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# *Leachia pacifica* (Cephalopoda, Teuthoidea): Spawning Habitat and Function of the Brachial Photophores[1]

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ABSTRACT: *Leachia pacifica* reaches about 80 percent of its maximum length in near-surface waters off Hawaii, then abruptly descends to depths greater than 1,000 meters where maturation and mating occur. At these latter depths, large photophores develop on the tips of the third arms in females. The photophores provide a possible means for sexual attraction.

SMALL SQUIDS of the genus *Leachia* have been thought to be epipelagic (Roper and Young, in press). However, off Hawaii the vertical distribution of *Leachia pacifica* reveals an unusual pattern, with captures as deep as 1,825 m. The pattern is closely associated with the stage of maturity and the development of the brachial organs in females. This information bears on two poorly understood subjects: the spawning habitats of oceanic squids and the function of their photophores.

## MATERIALS AND METHODS

Specimens were captured off the island of Oahu in the Hawaiian Archipelago at approximately 158° 18′ W, 21° 23′ N, over bottom depths of 1,500 to 4,000 m. Two types of trawls were used: a modified 3-meter Tucker trawl and a 3-meter Isaacs–Kidd midwater trawl (IKMT). The Tucker trawl opens and closes at the fishing depth; hence, capture of specimens during setting and retrieval of the trawl (i.e., contamination) cannot occur. The opening–closing mechanism utilizes a mechanical release that is activated by weighted messengers sent down the towing cable.

The IKMT is always open, and occasionally specimens are captured during the raising and lowering of the trawl. To minimize this contamination, the trawl was dropped as rapidly as possible and retrieved with the ship moving slowly ahead. The net is pulled horizontally at 3 to 4 knots. Depth records for both trawls were obtained with a Benthos time-depth recorder.

Sectioned material was fixed in Bouin's solution in seawater and embedded in Epon 812. Sections between 1 and 10 $\mu$ thick were cut on an A. O. rotary microtome with a steel knife and stained with Richardson's stain.

## DESCRIPTION

A brief description of *Leachia pacifica* is presented to facilitate subsequent discussion. A full description is desirable but is postponed until a later date.

*Leachia pacifica* (Cranchiidae) (Figure 1*c*) reaches a maximum mantle length of about 60 mm. The thin-walled mantle is long, slender, and transparent. A large pair of fins, elliptical in outline, is situated at the posterior end of the mantle. The eyes of adults are small, reaching a diameter of about 5.5 percent of the mantle length, and lie within the head (i.e., not on stalks); however, about 2 mm separate the optic lobes from the central mass of the brain. The third arms are nearly three times the length of the others. In males the right fourth arm is hectocotylized; it is longer than the left arm and has an expanded tip that carries large medial and reduced marginal suckers. Small photophores are present on the eyes. In mature or nearly mature females, a large organ (the brachial organ) occupies the distal portion of each third arm.

The larval stage (= pyrgopsis stage) is extended, as is typical of the genus.

