

New Records and Observations on the Flapjack Devilfish, *Opisthoteuthis californiana* Berry¹

WALTER T. PEREYRA²

IN JUNE 1961 the U. S. Bureau of Commercial Fisheries joined with the Atomic Energy Commission to undertake an investigation of the deep-water ocean fauna in the area contiguous to the Columbia River mouth at depths from 50 to 1050 fathoms (91–1920 m). The main objectives of this project are to describe the benthic fish and invertebrate communities inhabiting the study area, and to define their bathymetric distribution on a temporal basis. Associated with the faunal investigation is a monitoring of the various demersal forms to evaluate the biological transport of radionuclides which may have their origin in Columbia River waters.

Thirty-one specimens of the flapjack devilfish, *Opisthoteuthis californiana*, have been captured since initiation of the field program in 1961. Records of these captures, together with records of this species from other areas in the northeastern Pacific, are used here to describe the bathymetric and geographic distribution of *O. californiana* and to augment knowledge of its biology.

The flapjack devilfish was described and named by Berry in 1949 from two mature females captured in 188 fathoms (344 m) by a commercial trawler off Humboldt Bay, California. A second paper by Berry (1952) illustrates and gives additional descriptions of these specimens. A male and a juvenile female flapjack devilfish were taken two years later in 280 fathoms (512 m) off Humboldt County, California, also by a commercial trawler. The male specimen was described in detail, especially with

respect to the development of secondary sexual characteristics (Berry, 1954 and 1955). The four specimens reported by Berry (two mature females, one mature male, and a juvenile female) represent the only previous records of this species known to the author.

Throughout the world, six other species of this genus have been described. Two species are known from the Atlantic (the genus type *O. agassizii* Verrill, 1883 and an apparent pelagic species, *O. medusoides* Thiele, 1915), one from the Indian ocean off the west coast of Sumatra (*O. extensa* Thiele, 1915), two from Australian waters (*O. persephone* Berry, 1918 and *O. pluto* Berry, 1918), and one which has been taken repeatedly in Japanese waters (*O. depressa* Ijima and Ikeda, 1895).

Despite wide interest in the taxonomy and comparative morphology of this divergent cephalopod group (Robson, 1925 and 1929), very little is known of their feeding habits, mode of life, or behavior. As late as 1952 Berry (p. 187) wrote of his hope ". . . that we may not have long to wait before further examples of so strange and interesting an animal will be captured and that something may then be learned of its appearance in the living state, its behavior and habits."

ACKNOWLEDGMENTS

I am grateful to Dr. Paul Illg, Zoology Department, University of Washington; Mr. William High, International Pacific Halibut Commission; Mr. Clifford Fiscus, Marine Mammals Branch, Bureau of Commercial Fisheries; and Miss Patsy McLaughlin, Oceanography Department, University of Washington, for loaning specimens and/or data for several Gulf of Alaska and Washington coast records. The loan of specimens of *Opisthoteuthis depressa* and *Staurototeuthis albatrossi* from the U. S. National Museum by Dr. Fenner Chase and Dr. Harold

¹ The work was supported by the cooperative Bureau of Commercial Fisheries–U. S. Atomic Energy Commission deep-water investigation of the benthic marine fauna in the area contiguous to the Columbia River mouth. Manuscript received December 11, 1963.

² Fishery Biologist, Exploratory Fishing and Gear Research Base, Bureau of Commercial Fisheries, U. S. Fish and Wildlife Service, Seattle, Washington.

TABLE 1
COLLECTION DATA FOR THIRTY-NINE *Opisthoteuthis californiana*
TAKEN IN THE NORTHEASTERN PACIFIC

DATE	POSITION		DEPTH (fathoms)	TEMP. (°C)		BOT. SAL. ‰	NO.	SEX	SIZE (mm)	REMARKS
	Lat. N	Long. W		Surf.	Bot.					
SW of Columbia River off Oregon										
1 July 1961	46° 05'	124° 49.0'	300-303	16.1	1	undetermined		
3 July 1961	45° 51.8'	124° 48.5'	425	16.9	1	mat. F	225 × 250	
3 July 1961	45° 50.3'	124° 50.0'	450-500	16.3	1	immat. F	180 × 200	
16 Sept. 1961	45° 56.3'	124° 47.8'	372-374	16.1	1	mat. M	460 × 440	
							1	mat. F	225 × 224	
10 Dec. 1961	45° 58.5'	124° 49.1'	350	10.0	1	undetermined		
10 Dec. 1961	45° 52.2'	124° 53.7'	455-475	10.0	1	mat. F	195 × 175	Wt. 2 lb
11 Dec. 1961	45° 58.4'	124° 49.6'	335	9.9	1	mat. M	280 × 260	
11 Dec. 1961	45° 55.9'	124° 48.1'	372-380	10.0	1	mat. F	340 × 330	
							1	mat. M	280 × 260	
							1	mat. M	420 × 380	
							1	mat. M	205 × 200	
6 Mar. 1962	45° 52.4'	124° 49.7'	446-455	9.2	4.6	34.192	1	immat. F	170 × 180	Wt. 1.5 lb
7 Mar. 1962	45° 58.5'	124° 52.1'	415-427	8.3	4.6	34.137	1	mat. F	210 × 150	Wt. 1.5 lb
							1	immat. F	190 × 180	Wt. 1.5 lb
11 Mar. 1962	45° 55.5'	124° 46.1'	318-333	7.8	5.8	34.021	1	immat. M	145 × 140	Wt. 1 lb
26 May 1962	45° 58.8'	124° 50.6'	350	13.3	1	mat. M	440 × 420	
27 May 1962	45° 58.1'	124° 51.5'	375	12.2	1	mat. M	290 × 290	
27 May 1962	45° 59.3'	124° 52.2'	400	12.8	1	mat. F	205 × 205	
27 May 1962	45° 54.1'	124° 54.5'	450	13.3	1	mat. F	210 × 205	
30 Aug. 1962	45° 58.0'	124° 44.7'	250	16.7	1	mat. M	250 × 240	
31 Aug. 1962	45° 55.6'	124° 46.2'	350	16.7	1	mat. M	285 × 260	
							1	mat. M	200 × 220	
1 Sept. 1962	45° 54.0'	124° 47.2'	375	16.7	1	undetermined	small	
23 Jan. 1963	45° 50.9'	124° 52.8'	440-450	8.3	4.7	34.13	1	immat. M	140 × 125	
							1	mat. M	360 × 350	
23 Jan. 1963	45° 54.2'	124° 53.8'	405	8.3	5.1	34.09	1	immat. M	145 × 128	
24 Jan. 1963	45° 55.0'	124° 47.4'	348-354	8.9	4.6	34.18	1	mat. M	260 × 230	
9 May 1963	46° 00.1'	124° 50.8'	300	11.7	1	mat. M		
13 May 1963	45° 55.8'	124° 49.8'	375	12.2	1	mat. M	310 × 300	
13 May 1963	45° 52.3'	124° 52.0'	450	12.2	1	mat. M	360 × 340	

