The Biology of the Marquesan Sardine, *Sardinella marquesensis*[1]

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ABSTRACT: Data and samples obtained in the Marquesas Islands from 1954 to 1960 form the basis of this report. Various morphological traits of the Marquesan sardine, *Sardinella marquesensis,* are described, and measures of their variation are given. These sardines were found mostly in bays with clear to slightly turbid and clear-green to brownish-green water and with substrate of sand, rock, coral rubble, or a combination of these. The composition of their stomach contents was very similar to that of plankton obtained in sardine habitats. Ten of the 35 species of fish taken with sardines in the seine are probable predators of the latter. Sardine behavior in the field, in captivity, and as tuna bait is noted. Parasites included hemiurid trematodes, camallanid nematodes, and an ergasilid copepod. Attainment of sexual maturity is estimated at a standard length of 84 mm. Spawning is believed to occur throughout the year. Between 1,000 and 8,000 ova are deposited at a single spawning. The sex ratio favored males. The abundance of Marquesan sardines appears to be inadequate to sustain commercial live-bait tuna vessels like those operating from California ports.

BIOLOGISTS ABOARD a research vessel of the U.S. Bureau of Commercial Fisheries from Honolulu, Hawaii, scouted the Marquesas Islands (Fig. 1) in 1954 for small fish suitable as live bait for tuna fishing. Large quantities of a sardine-like fish were seen in Taiohae Bay on the island of Nuku Hiva (Royce, 1954). This fish was also found at the other islands, where it was not as abundant nor as readily available as at Taiohae.

During the subsequent six years, scientists of the Bureau of Commercial Fisheries made 12 more cruises to the Marquesas Islands to obtain fishery and environmental data for a survey of the tuna resources in this area (Austin, 1957; Wilson and Rinkel, 1957; Wilson, Nakamura, and Yoshida, 1958; Yoshida, 1960). When the Marquesan sardines were captured for use as live bait, samples were preserved, and observations on the ecology of the sardine were made. On eight of these cruises live sardines were brought back for introduction into Hawaiian waters, where they have become established (Brock, 1960; Murphy, 1960; Hida and Morris, 1963).

The Marquesan sardine was described as a new species by Berry and Whitehead (1968) who named it *Sardinella marquesensis.* Aside from faunal and taxonomic reports, very little has been published about the Marquesan sardine. The purpose of this paper is to present information on various aspects of the biology of this species in the Marquesas Islands.

METHODS

Observations and collections were made in the course of visual surveys for live bait during daylight and while fishing for live bait during both day and night.

The visual surveys were carried out by swimmers equipped with face plates and by observers either walking in shallow water or searching from a boat in deeper water. All the swimmers and observers were experienced fishermen. When a school of sardines was seen, a size estimate in "buckets" was made and recorded. Such a bucket, a container used to handle captured sardines, contains approximately 3.5 kg (8 pounds) of fish.

In seining for live bait during the day, the techniques for locating sardine schools were sim-

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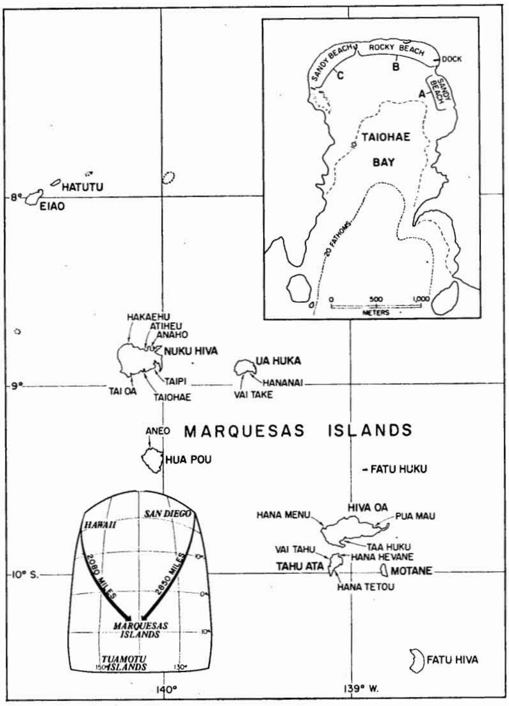

FIG. 1. The Marquesas Islands.

ilar to those used during the visual surveys. The method and gear were those of the Hawaiian skipjack fishery (June 1951). Captured sardines were placed in baitwells aboard the research vessels and were used as live bait for surface tuna fishing in the vicinity of the Marquesas.