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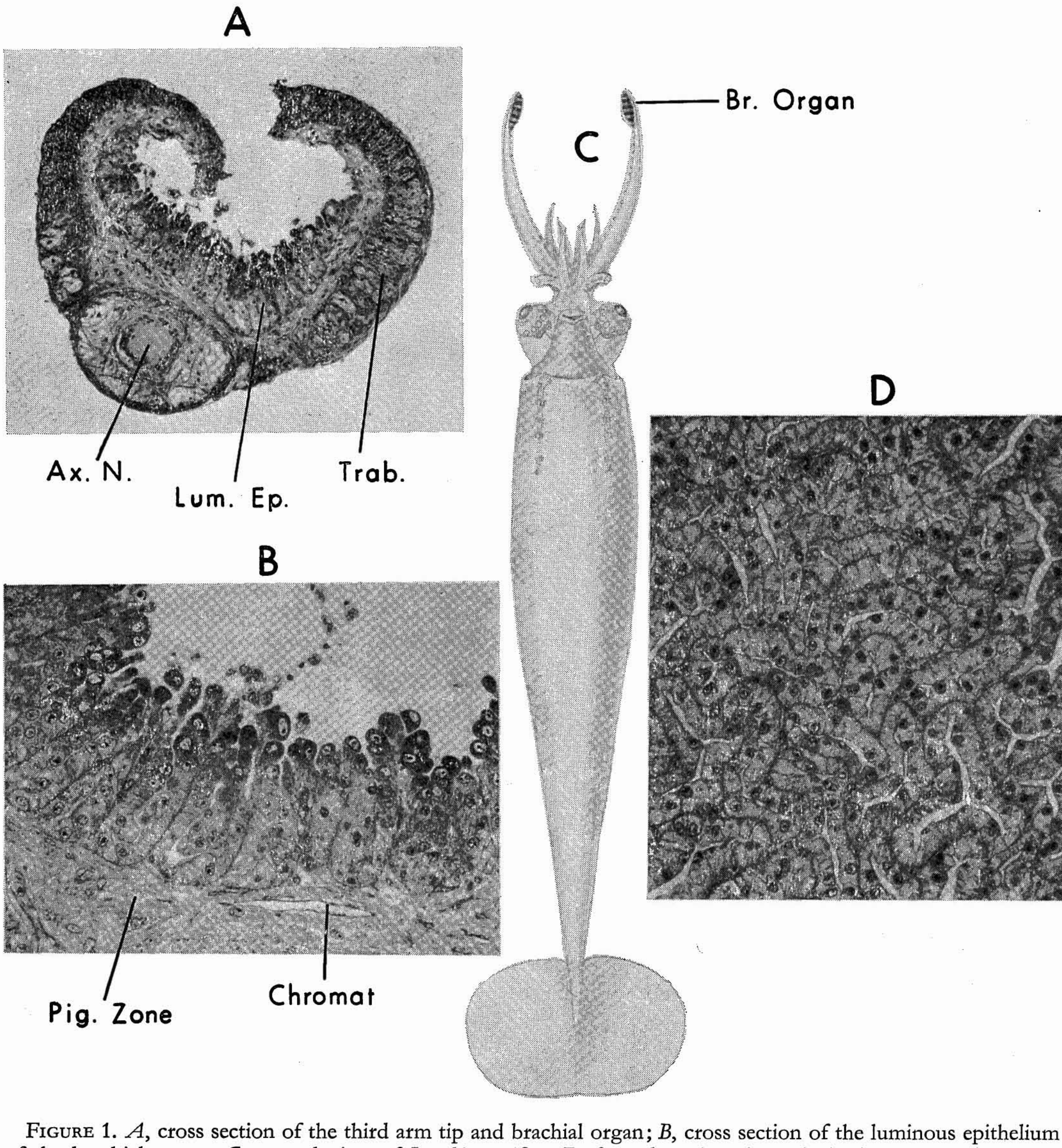


FIGURE 1. *A*, cross section of the third arm tip and brachial organ; *B*, cross section of the luminous epithelium of the brachial organ; *C*, ventral view of *Leachia pacifica*; *D*, frontal section through the base of the luminous epithelium.

ABBREVIATIONS: Ax. N., axial nerve; Lum. Ep., luminous epithelium; Trab., trabecula; Pig. Zone, pigmented zone; Chromat., chromatophore; Br. Organ, brachial organ.

*Vertical Distribution*

The catch records presented in Figure 2 provide a clear picture of the vertical distribution of *L. pacifica*. Symbols in the figure, however, require some explanation. Tucker trawl captures are represented by a vertical bar that indicates the total range fished by the net while open. Within this range the net usually fishes predominately within a narrow zone, the midpoint of which is indicated by either an open circle (male specimen) or a large solid circle (female specimen). The IKMT also fishes primarily within a narrow vertical range. The

