immature testis of 18-month-old animal. Large germ cells in the appendage, A. Follicles in the adjacent primary lobule, B. 125x

FIGURE 32. ***Immature testis of 18-month-old animal. Large germ cells in the appendage, A. Follicles in the adjacent primary lobule, B. 125x***

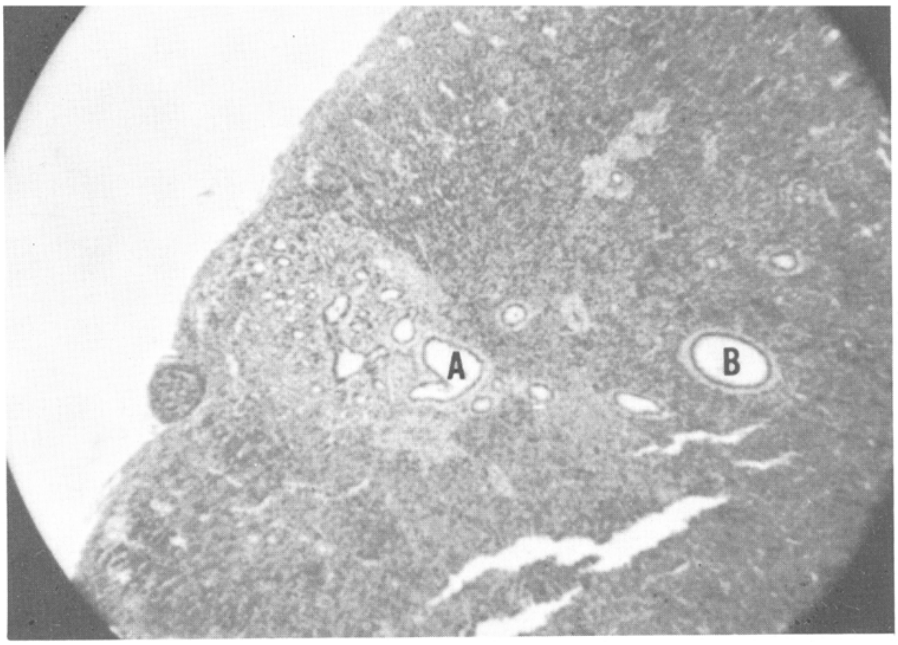


FIGURE 33. Immature primary lobule of 21-month-old animal. Large duct penetrating lobule, A; longitudinal duct seen in cross section, B. 44x

FIGURE 33. ***Immature primary lobule of 21-month-old animal. Large duct penetrating lobule, A; longitudinal duct seen in cross section, B. 44x***

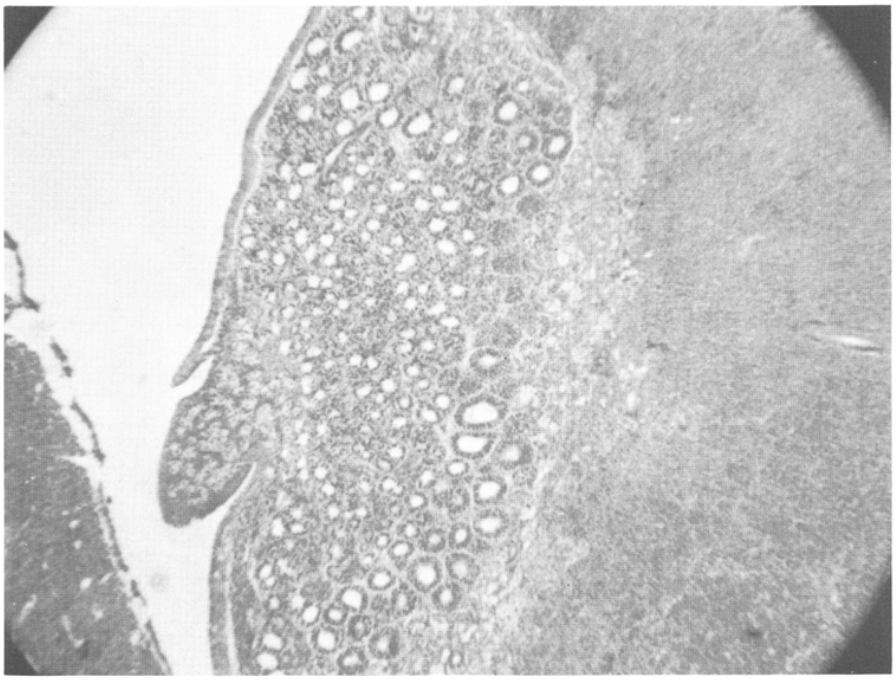


FIGURE 34. Large germ cells migrating from appendage into mature primary lobule. Follicles of primary lobule enlarging by cell divisions and moving away from base of appendage. 44x

FIGURE 34. ***Large germ cells migrating from appendage into mature primary lobule. Follicles of primary lobule enlarging by cell divisions and moving away from base of appendage. 44x***

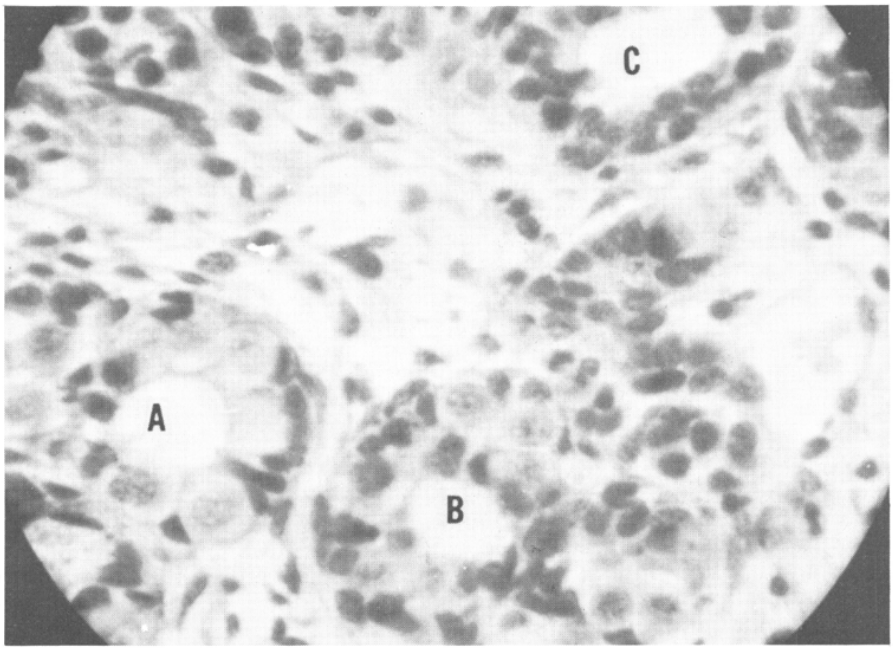


FIGURE 35. Early follicle of large germ cells at base of testicular appendage, A; follicle in which spermatogonial divisions have begun, B; follicle in which spermatogonia have replaced large germ cells, C. 562x

FIGURE 35. ***Early follicle of large germ cells at base of testicular appendage, A; follicle in which spermatogonial divisions have begun, B; follicle in which spermatogonia have replaced large germ cells, C. 562x***

4.4.2. Annual cycle of spermatogenesis

The first cycle of spermatogenesis begins in immature males soon after their primary testicular lobules are formed, at about 23 months of age. Sperm ripen in the secondary lobules approximately 8 months later when the animal is about 31 months old. I used the presence of ripe sperm as the criterion for determining sexual maturity. Mature males produce sperm annually.

It is difficult to follow the cell divisions that take place in the testes of the round stingray during spermatogenesis, and in order to accomplish this, some system must be devised. It is assumed that a follicle in a given stage of development which has been sectioned in a plane passing through its center, will as a result appear to have the largest lumen. It is thus possible to select a number of follicles in the same developmental stage, that have been so sectioned, and to determine the average number of sex cells appearing in them at that stage. Then by comparing the number of cells visible in different stages, it is possible to estimate the number of divisions that occur.

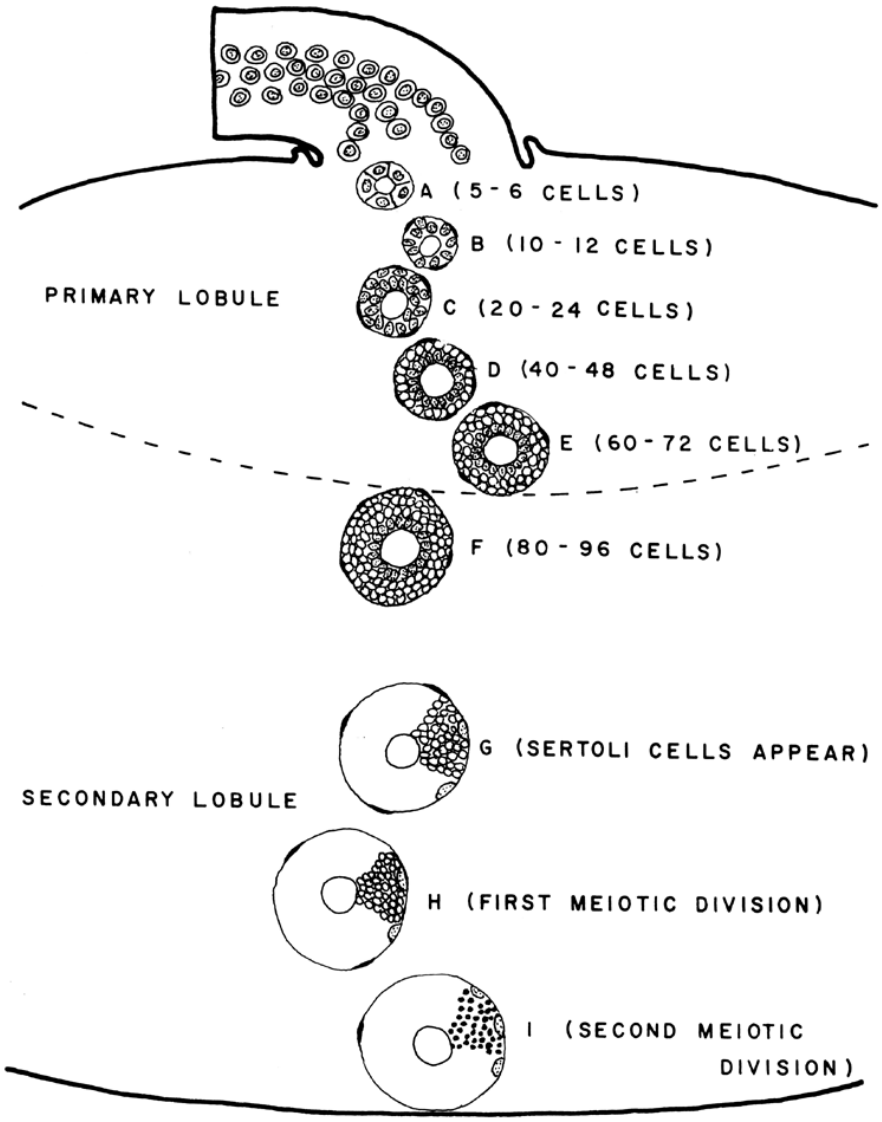
Five or six large germ cells can normally be seen in an early follicle that has been sectioned through its center (Figure 36A). Slightly deeper in the primary lobule, 10 or 12 smaller spermatogonia are found in a single layer around the lumen (Figure 36B). Still further from the appendage base, 20 to 24 cells are seen in each follicle, at first in a very irregular layer (Figure 36C) and later forming a single orderly layer around the cavity. In the next division, the 20 to 24 spermatogonia become encircled by an approximately equal number of primary spermatocytes (Figure 36D). The manner in which this occurs is not clear; possibly each spermatogonium divides, and one daughter cell retains its identity while the other becomes a primary spermatocyte. The alternative would be that one-half of the 20 to 24 spermatogonia produce daughter cells which are all primary spermatocytes, while the other 10 or 12 spermatogonia produce daughter cells which are all spermatogonia.

The next division results in three concentric layers of cells totaling 60 to 72 (Figure 36E); the layer immediately surrounding the cavity still consists of 20 to 24 spermatogonia; it is not known whether the additional 20 to 24 primary spermatocytes are produced by the spermatogonia or by the most peripheral layer of primary spermatocytes. This is the extent of divisions within the primary lobule.

The beginning of the annual gonadal cycle is marked by formation of additional follicles at the base of each appendage. All previously formed follicles of a primary lobule now move deeper into the testis and their cells resume divisions. A third concentric row of primary spermatocytes appears in the outlying follicles so that four rows of cells are arranged around the central cavity (Figure 36F). In this way, the secondary portion of the testicular lobule is begun.

When the most advanced follicles in the secondary lobules contain cells six layers deep (Figure 36G), the spermatogonia of these follicles disappear from their position around the cavity. Soon, approximately the same number of Sertoli cells are spaced around the follicle wall.

The large outlying follicles in the secondary lobule now have their full complement of primary spermatocytes, and they begin to undergo



FIGURES 36. Diagram showing stages of spermatogenesis in a primary and secondary lobule. (A thru I)

FIGURES 36. ***Diagram showing stages of spermatogenesis in a primary and secondary lobule. (A thru I)*** the first meiotic division; this division transforms each cell into two smaller secondary spermatocytes; concurrently the follicle enlarges to its ultimate diameter (Figure 36H), apparently by a slight growth of each secondary spermatocyte. Soon the second meiotic division occurs (Figure 36I), producing many noticeably smaller spermatids, arranged in clumps; each clump is associated with a Sertoli cell.

The spermatids in the peripheral follicles now begin to elongate and much of their cytoplasm is sloughed off. Each nucleus continues to

lengthen, forming a wavy, threadlike sperm head that stains lightly at first, but soon becomes very dark. Three stages of sperm development are sometimes found in three adjacent follicles (Figure 37).

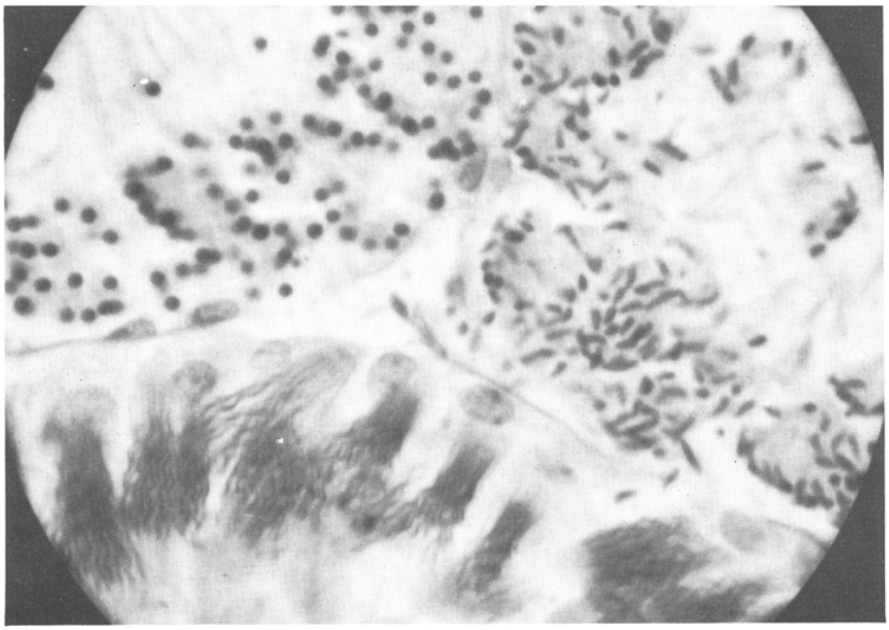


FIGURE 37. Three adjacent follicles with different stages of sperm development. Spermatids at upper left; elongating spermatids at upper right; sperm associated with Sertoli cells, below. 560x

FIGURE 37. ***Three adjacent follicles with different stages of sperm development. Spermatids at upper left; elongating spermatids at upper right; sperm associated with Sertoli cells, below. 560x***

The oldest and most advanced follicles of a secondary lobule are also the most peripheral ones. They ripen first and can be readily seen in an histological preparation because the sperm in them stain darkly. When these peripheral follicles become ripe, they form a dark border around the secondary lobule (Figure 38). Ripening progresses from the peripheral follicles toward the youngest follicles, which lie next to the associated primary lobule. The stage of ripening can be determined by the relative area of the secondary lobule that contains darkly-stained follicles (Figure 39).

The peripheral follicles are also the first to shed their sperm; after shedding they collapse and their walls consist only of Sertoli cells that will soon degenerate (Figure 40). When the oldest follicles have collapsed the youngest ones, adjacent to the primary lobule, are just becoming ripe. The ripening and shedding of sperm in an individual, may continue for a month.

Follicles of the primary and secondary lobules of a testis, contrast sharply in size when the secondary lobule is ripe (Figure 40). However, when the secondary lobule is still undergoing its annual cycle of development, the boundary between the two lobules is poorly defined because of the continuous gradation in follicles sizes (Figures 28, 30).

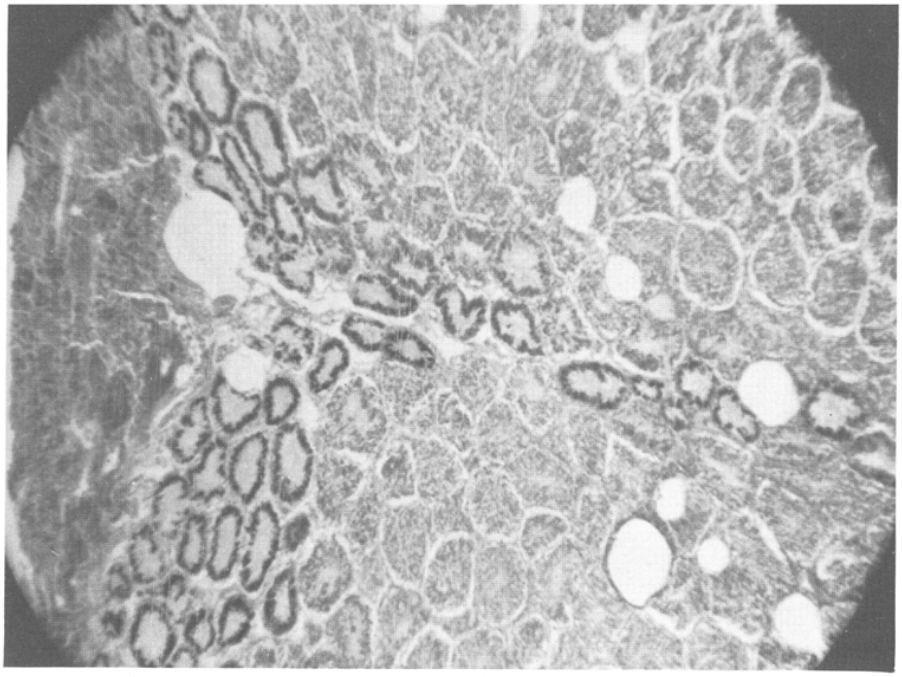


FIGURE 38. Two adjacent testicular lobules with ripe, darkly-stained sperm in the most periferal follicles. 44x

FIGURE 38. ***Two adjacent testicular lobules with ripe, darkly-stained sperm in the most periferal follicles. 44x***

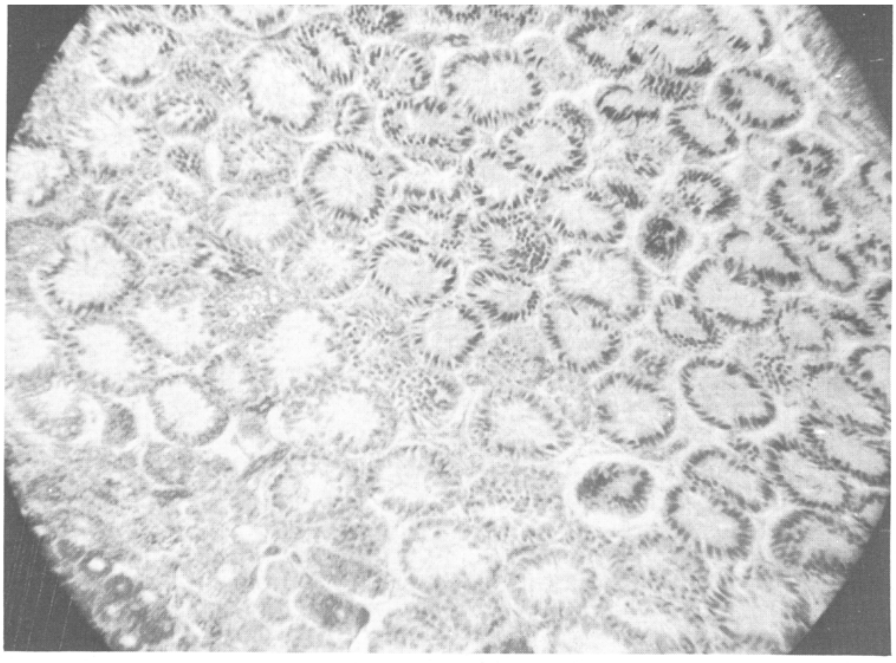


FIGURE 39. Secondary lobule with ripe sperm in more than half of the follicles; edge of primary lobule visible at extreme lower left. 44x

FIGURE 39. ***Secondary lobule with ripe sperm in more than half of the follicles; edge of primary lobule visible at extreme lower left. 44x***

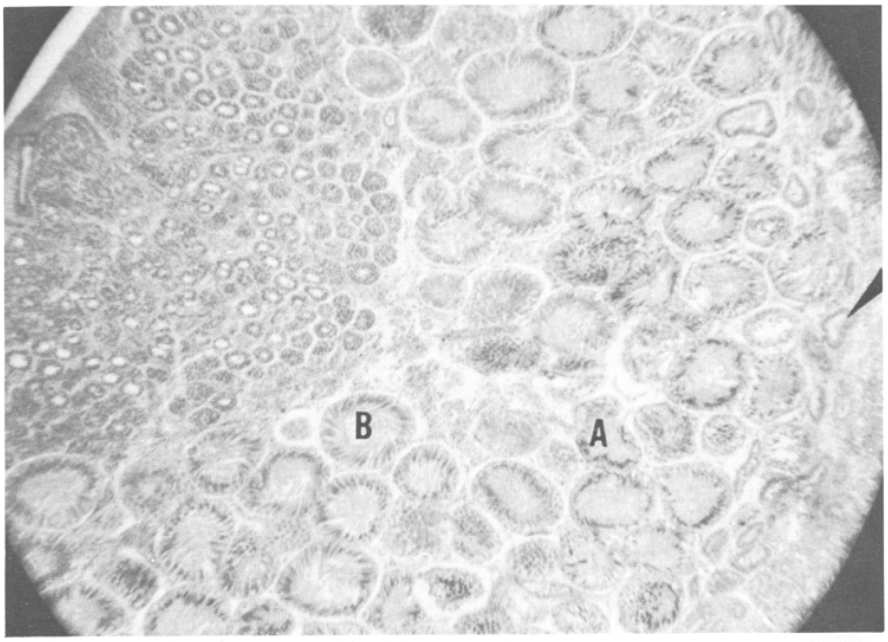


FIGURE 40. Secondary lobule with periferal follicles empty and collapsed (arrow); centrally located follicle shedding sperm, A; nearly ripe sperm in follicle adjacent to primary lobule, B. 44x

FIGURE 40. ***Secondary lobule with periferal follicles empty and collapsed (arrow); centrally located follicle shedding sperm, A; nearly ripe sperm in follicle adjacent to primary lobule, B. 44x***

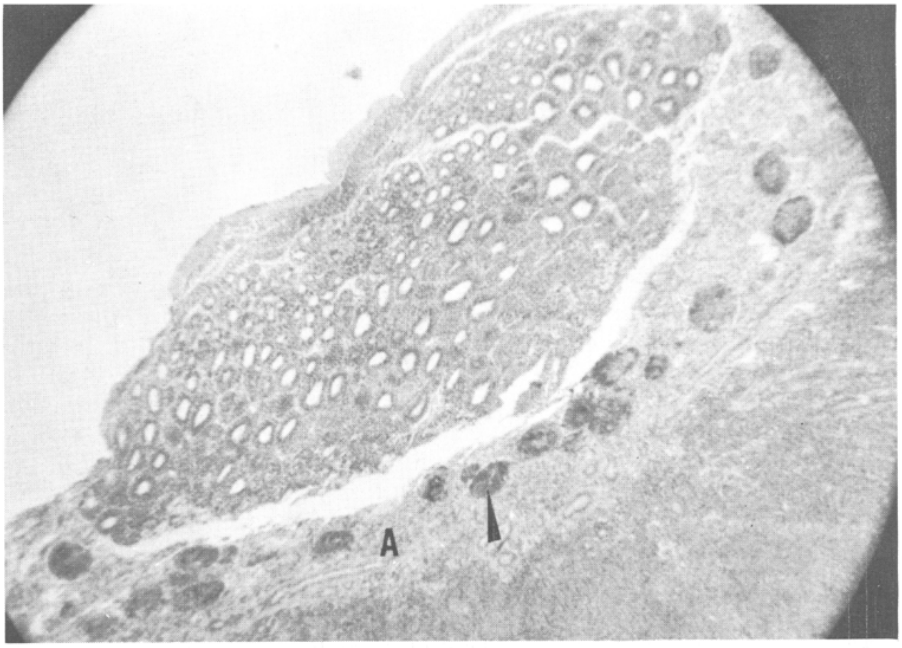


FIGURE 41. Collapsed secondary lobule is zone of lightly stained tissue, A; dark mass of trapped sperm (arrow). Primary lobule is above. 44x.