Often the water was so turbid that the crew made "blind" sets—that is, the bait seine was set even though a school of sardines had not been sighted. Most of these "blind" sets were made in Tai Oa and in Taipi bays on Nuku Hiva, where river waters account for the turbidity. Good catches were occasionally obtained by this method.

In fishing for live bait at night, we attracted the sardines to the vessel by a floodlight. On 10 occasions, those thus attracted were captured with a lift net of the type used in night baiting in the Hawaiian skipjack tuna fishery (June 1951). The vessel generally was anchored in water about 12 meters deep off shores where sardines had been seen in the shallows during the day.

Each time a bait set was made, the date, time, locality, water temperature, and water clarity were recorded. Fork-length measurements, sex determinations, and estimates of sexual maturity on about 25 sardines from each successful set were made aboard the vessel. Another 25 sardines plus specimens of other species caught in the set were preserved in 4 percent formaldehyde and brought back to the laboratory.

Laboratory procedures were as follows: Specimens were removed from the 4 percent formaldehyde and allowed to soak in fresh water for at least 1 hour, after which they were immersed in an alizarin solution until the fin rays were clearly stained. They were then placed on their right side so that morphometric measurements and meristic data could be taken uniformly on the left. After the measurements and counts were made, the specimens were dissected for sex determination. Stomachs and intestines were preserved for food studies, and ovaries for spawning and fecundity studies. Then the flesh on the left side was removed and the vertebrae counted.

Stomachs and intestines were opened with dissecting needles and their contents examined under a dissecting microscope. After the organisms were identified, their numbers were estimated.

In the measurement of ova, a section was cut from the middle of the right ovary. The ova were teased out of the section onto a Sedgwick-Rafter counting chamber. Diameters of the first 25 ova, beginning at the upper left corner of the chamber, were measured with an ocular micrometer with a calibration of 60 micrometer units equal to 1 mm. The measurements were taken at right angles to the lines of the counting chamber, on the assumption that axes of ova (which often were not spherical) were oriented randomly.

For the estimation of fecundity, the paired ovaries were dried on absorbent paper, then weighed to the nearest 0.001 gram on an analytical balance. A section was cut from one ovary, and the ovaries were weighed again to determine the weight of the section. The ova from the section were counted in a Sedgwick-Rafter counting chamber under a dissecting microscope. If two size groups were present, excluding primordial ova, they were easily differentiated, and separate counts were made of "large" and of "small" ova.

Occasional water samples from areas where bait was caught were taken for salinity determinations at the laboratory.

Plankton samples were obtained with a net constructed of netting with aperture width of 0.31 mm. The diameter of the mouth of the net was 45 cm. All hauls were made at the surface for a period of 10 to 15 minutes during the day. The organisms in these plankton collections were identified under a dissecting microscope and their abundance estimated.

MORPHOLOGY

The Marquesan sardine (Fig. 2) is a silvery fish with dark pigmentation on its dorsal and dorsolateral surfaces. Its body is laterally compressed and has a rather sharp ventral edge formed by spinous scutes. The imbricated cycloid scales are easily lost during handling of the fish. The largest Marquesan sardine in our records is 129 mm standard length, the smallest 28 mm.