Off Washington									
Date	Long.	Lat.	Depth	Time	Specimens	Depth	Time	Specimens	Notes
25 Sept. 1952	47° 29.3'	125° 11.0'	304-308	11.6	1	undetermined	1	1	Taken in off-bottom trawl app:ox. 3 fath. off bottom
14 May 1963	47° 57.7'	125° 35.5'	150	5.0	1	F	1	1	
Gulf of Alaska									
14 May 1961	53° 38.0'	165° 00.0'	230	5.8	1	mat. M	1	1	S of Unimak I.
4 May 1962	57° 29.0'	150° 09.5'	250-256	5.0	1	mat. M	1	1	E of Kodiak I.
6 Apr. 1962	54° 21.0'	159° 45.0'	300	...	2	mat. M	2	2	large
17 Sept. 1962	59° 34.0'	145° 45.0'	118	...	1	mat. M	1	1	WSW Cape St. Elias
17 Sept. 1962	59° 33.0'	145° 17.0'	68	...	1	mat. F	1	1	WSW Cape St. Elias

Rehder is greatly appreciated. Special thanks are due Dr. Grace Pickford, Bingham Oceanographic Laboratory, Yale University, and Mr. Clifford Fiscus for critical review of the manuscript.

METHODS AND MATERIALS

All the specimens agreed with Berry's description of *Opisthoteuthis californiana*, but no comparison was made with species types. Specimens were compared with representatives of two closely related species, *O. depressa* and *Stauroteuthis albatrossi*.

The majority of specimens reported in this paper were taken along a trackline running southwest from the Columbia River mouth. On this trackline standard stations were established at depths ranging from 50 to 1050 fathoms (91-1920 m). These stations were monitored four times a year, principally with a 400-mesh Eastern otter trawl, a 43-ft Gulf of Mexico shrimp trawl, and a 70-ft semi-balloon shrimp trawl. The latter two trawls were used when trawling at depths greater than 450 fathoms (823 m). Vessels used to survey the trackline were the M/V "Commando," a 65-ft purse-seine type vessel chartered from the College of Fisheries, University of Washington; and the M/V "John N. Cobb," the Bureau's 93-ft exploratory fishing vessel.

Observations on 39 flapjack devilfish collected in the northeast Pacific are reported in this paper (Table 1). Of this total, 31 specimens were taken on the Columbia River trackline by the M/V "Commando" and "John N. Cobb," two off the coast of Washington by the "Cobb," and six in the Gulf of Alaska by the "Cobb" and chartered vessels of the International Pacific Halibut Commission. All specimens were captured with the 400-mesh otter trawl, with the exception of one taken on the Washington coast in a large pelagic trawl rigged to fish just off-bottom. None of the sampling gear used was a closing net. Therefore, although all of these captures, with one exception, are treated as occurring on the bottom, the possibility exists that they could have been taken as the gear was being set or hauled back.

Observations on living animals were made in a 20-gallon aquarium with a sealed top aboard the M/V "John N. Cobb" during a cruise in January 1962. Motion pictures were taken at this time which allowed a more detailed behavioral analysis to be made on shore.

OBSERVATIONS

Geographic Distribution

Prior to this study the known geographic distribution of *O. californiana* was recorded from four specimens reported by Berry (1949:24; 1952:183; 1954:29; and 1955:219, 223). The exact locations for these captures are not given, but from Berry's descriptions they apparently were confined to a small area off Humboldt Bay, California (approximately 45°10'N, 125°10'W).

The data in Table 1 extend the geographic range northward 2200 miles along the continental shelf to off Unimak Island, Alaska—that is, from northern California to the Aleutian Islands, Alaska.

Bathymetric and Seasonal Distribution

The known bathymetric range of this species off northern California as recorded by Berry (ibid.) is from 188 to 280 fathoms (344–512 m). Specimens collected from the Columbia River trackline were taken at depths from 250 to 450 fathoms (457–823 m); those off Washington from 150 and 308 fathoms (274–563 m); and those from the Gulf of Alaska from 68 to 300 fathoms (124–548 m). The above records extend the known bathymetric range shoreward to 68 fathoms (124 m) and seaward to a depth of 450 fathoms (823 m). As has been observed for the western Pacific congener (*O. depressa*), *O. californiana* has been collected from shallower water at the northern end of its range, with the bathymetric range being wider to the north despite infrequent trawling in water deeper than 300 fathoms in northern waters.

The known bathymetric ranges of the other species of *Opisthotenthis* are not all similar (Robson, 1929:167–173). Both *O. depressa* from Japanese waters and *O. agassizii* from the North Atlantic have been reported at greater

depths (587 and 1058 fathoms [1073 and 1934 m], respectively) than *O. californiana*. The bathymetric ranges of the other four species, *O. extensa*, *persephone*, *pluto*, and *medusoides*, fall within that of *O. californiana*.

The temporal distribution of males and females by depth along the Columbia River trackline is presented in Figure 1. Although the number of specimens is small, males appear to occupy a greater bathymetric range than females. The latter were never captured at depths shallower than 375 fathoms (686 m). There are, however, three known records of females from levels shallower than 375 fathoms (686 m): one off California in 188 fathoms (344 m) (Berry, 1949:24), one off Washington in 150 fathoms (274 m), and one from the Gulf of Alaska in 68 fathoms (124 m).

On the trackline the data suggest that the males may move seasonally, being found at shallower depths in the summer. Perhaps mating takes place in late winter when the sexes occupy similar depth zones, but this is only a surmise.

In cephalopods a separation of the sexes by depth has been noted by several authors. Isgrove (1909:472) notes a disparity in the sex ratio of *Eledone*. She suggests that the disparity is caused by the females breeding in littoral waters, in which they are more frequently taken. Robson (1925:1325) presents figures for Octopodidae picked at random from selected reports, where inside of 200 fathoms (366 m) the percentage of females is greater and outside the percentage of males is greater. Both of the above findings, where the female Octopodidae predominate in shallow water, are reversals of the situation which has been found in this study for *Opisthotenthis*, where the males predominate in shallow water.