FIGURE 41. ***Collapsed secondary lobule is zone of lightly stained tissue, A; dark mass of trapped sperm (arrow). Primary lobule is above. 44x.***

When the entire secondary lobule has shed its sperm and has collapsed, it becomes a narrow band of light staining tissue, marked by dark masses of spermatozoa (Figure 41). Usually such masses represent follicles that for some reason did not rupture. In other instances, sperm from late-rupturing follicles appear to be trapped in the collapsed tissue. These masses soon begin to degenerate and large, redstaining phagocytic cells engulf the remaining debris before the next gonadal cycle begins. The ciliated ducts of a ripe testis contain varying amounts of sperm (Figure 42).

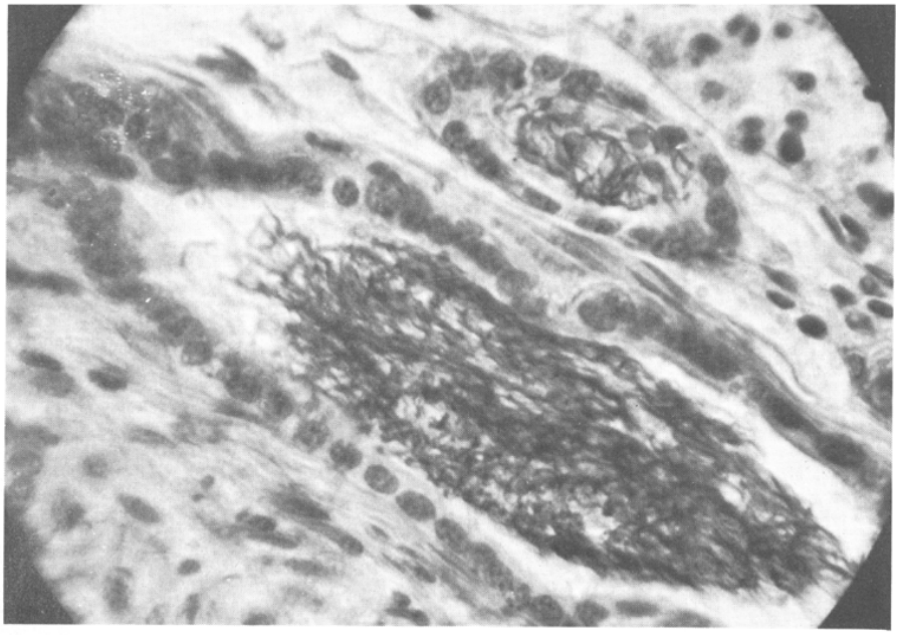


FIGURE 42. Sperm in ducts of a testis of *U. halleri*. 560x

FIGURE 42. ***Sperm in ducts of a testis of U. halleri. 560x***

Testes from 327 animals were collected and preserved during this study. Each month of the year was represented in the sample, by males ranging from immature to the largest available. From these, the testes of 168 animals were selected for histological examination. All testes which were enlarged or had prominent testicular lobules were chosen, as well as inactive-appearing testes from rays of a wide size range, and representing all months. From this histological study the typical cycle of spermatogenesis was determined (Table 1) .

Seventy-six of the 168 animals examined histologically, were shedding ripe sperm from the testes at time of capture. The percentage of these 76 males which were shedding each month, I believe, represents the temporal distribution of sperm production (Figure 43). January, February, and March are the peak months with 11 percent shed before that period and only 5 percent shed after.

TABLE 1

Typical Cycle of Spermatogenesis for *U. halleri*

July	Secondary lobules begin to form rapidly: follicles enlarge with additional primary spermatocytes.
August	Secondary lobules attain one-half maximum size; some follicles now contain secondary spermatocytes; spermatids appear in oldest follicles at periphery of lobule.
September	Secondary lobules approach maximum size; many follicles contain spermatids; a few peripheral follicles contain immature sperm clumps; primary lobules become dormant.
October	Follicles in peripheral one-third of each secondary lobule contain immature sperm clumps.
November	Follicles in peripheral two-thirds of each secondary lobule contain immature sperm clumps.
December	All follicles of secondary lobule contain immature sperm clumps.
January	A few peripheral follicles in each secondary lobule shed mature sperm; many peripheral follicles nearing maturity.
February	Many follicles shed mature sperm.
March	Secondary lobules collapse, begin to be reabsorbed.
April, May, June	Rest period; primary lobules remain dormant; reabsorption of secondary lobules is completed.

TABLE 1 ***Typical Cycle of Spermatogenesis for U. halleri***

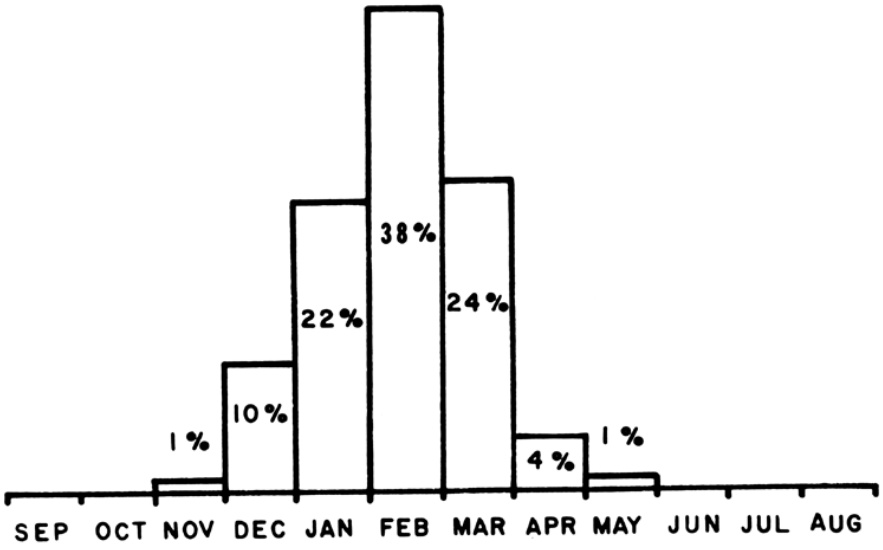


FIGURE 43. Temporal distribution of sperm production, based on histological examination of 168 males, 76 of which were shedding sperm when captured.

FIGURE 43. ***Temporal distribution of sperm production, based on histological examination of 168 males, 76 of which were shedding sperm when captured.***

4.5. GESTATION

4.5.1. Relationship of animal size to right uterus function

Previously, I pointed out that the right uterus of U. halleri develops more slowly and is used less than the left. Data for pregnant females taken at Newport Bay, September 17, 1959, demonstrate this relationship (Table 2) . When the animals are listed in order of size, it is seen that young females bear smaller litters, and when there is a single fetus it is usually carried in the left uterus. As the size of litters increases with age of the female, the right uterus comes into use, but the left still receives more ova. The largest ray had six fetuses of almost equal size, evenly distributed between the left and right uterus (Table 2). However, in the smaller females, when fetuses were present in both uteri, those in the right were usually smaller.

4.5.2. Uterine villi

Villi are present on the uterine mucosa of a number of elasmobranchs. These structures attain their highest development in the several

TABLE 2

Relationship of Uterus Function to Animal Size in *U. halleri*

Size and approximate age of mother		Number of fetuses	
Disc width (mm)	Age (months)	Left uterus	Right uterus
149	30	1	
151	31	1	
160	36.5	--	1
165	39.5	1	
166	40	1	1*
170	42.5	1	
171	43	1	1*
174	45	1	
175	45.5	2	
175	45.5	2	
175	45.5	1	1*
175	45.5	--	1
177	47	1	1*
188	57	2	
189	----	2	1*
191	----	2	1
245	----	3	3
Total	----	22	11

* Fetus smaller than that/those in left uterus.

TABLE 2 ***Relationship of Uterus Function to Animal Size in U. halleri***

families of stingrays. Alcock (1891) described the villi lining the uterus of Pteroplatea macrura (= Gymnura micrura) in considerable detail, calling them trophonemata, and expressing the belief, in which I concur, that they were instrumental in nourishing the embryo.

Immature U. halleri about 135 mm in disc width have trophonemata 3 mm long in the left uterus, while those lining the right are only about 2 mm long. Approximately 20 mm of the left uterus contains villi, and 16 mm of the right. The villi are flattened in cross section and about 0.25 mm wide at the middle, but taper to one-half that width at both the base and free end. Their epithelium consists of a single layer of uniform, cuboidal cells. One vein and two arteries traverse the length of each villus sending branches to just beneath the epithelium.

Just before ovulation, the uteri are somewhat enlarged and contain a clear watery fluid. The trophonemata are then longer, those of the left uterus having increased to 5 mm, and the right to 3 mm. An ovulated egg settles down among the villi, although there is no physical connection. If one uterus fails to receive an ovum, its trophonemata do not enlarge further but those of the gravid uterus undergo a remarkable change as gestation progresses.

At first, the embryos of U. halleri are nourished by yolk and the vitelline circulation, but early in development the uterine villi take over part of that function. Histotroph or uterine milk is probably at first absorbed by the embryo through its yolk sac and external gill filaments (Ranzi, 1934b). As the digestive tract forms in embryos of U. halleri, this fluid enters the stomach by way of mouth and spiracles. After about 2 months the half-depleted yolk sac shrinks as yolk moves up the stalk, directly into the intestine. Nourishment during the last month of development seems to be accomplished by histotroph alone.

By half-term (about 45 days) the trophonemata have reached their maximum development, measuring 15 mm in length; their shape is

that of a very elongated cone that is ovoid in cross section. A greatly enlarged axial vein can be seen traversing the center of one such villus for much of its length (Figure 44). The epithelium of the villus has become greatly complicated by many glandular pits (Figure 45), and each gland is surrounded by a plexus of capillaries from the lateral arteries. Clumps of trophonemata now extend into the spiracles and pharynx of embryos for as much as 13 mm.

Alcock (1892a) observed in Pteroplatea micrura (= Gymnura micrura) that the entire uterine lining was covered with villi at the start of gestation. Later the villi atrophied due to pressure from the growing embryos, except opposite the spiracles where large clumps persisted. No reduction of trophonemata occurs in U. halleri until the end of gestation (Figure 46). Following parturition the villi are reduced to small flattened filaments with simple epithelium (Figure 47).

4.5.3. Embryonic development

The gestation period of U. halleri is about 3 months. Fertilization typically occurs in June, and young are born in September. Following fertilization, cleavages begin on the surface of the germinal disc. The germinal disc is thickest at its center and tapers toward the circumference. Viewed from above, it appears as a small, light-colored, circular area on the ovum surface; around its edge is a narrow, almost transparent border, the zona pellucida. Balfour (1878), in a monographic work, described elasmobranch development. The early stages are similar in all elasmobranchs and will not be reviewed here.

When an embryo of U. halleri has attained a length of 9 mm, it is removed from the yolk sac by a stalk, several millimeters long; the eyes and visceral arches are plainly visible. At a length of 13 mm, rudimentary pectoral fins appear as small lateral flaps just posterior to the branchial arches; meanwhile two other lateral swellings arise on either side of the cloaca, forming the pelvic fins. Numerous flattened external gill filaments extend from between the gill arches. Up to this point, an embryo of U. halleri closely resembles that of a shark except for the absence of median fins. As development proceeds, the two forms are separated by a widening gulf.

When an embryo is 16 mm long (Figure 48A), its pectoral fins extend halfway back to the pelvics, along the lateral body walls to which they are fused. The pectorals still remain posterior to the branchial arches, however, due to the rapid forward growth of that region, and their lateral span is only 3 mm.

An embryo of 20 mm (Figure 48B), has a pectoral fin span of about 4 mm. Drawings of the 20 mm stage in dorsal, ventral and lateral view, show considerably more detail than the photograph (Figure 49). The pectoral fins now extend back almost to the pelvics but still remain posterior to the branchial region. The incomplete cranial roof between the orbits is visible through the thin covering membrane; that portion of the cranium housing the mesencephalon is open anteriorly. In the lateral head region, the spiracle can be seen, partially surrounded by a gill arch; five more well-formed arches lie exposed behind the spiracle.

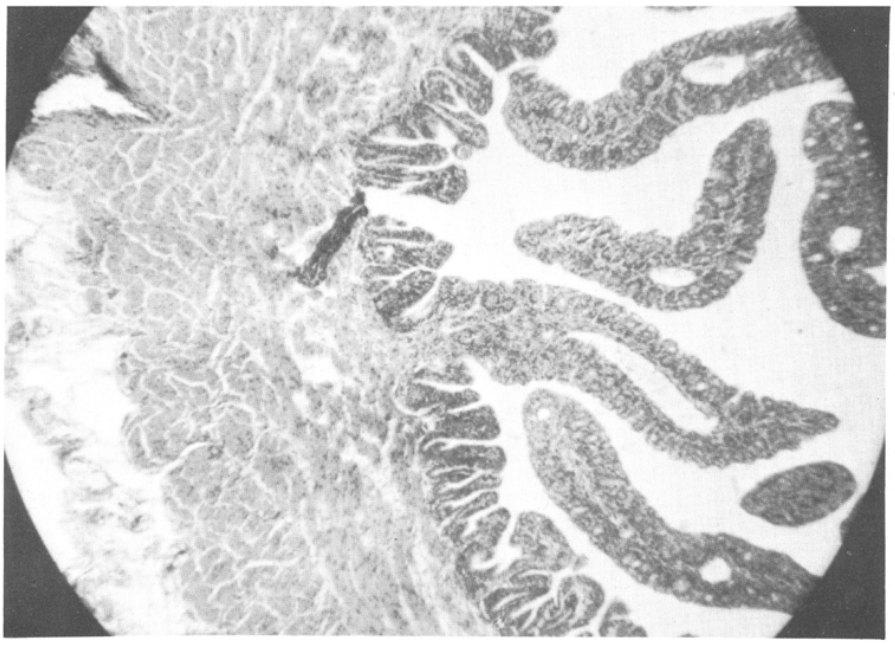


FIGURE 44. Longitudinal section through fully developed uterine villi at half-term, showing large axial vein at center. 44x

FIGURE 44. ***Longitudinal section through fully developed uterine villi at half-term, showing large axial vein at center. 44x***

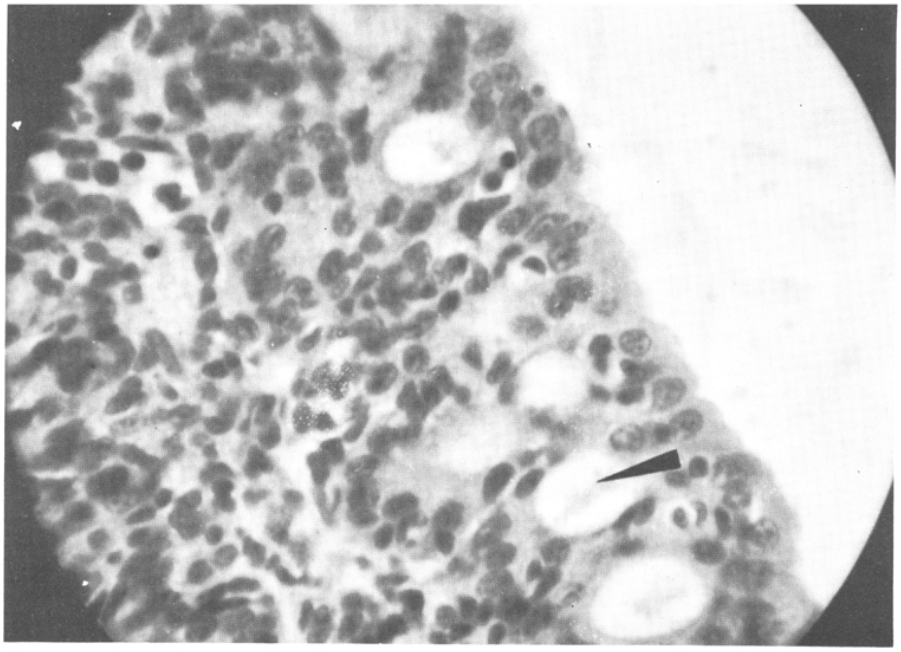


FIGURE 45. Glandular pits in epithelium of fully developed uterine villus (arrow). 560x

FIGURE 45. ***Glandular pits in epithelium of fully developed uterine villus (arrow). 560x***

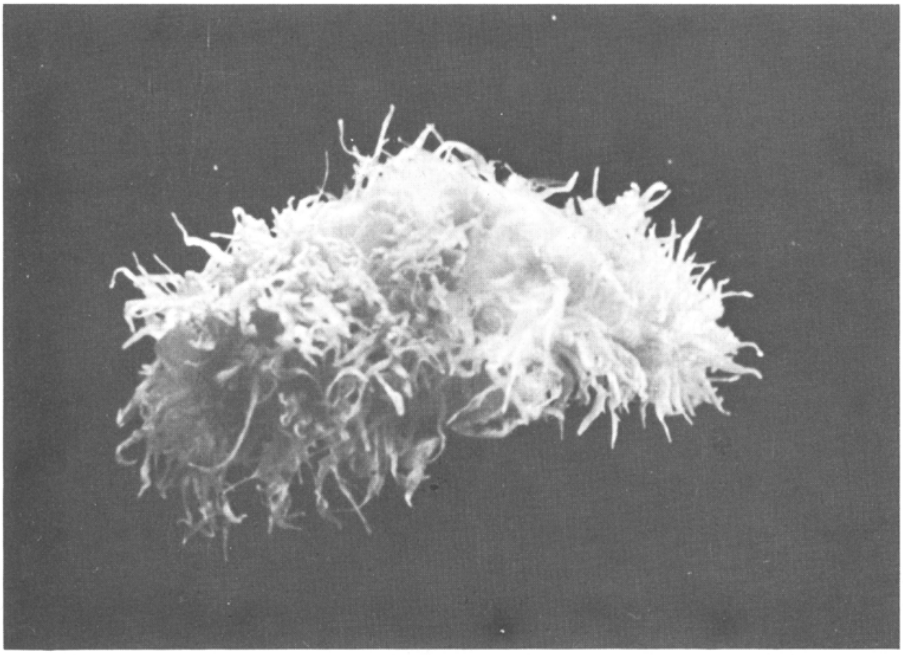


FIGURE 46. Uterus in third month of pregnancy, inverted to show dense growth of villi.

FIGURE 46. ***Uterus in third month of pregnancy, inverted to show dense growth of villi.***

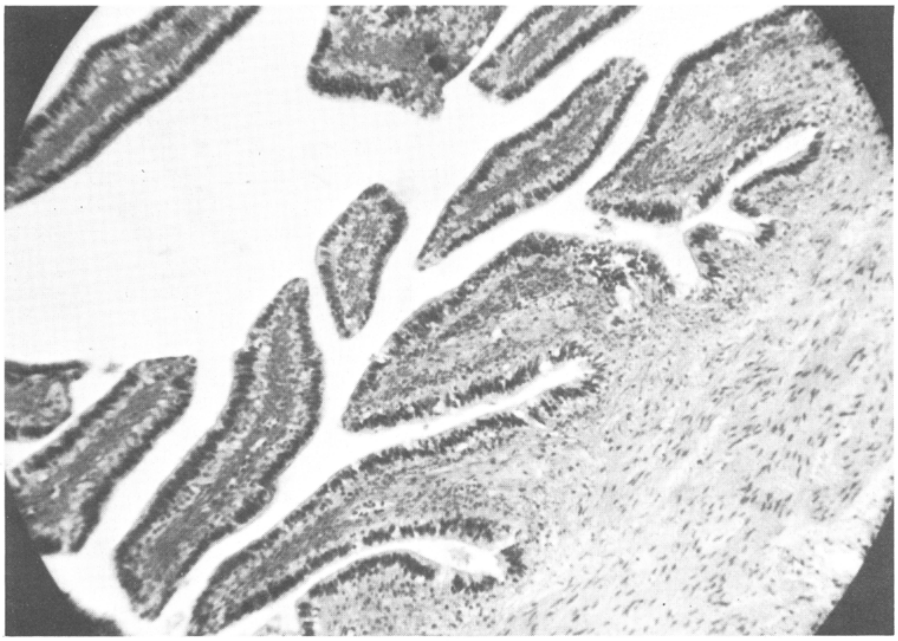


FIGURE 47. Longitudinal section through post-partum uterine villi showing reduction of blood vessels and glands. 125x

FIGURE 47. ***Longitudinal section through post-partum uterine villi showing reduction of blood vessels and glands. 125x***

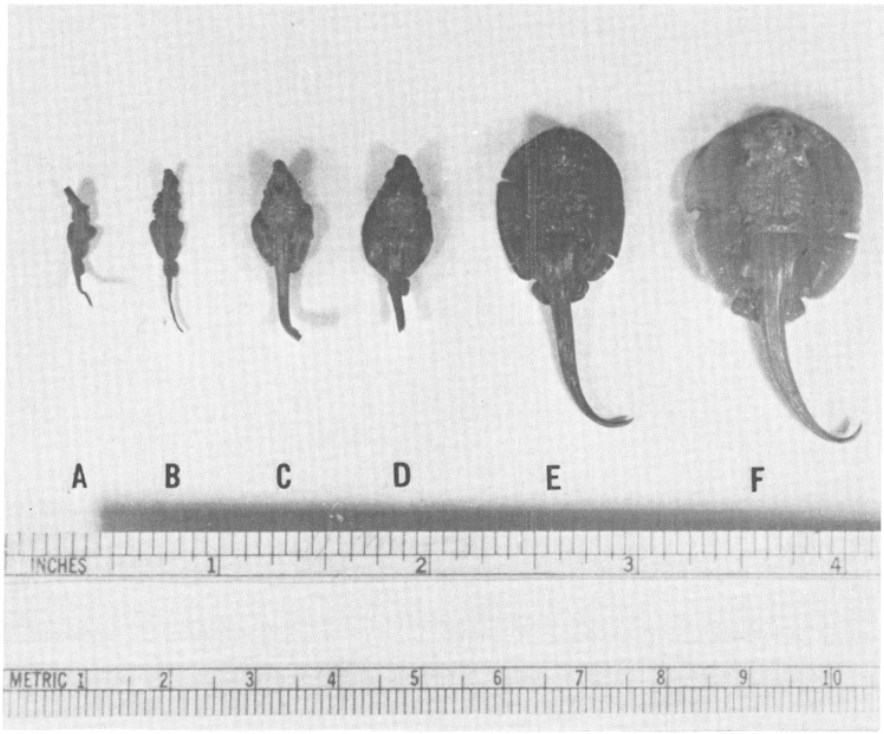


FIGURE 48. Early developmental stages. Embryo 16 x 3 mm, A; embryo 20 x 4 mm, B; embryo 24 x 7.5 mm. C; embryo 26 x 9 mm, D; embryo 40 x 14.5 mm, E; fetus 46 x 22 mm, F.

FIGURE 48. ***Early developmental stages. Embryo 16 x 3 mm, A; embryo 20 x 4 mm, B; embryo 24 x 7.5 mm. C; embryo 26 x 9 mm, D; embryo 40 x 14.5 mm, E; fetus 46 x 22 mm, F.***

In the ventral view, Meckel's cartilage of the lower jaw is discernible in outline, and its gill arch derivation is apparent. The external gill filaments are now about 5 mm long, and branchial rays have made their appearance on the ventral half of each arch, along its inner surface. The absence of branchial rays on the dorsal half of the arches seems to anticipate future development wherein the gill openings become restricted to a ventral position. A well-formed esophagus, stomach, and spiral valve are visible through the transparent ventral wall and the junction of the yolk stalk with the intestine can also be seen. The caudal fin is commencing to form as a narrow flap of tissue above and below the tip of the tail.

An embryo 24 mm long (Figure 48C), has a pectoral fin span of 7.5 mm. These fins have grown forward along the branchial region, but are not yet attached there (Figure 50). The branchial region has become dorsoventrally flattened, and its dorsal surface is covered over so that the gill openings are ventral. The external gill filaments now are about 7 mm long. The cranium remains open between the orbits, and the fusion line along the neural tube is discernible throughout the trunk region. In lateral view, the pectoral fin propterygium can be seen extending forward along the branchial region. Soon it will join with the propterygium of the opposite side, at the tip of the ethmoid. The caudal fin is now well formed, and the abdomen has begun to protrude noticeably.