To obtain measures of variations in certain selected morphological characteristics, approximately 10 specimens from each sample brought back to the laboratory were examined. Measurements were taken of the standard length, head length, and depth of body. The ventral scutes, longitudinal scales, transverse scales, dorsal fin rays, anal fin rays, pectoral fin rays, pelvic fin rays, gill rakers below the angle (lower limb) of the first gill arch, and vertebrae—including the urostylar vertebra (see Gosline, 1961)—were counted. Bilateral structures were counted on the left side only. Criteria used for the measurements and counts were those used by Storey (1938).

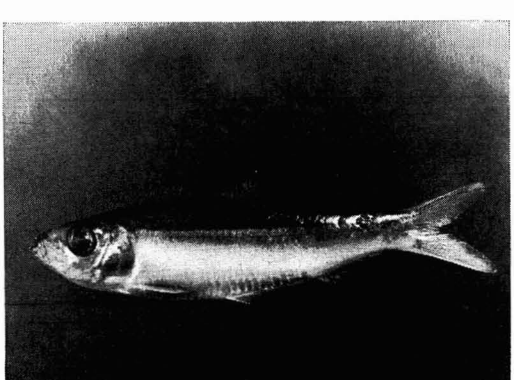

FIG. 2. The Marquesan sardine.

The variations in meristic data and the frequency of each count are listed in Table 1. The

TABLE 1

MERISTIC VARIATIONS OF THE MARQUESAN SARDINE

MERISTIC CHARACTER AND COUNT		FREQUENCY
Ventral scutes (n = 454)		
	15 + 12 = 27	1
	15 + 13 = 28	1
	16 + 12 = 28	18
	16 + 13 = 29	25
	16 + 14 = 30	1
	17 + 11 = 28	7
	17 + 12 = 29	232
	17 + 13 = 30	167
	17 + 14 = 31	2
Dorsal fin rays (n = 152)		
	15	4
	16	95
	17	51
	18	2
Anal fin rays (n = 151)		
	17	7
	18	35
	19	86
	20	23
Pectoral fin rays (n = 152)		
	13	10
	14	120
	15	22
Pelvic fin rays (n = 152)		
	7	1
	8	146
	9	5
Transverse scales (n = 146)		
	9½	7
	10½	49
	11½	84
	12½	6
Longitudinal scales (n = 145)		
	37	1
	38	2
	39	5
	40	15
	41	33
	42	30
	43	29
	44	15
	45	12
	46	2
	47	1
Vertebrae (n = 459)		
	41	20
	42	432
	43	7

count of the ventral scutes varied according to the number of scutes anterior to and posterior to the origin of the pelvic fins, the total ranging from 27 to 31. The fin ray counts varied from 15 to 18 in the dorsal fin, 17 to 20 in the anal fin, 13 to 15 in the pectoral fin, and 7 to 9 in the pelvic fin. The scales often were difficult to count because the overlapping pattern lacked uniformity, particularly in the area of the caudal peduncle. Also, because the scales are deciduous, scale pockets rather than scales frequently were enumerated. The transverse scale count ranged from 9½ to 12½, and that of the longitudinal scales ranged from 37 to 47. No difficulties were encountered in counting vertebrae. They ranged from 41 to 43. The ranges in most of these counts were greater than those reported by Berry and Whitehead (1968), owing to the larger sample size shown in Table 1.

Both head length and depth of body showed linear relationships to standard length. No sexual dimorphism was found. The regressions computed from measurements of 457 sardines ranging from 28 to 129 mm standard length are expressed below, where X = standard length, Y = head length, and Y′ = depth of body, all in millimeters:

$$Y = -0.11 + 0.2665X$$
$$Y' = -2.18 + 0.2881X$$

Because standard length was measured in the laboratory and fork length in the field, a regression of standard length on fork length was computed from measurements taken on 170 preserved specimens ranging from 28 to 115 mm standard length. The formula is as follows, where Y = standard length and X = fork length, both in millimeters:

$$Y = -1.31 + 0.9493X$$

The numbers of gill rakers on the lower anterior arches of 458 sardines were plotted against standard lengths. As shown in Figure 3, the number of gill rakers and its variation increased with size of fish. Differences in number of gill rakers between sexes were not evident.