Of the specimens collected off the north Oregon coast for which the sex is known, 18 males and 10 females are recorded. Since greater trawling effort was expended at the depths where the males predominate (in the shallow part of the range), the above ratio probably does not reflect the actual sex ratio.

Availability

Catch-per-hour trawling for *O. californiana* at various depths is given in Figure 2. The data

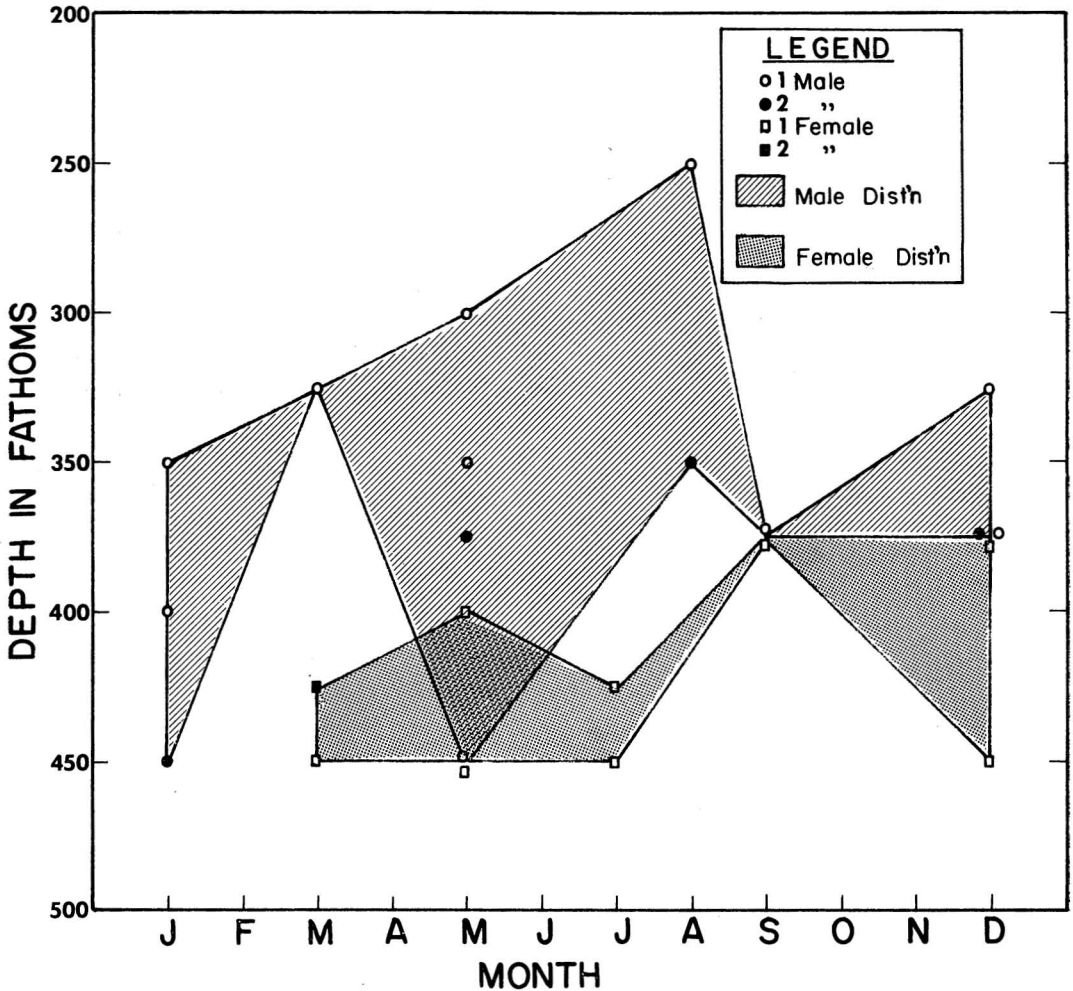


FIG. 1. Temporal and bathymetric distribution of male and female *Opisthoteuthis californiana* based on capture of 28 individuals on a trackline off the mouth of the Columbia River, July 1961–May 1963.

suggest that Berry (1949:26 and 1952:183) was correct in surmising that these animals are probably not unduly rare where suitable bottom conditions exist. The average catch rate over the depth range where they were taken on the Columbia River trackline was approximately 0.4 individuals per hour of trawling (Table 2). Within the range of depth where the species were found, they were most frequently encountered from 375 to 450 fathoms (686–823 m). Due to the low effort from 475 to 575 fathoms (868–1051 m), where only two drags have been made, its relative abundance in deeper water is not well known.

The bimodal nature of the catch-per-unit-of-effort curve may result from several factors. As shown earlier, the sexes are distributed unevenly, with the males found in shallower water than the females. This could create the apparent non-normal distribution. Another factor which may be responsible is the direct or indirect effect of bottom type on distribution. Green mud was found to predominate over the range where the species was encountered; but inside of 325 fathoms (594 m) and at 400 fathoms (731 m), where the catch per effort was low, the sand/mud ratio was higher (> .08) than was found at adjacent stations

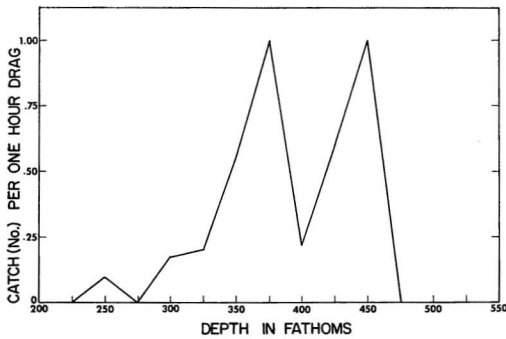


FIG. 2. Number of *Opisthoteuthis californiana* caught per one-hour of trawling by 25-fathom depth intervals from the Columbia River trackline.

(Dr. Dean McManus, unpublished data). Additionally, at 275 fathoms (503 m), where no specimens were captured, outcroppings were encountered. The above findings are presented as possible explanations, not conclusions.

Morphology

The external appearance of animals of this genus is quite peculiar. General descriptions in the past have invariably been made on preserved specimens or on specimens which were not alive in water; consequently the common name, flapjack devilfish, has arisen in the literature. Berry (1952:183) goes so far as to state that in the preserved state these animals resemble in about equal degree a soggy pancake or a very dirty floor mop. The lack of supporting structures, webbing between the arms, and the extent of gelatinous tissue makes this description true. But when the animal is observed alive in water, a different picture is presented (Fig. 3).