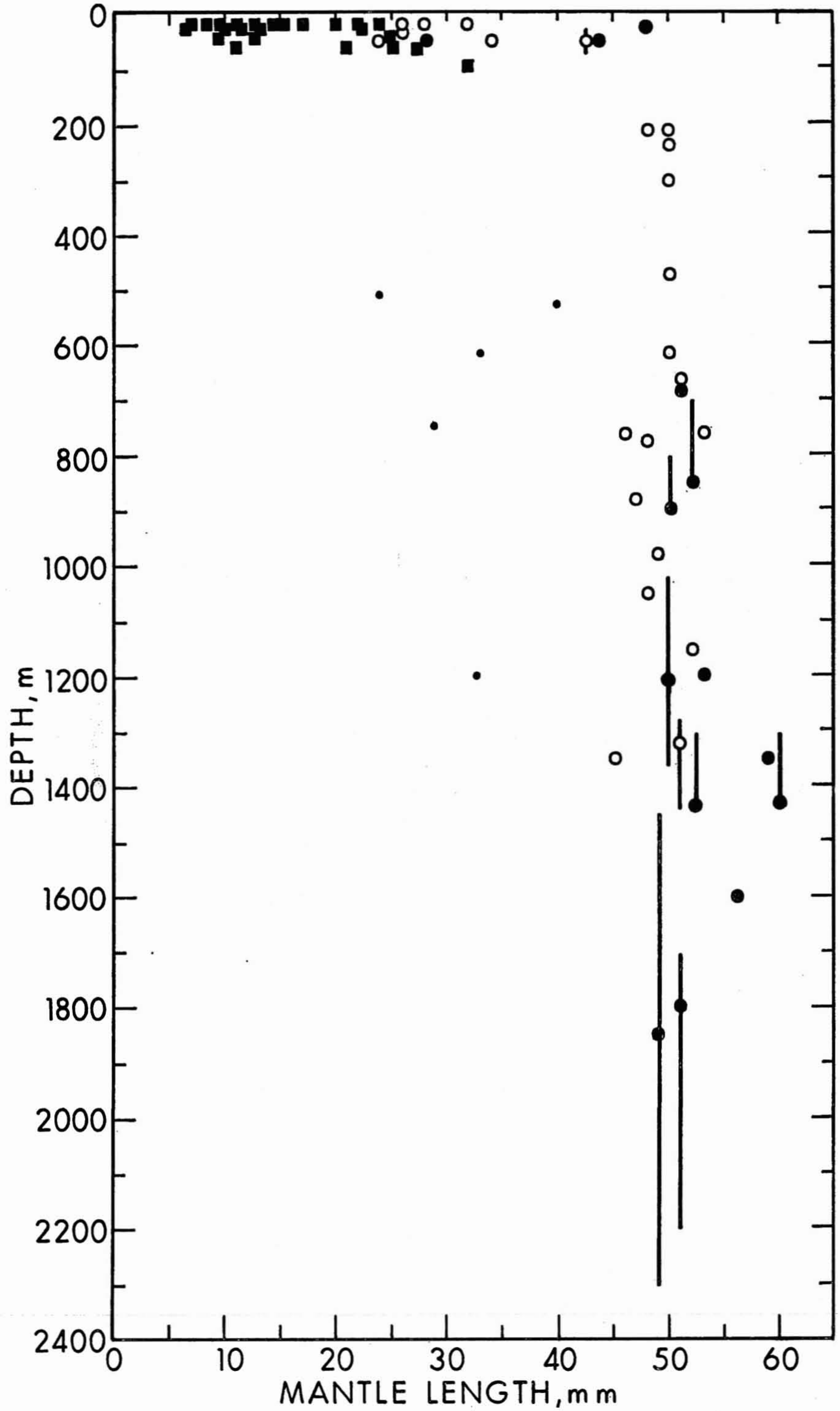


FIGURE 2. Vertical distribution of *Leachia pacifica* off Hawaii. Large solid circles = depth of capture of males; large open circles = depth of capture of females; small solid circles = presumed contaminants; bars = depth range of opening-closing tows; squares = depth of capture of specimens of undetermined sex.

total range, of course, extends to the surface and, therefore, is not represented in Figure 2. The probable depth of capture is determined from the horizontal phase of the tow in the same manner as for captures from the Tucker trawl. Every IKMT tow below 100 m passed through the habitat of the younger individuals during the setting and retrieval of the net. In such circumstances some contamination is expected. I have assumed that five specimens (represented by the smaller dots in the figure) were captured in this fashion. Numerous opening–closing tows in these same intermediate depths where the contaminants are recorded failed to capture small specimens.

The pattern of vertical distribution is peculiar. Excluding contaminants, specimens less than 45-mm mantle length (ML) were taken in the upper 100 m whereas larger specimens were captured throughout the water column from 30 to about 1,800 m. Day and night captures are intermingled at all depths; therefore, diel movements do not occur. Although multiple captures occur in near-surface waters, generally only one specimen is taken per tow at depths below 100 m, indicating a solitary habit for deep-living individuals.

*Maturation in Females*

The change in females from larvae to adults involves several structures besides the gonads. In larvae, the eyes are located on long stalks that extend laterally from the head (stalked eyes). In adults, stalks are absent and the eyes are included within the head (sessile eyes). In adults, the oviducal and nidamental glands are greatly enlarged, and large brachial organs develop on the tips of the third arms.