The shape and grooving of the scales of the sardine varied according to the region of the body from which they were taken. Those from the ventrad prepectoral region were generally

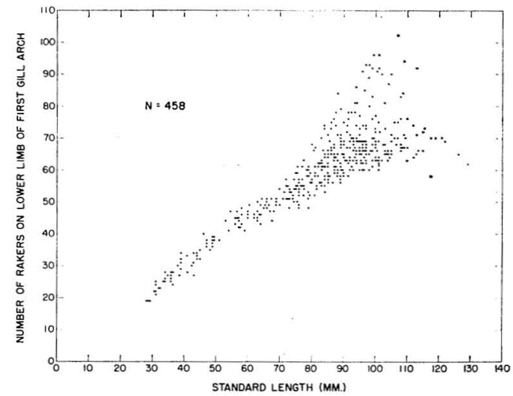

FIG. 3. Relationship between number of gill rakers and standard length of 458 Marquesan sardines.

shaped like an ellipse cut in half along its short axis, the rounded edge being anterior; one continuous transverse groove and many irregular ones were in the anterior half of the scale. Scales from the dorsum cephalad of the dorsal fin generally were round, with notches in the posterior edge; they had a single continuous transverse groove and several interrupted transverse grooves, the most anterior of which tended to be radial. Scales from the midlateral midsection (Fig. 4) also were generally round, and were feebly notched at the posterior edge; a single continuous transverse groove was immediately posterior to several pairs of interrupted transverse grooves. Scales from the midlateral caudal peduncle generally were similar to those of the midlateral midsection, although some were more oval; some but not all

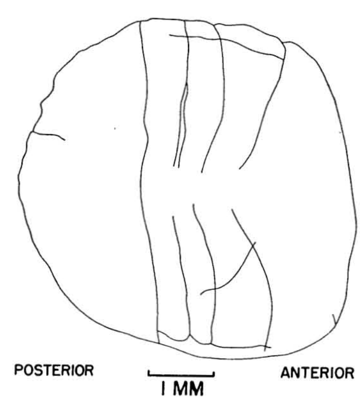

FIG. 4. Scale from midlateral midsection of a Marquesan sardine 93 mm standard length.

of the scales of the caudal peduncle had a single continuous transverse groove.

HABITAT

Marquesan sardines were found in habitats which ranged from white sand beaches where the water was clear and almost oceanic in salinity to bays where the water was very turbid and low in salinity and the substrate muddy and covered with debris. Large numbers of sardines most often were found in bay waters which were clear to slightly turbid and clear-green to brownish-green, and where the substrate was composed of sand, rock, coral rubble, or a combination of these materials.

Temperature in localities where bait was found varied from 25.1° to 31.1° C, and salinity ranged from 8.55‰ to 36.03‰ (Table 2). As a comparison, 48 samples of oceanic water in the Marquesas had a temperature range of 26.8° to 29.5° C and a salinity range of 35.58‰ to 36.15‰.

Plankton samples were obtained at most of the localities where sardines were found (Table 2). About 60 percent of the samples were taken in Taiohae Bay.

In tabulating the occurrence and abundance of items found in plankton samples (Table 3), the criteria used for determining plankter abundance were based on the estimated percentage (by number) of the sample that the item constituted: *Swarming,* 75 percent or more; *numerous,* at least 25 percent but less than 75 percent; *common,* at least 10 percent but less than 25 percent; *scarce,* less than 10 percent.

Swarming of copepods, pteropods, mysids, megalops, and salps was found in 16 instances. Of the 99 "numerous" occurrences (excluding sand grains), 67 were either crustaceans or molluscs. Of the 157 "common" occurrences, 94 were either crustaceans or molluscs. Thus, crustaceans and molluscs were the most abundant components of the plankton in sardine habitats.