With the mantle cavity and gelatinous tissues supported by water the shape, as viewed anteriorly, appears more like a wide bell than the plano-convex disc used to describe preserved material. Viewed from the side the anterior portion of the head and body proper slope gradually dorsad, with the dorsal surface being rather flattened. The posterior margin slopes very abruptly, almost perpendicularly, away from the dorsal surface. Thus, the cephalic mass is considerably expanded and raised, being displaced posteriorly.

The eye openings are not large and the

rounded eye prominences, which are noticeable on the upper surface of preserved material, disappear when the animal assumes a normal shape. Conversely, the ear-like fins become more noticeable on live specimens.

When the animal is at rest (Fig. 3a), there is a horizontal curvature of the distal portion of the arms anteriorly, a condition similar to that described for preserved specimens (Ijima and Ikeda, 1895:329). The lateral curving of the right and left arms anteriorly results in the dorsal or anterior arms facing each other with their concavity while the ventral or posterior arms face with their convexity. The ends of the latter pair of arms are, therefore, turned laterally away from each other.

When at rest in an aquarium, the oral surface did not lie flat to the bottom, as might be expected. Instead, the distal half of the animal was held off the bottom (an inch or so in larger specimens) with only the basal portions of the arms in contact with the bottom (Fig. 3b). Interestingly, this area of contact on the arms is the portion possessing the largest suckers (excepting the 6-7 enlarged suckers distally on the dorsal pair of arms on the males, which have a specialized function [Berry, 1955:221]). Yet, at no time were the animals observed to hold with these or other suckers. As

TABLE 2

NUMBER OF *Opisthoteuthis californiana* CAUGHT PER ONE-HOUR DRAG WITH A 400-MESH COMMERCIAL OTTER TRAWL BY 25 FATHOM DEPTH INTERVALS ON A TRACKLINE OFF THE MOUTH OF THE COLUMBIA RIVER.*

DEPTH (fathoms)	NO. SPECIMENS (C)	NO. DRAGS (f)	C/f
250	1	11	0.09
275	0	8	0
300	2	12	0.17
325	2	10	0.20
350	5	9	0.56
375	9	9	1.00
400	2	9	0.22
425	3	5	0.60
450	7	7	1.00
Σ	31	80	

* Only drags at depths where captures have been made in this area are included.

$$C/f = 31/80 = 0.388.$$

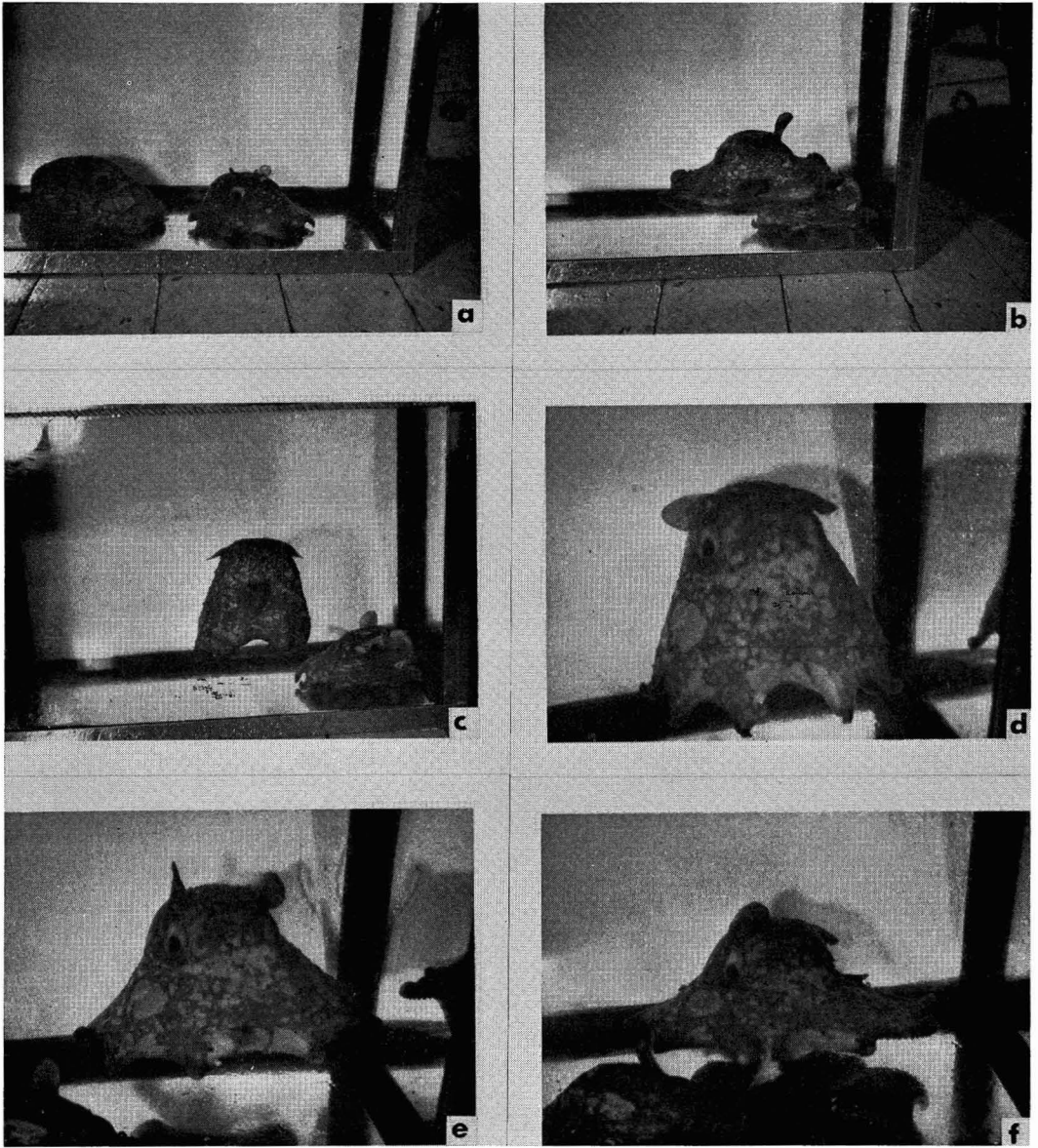


FIG. 3. Behavior of live *Opisthoteuthis californiana* in an aquarium. *a-d*, swimming off bottom; *e-f*, setting back to bottom.

the vessel rolled, flapjack devilfish moved back and forth in the aquarium. A small *Octopus* sp., placed in the aquarium at the same time, had no trouble "hanging on" or clinging to the aquarium. The inability of the flapjack devilfish to attach to the aquarium glass, even though the males possess many greatly enlarged suckers, sheds more light on the degeneracy of this

cephalopod group and allows questions as to the function of these enlarged suckers. Assuming that these animals behaved normally despite the fact that they had been brought to the surface, it would not seem that this cephalopod can apply itself to a rock as stated by Borradaile et al. (1935:602), or attach to a projecting substratum as stated by Ijima and Ikeda (1895:

328), or is a creeping or clinging form as Verrill (1896:74) thought.