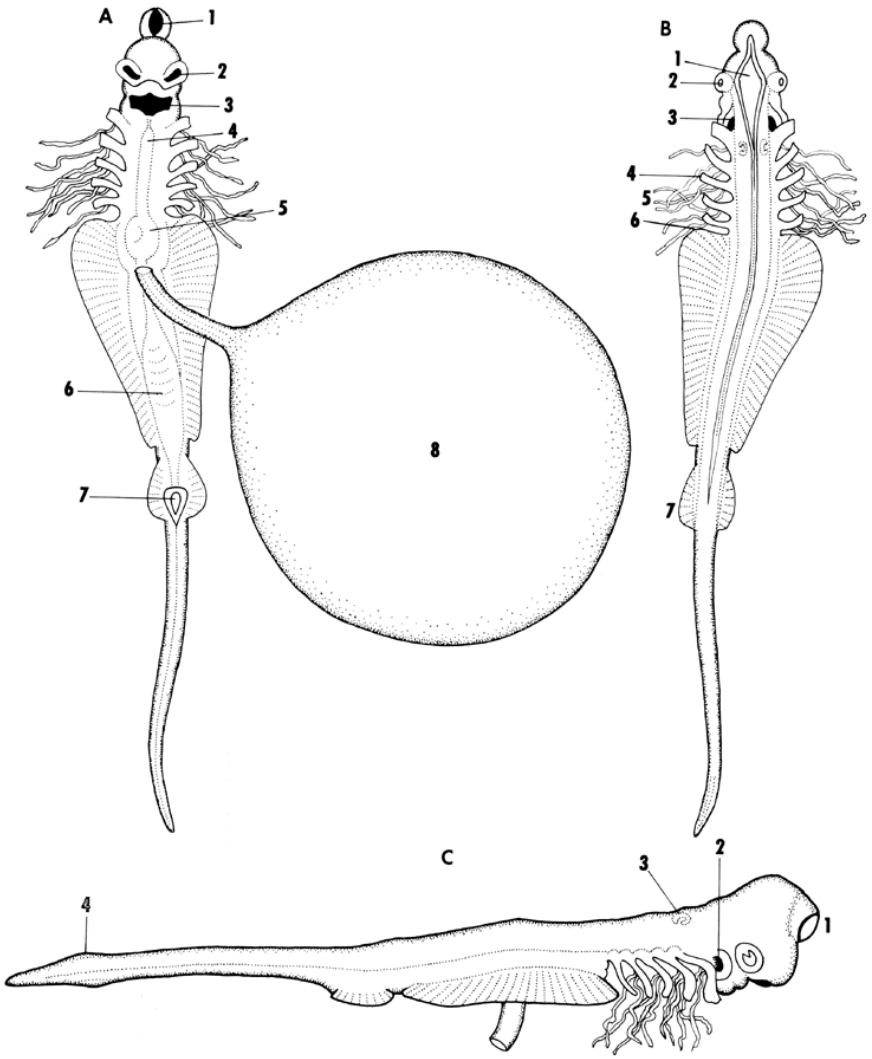


FIGURE 49. Twenty-millimeter embryo of *U. halleri*. Ventral View, A: open end of neural tube, 1; olefactory pit, 2; mouth, 3; esophagus, 4; stomach, 5; spiral valve, 6; cloaca, 7; yolk sac, 8. Dorsal view, B: unroofed cranium, 1; eye, 2; spiracle, 3; gill arch, 4; external gill filaments, 5; anterior tip of pectoral fin, 6; pelvic fin, 7. Lateral view, C: open end of neural tube, 1; spiracle, 2; auditory pit, 3; rudimentary caudal fin, 4.

FIGURE 49. ***Twenty-millimeter embryo of U. halleri. Ventral View, A: open end of neural tube, 1; olefactory pit, 2; mouth, 3; esophagus, 4; stomach, 5; spiral valve, 6; cloaca, 7; yolk sac, 8. Dorsal view, B: unroofed cranium, 1; eye, 2; spiracle, 3; gill arch, 4; external gill filaments, 5; anterior tip of pectoral fin, 6; pelvic fin, 7. Lateral view, C: open end of neural tube, 1; spiracle, 2; auditory pit, 3; rudimentary caudal fin, 4.***

After 1 month of gestation, the embryo is about 40 mm long and its batoidean characters are unmistakable (Figure 48E). The large pectoral fins span about 14 mm, and are completely fused to the branchial region and head, but they are not yet joined to the tip of the rostrum. The ventral gill openings are now quite small; the spiracles, however, are large commensurate with their postnatal function of pumping water over the gills when the animal lies buried (Figures 51, 52, 53).

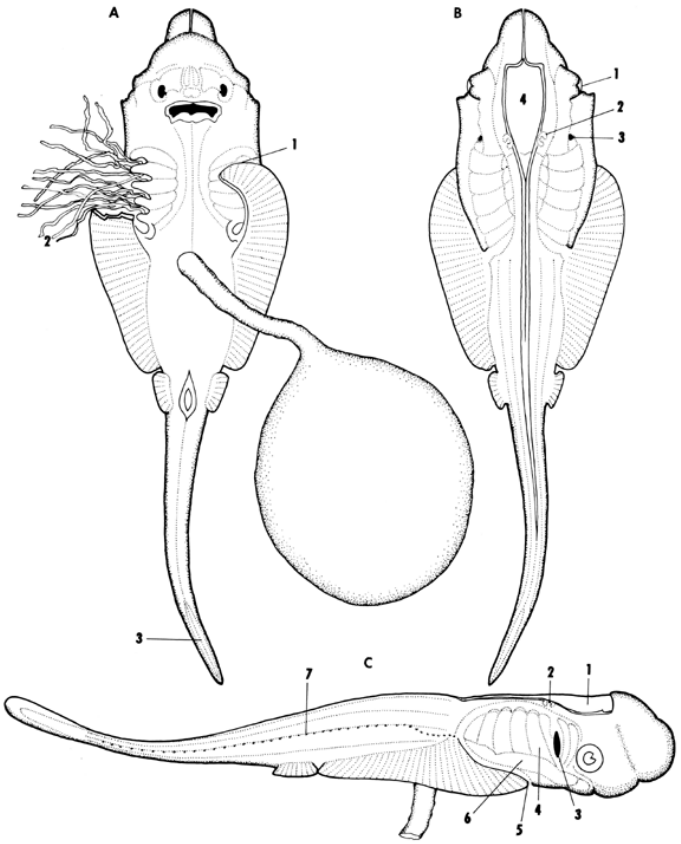


FIGURE 50. Twenty-four millimeter embryo of *U. halleri*. Ventral view, A: anterior tip of pectoral fin, 1; left pectoral partially removed to expose ventrally situated gill openings, 2; caudal fin, 3. Dorsal view, B: eye, 1; auditory pit, 2; spiracle, 3; unroofed cranium, 4. Lateral view, C: unroofed cranium, 1; auditory pit, 2; spiracle, 3; gill arch, 4; anterior tip of pectoral fin, 5; propterygium, 6; lateral line, 7.

FIGURE 50. ***Twenty-four millimeter embryo of U. halleri. Ventral view, A: anterior tip of pectoral fin, 1; left pectoral partially removed to expose ventrally situated gill openings, 2; caudal fin, 3. Dorsal view, B: eye, 1; auditory pit, 2; spiracle, 3; unroofed cranium, 4. Lateral view, C: unroofed cranium, 1; auditory pit, 2; spiracle, 3; gill arch, 4; anterior tip of pectoral fin, 5; propterygium, 6; lateral line, 7.***

At half-term (about 45 days) I have considered the developing ray a fetus. It is now about 46 mm long and there has been a great lateral expansion of the pectorals to a width of approximately 22 mm (Figure 48F). The external gill filaments have begun to be reabsorbed, and a cartilaginous structure is visible along the upper margin of each spiracle. One or both spiracles may now be penetrated for a few millimeters by a clump of trophonemata, but these are unattached and can be easily withdrawn. All trophonemata are deep-red, due to their intense vascularization. The yolk sac remains surprisingly large, indicating that a good part of the nutrition has been supplied by histotroph.

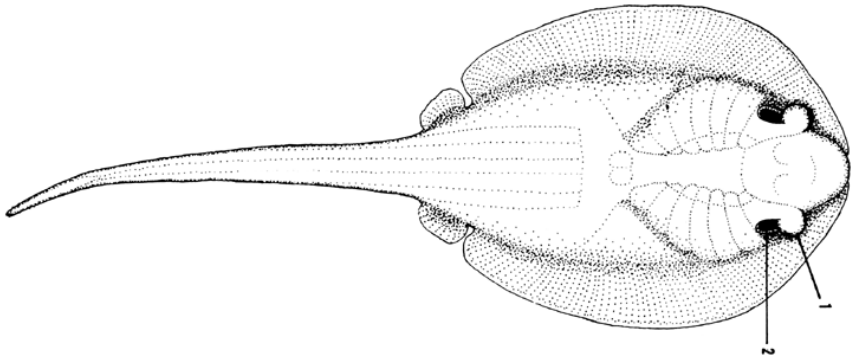


FIGURE 51. Dorsal view of embryo after 1 month of gestation. Eye, 1; spiracle, 2.

FIGURE 51. ***Dorsal view of embryo after 1 month of gestation. Eye, 1; spiracle, 2.***

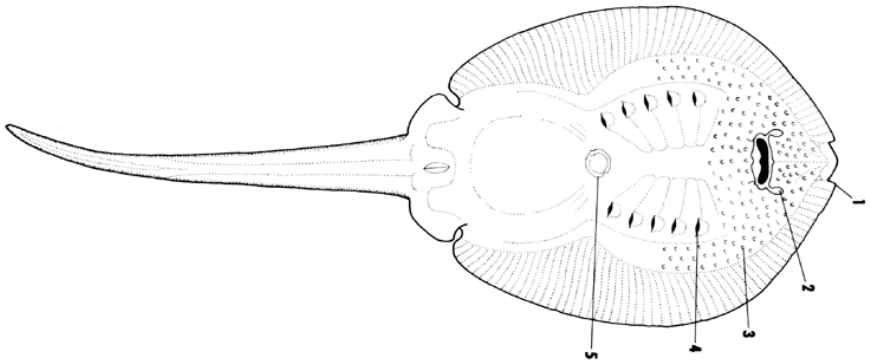


FIGURE 52. Ventral view of 1-month embryo. Anterior tip of pectoral fin (not yet fused with opposite fin), 1; olefactory pit, 2; papilla, 3; gill opening, 4; point of attachment of yolk stalk, 5.

FIGURE 52. ***Ventral view of 1-month embryo. Anterior tip of pectoral fin (not yet fused with opposite fin), 1; olefactory pit, 2; papilla, 3; gill opening, 4; point of attachment of yolk stalk, 5.***

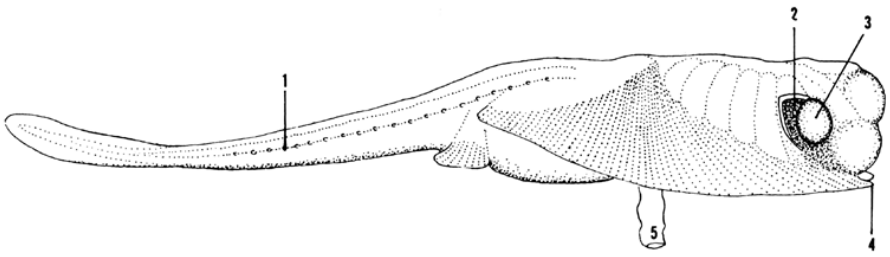


FIGURE 53. Lateral view of 1-month embryo. Lateral line, 1; spiracle, 2; eye, 3; anterior tip of pectoral fin, 4; yolk stalk, 5.

FIGURE 53. ***Lateral view of 1-month embryo. Lateral line, 1; spiracle, 2; eye, 3; anterior tip of pectoral fin, 4; yolk stalk, 5.***

Development is greatly accelerated after the mid-point in gestation. At 2 months, the fetus is about 64 mm long and 32 mm wide (Figure 54A). Absorption of the external gill filaments is by now complete. The spiracular cartilage has elongated and is free at its posterior tip, giving the fetus a horned appearance. The progressive growth of that process can be followed in fetuses of various ages (Figure 55); it reaches its greatest proportions in the full-term young, but is reabsorbed soon after birth.

The elongated yolk sac still contains almost one-half its yolk after 2 months, but now begins to shrink. The abdomen is greatly distended by this time from accumulating waste stored in the ileum. The swollen spiral valve apears bright-green through the thin abdominal wall, due to bile. Light pigmentation is present on the dorsum in the 3rd month (Figure 55), and at birth the color pattern is fairly well established.

When the fetus measures about 78 x 41 mm, its yolk sac is empty and is being reabsorbed (Figure 54B). The most posterior portion of the spiral value now contains a small greenish concretion that continues to enlarge and eventually fills half of the spiral value. In this unique manner, waste is stored during development; shortly after birth, the rock-like mass is dissolved.

At about midpoint in gestation (1½ months), when space becomes a problem in the uterus, the fetus's tail begins to bend forward and the pectoral fins fold at their free edges. As development proceeds, the tail curves forward more sharply so that it lies along the young animal's belly and is twisted in such a way that the caudal spine is directed away from the mother's uterine wall. Eventually, the pectoral fins fold over the belly and tail so that the fetus is literally rolled up. This position is normally maintained until birth (Figure 56).

The shock of capture frequently causes pregnant females to abort their young. In some cases, abortion is completed and the young emerge with tails fully extended and pectorals folded. In many instances, abortion is not completed, and the straightened tails of several young can be seen protruding from the mother's cloaca. Normal birth has not

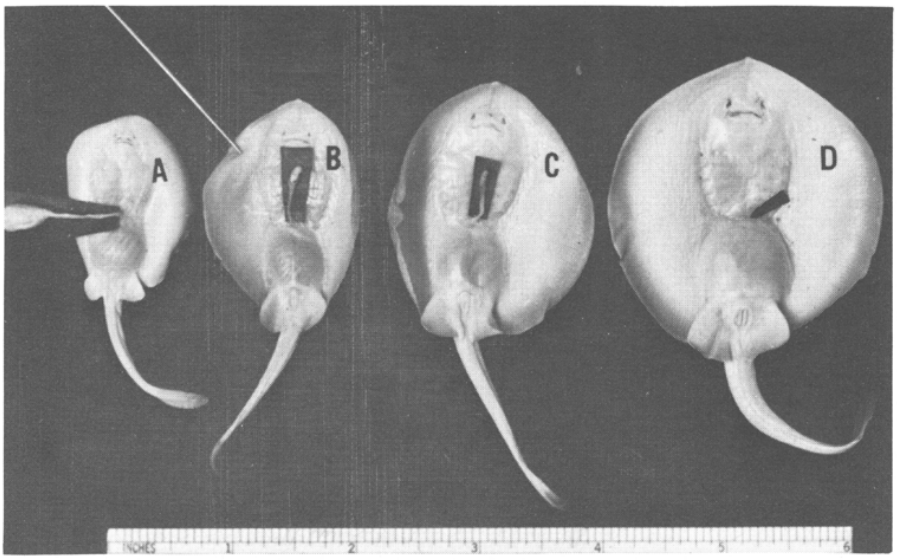


FIGURE 54. Ventral view of four fetuses in the last month of development. Sixty-day fetus (approx.); 64 x 32 mm, A; sixty-six-day fetus (approx.); 78 x 41 mm, B; seventy-two-day fetus (approx.); 91 x 46 mm, C; eighty-day fetus (approx.); 104 x 57 mm, D.

FIGURE 54. ***Ventral view of four fetuses in the last month of development. Sixty-day fetus (approx.); 64 x 32 mm, A; sixty-six-day fetus (approx.); 78 x 41 mm, B; seventy-two-day fetus (approx.); 91 x 46 mm, C; eighty-day fetus (approx.); 104 x 57 mm, D.***

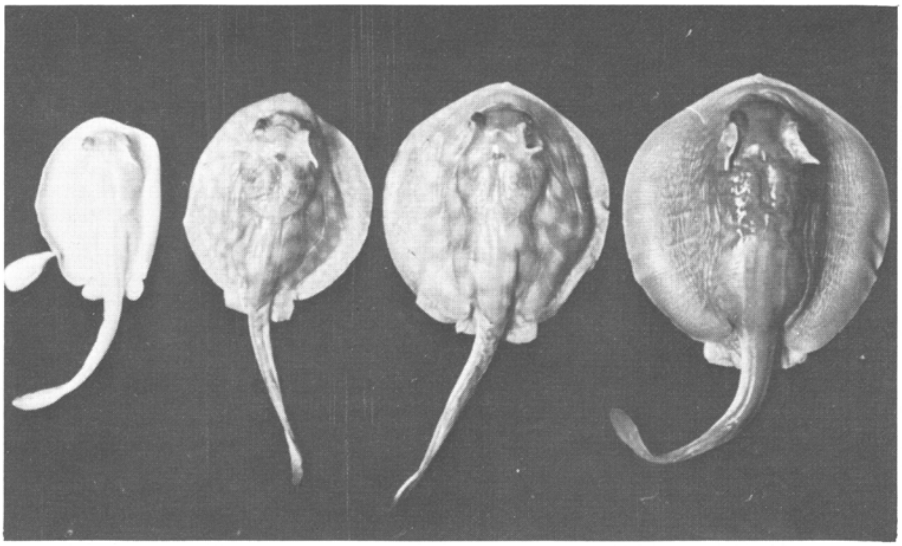


FIGURE 55. Dorsal view of same four fetuses seen in Figure 54.

FIGURE 55. ***Dorsal view of same four fetuses seen in Figure 54.***

been observed. Gudger (1914) noted that young of the spotted eagle ray, Aetobatus narinari, were rolled-up at birth.

When the tail commences its forward flexure in fetuses of U. halleri, the spine is poorly developed and lies beneath the integument. When the flexure is complete, the spine is about 7 mm long and is free from the tail for nearly 3 mm, although still well sheathed (Figure 57). In a nearly full-term embryo, the tips of six or more recurved barbs can be seen along each side of the spine, beneath the sheath (Figure 58).

FIGURE 56. Nearly full-term fetus removed from uterus in typical rolled-up position.

FIGURE 56. ***Nearly full-term fetus removed from uterus in typical rolled-up position.***

There is a cartilaginous terminal bulb which disappears after birth, but the sheath is retained. In one case, the bare spine of a fully-developed fetus was found protruding through the mother's uterus well into the coelom.

A fetus is most often found with its posterior end toward the mother's cloaca. When two young occupy the same uterus, they normally lie belly to belly, one enfolded within the other's pectorals so that the spiracles of both are against the uterus wall. When three fetuses occupy one uterus, the animal in the center of the roll has little or no contact with the uterus lining, but is as large and well-formed as the others. Adequate nutrition is apparently not dependent upon physical contact between fetus and trophonemata. A number of exceptions to the usual fetal orientation have been observed. Two individuals may be arranged head to tail. Where the female carries young in both uteri, those of the two sides may be headed in opposite directions. Large females of the round stingray bear more and larger offspring. Newborn animals vary in disc width from 63 to 80 mm with the average being approximately 75 mm.

5. SEX RATIO

In a sample of 164 one-third to fully-developed embryos, the female-male ratio was 1:1.6. A chi square test indicated this difference is highly significant (P 0.01). Thus a marked imbalance appears to exist between sexes during embryonic development. Breder (1941) found more male than female embryos in the stingrays Dasyatis sabina and D. hastatus (= D. americana) . Olsen (1954) reported the same situation in the shark Galeorhinus australis.

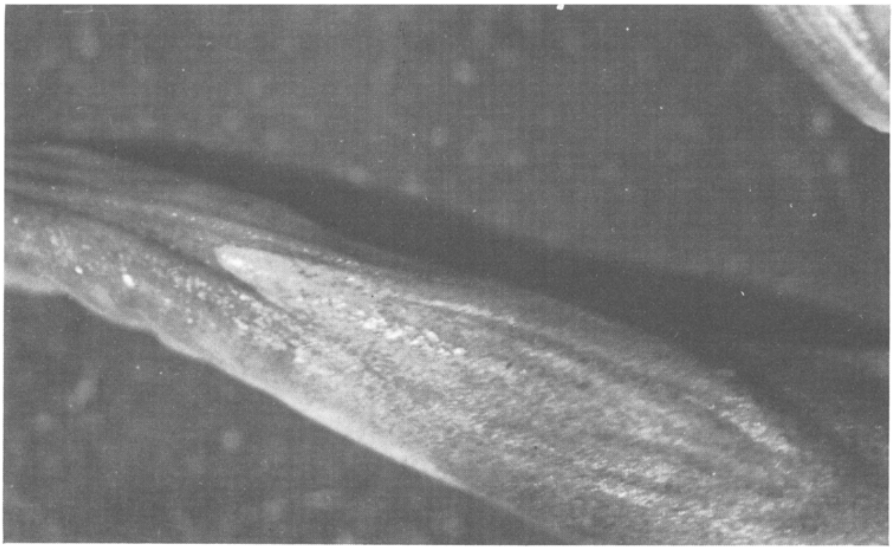


FIGURE 57. Incompletely formed caudal spine of fetus after about 65 days of development.

FIGURE 57. ***Incompletely formed caudal spine of fetus after about 65 days of development.***

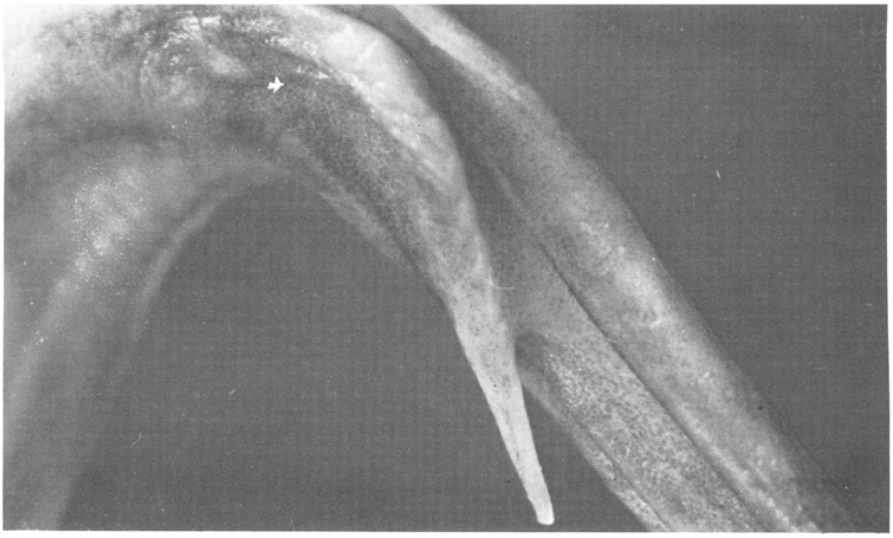


FIGURE 58. Sheathed caudal spine of nearly full-term embryo. Tail flexure turns spine away from mother's uterus wall.

FIGURE 58. ***Sheathed caudal spine of nearly full-term embryo. Tail flexure turns spine away from mother's uterus wall.***

In the newborn size class, females of U. halleri are slightly more numerous than males (Table 3-C) , apparently due to higher mortality among newborn males. Olsen (1954) similarly reported that the sex ratio of Galeorhinus australis began to approach parity after birth; by the end of the first year, females outnumbered males.

Most newborn U. halleri were taken at an inshore nursery. March and September seem to be the peak birth months. More young were actually captured in October than in September (Table 3A)). October also yielded the greatest number of young per seine haul (Table 4) . Absence

TABLE 3-A

U. halleri Sex Ratio In Inshore Waters, By Months

		Newborn Under 81 mm F.	M.	81–100 F.	M.	101–120 F.	M.	121–140 F.	M.	141–160 F.	M.	161–180 F.	M.	Over 180 F.	M.	Total catch F.	M.	140 and under F.	M.	141 and over F.	M.
February	Number	2	4	6		8		4	2	8	10	4	18	10		32	44	20	6	12	38
	Ratio	1	: 2					2	: 1	1	: 1.3	1	: 4.5			1	: 1.4	3.3	: 1	1	: 3.2
March	Number	10	6		6			3	2			5	4	2	3	20	21	13	14	7	7
	Ratio	1.7	: 1					1.5	: 1			1.3	: 1	1	: 1.5	1	: 1.1	1	: 1.1	1	: 1
April	Number	2	2			3	3			2	3					7	8	5	5	2	3
	Ratio	1	: 1			1	: 1			1	: 1.5					1	: 1.1	1	: 1	1	: 1.5
June	Number	2		5	2	2	2			2		7	4	6		24	8	9	4	15	4
	Ratio			2.5	: 1	1	: 1					1.8	: 1			2.5	: 1	1.5	: 1	3.8	: 1
July	Number			2	2	2		4		8	10	2	50	40		18	102	8	2	10	100
	Ratio			1	: 1					1	: 1.3	1	: 25			1	: 5.7	4	: 1	1	: 10
August	Number				2	24	20	20	20	6	14	6	36	6	24	62	116	44	42	18	74
	Ratio					1.2	: 1	1	: 1	1	: 2.3	1	: 6	1	: 4	1	: 1.9	1	: 1	1	: 4.1
September	Number	8	8	12	10	13	13	6	4	14	6	32	8	30	22	115	71	39	35	76	30
	Ratio	1	: 1	1.2	: 1	1	: 1	1.5	: 1	2.3	: 1	4	: 1	1.4	: 1	1.7	: 1	1.1	: 1	2.1	: 1
October	Number	68	56	46	28	16	13	5	4	2		2	2	2		141	113	135	111	6	2
	Ratio	1.2	: 1	1.2	: 1	1.3	: 1	1.3	: 1			1	: 1			1.3	: 1	1.2	: 1	3	: 1
November	Number	2	2													2	2	2	2		
	Ratio	1	: 1													1	: 1	1	: 1		
December	Number				2	2	2			4	4	2				8	8	2	4	6	4
	Ratio					1	: 1			1	: 1					1	: 1	1	: 2	1.5	: 1
Total	Number	94	78	71	62	70	53	42	32	46	47	60	122	46	99	429	493	277	225	153	268
	Ratios	1.2	: 1	1.1	: 1	1.3	: 1	1.3	: 1	1	: 1	1	: 2	1	: 2	1	: 1.2	1.2	: 1	1	: 1.8

TABLE 3-A
U. halleri Sex Ratio In Inshore Waters, By Months

TABLE 3-B

***U. halleri* Sex Ratio In Offshore Waters, By Months**

		Newborn Under 81 mm F.	M.	81–100 F.	M.	101–120 F.	M.	121–140 F.	M.	141–160 F.	M.	161–180 F.	M.	Over 180 F.	M.	Total catch F.	M.	140 and under F.	M.	141 and over F.	M.
January	Number							21	16	15	35	33	70	24	54	93	175	21	16	72	159
	Ratio							1.3	1	1	2.3	1	2.1	1	2.3	1	1.9	1.3	1	1	2.2
February	Number					*3		11	22	18	70	29	119	26	37	97	248	14	22	83	226
	Ratio							1	2	1	3.9	1	3.1	1	1.4	1	2.6	1	1.6	1	2.7
March	Number							1	3	10	9	12	22	6	53	29	87	1	3	28	84
	Ratio							1	3	1.1	1	1	1.8	1	8.8	1	3	1	3	1	3
April	Number					*3	1	6	4	3	4	16	37	12	49	40	95	9	5	31	90
	Ratio					3	1	1.5	1	1	1.3	1	2.3	1	4.1	1	2.4	1.8	1	1	2.9
May	Number									8	3	30	48	28	100	66	151			66	151
	Ratio									2.7	1	1	1.6	1	3.6	1	2.3			1	2.3
June	Number									1	1	4	17	3	42	8	60			8	60
	Ratio									1	1	1	4.3	1	14	1	7.5			1	7.5
November	Number							7	1	12	19	11	51	10	40	40	111	7	1	33	110
	Ratio							7	1	1	1.6	1	4.6	1	4	1	2.8	7	1	1	3.3
Total	Number					*6	1	45	46	67	141	145	364	109	375	373	927	52	47	321	880
	Ratios					6	1	1	1	1	2.1	1	2.5	1	3.4	1	2.5	1.1	1	1	2.7

* Only occurrence of young under 121 mm in offshore waters.