Some of the items found in the samples are not typical plankters, for example, anemones and sponges, which generally are sessile. Others, such as grass seeds, ants, beetles, chironomids, and millipedes, are terrestrial and probably were brought into sardine habitats by streams and winds.

Tabulation of the plankton data by season—23 summer, 26 fall, and 13 winter samples (none for spring)—indicated a general uniformity in composition. Except for the occurrence of a few swarms, no conspicuous abundance of any organism in any of the three seasons was noted. Among items in more than 10 percent of the plankton samples (Table 3), only isopods were not present in all three seasons (in summer only).

Sardines were found to be most abundant at Taiohae Bay (Fig. 1). The bay was horseshoe shaped with a southern entrance. Sardines were located and captured in the areas marked A, B, and C in the figure. In June 1958, area A had a beach of fine white sand, with several coral heads located about 70 meters offshore at the southern end. The coral heads had their bases in the sand and were about 2.5 meters high. The beach extended approximately 375 meters. Area B covered a distance of approximately 900 meters; for the most part its shoreline was covered with smooth black rocks ranging from less than 2 cm to 25 cm in diameter. A few large boulders were offshore in water 3 to 4.5 meters deep. Area C was approximately 650 meters long and had a white sand beach, as in area A. Its southern end was bounded by a coral bank. The other areas of the bay shoreline were characterized by rock cliffs and wave-cut benches. Areas A, B, and C were the only locations in the bay with beaches and surf. Sardines often were observed in the surf. A few small streams emptied into the bay, but, except after heavy rains, water in the bay was clear.

FOOD

Stomachs of 493 sardines were examined. The occurrence and abundance of the items found in these stomachs are summarized in Table 4. Criteria used in designating the degree of abundance were based on the estimated fullness of the stomach and the estimated percentage (by number) of the sample that the item constituted: *Numerous,* stomach at least one-fourth filled and the item 25 percent or more of the contents; *common,* stomach at least one-fourth filled and the item 10 percent or more but less than 25 percent of the contents, or stomach

TABLE 2

SUMMARY OF ENVIRONMENTAL DATA COLLECTED IN BAYS OF THE MARQUESAS ISLANDS WHERE SARDINES WERE FOUND, 1954–60

ISLANDS AND BAYS WHERE SARDINES WERE FOUND	NUMBER OF PLANKTON SAMPLES	NUMBER OF SALINITY AND TEMPERATURE MEASUREMENTS	SALINITY RANGE (‰)	TEMPERATURE RANGE (°C)	QUANTITY OF SARDINES AND WATER CLARITY OBSERVED ON INDICATED DATE		
					DATE	BUCKETS	WATER CLARITY
Nuku Hiva							
Taiohae	37	45	35.43–36.03	25.6–31.1	1-24-57	1,200	clear
Tai Oa	9	10	23.48–35.67	27.8–29.6	—	—	—
Taipi	7	9	8.55–35.89	25.1–30.6	2-4-57	none	very turbid
Anaho	3	2	35.70–35.90	26.2–28.5	1-31-57	500	clear
Atiheu	1	—	—	—	—	—	—
Hakaehu	—	—	—	—	—	—	—
Ua Huka							
Hananai	1	2	33.53–35.73	27.9–28.3	1-29-57	<1	intermediate
Vai Take	1	—	—	—	1-29-57	<1	intermediate
Hiva Oa							
Taa Huku	1	7	33.58–35.90	25.5–28.3	1-27-57	40	intermediate
Pua Mau	—	—	—	—	—	—	—
Hana Menu	1	—	—	—	—	—	—
Tahu Ata							
Vai Tahu	—	—	—	—	—	—	—
Hana Tetou	—	4	35.62–36.03	27.5–28.9	2-25-57	23	clear
Hana Hevane	—	—	—	—	2-25-57	11	clear
Hua Pou							
Aneo	1	—	—	—	—	—	—