The highly specialized dorsal arm-pair of the males, regarded as the hectocotylized or nuptial arms, with their 6-7 greatly enlarged globular suckers distally, is characteristic of this species (Berry, 1955:221-222). This condition, of course, reaches its highest degree of development in the mature males; but even with the smaller immature males, three of which are present in this series, the distal suckers of the dorsal arm-pair are slightly enlarged. The sexes are, therefore, always distinguishable by this male nuptial arm character.

The internal structuring of this group is more striking than the external. Many organs are completely lost with no new structures replacing them. There are no salivary glands, no ink sac, no well defined crop, no radula, and no right oviduct (Berry, 1952:185). The stomach is quite small, and is divided into two parts; the liver is bilobed. The reproductive apparatus of both sexes is massive, and in mature individuals it constitutes a considerable portion of the visceral mass (Figs. 4 and 5).

Color

In life the coloration differed slightly from that reported by Berry (1949:24 and 1952:186) for preserved material ("... light dull drab, very heavily concentrically streaked with dull dark reddish brown . . ."), being a more evenly distributed dark reddish brown with breaks of light blue in the background coloration.

There was no concentric streaking as Berry observed for preserved material, and no aboral spotting as is reported for several congeners (Berry, 1918:286, 291; Sasaki, 1929:11; and Verrill, 1883:114). The oral surface was likewise dark reddish brown but without the breaks in the background coloration. This dark reddish brown coloration diffuses to a pale reddish tan color in the region of the cirri, suckers, and the central portion of the arms. After preservation the coloration was similar to that reported by Berry (1952:186).

The light blue breaks in the reddish brown coloration were due to splitting of the delicate outer skin of the aboral surface by trawl abrasion and from the spines of fish in the catch. This point was verified by purposely splitting the outer skin of freshly caught specimens. The light blue coloration became evident immediately. The degree of skin splitting varied with the individual, some being so badly abraded that the brown coloration was almost completely wanting.

Fecundity

Egg counts and measurements were made on three mature females captured at different times of the year. These data are presented in Table 3.

The total egg count varied from 225 to 475 eggs. In none of the individuals examined was the egg size uniform; it varied from less than one mm to 11 mm in greatest diameter (length). The largest egg examined measured 11 by 6 mm, which is slightly larger than the largest

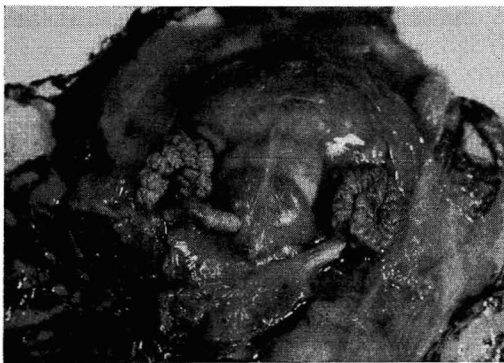


FIG. 4. Reproductive organs of a mature female *Opisthoteuthis californiana*, $\times .45$.



FIG. 5. Reproductive organs of a mature male *Opisthoteuthis californiana*, $\times .65$.

TABLE 3

FECUNDITY OBSERVATIONS ON THREE MATURE FEMALE *Opisthoteuthis californiana* TAKEN ON THE COLUMBIA RIVER TRACKLINE

DATE	DEPTH (fathoms)	SIZE (mm)	TOTAL VOLUME EGGS (ml)	NO. EGGS ≥ 3 mm (length)	NO. EGGS < 3 mm (length)	% LARGE EGGS	LARGEST EGG (mm) LENGTH \times WIDTH
3-7-62	425	210 \times 150	5.0	98	150-200	33-39	10 \times 5
7-3-61	425	255 \times 250	3.3	125	150-200	46-56	9 \times 5
12-11-61	375	340 \times 330	23.0	324	125-150	68-72	11 \times 6

egg reported by Berry (1952:185) (9 by 5 mm).

The percentage of large eggs (greater than or less than 3 mm in length was arbitrarily chosen to designate large and small eggs, respectively) differed for each individual, with a range from 33 to 72%. Likewise, the volume of eggs in the ovary ranged from 3.3 ml to 23.0 ml. In the specimen with 72% large eggs (egg volume of 23.0 ml), the majority of the large eggs were located in the upper part of the ovary with ripe eggs spirally arranged in a compact group just under the oviducal gland (Fig. 4). In no case was there any indication of stalk development.

The extent of egg development was used as circumstantial evidence indicating the season of ovulation. The highest degree of egg development was observed in a female containing ripe eggs, captured on the 11th of December. The least development was found for the March capture, while the female captured in July showed an intermediate degree of development. With only three samples represented no unequivocal conclusions are permitted, but indications are that ovulation occurs during the winter.

Food

The stomachs of eight specimens were examined to ascertain the food organisms (Table 4). Only one stomach was found completely empty and the remaining stomachs contained very little, never more than 5 ml. The material in greatest abundance was crustacean remains, mostly small mysids (approximately 7 mm in length) and large copepods. Only one non-crustacean organism was found, a polychaete; and this was partially digested and positive

identification was not possible. A few amphipods, isopods, and a masticated shrimp, probably a hippolytid or crangonid species, were also recognized. No quantities of mud were mixed in with the stomach contents, but a few sand grains were found in the stomach of the Unimak Island specimen. In some stomachs a brown organic material was found mixed with the food, but the exact composition of this material is not known. Fecal remains left in the aquarium by the live individual appeared to contain this same material.

The above summary of gut-contents partially substantiates the speculation by Berry (1952:187) that this species feeds mainly on micro-plankton or detritus swept down the disc by the radial series of cirri toward the mouth. The detrital element of its diet has not been substantiated, but the presence of the small crustaceans in the gut verified the planktonic feeding habit. The size of the plankton indicates that the animal is more of a macro- than a micro-plankton feeder.