These developmental changes are correlated with changes in vertical distribution. The two largest females found in near-surface waters have stalked eyes, small nidamental and oviducal glands (about 1 mm and 0.5 mm in diameter, respectively) and unmodified third arms. The three females captured between about 600 to 900 m depth have stalked eyes, slightly enlarged nidamental and oviducal glands (about 2 mm in length), and third arms with flat and expanded tips. The leaflike tips bear thin trabeculae and are colorless or nearly so. A fourth specimen captured at about 1,200 m depth shared the same features.

The remaining seven females were captured at depths greater than 1,000 to 1,200 m. Only a single specimen has undamaged eyes, and these are sessile. The eyes in the other specimens probably were sessile or nearly so. All undamaged specimens have nidamental and oviducal glands larger than 3 mm.

Four of the seven females have large heavily pigmented brachial organs at the tips of the third arms; the tips of these arms were missing on the three remaining females.

Three of the seven females appear to be near or just past the spawning stage. In one of them, captured between 1,450 and 2,310 m depth, the nidamental and oviducal glands greatly exceeded 8 mm in length (part of the gland was missing) and are greatly swollen, slightly pigmented, and gelatinous. Discharged spermatophores, imbedded in the dorsal surfaces of the head and mantle, indicated that mating had occurred. The specimen was flaccid and rather gelatinous, features typical of squids near or just past the spawning period (Young 1973). Unfortunately, the ovary was lost during capture, so the reproductive state cannot be positively determined; however, the swollen accessory reproductive glands suggest that spawning had not occurred. Two other specimens appear to be in the same state. These specimens, captured at depths between 1,305 and 1,445 m and between 1,700 and 2,200 m have large gelatinous and lightly pigmented remnants of the oviducal glands and a flaccid overall consistency. Both have lost the ovaries, nidamental glands, and most of the oviducal glands due to damage in the trawl. Although discharged spermatophores cannot be found in these two females, there is no doubt they are near or just past the spawning stage.

There is relatively little difference in mantle length between the largest larvae and mature adults. Since death probably follows spawning (Young 1973), this species apparently has an abbreviated adult life.

*Maturation of Males*

In males some correlation exists between vertical distribution and the development of the secondary sexual organs. Unfortunately, mature specimens are lacking. Initial phases of hectocotylus development are apparent in specimens at a mantle length of 25 mm that live in near-surface waters. Well-developed hectocotyli are found only in specimens captured at depths greater than 600 m. Also the penis and spermatophore glands are enlarged only in specimens found below 600 m. All males captured have stalked eyes and lack spermatophores.

### *Structure of the Brachial Organs*

The brachial organs are large spoon-shaped structures formed, in part, by the distal enlargement of the protective membranes and muscular supporting trabeculae of the third arms (Figure 1*A*). The enlarged trabeculae have a rather gelatinous core of loose, vacuolated, connective tissue with scattered transverse and diagonal muscle fibers passing from the oral to the aboral sides. Each trabecula has a broad muscle band over its entire aboral surface with fibers running from the base to the tip. A narrow muscle strand runs up the midline of each trabecula along its oral surface.

The epithelium that lines the oral surface of the organ is highly folded into a network of interconnecting ridges (Figures 1*B*, *D*). The epithelium at the base of the ridges has a rather uniform structure of short broad cells. In contrast, the epithelium along the ridge crests consists of cells with teardrop shapes, with the small ends attached to the basement membrane of the epithelium and with much of the bulbular ends free from contact with adjacent cells. These bulbular cells stain more heavily than the basal cells. Although no pigment granules were found in the oral epithelium in dissection of formalin-preserved organs, the bulbular cells have a slight brown tint. No evidence of a secretory function could be seen in the oral epithelium.

Each organ is heavily pigmented. Most of the pigment is not contained in chromatophores, although sections reveal the presence of at least one chromatophore in the median line beneath the oral epithelium (Figure 1*B*). Spherical pigment granules lie in the tissue immediately beneath the oral epithelium and lateral to it up to the ends of the trabeculate membranes. Although the pigment granules cannot be resolved in the photographs (Figure 1*A*, *B*), the pigmentation seems dense enough in the intact organ to prevent passage of light.