TABLE 3

OCCURRENCE AND ABUNDANCE OF ITEMS IN 62 PLANKTON SAMPLES TAKEN DURING DAYLIGHT IN BAITING AREAS
(Asterisks denote presence in plankton but not in stomachs)

ITEM	NUMBER OF SAMPLES IN WHICH ITEM WAS:				NUMBER OF SAMPLES IN WHICH ITEM OCCURRED	PERCENTAGE OCCURRENCE
	SWARMING	NUMEROUS	COMMON	SCARCE		
Copepods	9	42	9	1	61	98.4
Pteropods	2	7	18	20	47	75.8
Appendicularians	0	8	20	18	46	74.2
Chaetognaths	0	5	16	22	43	69.4
Fish ova	0	5	11	27	43	69.4
Gastropods (excluding heteropods and pteropods)	0	2	24	17	43	69.4
Polychaetes	0	1	2	40	43	69.4
Mysids	1	9	18	12	40	64.5
Shrimps	0	1	6	32	39	62.9
Megalops	1	3	8	22	34	54.8
Amphipods	0	2	3	24	29	46.8
Salps	3	3	9	12	27	43.5
Sipunculid larvae	0	0	2	24	26	41.9
Fish larvae	0	0	0	23	23	37.1
Pelecypods	0	0	6	15	21	33.9
Phytoplankters (not diatoms)*	0	10	2	4	16	25.8
Siphonophores*	0	0	0	15	15	24.2
Sand grains	0	3	0	11	14	22.6
Fish scales	0	0	0	13	13	21.0
Grass seeds	0	0	0	10	10	16.1
Stomatopods	0	1	0	8	9	14.5
Algae (filamentous)	0	0	0	7	7	11.3
Ants	0	0	0	7	7	11.3
Cypris	0	0	1	6	7	11.3
Isopods	0	0	0	7	7	11.3
Medusae*	0	0	0	7	7	11.3
Ctenophores*	0	0	1	5	6	9.7
Trochophores*	0	0	0	3	3	4.8
Beetles*	0	0	0	2	2	3.2
Chironomid larvae	0	0	0	2	2	3.2
Chironomid flies*	0	0	0	2	2	3.2
Foraminiferans	0	0	0	2	2	3.2
Hydroids	0	0	0	2	2	3.2
Phyllosoma*	0	0	0	2	2	3.2
Sponges*	0	0	0	2	2	3.2
Squid*	0	0	0	2	2	3.2
Anemones*	0	0	0	1	1	1.6
Diatoms	0	0	0	1	1	1.6
Echinoid larvae*	0	0	0	1	1	1.6
*Halobates**	0	0	0	1	1	1.6
Heteropods	0	0	0	1	1	1.6
Millipedes*	0	0	0	1	1	1.6
Ostracods	0	0	0	1	1	1.6
Polyclads*	0	0	0	1	1	1.6
Shrimp ova*	0	0	1	0	1	1.6

less than one-fourth filled and item 10 percent or more of the contents; *scarce*, other than these.

The most important food items were crustaceans and molluscs, particularly copepods, which were found most frequently and in greatest abundance. Copepods are a major food item for

TABLE 4

OCCURRENCE AND ABUNDANCE OF ITEMS IN 493 MARQUESAN SARDINE STOMACHS
(Asterisks denote presence in stomachs but not in plankton samples)