A few mysids found in the esophagus of one individual were entire, as were most of those found in the first stomach of the others. Only one organism was noticeably bitten, the small hippolytid or crangonid shrimp. Thus it appears that except for a few of the larger organisms the majority were taken entire and not first reduced by the strong beak. As Robson (1925:1348-1349) has suggested, the food is probably ground down in the muscular first stomach and digested in the second, instead of being partially comminuted by the radula with preliminary digestion in the crop, as occurs in species that possess the latter two structures.

Locomotion

Observations made on live individuals in an aquarium revealed a most interesting locomotory pattern. Although most octopods, with the exception of the pelagic species such as *Cirro-teuthis*, move about principally by two methods, "crawling" and rapid ejection of water from the siphon, the flapjack devilfish, owing to its unusual anatomical features, is not able to move effectively by these means. The very weak suckers and the loss of free arm movement due to webbing prevent crawling; and the reduction in the mantle aperture consequent to the posterior placement of the siphon greatly decreases the effectiveness of the siphon as a locomotory organ.

The principal means of progression, as observed in the aquarium, was by opening and closing of the webbed "umbrella" together with fin movement. The general pattern of this method of locomotion, which was analogous to that of a jellyfish, is seen in Figure 3 *a-f*.

From a resting state the animal initiated movement by extreme opening of the umbrella (Fig. 3*b*). This caused the oral surface to take on a convex shape with the arms curved slightly upwards and anteriorly. Following this, the umbrella was closed by a

powerful downward stroke, which reduced the opening into the concavity of the now closed umbrella to about one-half the diameter of the animal (Fig. 3*c*). This action forced the animal off the bottom by (1) the actual contact of the downward thrusting arms with the bottom and (2) the interaction of the closing oral surface with the water. This pattern of opening and closing the umbrella was repeated so that the animal remained off the bottom. The closing action was about twice as rapid as the opening. With each stroke the devilfish would move from 4 to 12 inches depending on the thrust of the closing stroke, and the tempo and direction of movement. The swimming motion was observed to progress as rapidly as one stroke every two seconds, although the usual tempo was once every four seconds. With movement at the higher rate the animal was carried to the surface of the aquarium in three to four strokes. Subsequent to termination of swimming, the animal opened its umbrella into the convex shape, thereby descending slowly (Fig. 3*f*). When swimming the animal occasionally made partial strokes instead of complete ones.

With contraction of the umbrella a jet of water was ejected from the siphon (Fig. 3*c*). This jet could be directed by the siphon left

TABLE 4

STOMACH CONTENTS OF EIGHT *Opisthotenthis californiana* COLLECTED IN THE NORTHEAST PACIFIC

DATE	DEPTH (fathoms)	LOCATION	ANIMAL SIZE (mm)	STOMACH VOL. (ml)	CONTENTS
5-14-61	425	Gulf of Alaska	350 × 340	<1	crustacean remains including 1 amphipod; some sand grains
7-3-61	425	off north Oregon coast	255 × 250	<1	nothing which could be made out
12-11-61	335	off north Oregon coast	420 × 380	empty
12-11-61	375	off north Oregon coast	280 × 260	2	crustacean remains; 3 mysids approx. 7 mm long
12-11-61	375	off north Oregon coast	340 × 330	4	8 mysids, largest 10 mm; 4 amphipods, 9 copepods, 2 isopods, 1 crangonid or hippolytid shrimp approx. 22 mm
3-7-62	425	off north Oregon coast	190 × 180	1	crustacean remains, mostly copepods
3-7-62	425	off north Oregon coast	210 × 150	3	same as above plus partly digested polychaete?
8-30-62	250	off north Oregon coast	250 × 240	1	crustacean remains, mostly copepods

or right, to the posterior, or down. But because the ejection was feeble, it added only slightly to the net movement. Verrill (1896:74) and Berry (1952:184) were correct in stating that the siphon appeared to be too small to be used for efficient locomotion.

The two dorsal fins, which heretofore had been considered as "inefficient looking" (Berry, 1952:183), moved in a highly coordinated manner, augmenting the effect of the umbrella movement. (This is consistent with their morphology, inasmuch as they are supported by a cartilaginous rod and possess ample musculature.) Balancing and orientation of the animal were the main functions of the fins, but during certain phases of swimming they appeared to assist locomotion.

When at rest the fins were positioned at the side of the head just behind the eyes in a down position, with the free-edge which contained the cartilaginous rod posterior (Fig. 3*a left*). The fins could point slightly posteriorly but never anteriorly.

Fin movement began with an up-stroke (Fig. 3*a right*). The supported posterior edge led on this stroke, resulting in the fin moving through the water with the least resistance (Fig. 3*d*). This stroke was terminated after the fin had moved upward almost 180° (Fig. 3*e*). On the down-stroke the supported posterior edge again moved the fin, but this time the transverse axis was perpendicular to the direction of fin movement, offering the greatest surface area to come in contact with the water (Fig. 3*c*). Because of this, fin movement on the up-stroke was faster than on the down-stroke. This pattern of least resistance on the up-stroke and greatest on the down-stroke created an upward resultant force. Both fins were usually moved together in the same direction, but occasionally they were moved alternately, or one might be moved while the other was not. (Fig. 3*b, f*).

Although the basic fin movement was always the same, the axis of movement could be shifted 90° forward from the up-down to an anterior-posterior direction or to any degree between these extremes. The greatest surface area of the fin was exposed on the posterior or down-stroke. This permitted net movement in any direction from upward to forward or anterior.

Thus, by moving the fins alternately or together, and by adjusting the axis of movement and the strength of the stroke, the animal had considerable control over the direction of movement created by the powerful undulations of the umbrella. The animal might swim up, sideways, or down depending on its attitude at the time of the umbrella closing.

The tempo of fin movement was always greater than that of umbrella movement. Usually it was in the ratio of three fin strokes to every umbrella stroke, but this varied. Also, the fin movement was coordinated so that a down-stroke coincided with the closing of the umbrella.

When the animal was at rest on the bottom, fin movement usually continued, but at a slower rate and in various directions. Also, the pattern of fin movement was generally alternate.

As the swimming undulations of the umbrella ceased and the animal settled to the bottom, the tempo of fin movement increased considerably in an alternate pattern. This increased fin activity probably helped to slow the animal's descent and provided for better attitude control.

The alternate fin movement pattern was surprising. Considering that both fins are supported by a common cartilaginous rod, this rod must be able to undergo considerable torsion for the fins to be moved alternately.