TABLE 3-B

U. halleri Sex Ratio In offshore Waters, By Months

of post-spiracular cartilages and slightly larger size of many October captures, however, indicated September birth.

The young begin venturing out along coastal beaches after attaining a disc width of about 90 mm. Their seaward range increases with age, but few go far enough offshore to be taken by trawl (2 fathoms), until reaching 121 mm (Table 3-B).

Throughout all the immature sizes in the catch (Table 3-C), females retained their slight numerical superiority. Eighty-three percent of immature animals were taken in shallow inshore waters by beach seine (Table 3-A); the remaining 17 percent were captured offshore by trawl (Table 3-B). Since neither type of net is believed selective of one sex, it seems likely that females outnumber males slightly, until maturity is reached at a disc width of about 150 mm.

The total catch (Table 3-C), comprising rays taken during all months, showed a sharp reversal in the sex ratio at maturity; in the 141–160 mm size class of the total catch, there were 1.7 males per female, and the disparity increased with size. The predominance of males following maturity, existed in both the inshore and offshore catches (Tables 3-A, 3-B). This disparity is believed due to a sex segregation rather than to high female mortality.

TABLE 3-C

***U. halleri* Sex Ratio for Total Catch (1955–1962)**

(Inshore and Offshore Waters)

Disc width (mm)	Number of females	Ratio	Number of males
Newborn under 81 mm	94	1.2:1	78
81–100	71	1.1:1	62
101–120	76	1.4:1	54
121–140	88	1.1:1	78
141–160	113	1:1.7	188
161–180	205	1:2.4	486
Over 180	155	1:3.1	474
140 and under	329	1.2:1	272
141 and over	473	1:2.4	1,148
Total catch	802	1:1.8	1,420

TABLE 3-C

U. halleri Sex Ratio for Total Catch (1955–1962) (Inshore and offshore Waters)

TABLE 4

Number of Newborn Rays Taken Per Siene Haul Each Month, From Same Nursery Ground

Month	Number of sets 65′ seine	Number of newborn rays taken	Number of rays taken per set
January	0	0	0
February	4	6	1.50
March	3	16	5.33
April	3	4	1.33
May	4	0	0
June	11	2	0.18
July	4	0	0
August	0	0	0
September	3	16	5.33
October	14	124	8.80
November	3	4	1.33
December	4	0	0
Total	53	172	

TABLE 4

Number of Newborn Rays Taken Per Siene Haul Each Month, From Same Nursery Ground

The scant trawling data from water deeper than 7 fathoms indicate that some females move into deeper offshore waters following maturity. Rays captured at various depths within a short period demonstrate the greater number of females below 7 fathoms (Table 5A, B) . A small sample from 13.5 fathoms, however, consisted entirely of males, two of which were quite large. The total offshore trawl catch contained 2.5 males for every female (Table 3-B) , probably due to inadequate sampling of deeper waters where mature females apparently spend much time.

TABLE 5

Relationship of Sex Ratio to Water Depth for *U. halleri*

A.	Number of rays taken					
	Off Belmont Shore 2–4 fathoms		Off Anaheim Bay 5–5.5 fathoms		Off Anaheim Bay 7–7.5 fathoms	
	F	M	F	M	F	M
1–31–57	33	64	--	--	32	27
2–1–57	51	118	7	14	12	6
2–4–57	16	16				
2–5–57	5	33	3	13	6	5
Total	105	231	10	27	50	38
Ratios	1:2.2		1:2.7		1.3:1	

B.	Number of rays taken					
	Off Seal Beach and Sunset Beach 3–4 fathoms		Off Bolsa Chica 7–10 fathoms		Off Oil Island 13.5 fathoms	
	F	M	F	M	F	M
4–25–58	17	24	9	2	--	4
Ratios	1:1.4		4.5:1			

TABLE 5

Relationship of Sex Ratio to Water Depth for U. halleri

My entire sample of 2,222 rays (Table 3-C), contained 1.8 males for each female. I examined another sample of 1,501 rays during June and July, 1962, at Seal Beach, and found that adults predominated; all size classes above 100 mm disc width were present. The female-male ratio was 1 :2. Russell (1955) reported a female-male ratio of 1 :2.4 in a sample of 1,196 round stingrays.

Two sharp, seasonal fluctuations occurred in the sex ratio of the adult population. Both seemed related to the reproductive cycle. The first was in June when females became quite scarce in offshore waters, at all depths sampled. The female-male ratio for the total June catch, offshore, was 1 :7.5 (Table 3-B). Trawl catches from various depths on three consecutive days in mid-June, 1958, show that only 8 of 67 animals were females (Table 6) . It is significant that seven of these had either just ovulated or possessed ripe ova.

In contrast, females outnumbered males inshore, during June, by a ratio of 2.1 :1, or more significantly, by a ratio of 3.5 :1 if only mature animals are considered (Table 3-A). Seining in a nursery on June 8, 1962, yielded 15 mature females and two males. One female had just

TABLE 6

June Trawl Catches, Demonstrating Seasonal Scarcity of Female *U. halleri* In Offshore Waters At All Depths Sampled

	Number of rays taken					
	Off Belmont Shore 2–4 fathoms		Off Anaheim Bay 5–5.5 fathoms		Off Bolsa Chica 7.5–9.5 fathoms	
	F	M	F	M	F	M
6–10–58	3	17				
6–11–58	--	--	0	4	1	25
6–12–58	4	13				
Total	7*	30	0	4	1	25
Ratios	1:4.3		------		1:25	

* These females had either just ovulated or were ready to ovulate.

TABLE 6

June Trawl Catches, Demonstrating Seasonal Scarcity of Female U. halleri In offshore Waters At All Depths Sampled

ovulated and the others were about to do so. Both males were in breeding condition; the lower ends of their vasa deferentia were distended with seminal fluid and the siphon glands were swollen. The foregoing suggests that ovulating females migrate shoreward during June to join the males and to mate.

A second seasonal fluctuation in the sex ratio of adult rays was noted in September. In the inshore nurseries at this time, mature females outnumbered males by a ratio of 2.1 :1 (Table 3-A). The females bear their young in these sheltered areas and soon return to open water.

6. GROWTH

6.1. Relationship of Disc Width to Total Length

In describing the embryonic development of U. halleri, it was noted that embryos are at first elongate and shark-like, becoming proportionately wider as the pectoral fins develop. At birth, the ratio of disc width to total length is about 1 :1.75; it remains essentially unchanged throughout life. A graph of disc width over length, made for 210 rays (including 10 embryos), showed a straight-line relationship between these two measurements from birth onward (Figure 59). The plotted points of the 10 embryos, however, all fell below the line.

6.2. Age and Growth Rate Determination (General)

Difficulty is generally experienced in determining age and growth rate of an elasmobranch because there are no suitable otoliths or scales. Four separate approaches to this problem were necessary in the case of U. halleri, since no single approach yielded sufficient data: (i) the Petersen method of width frequencies (Petersen, 1891); (ii) double sampling and comparing the two resultant frequency curves; (iii) tagging and recapture (Perlmutter, 1954); (iv) rearing in captivity.

6.3. Width Frequency Curves

Where a series of peaks occur on a width frequency curve, each peak supposedly represents a separate brood or age group in a fish population. The disc width at which a given peak occurs, should represent

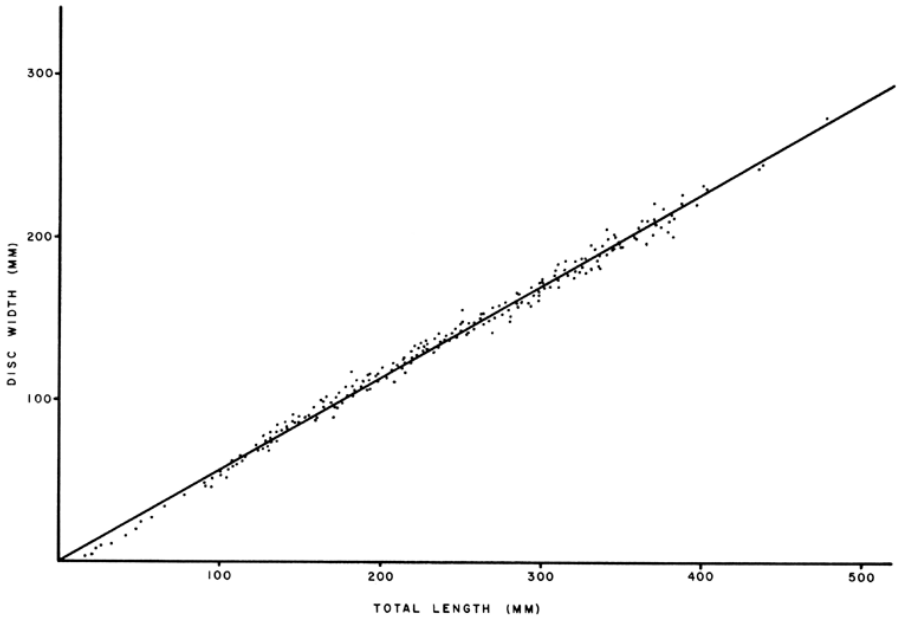


FIGURE 59. Disc width plotted over total length. The first 10 points represent embryos.

FIGURE 59. ***Disc width plotted over total length. The first 10 points represent embryos.***

the average disc width for that particular age group. The method is valid only if animal sizes in each age group are distributed normally and if the various age groups are sufficiently distinct to provide a series of individual peaks. The method must be used cautiously and is most reliable for samples of young fishes; beyond the first two age groups, there is increasing overlap due to unequal growth rates (Walford, 1932; Perlmutter, 1954).

In applying the Petersen method to U. halleri, it was first assumed that enough births occur in March to produce a prominent mode or peak. Evidence indicating a considerable number of March births, was previously presented (Figure 27 and Table 4). The second assumption was that the young of U. halleri are born during sufficiently short periods in spring and fall, to produce individually-recognizable peaks, even though the natal periods are but 6 months apart. Little is known about the actual length of the March birth period. Data on the September birth period are presented below.

Seventy-eight fetuses were taken from De Anza Cove, Mission Bay, near San Diego, on August 14, 1958. A second sample of 86 fetuses was collected September 17 and 18, 1959, at Newport Dunes, Newport Upper Bay. Width frequency distributions were plotted for both groups. The greatest width frequency of the De Anza Cove sample (upper curve) was 55 mm (Figure 60). Fetuses of this size are approximately three-quarters developed and would be born around September 5th. Since individuals in the sample ranged from one-half to almost fully developed, their births would probably be distributed between August 15 and September 28, a period of 44 days.

In the Newport Dunes sample, the greatest width frequency was 62 mm. Fetuses of this size would probably be delivered about 1 week later on September 25th. Individuals of the sample ranged in size from

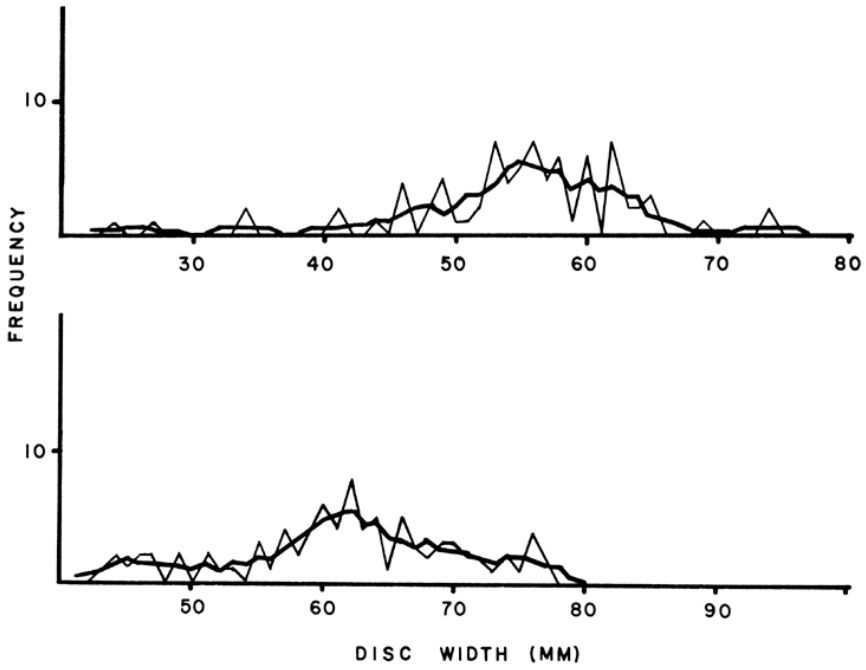


FIGURE 60. Width frequency distribution for two groups of fetuses of *Urolophus halleri*. Heaviest line represents smoothing of the frequencies by a moving average of five. Upper curve—78 fetuses from DeAnza Cove. Lower curve—86 fetuses from Newport Dunes.

FIGURE 60. ***Width frequency distribution for two groups of fetuses of Urolophus halleri. Heaviest line represents smoothing of the frequencies by a moving average of five. Upper curve—78 fetuses from DeAnza Cove. Lower curve—86 fetuses from Newport Dunes.***

over two-thirds to fully developed. The presence of postpartum females and newborn rays in the nursery indicated that a number of births had occurred prior to September 17th. Some of the young may have been born as early as September 1, judging from their size and by the absence of post-spiracular cartilages and intestinal concretions. No adult females were found there after October 10 and presumably the natal period was ended; its duration is estimated to have been between 40 and 45 days.

The temporal distribution of births in the two samples appears similar, and a fall natal period lasting about 40 days seems reasonable. If the March natal period is of equal length, there is a span of about 140 days between periods when only a few young are born. As might be expected, the autumnal natal period appears to be about 2 weeks earlier at the more southerly Mission Bay locale.

If an average growth rate of 3 mm per month is used, in disc width for newborn rays (based on the maximum observed rate of captive young, Table 8), it is possible to estimate roughly the extent of overlap of successive broods as follows: if an animal was born early in the natal period, at a maximum disc width of 80 mm, it would attain 98 mm by the beginning of the next natal period. If it were born late in the natal period, at a minimum disc width of 65 mm, it would attain 79 mm by the beginning of the next natal period. Therefore, the small, late-born individuals of the first brood would actually be slightly smaller (79 mm) than the large (80 mm) early arrivals of the following brood. The overlap is no doubt even more extensive, since

a few scattered births take place before and after each 40-day birth period. Variation in individual growth rates would produce further merging of age groups.

A sample of 268 rays ranging from 65 to 132 mm in disc width was taken between September 4, 1959, and October 25, 1959, from Newport Bay. Most of the very young animals were captured in the Newport Dunes nursery ground. Since the sample was collected during a period of 51 days, a correction was applied to the measurements, in order to simulate a single capture date of October 25 for the entire sample. In this way, the factor of growth increment was minimized. The corrections were made by assuming a growth rate of 3 mm per month in disc width for individuals under 96 mm (based on the maximum observed growth rate for captive young, Table 8); I do not believe this to be an excessive rate since the captive young were living under less than optimum conditions. A lower rate of 2.5 mm per month was used to correct disc widths of 96 mm or larger individuals.

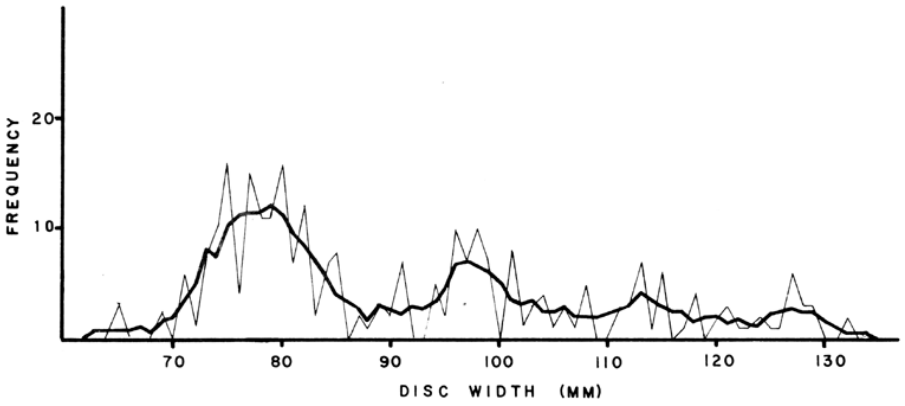


FIGURE 61. Width frequency curve for 268 young rays ranging from newborn to 132 mm in disc width.

FIGURE 61. ***Width frequency curve for 268 young rays ranging from newborn to 132 mm in disc width.***

Width frequencies were then plotted and smoothed by a moving average of five (Figure 61). Despite the small sample size, peaks could be distinguished at 79, 97, 113, and 127 mm. These peaks are believed to be the average disc widths of four successive broods produced at intervals of 6 months. If this is true, then the horizontal distance between peaks (in millimeters) represents the average growth increment for three periods of 6 months each. From this information, the beginning of a growth rate curve can be constructed by simply plotting modal lengths over age (points A, B, C, and D, Figure 62).

Since the greatest number of autumn births occurred near the end of September in the Newport Dunes nursery, and because animal sizes were adjusted to simulate a capture date of October 25, the average age of the youngest brood was considered to be 1 month at time of capture. The first peak on the width frequency curve should then represent the average disc width of the youngest age group, 1 month after birth.

Since the average disc width at birth is about 75 mm, the first peak then supposedly moved forward from 75 mm to 79 mm during the

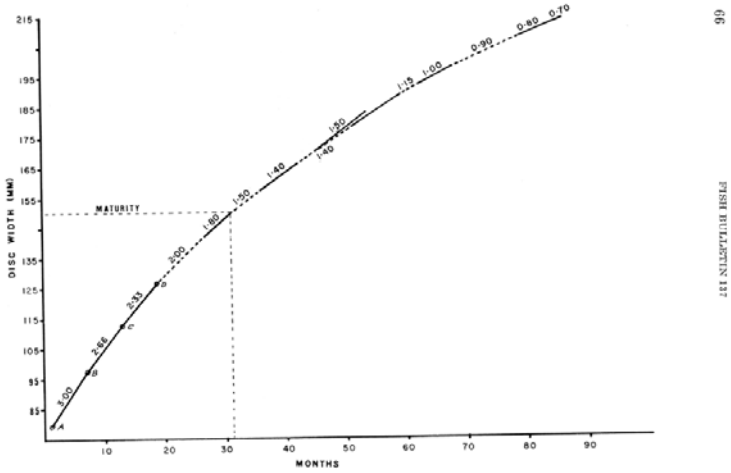


FIGURE 62. Growth curve for *Urolophus halleri*. Points A, B, C and D obtained from width frequency curve for young rays (Figure 61). Divergent segment, labeled 1.50, was obtained by double sampling method (Figure 63). All other solid segments of curve were obtained from tagging and recapture data (Table 7). Dotted segments of curve are not based on data, and simply assume a growth rate intermediate to known values on either side.

FIGURE 62. ***Growth curve for Urolophus halleri. Points A, B, C and D obtained from width frequency curve for young rays (Figure 61). Divergent segment, labeled 1.50, was obtained by double sampling method (Figure 63). All other solid segments of curve were obtained from tagging and recapture data*** *(Table 7)* ***. Dotted segments of curve are not based on data, and simply assume a growth rate intermediate to known values on either side.***

first month, indicating an initial growth rate of 4 mm per month. The growth rate for the next 6 months was only 3 mm per month; this rate is shown by the second segment of the growth rate curve, between points A and B (Figure 62). As would be expected, the growth rate decreases with increasing age. Between the 7th and 13th months, the rate is 2.7 mm per month; between the 13th and 19th months, it has declined to 2.3 mm per month.

6.4. Double Sampling Method

The doule sampling method was used in conjunction with the Petersen method, to obtain additional growth data. The first sample of 744 animals was collected by trawl in an 8-day period (January 30 through February 5, 1957), from the waters off Belmont Shore, Seal Beach, Sunset Beach, Bolsa Chica, and the entrance to Anaheim Slough. A second sample of 329 individuals was taken 3 months later from the same areas during an 8-day period (May 3 through May 10, 1957). The width frequency curves of the two samples were smoothed with a moving average of five and arranged one above the other on the same abscissa, for easy comparison (Figure 63).

The similarities between the curves are at once apparent. Only six animals under 120 mm in disc width are present in the two samples which total 1,073 animals. An increasing number of rays above 120 mm was taken by trawl, as shown by the ascending frequencies. The greatest frequency in both samples occurred roughly at 170 mm. Beyond this size, there was a sharp decline in numbers in both samples, presumably due to the combined effects of natural mortality and movement of many mature females into deeper waters. Seining of coastal beaches and inshore waters would give a better representation of immature rays.

Three well-defined peaks are visible on the lower curve at 169, 179 and 188 mm. Two similar prominences appear on the upper curve at 174 and 183 mm, while a third truncated peak is seen further to the right at C'. It would be risky, however, to assume that these peaks each represent a single age group. While the Petersen method is most reliable for the youngest age groups, it becomes progressively less so with older groups due to their increasing overlap (Perlmutter, 1954). Walford (1932) graphically demonstrated the phenomena of false age group peaks produced by several merging age groups in the California barracuda, Sphyraena argentea.

It seems possible that peaks A and A' represent the same group of merged age groups. Peaks B and B' appear similarly related while peak C may have its counterpart in the truncated peak at C'. Assuming the above analysis to be correct, an estimation of growth rate can be made from the interval between peaks A and A' and from that between B and B':

Peaks	Interval (mm)	Time interval (months)	Estimated growth rate (mm/month)
A, A'	5	3	1.66
B, B'	4	3	1.33

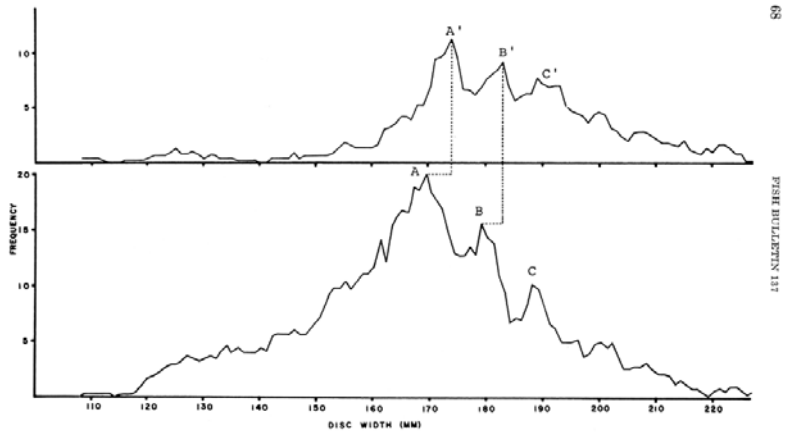


FIGURE 63. Comparison of width frequency curves from two samples of *U. halleri*, collected from the same offshore region. Lower curve represents first sample; upper curve represents animals captured 90 days later.

FIGURE 63. ***Comparison of width frequency curves from two samples of U. halleri, collected from the same offshore region. Lower curve represents first sample; upper curve represents animals captured 90 days later.***

By averaging the two rates, a growth rate of 1.5 mm per month for animals between the sizes of 169 and 183 mm is obtained. This figure agrees fairly well with the scanty data obtained from the tagging study.

6.5. Growth Data From Tagging and Recapture

In the 6 months from November 8, 1956, to May 10, 1957, 1,003 rays were marked and released. Forty-one tags (4 percent) were recovered by various means. Unfortunately, most fishermen who caught marked rays on hook and line, returned only the tag with a note as to time and place of capture. Migration data were obtained in such cases, but most growth information came from animals recaptured by trawl or beach seine.

Mortality of marked rays was apparently high. Physical pressure on fishes while in the net, time out of water, and shock caused by removal of the caudal spine and by fixing the tag, left most animals in a weakened state. Some recaptured rays were in poor condition, presumably from the effects of tagging; these animals were thin and showed little or no growth; in some, the tagging wound was not healed, probably due to snagging of the tag's trailing loop. Other factors such as impaired ability to evade enemies or to hide, may have contributed to mortality.

Recovery of marked animals ceased abruptly in September 1957, after fishermen returned three tags, and one large male was recaptured by beach seine in Anaheim Bay. The longest period of liberty for any marked animal was 284 days (Table 7). Two of the 41 tag returns were omitted since they contributed no information on growth or movement; one of these was recovered dead soon after being tagged; the other was retaken three times immediately after release. The 39 animals are arranged in order of size and divided into three size classes to facilitate study.