## DISCUSSION

### *The Brachial Organ*

The brachial organ is almost certainly a photophore. The layer of heavy pigment that envelops the oral surface of the organ must have a light-related function. This layer develops in depths of more than 1,000 m where bioluminescent light is the only detectable light. The trabeculate membranes provide a potential means of regulating emitted light. Although these membranes are usually found coiled over the luminous epithelium (Figure 1*A*) in captured specimens, the heavy aboral muscle layer of the trabeculae clearly indicates that the animals are capable of extending and exposing the oral surface of the organ. The action is similar to that which occurs when the fingers of the hand extend and close over the palm. This movement of the trabeculate membranes would allow the pigment layer to act as a screen, concealing or exposing a luminous epithelium.

The organ lacks the reflecting iridocytes characteristic of many cephalopod photophores, although the composite light organs of *Vampyroteuthis* and the tentacular organs of *Chiroteuthis* are known to lack iridocytes (Pickford 1946, Chun 1910). The tentacular organs of *Chiroteuthis* have been observed to luminesce (Y. Haneda, personal communication) and to have a luminous epithelium formed into high interconnecting ridges (Chun 1910) similar to that in *Leachia pacifica*. The photophores of *Chiroteuthis* and *Leachia pacifica* both lack a dioptric system.

### *Function of the Brachial Photophores*

The use of photophores in sexual attraction is well known in the terrestrial environment; e.g., fireflies (Buck 1948, Seliger et al. 1964). In neritic waters, photophores have been experimentally demonstrated to play a related role in courtship behavior in the fish *Porichthys notatus* (Crane 1965). In the midwater environment, evidence is circumstantial. In some groups (e.g., myctophids, ceratioids, idiacanthids) the occurrence of sexually dimorphic photophore patterns suggests a role in sexual attraction (Marshall 1954, Nicol 1967). The most convincing case has been made for the ceratioid angler fish, in which the luminous esca of the female is thought to be important in attracting males, although pheromones probably play a role as well (Bertelsen 1951, Marshall 1967). Sexual dimorphism alone is not unequivocal evidence for a sexual attraction function. Bolin (1961) presented evidence that the caudal photophores in the myctophid *Tarletonbeania crenularis*, which are present only in males, aid in diverting the attention of predators from females.

Circumstantial evidence also suggests that female *L. pacifica* use their brachial photophores as sexual attractants: (1) brachial photophores are present only in females; (2) the adult life apparently is abbreviated and brachial photophore development occurs just prior to sexual maturity and mating; and (3) brachial photophore development and mating occurs at depths greater than 1,000 to 1,200 m. At those depths, downwelling surface light is insignificant, and mate location, presumably, poses a serious problem for a visually dependent animal.

Mate detection through a bioluminescent signal has distance limitations. The concentration of *L. pacifica* in deep water, therefore, must be examined. Nine successful opening-closing tows below 1,000 m depth filtered an estimated 1,100,000 $m^3$ of water. If each of the five females captured was placed at the center of a separate cubic volume of water equal to one-fifth of the total volume filtered, the minimum separation of individuals would be 61 m. Such a distribution is, of course, highly unlikely; however, it indicates that the density of individuals is within a reasonable order of magnitude for sexual attraction by bioluminescence to be effective.

### *Possible Advantages of Spawning in Deep Water*

Deep waters lack detectable sunlight and are sparsely inhabited. These conditions presumably reduce the chances of predation upon gravid females. An indication of the low population densities can be seen from the series of four deep tows that captured two of the squid reported in this paper. These tows spent 18 hours at depths from 1,450 to 2,300 m and captured only 130 specimens (in addition to the squid) ranging from large copepods to fish. The same amount of trawling at a depth of 600 to 700 m would yield thousands of specimens and a similar high number would be found in the upper few hundred meters at night. Mating and spawning success is particularly critical in these squids, as they undoubtedly reproduce only once. By descending to great depths they are guaranteed a relatively undisturbed mating and spawning period. The presumed technique of mate location is, of course, far better suited to deep water where a flashing photophore is less likely to attract a predator.

Although young larvae of *L. pacifica* are found in surface waters, the depth of hatching is unknown. Therefore, the consequences of deep-sea spawning on embryos and newly hatched larvae cannot be determined.

## SUMMARY


1. *Leachia pacifica* obtains most of its growth in near-surface waters off Oahu, Hawaii, then abruptly descends to depths of 1,000 to, at least, 1,800 m.
2. Sexual maturity and mating occur at depths of more than 1,000 to 1,200 m.
3. At these depths, large organs, presumed to be photophores, develop on the third arms of the females prior to mating.
4. These photophores are presumed to function in sexual attraction.
5. The value of mating and spawning in deep waters may be related to lesser predation on the adults during this critical period.


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