The use of photofloods to take pictures revealed a negative light reaction. Prior to turning on the photofloods, the animals actively moved in the aquarium under subdued light. When the photofloods were turned on, activity continued for 15 to 20 seconds and then all movement ceased. As long as the photofloods were on, the animal remained perfectly still.

Several authors have hinted at the existence of the pulsating locomotory pattern from knowledge of the gross morphology of the species. Ijima and Ikeda (1895:328) stated "... that alternate closure and expansion of the arms is of much greater moment to *Opisthoteuthis* than to most other Cephalopods, since the ejection of water from the comparatively small branchial chamber and siphon must be of subordinate significance." Berry (1952:184) offered similar speculations, stating that the

undulations or opening and closing of the arms might be quite significant. Robson (1929:22, 28) also stated that the web is probably used in locomotion. He commented that the web becomes deep independently in the Cirromorpha and the abyssal Octopodidae and that this convergent resemblance is suggestive of some identity of adaptation.

Verrill (1896:74-75), by deducing function from structure, put forth several possibilities as to means of movement for members of this group that conflict with the above opinions. He felt that *Opisthoteuthis* was a crawling or creeping form, having concluded that the union of the eight arms with the web formed a disc-like ventral foot, and therefore, was analogous to that of a chiton or limpet. The small lateral fins indicated to him that *Opisthoteuthis* could swim, more or less, and that undulatory movements of the lateral edge of the pedal disc might be possible. But he felt that a pulsating swimming motion by the umbrella, similar to that of *Cirrotheuthis*, would not be possible because adhesion of the arms and web to the body would prevent their free use. It can be seen that, by approaching function in this manner, his deductive reasoning was, for the most part, erroneous.

Certain Octopodidae have also been observed to swim by opening and closing the web. Verrill (1882:373) states that *Bathypolypus arcticus* swims in this manner, as does *Eledone moschata*, according to Orbigny and Ferussac (1840). Wells (1962:3) comments that *Cirrothauma* employs a jellyfish-like locomotion. Another species of *Eledone*, *E. cirrosa*, uses its web only when sinking downwards (Isgrove, 1909:472-473).

The main function of the swimming pattern could be to facilitate travel from one area to the next. This is indicated by the fact that one specimen was apparently captured three fathoms above the bottom in an off-bottom trawl. If bottom currents were strong enough, the animal could travel considerable distances by swimming off the bottom and allowing the currents to carry it passively. Shorter movements could be made by orientation forward together with umbrella pulsations. A combination of these two methods would allow the greatest forward progress.

Another possible function might be food concentration. At times the animals were observed just off the bottom of the aquarium making incomplete swimming motions. Could this possibly represent a method whereby food is concentrated by means of the produced currents? Once the food was concentrated, the animal could settle to the bottom with the umbrella open. This might trap the food organisms under the umbrella and permit feeding.

An escape function is indicated from the reactions of provoked individuals in an aquarium: they moved rapidly upwards when prodded.

Habitat

It is generally felt that members of this group (with the exception of *O. medusoides*) are bottom dwellers. This conclusion has been deduced by several authors through arguments from structure to habitat (Berry, 1952:184; Dollo, 1912; and Meyer, 1906). The pigmentation, depressed form, dorsal eyes, and general body shape all are indicative of a benthic existence. Observations and data from this paper are further supporting evidence for a benthic existence.

Even though numerous drags along the Columbia River trackline have been made shallower and deeper than the known bathymetric range of this species, the captures of flapjack devilfish are restricted to the interval from 250 to 450 fathoms (457-823 m). This indicates that the species is benthic; for if it were pelagic, and if the trawl captured these animals while being set or hauled, we would expect to have captures over a wider depth range. The one off-bottom capture, which might be argued as being pelagic, should still be classed as a bottom capture, because of its proximity to the bottom.

Extensive midwater trawling off central and northern Oregon by Oregon State University personnel has not produced a single flapjack devilfish (Dr. William Percy, written communication). This is further supporting evidence of a non-pelagic existence.

Observational data further support a benthic existence. The negative buoyancy, together with the manner in which the animal swims off the

bottom and settles down again, are supporting evidence.

Although the animal is primarily a bottom dweller, it is doubtful that it burrows in the mud. The locomotory behavior of specimens in an aquarium, the capture of one specimen just off the bottom, and the lack of mud and infauna in the gut imply epibenthic existence. Although most of the food organisms recovered from the gut were not epi- or infauna, indicating a truly benthic feeding habit, none appeared morphologically to be pelagic.

Hydrographic data have been taken coincident with some of the captures of *O. californiana*. Bottom water temperature ranged from 4.6 to 5.8° C, and salinity was approximately 34.1 ‰, and bottom type consisted primarily of greenish silt, occasionally mixed with small amounts of sand and clay. Since this bottom type is associated with a smooth bottom which is, therefore, more conducive to trawling, flapjack devilfish may inhabit rocky areas which have not as yet been sampled.

Authors in the past have classified *Opisthoteuthis* as an abyssal animal (Dollo, 1912 and Meyer, 1906). According to Hedgpeth (1957: 21) the limits of the abyssal region are from 2000 or 3000 m (1092–1622 fathoms) downward to about 6000 m (3241 fathoms). The upper limit may better be defined as the region in which the temperature never exceeds 4° C. Bruun (1957:643) remarks that in the Atlantic Ocean this temperature is not reached until about 2000 m (1082 fathoms), whereas in the Indian and Pacific oceans it is as high as 1500 or 1000 m (811 or 541 fathoms). If we note the upper limit of the abyssal region in the areas of capture, then we must conclude that *Opisthoteuthis* has not been taken in the abyssal zone. With few exceptions, captures of *Opisthoteuthis* have been reported from the continental slope. These exceptions were a few specimens of *O. depressa* taken on the continental shelf off Japan at the higher latitudinal limits of this species' range (Sasaki, 1920: 170) where bottom temperatures are lower (Dr. Felix Favorite, personal communication); and one specimen of *O. californiana* captured off Alaska.

Evolutionary Considerations

From what is known of the morphology and habits of *Opisthoteuthis*, most authors have felt that members of this group are highly evolved, exhibiting numerous degenerate conditions (Berry, 1952; Dollo, 1912; Meyer, 1906; Robson, 1925 and 1929; and Verrill, 1896). The evolutionary significance of some of these conditions is not thoroughly understood and is questioned by Robson (1929).

The following observations are further additions to the concept of specialization and degeneration for *Opisthoteuthis*: (1) the presence of large suckers which are ineffective for holding on, and (2) a pulsating swimming motion through use of the web, together with highly coordinated fin movement.