Growth rates (Column E), are shown only for the rays which made significant gains. Due to the observed adverse effects of tagging in a large proportion of recovered rays, it is believed that the best rates found in tagged animals were at least equalled by untagged animals. Quick recapture accounted for lack of growth in a few cases. Most animals for which an actual decrease in size was recorded, had been frozen prior to measurement. Such treatment tends to dry out tissues and cause shrinkage so that accurate determinations are impossible. One small animal, in poor condition (No. 10243), was measured alive on the trawl boat and had decreased in both length and width. This phenomenon was also encountered in captive rays.

Among the smallest recaptured rays (Table 7), animal No. 10219 grew at an average rate of 1.8 mm per month over a period of 133 days, a large ray of 157 mm disc width (No. 10326), showed an average monthly increment of 1.4 mm during 195 days. In the second size group, a male with a disc width of 178 mm (No. 10254), grew at an average rate of 1.3 mm per month, over a period of 254 days. This is slightly less than the rate determined by the double sampling method for animals between 169 and 183 mm in width (Figure 63).

In the largest size group, three animals showed a good average monthly increment. Number 10260 was taken 182 days after release and had grown 1.0 mm per month. The other two (Nos. 10104, 10985)

TABLE 7

Data Obtained From Tagging *U. halleri*

A. Tag number	B. Sex	C. Measurements (mm) when tagged W.	L.	D. Growth (mm) W.	L.	E. Growth rate (mm/Mo.) in Disc Width	F. Period of liberty (Days)	G. Distance moved (naut. mi.)	H. Remarks
10582	Female	124	217	*		--	45	0.50	Tag recovered in beach seine.
10553	Male	135	234	0	0	--	30	0.75	Hook and line; carcass frozen.
10120	Male	138	240	*		--	184	1.25	Hook and line; tag only returned.
10219	Female	142	249	8	13	1.8	133	0.50	Trawl; excellent condition; released.
10001	Male	151	262	2	3	0.4	143	1.25	Steam plant intake; carcass frozen.
10526	Male	151	277	0	0	--	4	0.75	Trawl; fair condition; released.
10315	Male	153	280	0	1	--	79	0.75	Trawl; poor condition; released.
10243	Male	154	270	−1	−2	--	84	1.00	Trawl; poor condition; released.
10222	Male	156	272	*		--	215	1.00	Hook and line; tag only returned.
10409	Male	156	273	0	0	--	2	0.25	Trawl; fair condition; released.
10326	Female	157	278	9	15	1.4	195	1.25	Speared; excellent condition.
10971	Male	157	283	*		--	68	0.75	Hook and line; tag only returned.
10159	Male	159	281	1	2	0.7	46	1.25	Trawl; fair condition; released.
10588	Male	161	283	−1	0	--	87	1.50	Steam plant intake; carcass frozen.
10533	Male	162	279	0	0	--	5	0.75	Trawl; fair condition; released.
10390	Female	163	290	0	1	--	49	0.75	Trawl; fair condition; released.
10211	Male	163	295	4	6	0.9	133	0.50	Trawl; good condition; released.
10508	Male	163	283	*		--	63	1.00	Hook and line; tag only returned.
10393	Female	167	282	−1	−2	--	118	0.75	Hook and line; carcass frozen.
10766	Male	169	295	0	0	--	4	2.00	Trawl; fair condition; released.
10440	Female	171	315	2	3	0.7	92	1.25	Trawl; good condition; released.
10106	Male	173	307	1	0	--	109	1.50	Hook and line; carcass frozen.
10270	Male	173	311	*		--	189	1.50	Hook and line; tag only returned.
10150	Female	175	309	5	8	1.0	147	1.50	Beach seine; excellent condition; released.
10254	Male	178	319	11	18	1.3	254	2.00	Hook and line; excellent condition.
10458	Male	178	324	0	0	--	4	0.50	Trawl; good condition; released.
10208	Male	180	318	*		--	177	1.00	Hook and line; tag only returned.
10489	Male	183	312	*		--	210	0.50	Hook and line; tag only returned.
10206	Male	190	340	*		--	284	2.00	Hook and line; tag only returned.
10260	Male	192	334	6	11	1.0	182	2.25	Trawl; good condition; released.
10650	Female	192	336	*		--	132	1.75	Hook and line; tag only returned.
10320	Male	195	342	1	1	0.4	84	0.50	Trawl; good condition; released.
10317	Male	197	354	*		--	208	4.75	Hook and line; tag only returned.
10644	Female	200	332	0	−1	--	41	1.00	Trawl; carcass frozen.
10608	Male	204	377	*		--	135	3.50	Hook and line; tag only returned.
10607	Male	207	355	*		--	89	2.25	Hook and line; tag only returned.
10104	Female	208	340	4	7	0.8	141	2.00	Beach seine; excellent condition; released.
10085	Male	211	377	3	4	0.7	128	3.00	Beach seine; good condition; released.
10185	Male	216	378	*		--	28	2.50	Hook and line; tag only returned.

* No growth data (tag only returned).

TABLE 7
Data Obtained From Tagging U. halleri

were recaptured after 144 and 128 days, respectively. They were considerably larger than the first animal, and their growth rates were lower as would be expected; one grew at a rate of 0.8 mm per month while the other averaged 0.7 mm.

The growth curve (Figure 62) was begun by plotting the average disc width of successive broods of young animals obtained from a length frequency curve. Growth data for animals above 140 mm in disc width were obtained largely by tagging and recapture; these data were used to extend the growth curve. The dotted segments of the curve are not based on data and assume a growth rate intermediate to the known values on either side.

6.6. Growth in Captivity

On October 25, 1959, 33 young rays ranging from 65 to 108 mm in disc width, were captured in the nursery ground at Newport Dunes. They were transported in an aerated tank to Marineland of the Pacific and placed in a wooden aquarium already occupied by a number of fingerling yellowtail, Seriola dorsalis. The aquarium was lined with fiberglass and measured 4 feet by 6 feet by 2½ feet deep. Filtered sea water, at about 19° C, was continuously piped into the aquarium. Aeration was accomplished with plastic tubing and bubbling stones. No sand was used in the tank.

After an adjustment period, the rays were tagged and measured. This was accomplished by placing them, a few at a time, in a shallow white enameled pan containing 1 inch of fresh sea water. Here they were lightly anesthetized with tertiary amyl alcohol and tagged by slipping a numbered vinyl plastic sleeve over the caudal spine. Total length and disc width were then determined to the nearest 0.5 mm. Measurements were made without removing the animals from the water, by placing a transparent plastic ruler on the bottom of the pan. The sex of each animal together with remarks on its behavior and appearance were also recorded. Subsequent measurements were made at intervals of 1 month, following the same procedure.

It is believed that conditions for growth and survival during the 10 months of captivity were less favorable than those in nature. The diet lacked polychaetes which are eaten in quantity by young rays. The smallest animals seemed unable to masticate or swallow morsels of chopped food, so they subsisted largely on frozen brine shrimp. The older rays ate the chopped food to varying degrees, but had to compete for it with the aggressive yellowtail fingerlings.

After 3 months, the 24 surviving rays were placed by themselves in a small aquarium with a glass front. Although competition for food was reduced, the space was inadequate. Sand was added to provide a more natural environment, but sanitation suffered as a result and bacterial skin infection appeared on many individuals. This was successfully treated by introducing a stream of 2 percent copper sulphate solution for 1 week. The treatment was repeated periodically as needed.

Survival was highest among the larger individuals, although three large rays met early, accidental deaths (Table 8). There was great variation in growth rates during the first month (Column I). It is significant, however, that five animals grew 3 mm in disc width during

TABLE 8

Captivity Study of *U. halleri*

Ident. number	Original measur. W.	Original measur. L.	Growth in width and total length, by months: I W.	I L.	II W.	II L.	III W.	III L.	IV W.	IV L.	V W.	V L.	VI W.	VI L.	VII W.	VII L.	VIII W.	VIII L.	Total gain or loss (mm) W.	Total gain or loss (mm) L.	Average gain or loss (mm/Mo.) W.	Average gain or loss (mm/Mo.) L.	Condition: after 8 months
28	73	124	1.0	1.0	1.0	1.0	0.0	2.0	Missed		0.0	0.0	−0.5	−1.0	−0.5	−1.0	−0.5	1.5	0.5	3.5	0.06	0.4	Poor
20	75	127	2.0	3.0	0.0	0.0	1.0	1.0											3.0	3.0	1.0	1.0	
11	77	124																					
16	77	131	0.0	2.0	0.0	−0.5	0.0	0.5	0.0	1.0	0.0	1.0	−0.5	−1.0					−0.5	2.0	−0.1	0.3	
21	77	122	0.0	1.0	0.0	0.0													0.0	1.0	0.0	0.5	
22	77	126	1.0	2.0	1.0	0.0	−0.5	0.0											1.5	2.0	0.5	0.7	
7	78	130	1.0	2.0	1.0	0.0	1.0	3.0	0.0	0.0	1.0	2.0	0.0	0.0	0.0	1.0	0.0	−1.0	4.0	7.0	0.5	1.2	Good
13	78	130	3.0	5.0	2.0	3.0	0.5	1.0	0.0	1.0	−0.5	1.0	0.0	0.0					5.0	11.0	0.8	1.8	
8	79	140	1.0	2.0	0.0	0.0	−1.0	0.0	−0.5	−1.0	0.0	0.0							−0.5	1.0	−0.1	0.2	
9	79	132	2.0	4.0	0.0	0.5													2.0	4.5	1.0	2.3	
29	79	131	3.0	4.0															3.0	4.0	3.0	4.0	
32	79	138	2.5	3.5	2.0	3.0	Mined		1.5	2.5	0.0	0.5	−0.5	−0.5	0.0	0.5	−1.5	−2.0	4.0	7.5	0.5	0.9	Fair
6	80	134	0.0	1.0															0.0	1.0	0.0	1.0	
23	81	141	3.0	4.0	1.0	2.0	−1.0	0.0	0.0	−0.5	−1.0	−0.5							2.0	5.0	0.4	1.0	
19	82	141	1.0	0.0	1.0	2.0	−0.5	1.0											1.5	3.0	0.5	1.0	
2	83	144	3.0	5.5	2.0	3.0	2.0	3.0	0.0	0.0	0.0	−1.0	0.0	0.0	0.0	1.0	−1.0	−1.0	6.0	10.5	0.8	1.3	Poor
5	83	143	0.0	0.0	0.0	1.0													0.0	1.0	0.0	0.5	
27	83	135	1.0	2.0															1.0	3.0	1.0	3.0	
31	83	145	0.0	1.0	1.0	1.0	0.5	0.0	−1.0	0.5	−0.5	−1.0	0.0	0.0	0.0	0.5	−0.5	−1.0	−0.5	0.5	−0.1	0.1	Poor
33	84	143	1.0	2.0	0.5	0.5	0.5	0.5	−0.5	0.5	−0.5	0.0	1.0	−0.5	0.0	0.0	−0.5	0.0	1.5	3.0	0.2	0.4	Fair
17	86	148	2.0	3.0	2.0	3.0	1.0	2.0	−1.0	−1.0	1.0	2.0							5.0	9.0	1.0	1.8	
26	86	149	1.0	0.0	0.0	0.5	0.0	0.5	0.0	1.0	0.0	0.0	0.0	−1.0	0.0	0.0	0.5	−1.0	1.5	0.0	0.2	0.0	Fair
24	87	140	2.0	2.0	0.0	1.0	1.0	0.5	−0.5	−1.0	−0.5	0.5	−1.0	0.0	0.0	−1.0	0.5	0.5	1.5	2.5	0.2	0.3	Poor
25	87	140	2.5	4.0	1.0	0.5	Missed		0.5	0.5	Missed		−1.5	0.0	1.0	0.5			3.5	3.5	0.5	0.8	
30	87	146	Jumped out of tank																				
12	92	155	1.0	2.0	1.5	2.0	−1.5	0.0	0.0	−1.0	0.0	−1.0	0.0	0.0	−1.5	−0.5	0.5	0.5	0.0	2.0	0.0	0.3	Good
1	94	159	1.0	1.0	0.5	1.0	−0.5	0.0	0.0	0.0	−0.5	−1.0	−0.5	−1.0	0.0	0.0	−0.5	0.0	−0.5	0.0	−0.1	0.0	Fair
3	96	164	1.0	2.0	1.0	1.0	1.0	2.0	0.5	0.5	−0.5	0.5	0.0	−1.0	0.0	1.5	−1.0	−1.0	2.0	5.5	0.3	0.7	Poor
10	98	165	2.0	4.0	Tail crushed														2.0	4.0	2.0	4.0	
4	101	180	Crushed by piling																				
15	102	172	1.0	0.0	1.0	1.0	0.0	1.0	−1.0	0.0	1.5	−1.0	−1.5	1.5	1.0	−0.5	−1.0	−0.5	1.0	1.5	0.1	0.2	Good
18	106	182	1.0	1.0	0.5	1.0	0.5	2.0	−1.0	0.5	2.0	2.0	1.0	−0.5	1.0	1.0	0.0	1.0	5.0	8.0	0.6	1.0	Good
14	109	187	3.0	5.0	2.0	4.0	2.0	2.5	−1.0	1.0	2.0	2.0	2.0	3.0	0.0	0.0	1.0	2.5	11.0	20.0	1.4	2.5	Good
Av. growth (mm)			1.4	2.3	0.9	1.2	0.2	0.9	−0.2	0.2	0.2	0.3	−0.1	−0.1	0.1	0.2	−0.3	−0.1					
Percent mortality by months			9		21		30		39		39		48		55		58						

TABLE 8

Captivity Study of U. halleri

this initial period; this rate equals the growth rate previously determined for newborn animals, from the width frequency curve (Figure 61); thus, the captivity growth data lend support to that obtained for young animals by the Petersen method. It seems probable that the highest growth rate recorded in captivity is equalled by young rays living under natural conditions.

Most animals grew very slowly after the first month. In some, a decrease in both disc width and total length was observed. This phenomenon is unexplained. A notable exception was seen in the largest ray of the group (Number 14) which continued to grow at a much higher rate than any other. Its relative success probably resulted from its ability to eat all types of food offered. The growth rate of this individual during its first month was actually greater than that indicated for animals of like size, by the frequency curve (Figure 61).

Unhealthy animals generally have a faded color pattern. The dorsum takes on a light-grayish tone, and the markings become less distinct. Loss of weight and listlessness are also characteristic. Eight months after the initial measurements, mortality had reached 58 percent (Table 8). Five of the survivors were in poor condition, four were only fair, and five still appeared healthy. Growth had virtually ceased even in the seemingly healthy rays, with the exception of the largest animal which continued to make appreciable gains. Four of the five that appeared in good condition were large individuals, further demonstrating the advantage of age in survival. By the end of 10 months, mortality had reached 100 percent.

6.7. Sexual Maturity

There is evidence that both sexes of U. halleri grow at about the same average rate to sexual maturity. This evidence is found in the nearly equal size distribution of both sexes throughout samples of immature animals. No evidence to the contrary was found in the study of young captive rays. The average growth rate to maturity for both sexes is about 2.4 mm per month (Table 9) .

TABLE 9

Sexual Maturity Data for *U. halleri*

	Average growth rate to sexual maturity (mm/Mo.)	Average disc width at sexual maturity (mm)	Approximate average age at sexual maturity (years)	Width at first maturity (mm)	Maximum recorded width (mm)	Ratio of width at first maturity to maximum width
Male	2.4	150	2.6	146	250	0.588
Female	2.4	150	2.6	145	310	0.467

TABLE 9

Sexual Maturity Data for U. halleri

Furthermore, both sexes appear to attain sexual maturity at about the same size and, therefore, at about the same age. The average size at which maturity is attained, was estimated for males by histological examination of 41 young males ranging from 130 to 155 mm in disc width. Males were considered mature when the enlarged testicular lobules contained all stages of spermatogenesis including fully-formed sperm. The average size at maturity was estimated for females by gross

examination of 50 individuals ranging from 125 to 155 mm in disc width. A female was considered mature when a large ovum was found in the functional ovary or in either oviduct. The average disc width at maturity, for both sexes, is about 150 mm (Table 9); at this size they are about 31 months old (Figure 62). Thus, round stingrays attain maturity much more rapidly than do other elasmobranchs for which growth data are available.

First maturity, or earliest maturity, is defined as the smallest size at which individuals of a species are sexually mature (Olsen, 1954). First maturity was estimated for both sexes of U. halleri using the same criterion described above. The smallest mature male was 146 mm in disc width, while the smallest mature female measured 145 mm (Table 9).

The ratio of size at first maturity to maximum size, has been used by previous workers to indicate at what stage of growth various elasmobranchs become sexually mature. This ratio for U. halleri (Table 9) showed that a few males matured upon reaching about 59 percent of their maximum size, while earliest maturity in females occurred before one-half the maximum disc width was attained. The ratio would seem more valid if it were not based on the two extremes, either of which might be atypical. However, it gives a basis for comparison with other elasmobranch species (see Discussion).

Males apparently do not grow as large as females, which is a common condition in elasmobranchs. The maximum width I recorded for males was based on 2,921 animals. Although larger specimens may exist, it seems significant that several of a considerably smaller number of females (1,302) exceeded the largest male in size. The maximum width for females is based on a record animal captured by the California Department of Fish and Game.

7. MOVEMENTS

The tagging study yielded some specific knowledge about the movements of U. halleri, and additional information was obtained through trawling and seining. Trawled animals were captured offshore at depths of 2 or more fathoms and were released in the general area of capture. Individuals from each haul were tagged, placed in a holding tank, and released together. The point of release was located roughly by sightings on landmarks, and by estimation of distances. Depths were determined by fathometer. The distances moved by tagged rays were estimated to the nearest one-quarter-mile (nautical) and are subject to an error of one-quarter mile, plus or minus.

The greatest movement recorded, from 39 tag returns, was 4.75 miles (Table 10) . This animal was a large male (No. 10337), recaptured down-coast (south), and inshore from the point of its release, after 208 days of liberty. A large female (No. 10644) was retaken 4 miles up-coast (north), from the point of release, after 41 days of liberty. Both rays moved between Sunset Beach and Belmont Shore, but in opposite directions. Ray No. 10766 was recaptured 2 miles down-coast, just 4 days after release. Such rapid movement supports previous evidence from trawling records, that large areas can be evacuated by the animals in a short time.

TABLE 10

Movement Data from *U. halleri* Tagging Study

Tag number	Sex	Width (mm) when tagged	Liberty period (days)	Distance moved (naut. mi.)	Direction moved*
10582	F	124	45	0.50	2
553	M	135	30	0.75	2
120	M	138	184	1.25	1
219	F	142	133	0.50	2
001	M	151	143	1.25	1
536	M	151	4	0.75	2
315	M	153	79	0.75	2
243	M	154	84	1.00	3
232	M	156	215	1.00	1
409	M	156	2	0.25	2
326	F	157	195	1.25	1
971	M	157	68	0.75	1
159	M	159	46	1.25	3
588	M	161	87	1.50	1
533	M	162	5	0.75	2
390	F	163	49	0.75	2
211	M	163	133	0.50	2
598	M	165	63	1.00	1
393	F	167	118	0.75	2
766	M	169	4	2.00	3
440	F	171	92	1.25	3
106	M	173	109	1.50	1
270	M	173	189	1.50	1
150	F	175	147	1.50	1
254	M	178	254	2.00	4
458	M	178	4	0.50	2
208	M	180	177	1.00	1
489	M	183	210	0.50	1
296	M	190	284	2.00	4
260	M	192	182	2.25	3
689	F	192	132	1.75	4
320	M	195	84	0.50	2
337	M	197	208	4.75	4
644	F	200	41	4.00	3
608	M	204	135	3.50	4
607	M	207	89	2.25	4
104	F	208	144	2.00	4
985	M	211	128	3.00	1
185	M	216	28	2.50	1

*1. Moved shoreward to open beach or bay (14 animals).
2. Recaptured in open water near point of release (12).
3. In open water, up or down-coast from release point (6).
4. Up or down-coast and shoreward to open beach or bay (7).

TABLE 10

Movement Data from U. halleri Tagging Study

Twenty-one animals were retaken near open beaches or in bays (Table 10). Many of these were caught either in June or September and their presence there seems related to breeding or bearing of young. Twelve rays were recaptured offshore by trawl, three-fourths of a mile or less from point of release. Three of these were at liberty for more than 100 days, and may have moved in and out of this general area several times during the interim. The tendency to be recaptured in the same locale, appears more pronounced among rays of 167 mm disc width or less. Seven rays were retaken offshore, 1 to 4 miles up- or down-coast from the release point.

A marked relationship exists between animal size and distances moved (Table 11) . All except four recaptured rays were probably sexually mature at time of tagging. The range of movement apparently increases as an animal grows, even after maturity is reached. This finding supports similar evidence from trawling and seining records; those records show a marked tendency for young rays to remain near shore; few young venture offshore to a depth of 2 fathoms until they have

reached 120 mm in width; the largest animals are found farthest offshore at greatest depths. Large rays remained at liberty longer, on an average, than smaller rays (Table 11).

TABLE 11

Tag Return Data for *U. halleri* Showing Relationship Between Animal Size and Distances Moved

Disc width (mm)	Number of animals tagged	Number of recaptures	Percent of size group recaptured	Average period of freedom (days)	Average distance moved (naut. miles)
160 and under	272	13	4.8	94	0.86
161 to 180	410	14	3.4	102	1.18
181 and over	321	12	3.7	138	2.42
Total	1,003	39			

TABLE 11

Tag Return Data for U. halleri Showing Relationship Between Animal Size and Distances Moved

8. FOOD HABITS

8.1. Stomach Content Analysis

An effort was made in the food study, to obtain data representative of the species. Inshore and offshore waters were sampled from Long Beach to Newport during most months of 1956. Stomachs were collected from 217 rays of a wide size range, at the various locales. The percentages of different animal forms eaten by U. halleri are based on the contents of 180 stomachs. About 12 percent of the total food volume in these stomachs was unidentifiable and was used only in obtaining the average volume per stomach. Twelve additional stomachs were empty and enter only into calculation of the average volume per stomach. Stomachs of another 25 rays were examined and discarded as non-representative; the animals had apparently been restricted to a lagoon where food was scarce.

All animal groups taken as food by U. halleri, were listed phylogenetically (Table 12) . Food items were identified to the specific level whenever possible. Three classes of animal were best represented; Pelecypoda, Polychaeta, and Crustacea. Thirteen pelecypod, 16 polychaete, and 18 crustacean genera were identified. Nine crustacean genera were of the order Decapoda.

TABLE 12

List of Animals Collected from Stomachs of *Urolophus halleri*

* Animals not identifiable below this level

Phylum Nemertea
  * Nemerteans
Phylum Aschelminthes
  Class Nematoda
    * Nematodes
Phylum Echinodermata
  Class Ophiuroidea
    Ophioplocus esmarki Lyman
  Class Holothuroidea
    * Holothuroideans

TABLE 12

List of Animals Collected from Stomachs of Urolophus halleri

Phylum Sipunculoidea
  * Sipunculids
Phylum Annelida
    Class Polychaeta
      Polynoidae
        Nephtys sp.
        Platyneris bicanaliculata (Baird)
      Glyceridae
        Glycera americana Leidy
      Goniadidae
        Goniada sp.
        Goniada brunnea Treadwell
      * *Eunicidae*
      Onuphidae
        Diopatra sp.
        Lumbrineris sp.
        L. erecta (Moore)
        L. minima Hartman
        Arabella sp.
      Dorvilleidae
        Dorvillea articulata (Hartman)
      Orbiniidae
        Haploscoloplos elongata (Johnson)
        Prionospio sp.
        Chaetopterus sp.
        Tharyx parvus Berkeley
        Capitata ambiseta Hartman
      * Maldanidae
      Opheliidae
        Pectinaria sp.
        P. californiensis Hartman
      Ampharetidae
        Pista alata Moore
      Sabellidae
        Chone sp.
Phylum Arthropoda
    Class Pycnogonida
      Phoxichilidiidae
    Class Crustacea
      Order Amphipoda
        Phoxocephalidae
          Paraphoxus sp.
        * Calliopiidae
        Pontogeniidae
          Elasmopus rapax Costa
        Photidae
          Photis californica
          Corophium acherusicum Costa
        Oedoceratidae
          Ampithoe sp.
      Order Isopoda
        Tribe Flabellifera
          Idothea (Pentidotea) resecata (Stimpson)
          Edotea sp.
          Edotea sublittoralis Menzies & Barnard
      Order Cumacea
          Leptocuma sp.
          Diastylopsis tenuis Zimmer
      * Order Mysidacea
      Order Decapoda
          Penеus sp.
          P. californiensis

TABLE

Hippolyte sp.
Hippolyte californiensis Holmes
Spirontocaris sp.
S. palpator (Owen)
Crangon dentipes (Guerin)
C. californiensis
Betaeus longidactylus Lockington
Callianassa sp.
C. californiensis Dana
Pagurus sp.
Emerita sp.
Cancer sp.
C. productus Randall
C. antennarius Stimpson

Phylum Mollusca
Class Pelecypoda
Mytilus edulis Linnaeus
M. californianus Conrad
Laevicardium substriatum (Conrad)
Tivela stultorum (Mawe)
Saxidomus nuttalli Conrad
Chione undatella (Sowerby)
Macoma sp.
M. nasuta (Conrad)
Tagelus sp.
T. californianus (Conrad)
Donax sp.
D. californicus Conrad
Solen sp.
S. rosaceus Carpenter
Spisula sp.
Mactra californica Conrad
Tresus nuttalli (Conrad)
Barnea pacifica (Stearns)

Phylum Chordata
Class Leptocardii
Branchiostoma californiense Cooper
Class Osteichthys
Clevlandia ios (Jordan & Gilbert)
* Embiotocidae

TABLE

Pelecypods, polychaetes, and crustaceans comprised over 94 percent of the total food volume (Table 13) . The remaining groups can be considered merely incidental to the diet of the round stingray. Bivalves were the most important single class of food, comprising over 42 percent of the total volume, while polychaetes (30 percent) and crustaceans (21 percent) ranked second and third respectively. of the various crustacean orders, decapods formed by far the greatest volume (80 percent of the crustacean category), the other orders being relatively minor in importance.