The adaptive significance of the deepening of the web convergently in many of the Octopodidae is suggested by the locomotory pattern exhibited by *Opisthoteuthis* and others (*Bathypolypus arcticus*, *Eledone moschata*, *E. cirrosa*, *Cirrotoeuthis*, and *Cirrothauma*). All have an extended web and use it in some phase of swimming. When the behavior patterns of more deep-webbed species are known, we probably will find that the extension of the web is primarily a locomotory adaptation.

SUMMARY

1. Thirty-nine records of the flapjack devilfish, *Opisthoteuthis californiana*, from off the coasts of Oregon, Washington, and Alaska are reported.

2. The known geographic range of this species is extended from northern California to the Aleutian Islands, Alaska, and the known bathymetric range is now defined from 68 to 450 fathoms (124–823 m).

3. Males occur in shallower water than females, and there is an indication that the males move seasonally, being found in shallower water during the summer. The overall sex ratio appears to be close to 1:1.

4. At the depths of greatest availability (375 and 450 fathoms [686 and 823 m]) off northern Oregon a catch rate of one specimen per one-hour drag was recorded.

5. Observations on living animals revealed that the general appearance was more nearly a bell-shape than a plano-convex disc, with the

eye prominences not noticeable; that at rest there was a horizontal curvature of the distal portion of the arms anteriorly and that the oral surface was not completely in contact with the bottom; that the suckers were ineffective or not used by the animal to hold to the bottom; that contraction and expansion of the umbrella together with coordinated fin movement were the means of movement, with ejection of water from the siphon being of very minor importance; and that the color in life was dark reddish brown with the bluish blotches being the result of rough treatment in the trawl. There was no concentric streaking.

6. Hectocotylization of the dorsal arm-pair can be detected in all males, regardless of maturity.

7. The total egg count of mature females examined ranged from 225 to 475 eggs, with the largest egg found measuring 11 by 6 mm at the greatest diameters. Ovulation was tentatively concluded to occur in the winter.

8. Gut-content analysis showed that these animals feed on small crustacea, mostly large copepods and small mysids. A brown organic substance was found in several stomachs.

9. The benthic existence of this species was further substantiated from catch records and observational data.

the presence of the large ineffective suckers

10. The specialized locomotory behavior and further substantiate the degenerate and specialized nature of *Opisthoteuthis*.

ADDENDUM

After the present paper was submitted, Dr. D. B. Quayle, Fisheries Research Board of Canada, Nanaimo, B. C., provided the author with the following two additional records from the northeastern Pacific: (1) Off Unimak Island, Alaska (53°39'N, 164°44'W) at 238–252 fathoms on August 13, 1964; and (2) off northern Washington (47°58'N, 125°47'W) at 505–510 fathoms on September 6, 1964. The latter record extends the bathymetric range to 510 fathoms.

REFERENCES

BERRY, S. STILLMAN. 1918. Report on the Cephalopoda obtained by the F.I.S. "En-

deavor" in the Great Australian Bight and other Southern Australian localities. Biol. Results Fishing Experiments carried on by F.I.S. "Endeavor," 1909–1914, Fisheries 4 (5):201–298.

———. 1949. A new *Opisthoteuthis* from the eastern Pacific. Leaflets in Malacology 1(6): 23–26.

———. 1952. The flapjack devilfish, *Opisthoteuthis*, in California. Cal. Fish and Game 38(2):183–188.

———. 1954. The male flapjack devilfish. (Abstract) Amer. Malacol. Union, Ann. Rept. 1953:29.

———. 1955. The male flapjack devilfish. Cal. Fish and Game 41(3):219–224.

BORRADAILE, L. A., et al. 1958. The Invertebrata. 3rd ed. Univ. Press, Cambridge. 795 pp.

BRUUN, ANTON F. 1957. Deep sea and abyssal depths. In: Treatise on marine ecology and paleoecology. Geol. Soc. Amer., Memoir 67, Vol. 1, Ecology, Chap. 22:641–672.

DOLLO, L. 1912. Les céphalopodes adoptés à la vie nectique secondaire et à la vie benthique tertiaire. Zool. Jahrb. Suppl. 15(1):105–140.

HEDGPETH, JOEL W. 1957. Classification of marine environments. In: Treatise on marine ecology and paleoecology, Geol. Soc. Amer., Memoir 67, vol. 1 Ecology, Chap. 2:17–28.

IJIMA, I., and S. IKEDA. 1895. Description of *Opisthoteuthis depressa* n. sp. J. Coll. Sci., Imp. Univ., Tokyo, 8:323–335.

ISGROVE, A. 1909. *Elydone*. L.M.B.C. Memoirs, London (not seen).

MEYER, WERNER T. 1906. Die anatomie von *Opisthoteuthis depressa* (Ijima und Ikeda). Zeits. wiss. Zool. 85(2):183–269.

D'ORBIGNY, A., and A. DE FERUSSAC. 1840. Histoire naturelle générale et particulière des céphalopodes acétabulifères, vivant et fossiles. Paris, 1834–48 (not seen).

ROBSON, G. C. 1925. The deep-sea Octopoda. Proc. Zool. Soc. London, 1925, Part 2:1323–1356.

———. 1929. A monograph of the recent Cephalopoda, based on collections in the British Museum (Natural History) Part I, Octopodinae, 236 pp. Part II, The Octopoda (excluding the Octopodinae) (1932), 359 pp. London.

- SASAKI, MADOKA. 1920. Report on cephalopods collected during 1906 by the United States Bureau of Fisheries Steamer "Albatross" in the northwestern Pacific. Proc. U. S. Nat. Mus. 57(2310):168-170.
- 1929. A monograph of the dibranchiate cephalopods of the Japanese and adjacent waters. Hokkaido Imp. Univ., Sapporo, J. Coll. Agric., vol. 20, 357 pp. (suppl. no.).
- THIELE, J. 1915. See Chun, C., 1915.
- VERRILL, A. E. 1882. Report on the cephalopods of the north-eastern coast of America. Rept. U. S. Comm. Fish. for 1879. Part 7: 211-445.
- 1883. Supplementary report on the "Blake" cephalopods. Bull. Mus. Comp. Zool., Harvard College, 11(5):105-115.
- 1896. The Opisthoteuthidae. A remarkable new family of deep sea Cephalopoda, with remarks on some points in molluscan morphology. Amer. J. Sci. II, art. 11:74-80.
- WELLS, M. J. 1962. Brain and behavior in cephalopods. Stanford Univ. Press, Stanford, California. 171 pp.