It was noted that the feeding habits of U. halleri changed with age (Table 14) . Crustaceans formed over one-half the food volume of the smallest rays; small decapod crustaceans seemed to be preferred, and as many as 50 tiny shrimp were found in one stomach. Annelids were next in importance; masses of small, thread-like polychaetes of the family Goniadidae were commonly found in young rays. Few pelecypods appeared to be eaten by young rays, probably because they are

TABLE 13

Percentage and Percentage-of-Occurrence, of Different Food Types in Stomachs of *U. halleri*

(Based on 180 animals)

Food	Percentage of total food volume		Percentage of occurrence	
Polychaeta		30.42		72.0
Crustacea		21.38		56.1
Decapoda	17.14		43.9	
Amphipoda	1.40		35.4	
Isopoda	1.00		19.4	
Mysidacea	1.68		3.8	
Cumacea	0.16		3.6	
Pelecypoda		42.35		45.1
Nematoda		0.23		8.5
Osteichthys		1.98		7.5
Sipunculoidea		1.10		7.3
Nemertea		0.93		7.1
Echinodermata		0.40		6.1
Leptocardii		1.17		1.3
Pycnogonida		0.02		1.1

TABLE 13

Percentage and Percentage-of-Occurrence, of Different Food Types in Stomachs of U. halleri (Based on 180 animals)

TABLE 14

Percentage of Various Types of Food Found in Rays of Different Size Groups

(Based on 180 animals)

	I 36 Rays 120 mm & under		II 27 Rays 121–140		III 27 Rays 141–160		IV 31 Rays 161–180		V 59 Rays 181 & over	
Class Pelecypoda		1.46		17.91		56.25		68.13		44.22
Class Polychaeta		36.74		47.91		13.34		21.63		33.29
Class Crustacea		55.96		26.41		21.87		6.61		17.56
O. Decapoda	41.36		12.09		20.08		5.83		17.15	
O. Amphipoda	6.81		2.52		0.69		0.52		0.35	
O. Isopoda	6.33		0.90		1.10		0.26		0.06	
O. Mysidacea	0.24		10.60							
O. Cumacea	1.22		0.30							
Class Osteichthys				1.19				3.63		2.88
Phylum Sipunculoidea				6.12						0.35
Phylum Nemertea		5.35								1.05
Phylum Echinodermata		0.49				1.24				0.35
Class Nematoda				0.45		0.41				0.23
Class Leptocardii						6.88				
Class Pycnogonida										0.06

TABLE 14

Percentage of Various Types of Food Found in Rays of Different Size Groups (Based on 180 animals)

unable to crush the shells. However, as growth continued, bivalves assumed greater importance while annelids and crustaceans became relatively less important. The large rays tended to eat more bony fishes, although these were not important as food.

Although the relative volumes of the three major classes of food varied from one size group of ray to another, their combined volumes never dropped below 91.5 percent of the total volume consumed by any size group; nor did their combined volumes exceed 96.4 percent of the total food volume for any size group. Thus, the forms that were eaten incidentally, comprised only 3.6 to 8.5 percent of the total food volume.

Rays of all sizes browse on the extended siphons of bivalves. This habit has been reported for several fishes including the starry flounder, Platichthys stellatus (Orcutt, 1950). Although shell fragments and body parts of thin-shelled bivalves, such as Solen rosaceus, were more often

found in U. halleri, large rays are capable of crushing moderately thick shells.

Although pelecypods were foremost in volume consumed when all sizes of U. halleri are considered together (Table 13), their overall percentage of occurrence was lower than either annelids or crustaceans, because they were eaten mainly by larger rays. Polychaete worms are eaten by all sizes and consequently were found in 72 percent of stomachs; the larger species of polychaetes were preferred by mature rays, however. Crustaceans which formed 21 percent of the total food volume, were found in 56 percent of stomachs and decapods alone occurred in nearly 44 percent of individuals.

U. halleri seems to eat more or less continuously, at least during the day, without gorging. Only 12 of 192 stomachs (6 percent) were empty. No stomach contained more than 3.2 ml. In contrast, the barred surfperch, Amphistichus argenteus which does not differ greatly in body weight, appears to gorge itself periodically. Carlisle, Schott, and Abramson (1960) found 28 percent of stomachs in this species to be empty. Those containing food averaged 2.29 ml per animal and one fish contained 27 ml.

Rays from Belmont Shore ate more annelids and crustaceans but fewer bivalves than those from Newport Bay. At both places, however, these three classes of food taken together, formed over 90 percent of the total food volume. Availability may determine the relative volumes of the three most important classes of food, but no quantitative study of invertebrate fauna was made at either locale.

8.2. Feeding and Behavior, in Nature and in Captivity

Round stingrays obtain much of their food by burrowing in the substrate. At low tide, excavations measuring as much as 18 inches in diameter and 5 inches deep are found along the edges of inlets. Such activities may account for the red, abraded areas frequently found on the venter of captured rays.

Burrowing is also used for procryptic or defensive purposes and the ability seems to be innate, since newborn rays possess it. The act of concealment was photographed in slow motion in the laboratory at a shutter speed of 80 frames per second, and numerous observations were made. After settling to the bottom, the fish suddenly arches its back, keeping the outer edges of the pectoral fins on the substrate and drawing the posterior margin of the disc slightly forward. Sand and water appear to be drawn toward that margin by hydraulic action. Then as the body is quickly flattened, loose sand is scooped up posteriorly and propelled forward and upward by a rippling action of the pectorals. Settling debris quickly covers the animal's back and is held there by mucous secretions. Finally, the spiracles are cleared by an expulsion of water. The entire act is completed in about 5 seconds and only the caudal fin and eyes are normally left exposed.

U. halleri is able to develop considerable suction between its belly and any smooth surface, and can thus remain attached to a vertical surface. Captive animals, when hungry, will rise to the top of the aquarium by swimming up a wall, but they seldom venture away from contact with some surface. When a ray is released at the water's surface, away

from the sides of the aquarium, it immediately sounds, seeming to shun exposure of its underside. The same type of behavior has been noted in nature, the only exceptions being in mid-June during mating. Then, adult animals sometimes skim in a straight line along the surface of inland waters for 50 yards or more.

When young rays are fed in captivity, they move about the bottom searching by scent as well as by sight. An animal may pass directly over a morsel, then move backwards to it again, presumably as the olfactory organs receive stimulation. A concealed ray generally lies quietly when food is first placed in the tank; apparently not until it is stimulated by scent does it emerge to search the sand. Feeding rays ruffle their pectoral fins and pivot rapidly to right and left over their food to ward off other fishes; no threatening movements of the tail and caudal spine were ever observed, however. Newly-captured animals flinch violently at sudden motions or sounds outside the aquarium. After prolonged captivity and repeated handling, they generally become more placid.

9. PHYSICAL ENVIRONMENT

9.1. Temperature

The distribution of U. halleri seems to depend on several physical factors in the environment; probably the most important of these is water temperature. This benthic animal is limited to a relatively shallow coastal zone. The density of round stingrays is greatest from shore out to a depth of 8 fathoms, and is especially great at depths of 4 to 6 fathoms (Table 15) . The few hauls that were made below 7.5 fathoms, indicate that the yield per haul diminishes with depth.

Biologist-divers of the California Department of Fish and Game kept a monthly record of water temperature at three sites in Santa Monica Bay from August 1960 to August 1961, as part of an environmental study. Three stations were established on the ocean floor, 0.5 to 0.75 miles offshore. Obsolete streetcars were sunk at each site and the effect on animal population densities was studied. Monthly temperature measurements were made at the stations and near the surface directly above them (Figure 64, Graphs A, B, C). Temperatures from November through February at 10 fathoms were relatively high, and only slightly below those at the surface. This phenomenon was the result of the Davidson Current (Sverdrup, Johnson, and Fleming, 1942). During winter the Current brings warm water northward along the coast, close to the surface.

The water temperature at 10 fathoms remained above 10°C throughout the year at the three stations. The lowest temperatures at that depth were during September and June. Many mature females move inshore to warmer water during those months, to bear young and to mate. The bulk of the population seems restricted to depths of 10 fathoms or less, where temperatures remain above 10°C. That large rays are relatively more abundant in deepest water, seems to indicate greater tolerance by them for low temperatures.

Unfortunately, temperatures recorded by the California Department of Fish and Game during trawling and beach seining operations of 1955 to 1957, were made only slightly below the surface. By averaging

TABLE 15

Relation of Population Density to Water Depth
(Based on trawls made along the coast, mainly between Long Beach and Newport, during most months of the year.)

Depth fathoms	Number of hauls	Number of rays taken	Number of rays per haul
2.0	21	246	11.6
2.5	42	549	13.1
3.0	47	627	13.3
3.5	26	298	11.5
4.0	12	428	35.6
4.5	3	31	10.3
5.0	6	134	22.3
5.5	6	181	30.3
6.0	6	150	25.0
6.5	2	29	14.5
7.0	5	58	11.6
7.5	4	56	14.0
8.0	1	13	13.0
8.5	--	--	--
9.0*	1	11	11.0
9.5	1	6	6.0
10.0	1	0	0.0
10.5	--	--	--
11.0†	1	0	0.0
11.5†	1	0	0.0
12.0*	1	7	7.0
12.5	--	--	--
13.0†	1	0	0.0
13.5	1	4	4.0
14.5†	1	0	0.0
18.5†	1	0	0.0
Total	191	2,828	

* Trawls made at Black Warrior Lagoon, Baja California.
† Trawls made between Malibu and Ventura, California.

TABLE 15
Relation of Population Density to Water Depth
(Based on trawls made along the coast, mainly between Long Beach and Newport, during most months of the year.)

a large number of these readings collected from the Belmont Shore-Newport region, I graphed the monthly surface temperature for this region (Figure 64,D). This graph is similar in configuration and range to those of Santa Monica Bay. It therefore seems safe to assume that water temperatures of the two regions are also similar at 10 fathoms.

Another indication of the species' preference for warm water is seen in the high concentration of rays in the warm water near the outlet of the Seal Beach steam plant. The density was greater there during June 1962, than any I previously encountered in 6 years of study. Many of the adult rays captured there were in breeding condition. On June 14, 1962, 1,384 round stingrays were taken in a single set, using a 100-foot seine. On June 26, another set yielded 1,047 rays. On the latter date, the surface water temperature in the seining area was 24.4°C, while Belmont Shore registered 18.4°C, and Anaheim Landing was 18.1°C. The area of water affected around the steam plant, and the degree of temperature elevation vary with winds and currents.

Belmont Shore and Anaheim Landing were not seined at the time of the Seal Beach seining, but, the density of rays was probably much

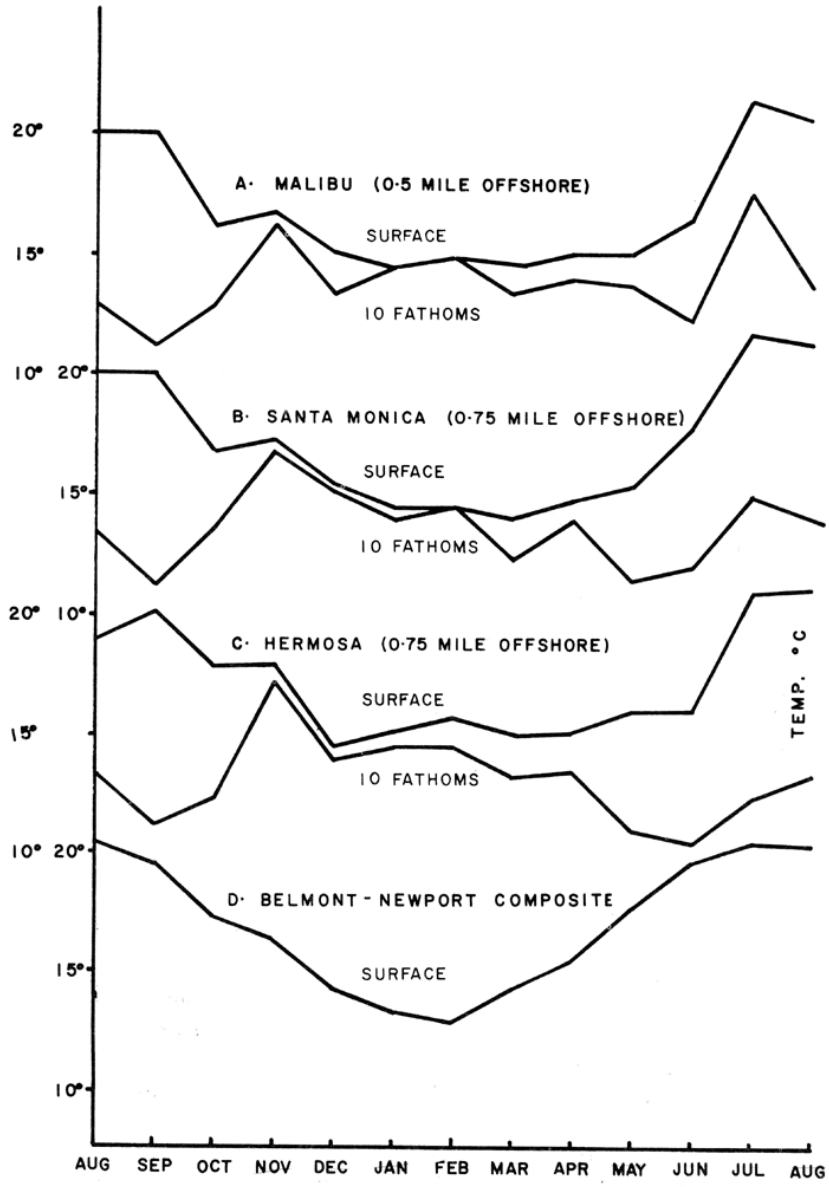


FIGURE 64. Monthly record of water temperature at surface and at ten fathoms for three offshore stations in Santa Monica Bay, A, B, C; monthly surface temperatures obtained by averaging readings collected from Long Beach and Newport, 1955–57, D.

FIGURE 64. ***Monthly record of water temperature at surface and at ten fathoms for three offshore stations in Santa Monica Bay, A, B, C; monthly surface temperatures obtained by averaging readings collected from Long Beach and Newport, 1955–57, D.***

lower at these two locales, judging from the low incidence of injuries reported there during the same period. Lifeguards estimated over 500 injuries at Seal Beach, between mid-May and the end of July, 1962.

Inshore water temperatures along the southern California coast are generally higher than those offshore throughout most of the year. In December, January, and February, however, the situation is reversed and shallow inlets become colder because of rapid heat loss to the air. Temperatures become particularly low (11°C) in the uppermost reaches

of such waters and are believed unattractive to both adults and young of U. halleri. Adults generally move offshore in winter; some re-enter mouths of inlets apparently to feed, but are not permanent residents. Young rays remaining inshore move closer to an inlet's mouth where temperatures more nearly approximate those in the ocean.

The role of temperature in the distribution of U. halleri needs further investigation employing controlled experiments, since the evidence presented here is based solely on the incidence of animals and temperatures in the field.

9.2. Substratum and Inlets

Coastal localities which have the highest density of round stingrays, seem to possess two physical characteristics: namely, a soft substratum just offshore, and protected inlets or bays which also have a soft bottom. The animals need loose sand or mud in which to burrow for food and concealment, while protected waters seem most attractive to mating individuals, and as nursery grounds.

Although Santa Monica Bay has water temperatures quite similar to the Belmont-Newport region, it has very few round stingrays. Trawling records over a period of several years, as well as recent observations by biologist-divers of the California Department of Fish and Game, bear out this fact. The scarcity seems due to hard-packed sand and rock on the bay floor, and to a lack of sufficiently large inlets adjacent to the bay.

In the Belmont-Newport region, which has a high population density, the substratum of coastal waters is shown by U.S. Coast and Geodetic Survey Chart 5101 (1959) to be predominantly gray sand. I took bottom samples off Belmont Shore and Seal Beach during trawling operations in 1957, using an orange-peel sampler, and these samples consisted mainly of loose, gray sand. Information obtained from divers indicates extensive areas of loose sand, offshore between Belmont Shore and Newport.

Numerous samples of the substratum in Alamitos, Anaheim, and Newport Bays have been obtained in the beach seine bag, and some of these were screened for their faunal contents. The substratum of Anaheim Bay is predominantly gray mud, with mixtures of sand in some areas. Reish and Winter (1954) made an ecological study of Alamitos Bay, and reported the bottom to be almost uniformly fine gray mud, except for limited rocky or sandy areas. Many of the benthic invertebrate forms listed by these authors are important to U. halleri as food.

Barnard and Reish (1959) found a variety of substrata in Newport Bay. Samples taken in the channel between Balboa Island and Harbor Island were of gray mud. That site is of particular interest, because I took rays there in all months of the year. The shallow Upper Bay which extends north of Highway 101, is a favored habitat of the species during the warm months. Here, much of the substratum is fine black and gray mud, or a mixture of sand and shell fragments.

9.3. The Effect of Man's Activities on the Environment of U. halleri

The enlargement of coastal inlets by dredging, and the erection of sea walls and breakwaters along the coast, is improving the physical environment of U. halleri. The Newport Dunes Marina represents such

an improvement. This sizeable body of water was created in 1956 by dredging a tidal marsh in Newport Upper Bay. The Marina's swimming lagoon measures about 200 by 500 yards. Its shores and bottom are sandy except at the deepest part near its approximate center, where the floor is fine gray mud. In September, 1959, I found a large number of pregnant rays and young in the swimming lagoon. Stomachs of 25 adults contained mud and occasional fragments of polychaete worms. Screening of sand and mud taken from the beach seine revealed two polychaete species, Lumbrineris minima and L. erecta; three mollusks, Solen rosaceus, Chione undatella and many bubble snails, Bulla gouldiana; one crab, Pagurus, and two unidentified amphipods. The most plentiful bony fishes were the atherinid, Atherinops affinis, bay anchovy, Engraulis mordax, staghorn aculpin, Leptocottus armatus, and the embiotocid, Micrometrus minimus. Small patches of Zostera were beginning to appear along the lagoon's east side.

Continued observation of the lagoon over a 33-month period showed round stingrays there throughout the summer months. Increasing numbers of rays used the area as a nursery ground each September. New animal species gradually added to the lagoon's fauna included pistol shrimp, Crangon dentipes, the shrimp, Peneus californiensis, an octopus, Octopus sp., and the bryozoan Zoobotryon verticillatum. The two polychaete species already present, became more plentiful. Ten of 22 species of bony fishes taken in the lagoon became more-or-less permanent residents. The eel-grass beds also became more extensive. Thus, dredging created an additional inshore nursery and eventually should provide more food for U. halleri when a benthic fauna becomes established.

10. BIOLOGICAL ENVIRONMENT

10.1. General

Although few of the animals captured in the trawl net with the round stingray were found in its diet, they are of interest because of their association with the ray. Fishes, though taken in quantity by trawl, comprised less than 2 percent of the ray's food (Table 13). The invertebrates eaten by U. halleri are generally too small to be taken by trawl, and many of them lie beneath the surface of the substratum.

The relative abundance of associated species (Tables [17], [18] and [19]) is based on Department of Fish and Game trawling records from January 28 through April 26, 1957. These records were selected because they included samples from locales having a high population density of rays as well as from locales with low density. By comparing the fauna of a favorable habitat with that of a less favorable one, a better understanding of both might be gained. Belmont Shore and Surfside are considered nearly optimum for U. halleri while the Oceanside and San Diego sites are much less favorable.

10.2. Animal Species Associated with U. halleri

Only 14 elasmobranch species were taken at the four trawling sites as compared to 31 bony fish species. However, the total elasmobranch catch per unit effort (Table 16), was only slightly below that for bony

fishes (Table 17). Benthic forms of both classes were taken in far greater number than nektonic ones, due to the heavily-weighted trawl net.

TABLE 16

Number of Elasmobranchs Taken Per Trawling Hour at Belmont Shore, Surfside, Oceanside, and San Diego

	Jan. 28 to Feb. 6, 1957		Mar. 18 to Mar. 26, 1957	April 17 to April 26, 1957		
	Belmont Shore	Surfside	Belmont Shore	Belmont shore	Oceanside	San Diego
Triakidae						
Mustelus californicus	15.4	1.1	0.8	2.9	0.1	0.3
Triakis semifasciata			0.1			0.3
Triakis henlei	0.2		0.1	0.5	0.3	
Carcharhinidae						
Galeorhinus zyopterus			0.1			0.3
Squatinidae						
Squatina californica	0.7	0.0	1.1	0.8	0.9	
Total Sharks	16.3	1.1	2.2	4.2	1.3	0.9
Rhinobatidae						
Rhinobatos productus	102.3	13.6	99.7	86.1	22.8	18.2
Platyrhinidae						
Platyrhinoidis triseriata	6.3	117.5	12.8	5.8	9.5	26.4
Rajidae						
Raja inornata					3.4	0.3
Dasyatidae						
Urolophus halleri	62.1	35.3	23.0	12.3	2.7	7.6
Gymnura marmorata			0.1	0.2	0.1	
Dasyatis dipterurus	0.2	0.0	0.3			
Myliobatidae						
Myliobatis californicus	3.5	0.6	11.7	5.2	6.0	15.2
Torpedinidae						
Torpedo californica	6.5	6.1	4.0	2.3	0.1	0.6
Total Rays	180.9	173.1	151.6	111.9	44.6	68.3
Chimaeridae						
Hydrolagus colliei			0.1		0.1	
Total Elasmobranchs	197.2	174.2	153.9	116.1	46.0	69.2

TABLE 16

Number of Elasmobranchs Taken Per Trawling Hour at Belmont Shore, Surfside, Oceanside, and San Diego

The guitarfish, Rhinobatos productus, was highest of all fishes in numbers taken per trawling hour. The California halibut, Paralicthys californicus, ranked second maintaining a high density even at the poorer sites near Oceanside and San Diego. The thornback, Platyrhinoidis triseriata, was third in numbers and U. halleri fourth. Although these four dominant, benthic species commonly associate, the round stingray appears more restricted in habitat than the other three. An indication of this is seen in the ray's relatively low density at the Oceanside and San Diego locales. Not only does U. halleri require a loose substratum offshore, but also prefers adjoining inlets or bays with suitable substrata, requirements not found in Rhinobatos, Paralichthys, or Platyrhinoidis.

The high density of guitarfishes at Belmont Shore remained fairly constant over the 3-month period of this study (Table 16). Meanwhile, numbers of U. halleri steadily declined. This general movement of rays

away from Belmont Shore may indicate some degree of feeding competition between these two dominant batoideans, which occupy the same habitat. Roedel (1953) reported R. productus eats crabs and clams although no detailed food study appears to have been made on the species.

If the densities of R. productus and P. triseriata are compared at Belmont Shore and Surfside in all months of the study (Table 16), a segregation seems to exist between them. Belmont Shore had many guitarfishes but few thornbacks, while the situation was exactly reversed at Surfside. Although this segregation may be due to differing environmental requirements, it seems likely that a more rigorous competition exists between these two closely-related batoideans than exists between either of them and U. halleri. Little was found concerning feeding habits of P. triseriata.

Among the bony fishes (Table 17), the benthic flatfishes were taken at the four trawling sites in greatest numbers, per unit effort. However, two embiotocids were also quite prominent; the sea perch, Phanerodon furcatus, ranks second to the California halibut, and just ahead of the flatfish, Hypsopsetta guttulata; the barred surfperch, Amphistichus argenteus is fourth in numbers per trawling hour while the flatfish, Pleuronichthys ritteri, is fifth. All five species are found in considerable numbers with U. halleri at Belmont Shore and Surfside but at Oceanside and San Diego, only the California halibut maintains its density.

Some competition for food is believed to exist between U. halleri and the valuable flatfishes. However, the diets of flatfishes associated locally with U. halleri are not well known. One of the two dominant embiotocids, Amphistichus argenteus, is not a competitor with the stingray for food (Carlisle, Schott, & Abramson, 1960), but the diet of the other, Phanerodon furcatus, is unknown.

Most invertebrates taken by trawl are forms that live on the surface of the substratum (Table 18). Shrimps and other small invertebrates no doubt frequently passed through the net, so their relative abundance is not accurately reflected.

of the echinoderms, Astropecten armatus was most abundant at every locale. Its density was lower, however, at Oceanside and San Diego. Echinoderms as a whole are unimportant in the diet of U. halleri, comprising only 0.4 percent of the total food volume (Table 13). None of the mollusks captured in the trawl net had been eaten by the ray.

The decapods Cancer anthonyi and C. gracilis were captured more frequently than other crustaceans. Their density again was lower at Oceanside and San Diego than at the more northerly trawling sites. These and other decapod crustaceans provided almost 44 percent of the ray's total food volume (Table 13).

The general scarcity of animal life at the two most southerly trawling sites was amply evident. A clue to the cause of low densities at San Diego was found in the quantity of kelp netted there (Table 18). The rocky bottom commonly associated with that plant (Scofield, 1959), would directly or indirectly limit many forms including U. halleri. Nothing is known about the nature of the substratum of the Oceanside locale.

TABLE 17

Number of Bony Fishes Taken Per Trawling Hour at Belmont Shore, Surfside, Oceanside, and San Diego

	Jan. 28 to Feb. 6, 1957		Mar. 18 to Mar. 26, 1957	April 17 to April 26, 1957		
	Belmont Shore	Surfside	Belmont Shore	Belmont shore	Oceanside	San Diego
Bothidae						
Paralichthys californicus	43.9	32.5	70.1	79.6	35.0	71.8
Xystreurys liolepis	3.6	0.6	4.0	4.2	4.4	0.3
Citharichthys sordidus					0.3	
C. stigmaeus				0.3	0.8	
Hippoglossina stomata					0.3	
Pleuronectidae						
Hypsopsetta guttulata	22.8	12.5	20.6	11.9	1.0	8.8
Pleuronichthys ritteri	12.0	13.0	3.3	3.5		2.1
P. decurrens		6.1			0.6	0.3
P. verticalis	0.3	2.2		1.8	11.4	
Parophrys vetulus				0.2	23.0	2.7
Eopsetta jordani					1.1	
Symphurus atricauda		0.3				
Total Flatfishes	82.6	67.2	98.0	101.5	77.9	86.0
Embiotocidae						
Phanerodon furcatus	14.0	0.3	30.4	39.2	0.9	
Amphistichus argenteus	18.4	7.8	6.1	3.6	0.3	
Hyperprosopon argenteum	0.2	2.5	2.1	0.8		
Rhacochilus vacca	0.5		1.5	0.5	0.8	1.2
Embiotoca jacksoni				0.2		0.6
Cymatogaster aggregata	0.2	60.3	0.3	0.5		
Total Perches	33.3	70.9	40.4	44.8	2.0	1.8
Sciaenidae						
Genyonemus lineatus	0.9	2.5	4.9	2.6	6.8	4.8
Cynoscion nobilis	3.7		0.9	0.2	0.2	
Roncador stearnsi	5.9		1.3	1.0	0.3	
Seriphus politus			1.0		0.7	
Menticirrhus undulatus	0.6	0.3	0.2		0.3	
Total Sciaenids	11.1	2.8	8.3	3.8	8.3	4.8
Scorpaenidae						
Scorpaena guttata		0.6			0.3	4.5
Serranidae						
Stereolepis gigas			0.1			
Batrachoididae						
Porichthys myriaster	1.6	0.3	3.7	4.7	0.6	0.6
Stomateidae						
Palometa simillima		1.4			3.2	
Cottidae						
Artedius notospilotus	0.3	1.7				
Leptocottus armatus	0.1	0.3	0.1		0.3	
Chitonotus pugutensis				0.1		
Zaniolepidae						
Zaniolepis latipinnis					0.1	
Total Bony Fishes	129.0	145.2	150.6	154.9	92.4	97.7

TABLE 17

Number of Bony Fishes Taken Per Trawling Hour at Belmont Shore, Surfside, Oceanside, and San Diego

11. DISCUSSION

11.1. Reproduction

11.1.1. Female Urogenital System

Unilateral Development of the Reproductive System. The right ovary and oviduct have undergone varying degrees of atrophy in the stingrays. Although the right ovary of U. halleri is small and non-functional, only one specimen was examined which lacked a right ovary; no cases were found in which the right uterus was lacking or even non-functional,

TABLE 18

Number of Invertebrates Taken Per Trawling Hour at Belmont Shore, Surfside, Oceanside, and San Diego

	Jan. 28 to Feb. 6, 1957		Mar. 18 to Mar. 26, 1957	April 17 to April 26, 1957		
	Belmont Shore	Surfside	Belmont Shore	Belmont Shore	Oceanside	San Diego
Echinodermata						
Astropecten armatus	96.0	53.6	144.6	164.5	28.0	1.2
Pisaster ocraceus	8.0		2.8	1.5	1.3	
P. giganteus	1.7		0.6	0.2	0.1	
Asterina		0.3				
Crustacea						
Cancer anthonyi	41.3	52.5		40.5	2.2	6.7
C. gracilis	13.5	561.7	48.7	9.5	0.2	10.6
C. antennarias	2.0	0.3	2.2	1.8	0.3	0.6
C. productus					0.1	
C. sp.			0.1			
Lozorhynchus sp.	1.7	1.4	3.8	4.7	0.6	
L. sp.	3.5	3.1	3.5	1.8	0.2	0.6
Portunas	0.3		0.1			0.6
Randallia					1.4	
Heterocrypta					0.3	
Pugettia			0.1		0.1	0.3
Panulirus	0.1	1.4	0.6	0.3		
Hermit crab	2.3	0.6	0.6	1.3	4.5	36.1
Shrimp		3.3				
Pennatulacea						
Renilla		0.6			1.5	
Mollusca						
Sea hares	6.6		2.9	1.5		
Nudibranchs	1.5		0.4	1.8		
Octopus		0.1	0.2	0.5		
Squid					0.3	
Jellyfishes				1.3	11.4	
*Bryozoans	3.2	6.7	1.4			
*Kelp	2.6	2.9	3.7	8.1	3.3	27.9

* Measured by grain scoops.

TABLE 18

Number of Invertebrates Taken Per Trawling Hour at Belmont Shore, Surfside, Oceanside, and San Diego

although its development is somewhat retarded. Giacomini (1896) found both the right ovary and uterus to be small and non-functional in Myliobatis bovina (= Pteromylaeus bovina) and M. nieuhofii (= Aetomylaeus nichofii) . Alcock (1892) reported the right ovary and uterus to be entirely absent in Trygon bleekeri (= Dasyatis bleekeri) . Selachians, on the other hand, tend to lose the function of the left ovary. Daniel (1934) reported an atrophied left ovary in Scyllium (= Scyliorhinus) , Pristiophorus, Carcharhinus, Galeus, Mustelus and Zygaena (= Sphyrna) .

Islands of cells having a glandular appearance were described in the atrophied right ovary of U. halleri. These cells appear most active during ovulation and may be involved in preparing the uteri to receive eggs. Te Winkel (1950) suggested a glandular function for the atrophied left ovary of Mustelus canis but did not indicate what it might be.

Movement of Ovulated Eggs to the Oviducal Funnel. The means by which ovulated eggs move anteriorly from the one functional ovary of U. halleri, to the oviducal funnels, has not been determined. Investigations by other workers, however, suggest that this movement is accomplished

by ciliary action. Rugh (1935) found that ova of amphibians seldom, if ever, fail to enter the funnels, and that their anterior movement is due to currents produced by cilia. Metten (1939) reported a similar situation in the dogfish, Scyliorhinus caniculus. He opened the abdominal cavity of anesthetized female sharks and was able to follow the movement of ovulated eggs. Cilia were found on the peritoneum of the anterior coelomic walls, the liver and on the outer surface of the oviducts. The cilia beat toward the ostium carrying eggs forward to its mouth. Metten was unable to find cilia within the coelomic cavity of male dogfish or immature females; however, he believed cilia to be generally present in mature female elasmobranchs of all species.

Sperm Storage in Females. Four female U. halleri, captured in September, were examined for sperm storage. Sections were taken from both zones of the oviducal gland with negative results. However, an examination of females which have been captured in September, with large ova in their ovaries, would be advisable before ruling out the possibility of sperm storage. There is some evidence that these females mate in September, and since they do not ovulate until December, they may store the sperm for 3 months.

Sperm storage has been reported in females of several elasmobranch species. Metten (1939) found sperm in the oviducal gland of Scyliorhinus caniculus during all months. The sperm were stored in the tubules of the shell-secreting zone of the gland. Metten examined fresh tissue from this zone and found cilia lining the tubules. The cilia beat toward the tubule mouth so that sperm were forced to swim upstream to remain in the tubule. Sperm were never found in the gland's albumin-secreting zone, supposedly due to inadequate nourishment there.

Clark (1922) reported sperm storage in females of several species of Raja. One female Raja brachyura laid 30 fertile egg-cases after being isolated from males for 5 weeks. Prasad (1945) found sperm in the shell gland of the tiger shark, Galeocerdo tigrinus, both before and for a while after ovulation.

Fertilization. The site of fertilization in the round stingray is not known. Metten (1950) found that fertilization in Scyliorhinus caniculus takes place in the shell-secreting zone of the oviducal gland. Only some of the sperm are emitted from the gland during fertilization of an ovum. Mating is believed to occur again before the shell gland exhausts its sperm supply.

Female Urinary System. The urinary system of the female round stingray is generally similar to that of other batoideans described by Semper (1875), Borcea (1906), and Daniel (1934). The mesonephros of females of U. halleri is quite broad posteriorly but is reduced to a narrow ribbon of tissue anteriorly. In most batoideans, the Wolffian duct is unimportant in urine drainage, being largely replaced by a branched ureter which drains the broad posterior portion of the kidney and empties into the urinary sinus. In females of the stingray Trygon (Daniels, 1934), and in U. halleri, the kidney is drained entirely by a ureter. The urinary sinus of all female elasmobranchs is a part of the urinary tract, having no sexual function as it does in males.

11.1.2. Male Urogenital System

Testicular Appendages and Vas Efferens. The urogenital systems of various male batoideans studied by Semper (1875), Borcea (1906), and Daniel (1934) agree in most details with that of U. halleri, but two structures were not reported by these authors. One is the testicular appendages on the dorsal gonadal surface; the other is a coiled duct overlying two or more lobules at the anterior end of the testis. The duct is lined with highly-folded, pseudostratified, columnar epithelium, and apparently is an extension of the vas efferens (Figures 8, 9). Its function may be to produce fluid to carry the spermatozoa through the epididymis to the vas deferens.

Borcea (1906) traced the embryonic development of the vasa efferentia in elasmobranchs. These structures are at first the anterior nephric tubules of the kidney whose funnels open into the testis. Sharks may have as many as six vasa efferentia extending from each testis to the epididymis. All rays examined by Borcea possessed only one, as is the case in U. halleri.

Gland of Leydig. The narrow, anterior portion of the kidney has lost its excretory function in males of U. halleri. Its tubules have become part of the genital system, emptying secretions into the vas deferens posterior to the epididymis. Borcea (1906) described a similar situation in several batoideans and called the secretory tubules "la glande de Leydig." Daniel (1934) confirmed Borcea's findings and Matthews (1950) reported Leydig's gland to be present in the basking shark, Cetorhinus maximus.

Siphon Gland. A siphon sac is present in all elasmobranchs, but only the more specialized batoideans possess a siphon gland on the sac's dorsal wall. Leigh-Sharpe (1920, 1921) and Friedman (1935) found this gland in all batoideans which they examined. The gland is also present in U. halleri and its functional similarity to the mammalian prostate is interesting.

Copulation. Agassiz (1871) and Friedman (1935) reported observing belly-to-belly copulation by skates, and Agassiz noted that both claspers of the male were inserted simultaneously, one into each vagina. I did not observe mating in U. halleri, but the belly-to-belly method seems most feasible, in view of the body shape and dorsal spine.

Sperm Storage in Males. Urolophus halleri apparently represents the first reported case of sperm storage in a male batoidean. Matthews (1950) reported for the first time, sperm storage by a male elasmobranch. He found quantities of peculiar gelatinous nodules or spermatophores in the vas deferens of the basking shark, Cetorhinus maximus. These spermatophores were stored among the transverse folds in the posterior part of the vas deferens, and their cores contained sperm. The author believed that secretions from the gland of Leydig nourished the sperm within the nodules. In U. halleri the lower end of the vas deferens is modified for sperm storage with numerous internal folds. No spermatophores were present in the duct; the sperm were simply suspended in a viscous, milky fluid.

Most males of U. halleri are in mating condition in late May, June or early July as determined by their swollen siphon glands and distended

vasa deferentia. The majority of females ovulate at this time (Figure 27), and soon afterward small embryos are found in their uteri. Some males, however, store sperm until September; it is believed that they mate with the few females which ovulate in December (Figure 27). If this is the case, those females must store the sperm for approximately 3 months until ovulation and fertilization can occur.

11.1.3. Egg Development

Egg Membranes. Two egg membranes surround the ova of elasmobranchs; the zona radiata lies against the yolk and is covered by the more peripheral follicular epithelium. It seems likely that the zona radiata is equivalent to the vitelline membrane of other vertebrate eggs. Balfour (1878) and Giacomini (1896) reported a third membrane lying between these two. Balfour called it the vitelline membrane, although it seems quite distinct from the vitelline membrane of other vertebrate eggs which lies directly against the yolk. Wallace (1903) did not find Balfour's vitelline membrance in Squalos spinax, (=Squalus acanthias) , nor did I observe it in U. halleri.

There exists in the literature a considerable variation in the number and structure of membranes described for elasmobranchs eggs. Wallace (1903) suggests that some of the variation may be more apparent than real. He observed that the membranes change with age and even differ in structure at opposite poles of the ovum. It is likely also that the method of fixing and staining affects their appearance.

Infolding of Follicular Epithelium. One of the most interesting features of oogenesis in U. halleri is the unusual proliferation and infolding of the follicular epithelium. It begins when the egg has a diameter of about 1.5 mm, and by 4.5 mm, extensive folds reach far in toward the egg's center. The folds carry with them the inner layers of fibrous theca which provide a central stratum of connective tissue and blood vessels within each fold.

Giacomini (1896) found similar infoldings in the stingray, Myliobatis bovina (=Pteromylaeus bovina) . The ova that he examined were not yet mature, and he believed the pleats would be forced to unfold as the egg enlarged with yolk. He reasoned that in this way the follicular layer would be freed from the ripe ovum and would remain in the ovary to produce luteal cells.

Origin of the Corpus Luteum. It seems that the corpus luteum in U. halleri is derived entirely from the external theca. The corpus luteum is generally reported to arise from follicular cells in elasmobranchs. This is also the case in some viviparous reptiles and in mammals. Samuel (1943) was the first to describe a corpus luteum of mixed origin in lower vertebrates. She observed that luteal cells in Rhinobatus granulatus arise by hypertrophy of both theca interna and follicular epithelium. Samuel's findings lend support to my belief that the corpus luteum in U. halleri is derived from thecal cells.

In freshly-ovulated eggs of the round stingray the pleated follicular epithelium is still present (Figure 24). Completely surrounding the ovum is a thin layer of inner theca, while the empty cavity in the ovary contains only the external theca (Figure 25). It therefore seems likely that cells of the external theca give rise to the corpus luteum

in U. halleri. The same method of corpus luteum formation probably exists in P. bovina because egg development as described for this species by Giacomini (1896) is almost identical to that of U. halleri. In fact, this same pattern of corpus luteum formation may be general among dasyatids and myliobatids, although it has not been previously described.

Nutritive Cells. Certain cells of the follicular epithelium enlarge when an ovum of U. halleri reaches a diameter of about 0.3 mm, and before the epithelium begins to fold inward. Wallace (1903) believed that the hypertrophied cells produced yolk or a precursor substance in Myliobatis and some other elasmobranchs. In Squalus spinax, (= Squalus acanthias) he observed delicate processes extending from the large "nutritive cells", through the zona radiata; material was reported to move along these processes into the egg. In U. halleri the large cells contain globules identical in appearance to yolk globules within the egg. No processes, however, were observed extending from the nutritive cells into the egg. Reduced globule size is evident in a narrow zone along both sides of the zona radiata (Figure 21) and may indicate that the nutrient material diffuses into the egg through minute pores in the zona radiata.

Time of Ovulation. Most female U. halleri ovulate in June; a small number ovulate in December. A somewhat similar situation has been reported in two other elasmobranch species. Templeman (1944) found that females of Squalus acanthias are divided into two groups which bear their young on alternate years. Olsen (1954) reported the same findings in Galeorhinus australis.

11.1.4. Sperm Development

Testicular Appendages. The small, finger-like appendages observed on the dorsal surface of the testis of newborn round stingrays, have not been described previously. Very large, lightstaining cells occupy the center of each appendage (Figure 32). Further histological study is needed to determine if these large cells have undergone divisions in the embryonic gonad. If not, they must be considered primordial germ cells. In this discussion they are referred to as large germ cells.

Herrmann (1882) described similar cells in the testis of certain unnamed rays. These *"ovules primatifs,"* first seen in the germinal epithelium of the embryonic genital ridge, are carried into the developing gonad by epithelial invagination. There, in the "progerminative region" of each testicular lobule, they become organized into progerminative cords which remain in contact with the germinal epithelium of the testis. Scattered over the dorsal surface of the testis in very young animals, Herrmann found a number of small gray areas. Each area represents an aggregation of progerminative cords just beneath the epithelium which will become a testicular lobule. He did not, however, find any appendages associated with the gray areas. At an unspecified age in young males, the cords of large germ cells lose contact with the germinal epithelium, sink deeper into the testis and gather into a number of hollow balls or follicles.

Matthews (1950) did not find testicular appendages in the basking shark, Cetorhinus maximus. He did, however, describe a region of connective

tissue at the center of each testicular "lobe" or lobule, in mature animals. In this region, are a number of large "central cells," arranged singly. Their description matches closely the large germ cells in the appendages of U. halleri. The central cells migrate out into the lobule and aggregate into "nests." The nests then begin dividing to form hollow ampullae or follicles.

The cell migrations described by Herrmann (1882) and Matthews (1950), correspond to the movement of large germ cells from the testicular appendages into the lobules of the testes of U. halleri at about 12 months. The migration initiates formation of the 12 or more primary lobules just beneath the dorsal surface of each testis.

Sertoli Cells. During spermatogenesis in U. halleri, when the most advanced follicles of a secondary lobule gain six concentric layers of cells (Figure 36-G), the spermatogonia disappear from their central position around the follicle lumen. Soon, approximately the same number of Sertoli cells appear, spaced around, inside the follicle wall.

Semper (1875) reported that in Scyliorhinus and several of the Rajidae the Sertoli cells appear soon after disappearance of the spermatogonia, but he failed to relate the two events. Matthews (1950) found spermatogenesis in the basking shark, Cetorhinus maximus, essentially as described by Semper. Matthews was able to trace migration of the spermatogonia from their central position around the follicle lumen to their new position as Sertoli cells.

Primary Testicular Lobule. I named the central portion of each testicular lobule of U. halleri the primary lobule. This distinction was made because it is the first part of a lobule to form in young males, and because it is permanent. Previous workers have not distinguished between permanent and temporary parts of a testicular lobule in elasmobranchs; however, the similarity of the patterns of spermatogenesis described by Semper (1875), Herrmann (1882) and Matthews (1950), with what I have described, suggest that permanent germ cell reservoirs are also maintained in other male elasmobranchs.

Possible Mechanisms Regulating Spermatogenesis. It is interesting to speculate on the possible mechanisms regulating spermatogenesis in U. halleri. Formation of the primary lobules in a young male may be controlled by some inherent hormonal mechanism; the process appears to begin when an individual is about 12 months old, regardless of whether that age is reached in March or September. The annual gonadal cycle, which involves both the primary and secondary lobules, seems more likely controlled by environmental factors, perhaps acting through the pituitary. This is suggested by the fact that in most males the testes become active in July and August when the photo-period is long and when solar intensity and water temperature are high.

11.1.5. Gestation

Uterine Villi and Embryo Nourishment. Embryonic development is rapid in the stingrays. Ranzi (1934a) observed that the gestation period is 4 months for Myliobatis bovina, (= Pteromylaeus bovina) and only 2 months for Trygon violacea, (= Dasyatis violacea) . Three months are required for development in U. halleri. The viviparous shark, Mustelus laevis, which nourishes its young by a yolk-sac placenta, requires

10 months for gestation (Ranzi, 1934a), while some ovoviviparous sharks, including Squalus acanthias, require almost 2 years (Hisaw, 1947).

The uterine mucosa in a number of batoideans and in some selachians, is covered by villiform papillae. These structures reach their greatest development in the stingrays, all of which are viviparous. Alcock (1891) described the villi in the stingray, Pteroplatea micrura, (= Gymnura micrura) surmising that their milky secretion nourishes the embryo.

Ranzi (1934a, 1934b) made an exhaustive study of the fetal-maternal relationships of 16 different elasmobranchs. His studies included ovoviviparous and viviparous species. In those ovoviviparous species which tend toward viviparity, the egg-case dissolves at some stage of gestation, making possible some nourishment of the embryo by the mother. Ranzi (1934b) found that as ovoviviparity gave way to viviparity, there was an increase in the organic substance transported from mother to embryo. In ovoviviparous forms whose uterine fluid contained less than 3 percent organic matter, the young at birth actually contained less organic matter than did the original fertilized egg. In ovoviviparous forms where the organic content of the histotroph exceeded 3 percent, the young showed a net gain in organic matter over the egg. Ranzi found that the three genera of stingrays studied, produced richer histotroph than the other elasmobranchs. In Trygon violacea, (= Dasyatis violacea) the organic content was 13 percent.

In the viviparous Mustelus laevis, the weight of organic substance deposited in the embryo during development is 1,000 percent greater than that found in the newly-fertilized egg. This represents a great advance when compared to some ovoviviparous forms whose embryos at birth contain less organic substance than did the egg. Ranzi, however, found a much greater transfer of organic substance from mother to young in the viviparous stingrays; young of Pteroplatea micrura (= Gymnura micrura) gain 5,000 percent in organic matter while those of Myliobatis bovina (= Pteromylaeus bovina) and Trygon violacea (= Dasyatis violacea) increase 3,120 and 1,680 percent respectively.

Ranzi (1934b) found that embryos of the stingray Trygon violacea at first absorb uterine milk through the yolk sac and external gill filaments; later on, injections of Chinese ink showed that the material enters the gut through the mouth and spiracles. Small external gill filaments first appear on embryos of U. halleri when they attain a length of about 13 mm. The digestive tract is complete in embryos of 20 mm and yet the yolk sac is only slightly depleted at that stage (Figure 49). It seems likely, therefore, that uterine milk provides some embryonic nutrition very early. The fluid may first be absorbed through the yolk sac and external gills as in D. violacea. Some time after the 20 mm stage, when the digestive tract is formed, uterine milk can be taken in through the mouth and spiracles.

Pitotti (1936) reported the presence of proteases in the uterine milk of Torpedo and Mustelus; these enzymes did not seem to act at the pH of the uterine fluid and may become active only when they have reached the fetal digestive tract. He demonstrated that the digestive glands of Torpedo ocellata embryos are all functional at a very early stage (46 mm), and while histotroph is being digested by the stomach, yolk is

being digested in the intestine. The well-formed alimentary tract in a 20 mm embryo of U. halleri, suggests that the digestive glands probably begin to function at about that stage.

Embryos of U. halleri develop rapidly after the mid-point in gestation. The acceleration coincides with a maximum development of the uterine villi at about this time. Breder and Krumholz (1941) reported rapid growth in advanced embryos of the stingray Dasyatis sabinas. Adults of this species are about the same size as the round stingray and bear from one to seven young. The young, however, attain a mean disc width of 100 mm at birth while those of U. halleri average only 75 mm. Breder and Krumholz found that the mean disc width of D. sabinas embryos increased from 35.8 to 99.6 mm in 22 days. There was no overlapping of the means and extremes of the two samples, collected 22 days apart. Development in this species, therefore, appears to be more rapid than in U. halleri.

I believe that U. halleri is a truly viviparous elasmobranch. Although no physical connection exists between mother and embryo as in viviparous Mustelus laevis, an efficient physiological placenta is established quite early.

11.1.6. Reproductive Adaptations

The reproductive success of round stingrays seems due partly to certain adaptations. Sperm storage by males (and possibly by females) allows two breeding seasons per year and thus greater reproductive flexibility. Both uteri are functional in U. halleri as compared to a single functional uterus in some elasmobranchs. Gestation is brief (3 months), and most females bear young every year. Although egg-development requires 2 years, two staggered groups of ova develop simultaneously, one group ovulating each year. The extensively folded follicular epithelium within an ovum accelerates yolk deposition and egg growth. Finally, newborn rays are large and capable of protecting themselves.

By way of comparison, Hisaw and Albert (1947) found that Squalus acanthias has a gestation period of 22 months, thus ovulation occurs at 2-year intervals. Olsen (1954) reported the gestation period to be only 6 months in the school shark Galeorhinus australis; however, females ovulate and bear only every other year.

11.2. Sex Ratio

11.2.1. Sex Ratio of Embryos and Newborn of U. halleri

The disparity between sexes in embryos of U. halleri is not without precedent among elasmobranchs. Breder (1941) found a female-male ratio of 1:1.27 in Dasyatis sabinas embryos and 1:1.25 in embryos of D. hastatus; both his samples were small. Olsen (1954) reported a female-male ratio of 1:1.2, among 941 almost fully-developed embryos of Galeorhinus australis. He observed that following birth, the ratio began to approach parity; after the first year there were more females than males. Olsen did not believe that his collecting gear or techniques were selective for females, and therefore he concluded the death rate was higher for young males.

11.2.2. Sex Ratio of Adult Rays

The sex ratio of U. halleri approaches parity soon after birth and remains so until maturity is reached. Following maturity, however, there is evidence of a partial segregation of adult males and females. I found 2.4 males for every female in 1,621 adult rays, and two males per female in a random sample of 1,501 rays, mostly adults. Russell (1955) reported 2.4 males per female in 1,196 rays, mostly adults. Herald, Schneebeli, Green and Innes (1960) also observed the imbalance in sexes and suggested a segregation. The scant trawling data I obtained at depths below 7 fathoms, showed more females than males; this indicated that many females move into deeper offshore water following maturity (Tables 3-A, B).

11.3. Growth

11.3.1. Double Sampling Method

Walford (1932) demonstrated false age groups in the California barracuda, Sphyraena argentea. He constructed a length frequency curve from a large sample and also determined ages for the sample by means of scales. The first three peaks on his frequency curve coincided accurately with the 0, I and II age groups determined by scales. The fourth peak on his curve, however, was quite large and contained animals of five different ages.

It seems likely that peaks A, A', B, and B' on the two frequency curves of U. halleri (Figure 63), contain merged age groups. I do not believe, however, that this fact invalidates the assumption that the 90-day growth increment, measured between corresponding peaks A and A' and between peaks B and B', represents the average growth rate for animals within those size ranges.

11.3.2. Growth Data from Tagging and Recapture

The round stingray should be an ideal species for a tagging study since the population densities are high and movements are quite limited. The poor results obtained in my study are attributed to several factors previously discussed. Probably the most important of these was my method of tagging.

Steven (1936) obtained excellent growth data on young thornback rays, Raja clavata, in the English Channel off Plymouth. He marked 614 animals and recaptured 33 percent of them over a period of nearly 4 years. Most recaptures were made by trawl and the periods of liberty ranged from 12 to 1,357 days. Steven's tag consisted of two vulcanite discs placed on opposite sides of the right "wing", and presumably held in place by a plastic leader threaded through the fin. He attributed poor recovery of the smallest rays to high mortality from tagging. The encumbrance of the two discs and the injury caused by attaching them, were both believed to be detrimental.

I devised a sleeve-type tag later and used it for captive rays. Mortality could be minimized, in any future marking experiment with U. halleri, by using this tag. It is simple to install, stays in place well and expands to accommodate growth of the caudal spine. Furthermore, it causes no injury or impairment to movement.

11.3.3. Growth in Captivity

Clark (1922) observed the incubation, hatching, and early life of several skates in the laboratory. Newly-hatched fishes were given a natural diet, but did not eat well under artificial conditions. Their growth usually ceased after 1 to 3 months, and death soon followed. In some individuals, a regression in size occurred after initial growth, which Clark attributed to lack of feeding. Some captive young U. halleri also decreased in total length and dise width, apparently because of failure to eat.

Growth recorded by Clark for two of the more successful young skates is compared below with that of a newborn round stingray fed in captivity:

	Disc width when hatched or born (mm)	Growth Rate (mm/mo.)			
		First month	Second month	Third month	Fourth month
Raja brachyura	100	16	6	–	–
R. naevus	62	3	2	–1	
U. halleri	78	3	2	0.5	0.0

TABLE

Clark believed that growth of the young Raja brachyura shown here, was about normal during the first two months. Adults of this species are much larger than those of U. halleri which accounts for its comparatively high monthly increment in disc width. Raja naevus also grows somewhat larger than U. halleri.

11.4. Sexual Maturity

Urolophus halleri appears unique in several respects, among elasmobranchs for which growth and maturity data are known. Both sexes reach maturity comparatively early in life and at about the same size and age. Characteristically in elasmobranchs, the sexes become mature only after attaining 60 percent or more of their maximum size, and males usually mature earlier and at a smaller size than females (Ford, 1921; Sato, 1935; Steven, 1936; Ripley, 1946; Bonham, 1949; Olsen, 1954).

Early sexual maturation in U. halleri results in a short time-span between generations, and a relatively longer reproductive life. Both factors increase the animals' biotic potential. In comparing six elasmobranchs, the ratio of width at first maturity to maximum width is markedly lower for U. halleri (Table 19).

Both sexes of U. halleri appear to grow at the same rate to maturity (Table 20). Both sexes of Raja clavata also grow at the same rate to maturity, and the growth rates of the two sexes of Galeorhinus australis are similar. Templeman (1944), likewise found no difference in growth rates of the two sexes of Squalus acanthias. Urolophus halleri, however, appears unique in that males and females attain maturity at the same size and therefore, at the same age, (Table 20) . Furthermore, maturity is reached by U. halleri in the remarkably short time of 2.6 years. In contrast, males of Raja clavata and Galeorhinus australis require 7 and 8 years respectively, while females of these species take even longer (Table 20). Templeman (1944) found that males of Squalus acanthias mature in 4.5 years while females require 7.5 years.

TABLE 19

Ratio of Length at First Maturity to Maximum Length for Several Elasmobranchs

	Sex	Smallest length or width at maturity (cm)	Maximum recorded length or width (cm)	Ratio	Source of data
Galeorhinus australis	Male	120	155	0.77	Olsen (1954)
	Female	135	174	0.775	
Galeorhinus zyopterus	Male	135	185	0.73	Ripley (1946)
	Female	150	195	0.769	
Squalus acanthias	Male	59	83	0.71	Ford (1921)
	Female	71	110	0.645	
Squalus suckleyi	Male	72	100	0.72	Sato (1935)
	Female	78.5	130	0.604	
			124	0.633	Bonham (1949)
Raja clavata	Male	50*	60*	0.833	Steven (1936)
	Female	67*	80*	0.837	
Urolophus halleri	Male	14.6*	25*	0.588	Present author
	Female	14.5*	31*	0.467	

* Disc width used for two batoidean species in place of length.

TABLE 19

Ratio of Length at First Maturity to Maximum Length for Several Elasmobranchs

TABLE 20

A Comparison of Growth Data for Three Elasmobranchs

	Sex	Average growth rate to sexual maturity (mm/mo.)	Smallest length or width at maturity (mm)	Average age at sexual maturity (years)	Maximum recorded length or width (mm)	Percentage growth rate to maturity (based on max. size)	Percentage growth rate to maturity (based on min. size)
Galeorhinus australis	M	9	1,200	8	1,550	0.58	0.75
	F	8	1,350	10.5	1,740	0.46	0.59
*Raja clavata**	M	5	500	7	600	0.83	1.00
	F	5	670	9	800	0.63	0.75
*Urolophus halleri**	M	2.4	146	2.6	250	0.96	1.64
	F	2.4	145	2.6	310	0.77	1.65

* Disc width was used in the batoideans for determining growth rate.

TABLE 20

A Comparison of Growth Data for Three Elasmobranchs

Percentage growth rates allow a better comparison of species of differing sizes. Males of U. Halleri, on an average, accrue 0.96 percent of the maximum recorded width each month, until maturity, which is significantly higher than for males of the other two species (Figure 20). Females of U. halleri also have a higher rate than females of G. australis and Raja clavata.

If the percentage growth rate is based on size at first maturity, rather than on maximum recorded size, then U. halleri by comparison, has an even higher percentage rate than the other two species (Table 20). Each month, on an average, both sexes of U. halleri accrue 1.6 percent of the width recorded for the smallest mature individuals of this species.

11.5. Movements

11.5.1. Information from Trawling and Seining Records

Trawling and seining records have provided some information about the movements of U. halleri. Movements of young rays are limited. For

a time after birth they remain inshore, then begin spreading out along open beaches. Trawl catches show that most young stay near shore, at depths of less than 2 fathoms, until attaining a disc width of 120 mm. A gradual seaward expansion of range accompanies growth, and the largest animals move furthest offshore. Mature females partially segregate from mature males during much of the year, seeming to stay at greater depths offshore. Conversely, mature males usually outnumber females at depths of less than 7 fathoms. Most animals within the area of this study appear restricted to a narrow coastal belt which extends offshore only to a depth of about 10 fathoms. Large numbers of mature females move shoreward in June to breed, and again in September to bear young. Mass movements for distances of 1 to several miles, are common in offshore waters. These are believed related to feeding activities. Adults prefer the warmer offshore waters in winter, only entering the inlets and bays to forage.

11.5.2. Movement Information from Tagging and Recapture

My tagging study suggested that even large adults normally move only short distances. The greatest movement recorded for 39 recaptured rays was 4.75 nautical miles (Table 10). Russell (1955) marked 482 round stingrays, and recaptured 61 of them after 4 to 14 months. He observed a strong tendency for animals to return to the same inshore waters in summer. Thirty-two rays were recaptured in the same bay where marked: 18 had moved less than 15 miles while 10 had traveled farther than 15. The fishes were marked by amputating the tail anterior to the caudal spine in such a manner as to denote place and month of original capture. There are two apparent objections to this system. First, such a mark might be misinterpreted and secondly, commercial and sport fishermen are known to perform similar amputations.

Steven (1936) found that immature thornback rays, Raja clavata are non-migratory, although larger than U. halleri and probably stronger swimmers. Sixty-one percent of his recaptures were found almost precisely where released, after periods of 12 to 1,357 days. There was simply a slow outward "diffusion" of some rays as maturity was approached. Seventy-one percent of his recaptures moved less than 5 miles while about 5 percent traveled more than 20. Presumably the 24 percent not accounted for, moved from 5 to 20 miles.

11.5.3. Movement Related to an Environmental Change

Individuals of U. halleri may migrate great distances when environmental conditions permit. A single specimen was captured at Humboldt Bay, Eureka, California, in December, 1960 (Best, 1961). Monterey Bay, some 300 miles farther south, was previously considered the extreme northern limit of the species. This northward capture is believed to have been related to a northward shift of isotherms along the California coast (Radovich, 1960, 1961).

11.6. Food Habits

11.6.1. Change of Feeding Habits with Growth

The feeding habits of U. halleri changed with size, which appears to be generally true of fishes. Steven (1947) reported that young Raja

clavata remain in shallow water, feeding largely on small crustaceans, while the adult diet consists principally of fishes.

11.7. Physical Environment

11.7.1. Water Temperature and Distribution of U. halleri

Evidence of the round stingray's preference for warm water is seen in its southward range which extends to Panama (Bigelow and Schroeder, 1953). The recent northward extension of range to Humboldt Bay, seems also related to elevated water temperatures.

The round stingray is benthic and is restricted, at least within the area of this study, to a shallow coastal zone. It is my belief that the decrease of water temperature with increasing depth is the principal restricting factor. Only four rays have been taken locally as deep as 13.5 fathoms (Table 15). Russell (1955) reported taking one animal by setline at almost 17 fathoms off Huntington Beach. Limbaugh (1955) made an extensive underwater study of the California coast and found round stingrays to a depth of 12 fathoms, with most of the population concentrated from shore out to 8 fathoms; Limbaugh's zone of greatest population density coincides well with that determined by trawling (Table 15).

Water temperatures in the shallow inlets, lagoons and bays within the study area, often become quite cold during winter. Stevenson and Emery (1958) reported a temperature of 10.4°C in Newport Bay in January, and readings of 11.5° and 12°C are not uncommon there in winter. Both adults and young desert the shallowest waters during the cold months.

11.8. The Effect of Man's Activities on the Environment of U. halleri

Some of man's activities have actually improved the environment for U. halleri, and may be contributing to a population increase along the southern California coast. For example, the San Pedro Bay breakwater, which forms the Los Angeles and Long Beach harbors, has created a large, shallow, protected bay ideal for these animals. Jetties which project out from shore at many points along the coast give some protection from currents and waves, and tend to increase the local water temperature. Dredging projects such as the one which created Newport Dunes Marina, have further benefited the round stingray. Elevation of water temperature by the Seal Beach Southern California Edison steam generating plant and by other such installations also is believed to create desirable conditions for these animals.

The apparent increase in stingray injuries in the Long Beach-Newport region since 1950 probably indicates a population growth for U. halleri. The increased number of injuries is due in part, but certainly not wholly, to greater recreational use of coastal waters. Russell (1953) reported 474 attended cases of stingray injury between April and November 1952, along the southern California coast. Most of these were attributed to U. halleri. Over 500 injuries by U. halleri are believed to have occurred during May, June, and July, 1962, at Seal Beach alone.

11.9. Biological Environment

11.9.1. Feeding Relationships

A discussion of the feeding relationships between U. halleri and other associated fishes, is limited to a very few species for which comprehensive food studies have been made. The barred surfperch, Amphisticus argenteus, is frequently taken in considerable numbers with U. halleri. Little competition for food exists between the two, however. Carlisle, Schott, and Abramson (1960) found that over 90 percent of the surfperch's diet was provided by the common sand crab, Emerita analoga. U. halleri eats few of these crustaceans.

Since flatfishes are generally benthic carnivores, the diets of some may overlap that of U. halleri. An indication of this competition is seen in the food of the starry flounder, Platichthys stellatus; it ranges northward from Point Conception so it seldom competes with the ray. Orcutt (1950) found that young P. stellatus, between a standard length of 40 and 100 mm, eat amphipods of the genera Grammarus and Corophium; young of U. halleri eat both these crustaceans. Flounders of 100 mm feed on some bivalves preferred by mature rays, and after reaching 200 mm, eat mollusks, crustaceans, and annelids also found in the diet of U. halleri.

12. LITERATURE CITED

Agassiz, Louis J. 1871. Note on copulation among selachians. Proc. Boston Soc. Nat. Hist., **14** :339–341.

Alcock, Alfred W. 1891. On the uterine villiform papillae of Pteroplataea micrura. Proc. Roy. Soc. London, **49** :359–367.

Alcock, Alfred W. 1892a. On utero-gestation in Trygon bleekeri. Ann. Mag. Nat. Hist., Ser. 6, **9** :417–427.

Alcock, Alfred W. 1892b. Observations on the gestation of Indian rays. Proc. Roy. Soc. London, **50** :202–209.

Balfour, Francis M. 1878. A monograph on the development of elasmobranch fishes. Macmillan Co., London, pp. 295.

Barnard, J. Laurens, and Donald J. Reish. 1959. Ecology of Amphipoda and Polychaeta of Newport Bay, California. Allan Hancock Found. Publ., Occ. Paper **21** :1–96.

Barnhart, Percy S. 1932. Notes on the habits, eggs and young of some fishes of southern California. Scripps Inst. Ocean., Cal. U. Tech. Ser., **3** (4) :88–89.

Best, E. A. 1961. Occurrence of the round stingray, Urolophus halleri Cooper, in Humboldt Bay, California. Calif. Fish and Game, **47** (7) :335–338.

Bigelow, Henry B., and William C. Schroeder. 1953. Fishes of the western North Atlantic. Mem. Sears Found. for Mar. Res. No. I. Part 2, Sawfishes, guitarfishes, skates, rays and chimaeroids. 562 p.

Bonham, Kelshaw S., Francis B. Sanford, William Clegg and Glenn C. Bucher. 1949. Biological and vitamin A studies of dogfish landed in the state of Washington (Squalus suckleyi) . Wash. Dep. Fish. Biol. Rep., **49**A :83–114.

Bostock, J., and H. Riley. 1890. The natural history of Pliny, Vol. I. G. Bell and Sons, London. Pp. 693.

Borcea, Ioan. 1906. Recherches sur le Systeme Uro-genital des Elasmobranches. Arch. Zool. exper et gen., **4** (4) :199–484.

Breder, Charles M., Jr. 1928. Elasmobranchii from Panama to Lower California. Bull. Bingham Ocean. Coll., **2** (1) :1–13.

Breder, Charles M., Jr. and Louis A. Krumholz, 1941. On the uterine young of Dasyatis sabinus (Le Sueur) and Dasyatis hastatus (De Kay). Zoologica New York, **26** :49–53.

Carlisle, John G., Jr., Jack W. Schott and Norman J. Abramson. 1960. The barred surfperch. Amphistichus argenteus Agassiz, in southern California. Calif. Dept. Fish and Game, Fish Bull., (109) :1–79.

Campbell, Berry. 1951. The locomotor behavior of spinal elasmobranchs with an analysis of stinging in Urobatis. Copeia 1951 (4) :277–284.

Clark, Robert S. 1922. Rays and skates (Raiae). No. 1, Egg-capsules and young. Jour. Mar. Biol. Ass. U. K., **12** (4) :577–643.

Cooper, J. G. 1863. On new genera and species of California fishes No. II. Proc. Cal. Acad. Sci., **3** (1) :93–97.

Coupin, Henri. 1899. Dangerous fishes. Med. Moderne, **10** (86) :681–684.

Daniel, John F. 1934. The elasmobranch fishes. Univ. Cal. Press, Berkeley. Pp. 313.

Ford, E. 1921. A contribution to our knowledge of the life histories of dogfishes landed at Plymouth. Jour. Mar. Biol. Ass. U. K., **12** (3) :468–505.

Friedman, M. H. F. 1935. The function of the claspers and clasper glands in the skate. Jour. Biol. Bd. Canada, **1** (4) :261–268.

Fry, Frederick E. J. 1957. The aquatic respiration of fish., in Brown's "Physiology of Fishes" 1957. Vol. 1 Academic Press, N. Y. Pp. 398.

Garman, Samuel. 1913. The Plagiostomia (sharks, skates and rays) Mem. Mus. Comp. Zool., Harvard. Pp. 528.

Giacomini, Ercole. 1896. Contributo all 'istologia dell' ovario dei Selaci con speciale rigardo sopra ad alcune particolarita di struttura riscontrate nell' ovario di Myliobatis bovina. Geoffr. Ric. Labor. Anat. Roma. **5** :221–274.

Gudger, Eugene W. 1914. History of the spotted eagle ray, Aetobatus narinari. Papers from Tortugas Lab., Carnegie Inst. of Wash., **6** (183) :241–323.

Hamilton, William J., Jr. 1941. Notes on the stingray Dasyatis say (Le Sueur) Copeia 1941 (3) :175.

Herald, Earl S. 1953. The 1952 shark derbies at Elkhorn Slough, Monterey Bay and San Francisco Bay. Calif. Fish and Game, **39** (2) :237–243.

Herald, Earl S., Walter Schneebeli, Norval Green and Kenneth Innes. 1960. Catch records for seventeen shark derbies held at Elkhorn Slough, Monterey Bay, Calif. Calif. Fish and Game, **46** (1) :59–67.

Herrmann, Gustave. 1882. Recherches sur la spermatogenese chez les selaciens. des Elasmobranches., Jour. de l'Anat. et Physiol., **18** :373–432.

Hisaw, Frederick L. and A. Albert. 1947. Observations on the reproduction of the spiny dogfish, Squalus acanthias. Biol. Bull., **92** :187–199.

Holloway, John E., Norman C. Bunker and Bruce W. Halstead. 1953. The venom of Urobatis halleri (Cooper), the round stingray. Calif. Fish and Game, **39** (1) :77–82.

Holmgren, Nils. 1940. Studies on the head in fishes. Part I, Development of the skull in sharks and rays. Acta Zool. Stockholm, **21** (1) :50–267.

Holmgren, Nils. 1941. Studies on the head in fishes. Part II, Comparative anatomy of the adult selachian skull. Acta Zool. Stockholm, **22** (2) :1–100.

Hubbs, Carl L. 1948. Changes in the fish fauna of western North America correlated with changes in ocean temperature. Jour. Mar. Res., **15** (3) :459–482.

Ishiyama, Reizo. 1951. Studies on rays and skates of the family Rajidae found in Japan. Age determination of the black skate, Raja fusca. Bull. Japan. Soc. Sci. Fish. **16** (12) :112–124.

Jordan, David S., and Charles H. Gilbert. 1882. Synopsis of the fishes of North America. Bull. U. S. Nat. Mus. **16** :1–1018.

Jordan, David S. and Barton W. Evermann. 1896. The fishes of North and Middle America. Bull. U.S. Nat. Mus. **47** (1) :1–1240.

Leigh-Sharpe, W. Harold. 1920. The comparative morphology of the secondary sexual characters of elasmobranch fishes. Jour. Morph., **34** :245–265.

Leigh-Sharpe, W. Harold. 1921. The comparative morphology of the secondary sexual characters of elasmobranch fishes. Jour. Morph., **35** :349–380.

Leigh-Sharpe, W. Harold. 1922. The comparative morphology of the secondary sexual characters of Holocephali and elasmobranch fishes. Jour. Morph., **36** :221–243.

Limbaugh, Conrad. 1955. Fish life in the kelp beds and the effects of kelp harvesting. Univ. Cal. Inst. Mar. Resources, La Jolla, Calif. Pp. 157.

Matthews, L. Harrison. 1950. Reproduction in the basking shark, Cetorhinus maximus (Gunner). Phil. Trans. Roy. Soc. London, B **234** :247–316.

Metten, H. 1939. Studies on the reproduction of the dogfish. Phil. Trans. Roy. Soc. London, B **230** :217–238.

Olsen, A. M. 1954. The biology, migration and growth rate of the school shark, Galeorhinus australis in southeastern Australian waters. Australian Jour. Mar. and Fresh Water Res., **5** (3) :353–404.

Orcutt, Harold G. 1950. The life history of the starry flounder, Platichthys stellatus (Pallas). Calif. Div. of Fish Game, Fish Bull. **78** :1–61.

Perlmutter, Alfred. 1954. Age determination of fish. Trans. N. Y. Acad. Sci., **16** (6) :305–311.

Petersen, Carl G. J. 1891. Eine Methode zur bestimmung des Alters und Wuchses der Fische. Reichsverband der deutschen Fischerei, Mitt. deut. Seefischerei., **11** :226–235.

Pitotti, Milena. 1936. Sull' assorbimento del tuorlo negli embrioni di Torpedo. Pubbl. Staz. Zool. Napoli, **15** :217–222.

Prasad, R. R. 1945. Further observation on the structure and function of the nidamental glands of a few elasmobranchs of the Madras coast. Proc. Ind. Acad. Sci., **22**B :368–373.

Radovich, John. 1960. Redistribution of fishes in the eastern north Pacific ocean in 1957 and 1958. Calif. Coop. Fish. Invest. Report, **7** :163–171.

Radovich, John. 1961. Relationships of some marine organisms of the northeast Pacific to water temperatures particularly during 1957 through 1959. Calif. Dept. of Fish and Game, Fish Bull. **112** :1–56.

Ranzi, Silvio. 1934a. Le basi fisio morphologiche dello sviluppo embrionale dei Selaci. Pubbl. Staz. Zool. Napoli., Parti II e III, **13** :331–437.

Ranzi, Silvio. 1934b. Sulle funzione dei Leucociti nell' utero del Selaci. Arch. Zool. Italiano **20** :569–577.

Reish, Donald J. and Howard A. Winter. 1954. The ecology of Alamitos Bay, California, with special reference to pollution. Calif. Fish and Game, **40** (2) :105–121.

Ripley, William E. 1946. The soupfin shark and the fishery. Calif. Div. Fish and Game, Fish Bull. **64** :1–37.

Roedel, Phil M. 1953. Common ocean fishes of the southern California coast. Calif. Dept. of Fish and Game, Fish Bull. **91** :1–184.

Roedel, Phil M. and William E. Ripley. 1950. California sharks and rays. Calif. Dept. of Fish and Game, Fish Bull. **75** :1–88.

Rugh, Roberts. 1935. Ovulation in the frog. II. Follicular rupture to fertilization. Jour. Exp. Zool., **71** :149–193.

Russell, Findlay E. 1953. Stingray injuries; a review and discussion of their treatment. Am. Jour. Med. Sci., **226** (2) :611–622.

Russell, Findlay E. 1955. Multiple caudal spines in the round stingray, Urobatis halleri. Calif. Fish and Game, **41** (3) :213–217.

Russell, Findlay E. and A. Van Harreveld. 1954. Cardiovascular effects of the venom of the round stingray, Urobatis halleri. Arch. Int. de Phys., **57** (3) :322–333.

Samuel, Mary. 1943. Studies on the corpus luteum in Rihnobatus granulatus Cuvier. Proc. Ind. Acad. Sci., **18**B :133–157.

Sato, S. 1935. A note on the Pacific dogfish, Squalus suckleyi Girard, in the coastal waters of Hokkaido, Japan. Jour. Fac. Sci., Hokkaido Univ., (6) **4** (3) :127–141.

Scofield, W. L. 1959. History of kelp harvesting in California. Calif. Fish and Game, **45** (3) :135–157.

Semper, Carl. 1875. Das Urogenitalsystem der Plagiostomen und seine Bedeutung fur das der ubrigen Wirbelthiere. Arb. Zool. Zoot. Inst. Wurzburg., **2** :195–509.

Starks, Edwin C. 1907. Marine fishes of southern California. U. Calif. Publ. in Zool., **3** (11) :159–251.

Steven, G. A. 1936. Migration and growth of the thornback ray, Raia clavata. Jour. Mar. Biol. Ass., United Kingdom, **20** (3) :605–614.

Steven, G. A. 1947. The British Raiidae. Sci. Progress **35** (138) :220–236.

Stevenson, Robert E. and Kenneth O. Emery. 1958. Marshlands at Newport Bay, California. Allan Hancock Found. Publ., Occ. Paper **20** :1–57.

Sverdrup, H. U., Martin W. Johnson and Richard H. Fleming. 1942. The oceans. Prentice-Hall, Englewood Cliffs, N. J. Pp. 1087.

Templeman, Wilfred. 1944. The life-history of the spiny dogfish, Squalus acanthias and the vitamin A values of dogfish liver oil. Res. Bull. Newfoundland Dep. Nat. Res., **15**: 1–102.

Te Winkel, Lois E. 1950. Notes on ovulation, ova and early development in the smooth dogfish, Mastelus canis. Biol. Bull., **99** :474–476.

Walford, Lionel A. 1932. The California barracuda, Sphyraena argentea. Calif. Div. of Fish and Game, Fish Bull. **37** :1–122.

Wallace, William. 1903. Observations on ovarian ova and follicles in certain teleostian and elasmobranch fishes. Quart. Jour. Mic. Sci., **47** (186) :161–213.