ITEM	NUMBER OF STOMACHS IN WHICH ITEM WAS: NUMEROUS	COMMON	SCARCE	NUMBER OF STOMACHS IN WHICH ITEM OCCURRED	PERCENTAGE OCCURRENCE
Copepods	155	109	126	390	79.1
Sand grains	49	78	64	191	38.7
Pelecypods	4	24	83	111	22.5
Gastropods (excluding heteropods and pteropods)	0	3	79	82	16.6
Cypris	1	15	55	71	14.4
Pteropods	0	21	50	71	14.4
Amphipods	23	8	38	69	14.0
Megalops	16	11	24	51	10.3
Shrimps	0	4	39	43	8.7
Salps	19	14	7	40	8.1
Polychaetes	3	6	26	35	7.1
Appendicularians	17	8	4	29	5.9
Mysids	9	9	11	29	5.9
Fish ova	0	1	26	27	5.5
Sipunculid larvae	2	4	19	25	5.1
Fish scales	0	3	16	19	3.9
Chaetognaths	0	7	9	16	3.2
Barnacle nauplii*	12	1	1	14	2.8
Grass seeds	0	0	13	13	2.6
Algae (filamentous)	2	2	6	10	2.0
Fish larvae	0	0	8	8	1.6
Invertebrate ova	6	0	0	6	1.2
Ostracods	0	0	5	5	1.0
Foraminiferans	0	3	1	4	0.8
Ants	0	0	3	3	0.6
Chironomid larvae	0	0	3	3	0.6
Heteropods	0	1	2	3	0.6
Hydroids	0	0	3	3	0.6
Isopods	0	2	2	2	0.4
Aphids*	0	0	1	1	0.2
Diatoms	1	0	0	1	0.2
Euphausiids	0	0	1	1	0.2
Stomatopods	0	1	0	1	0.2
Wasps*	0	0	1	1	0.2

many clupeids (Davies, 1957; Hand and Berner, 1959; Radovich, 1952; Suarez Caabro, Duarte, and Reguera, 1961; Yamashita, 1955).

Observations of their predation upon copepods in the baitwells of our research vessel and the occurrence of relatively large crustaceans, such as euphausiids, mysids, and amphipods, in their stomachs indicate that the sardines are active particulate feeders. On the other hand, the abundant occurrence of extremely small organisms, such as barnacle nauplii and diatoms, in individual stomachs indicates filter feeding. Most probably, the Marquesan sardine is both a particulate and filter feeder. Similar conclusions have been reached concerning the feeding habits of other clupeids (Davies, 1957; Hand and Berner, 1959).

Further evidence of filter feeding was the presence of sand grains in the stomachs. At first the ingestion of sand was believed to have been forced upon the sardines during seining when the bottom was agitated. However, sand grains were sometimes present throughout the digestive tract. Since sardines often were observed in the surf zone, where the sandy bottom is continually stirred, it seems more reasonable to conclude that sand grains are ingested incidentally during filtration of the water for food organisms. Sand grains also have been found in the stomachs of *Sardinella fimbriata, S. longiceps,* and *S. albella* from India (Venkataraman, 1960).

Since most of the fish scales in the stomachs were sardine scales, their presence may have resulted largely from crowding in the bait seine. The fish may have ingested the deciduous scales in their attempts to pass water over their gills. Only occasionally was a scale found in the intestine.

As the lists of items in Tables 3 and 4 indicate, sardines fed primarily upon zooplankton. Of the items in Table 3, 16 were not found in stomachs, but one of these (chironomid flies) was found in the intestines. Some plankters (medusae, phyllosomas, polyclads, siphonophores, and squids) were not expected in stomachs, because they were too large to be ingested. *Halobates,* a marine insect, may be difficult for sardines to capture because it travels swiftly on the surface of the water. Barnacle nauplii were the only plankters found in stomachs but not in plankton samples. The mesh size of the plankton net was large enough to allow them to pass through.

The only items present in the intestines but not in the stomachs were adult chironomids. The larvae of these flies were in several stomachs.

Separation of the food data by seasons showed only slight variations in the diet of the sardine. Of the items which occurred in more than 5 percent of all stomachs examined, pteropods were absent in the spring samples and salps and appendicularians in winter ones. Sipunculids were present only in fall samples. The numbers of stomachs examined for the Southern Hemisphere summer and fall (164 and 227, respectively) were much greater than for winter and spring (41 and 61).

Stomach contents of small sardines (less than 60 mm standard length) and large sardines (greater than 95 mm standard length) were compared for a study of variations in diet with size. The data were similar for the two size groups. Of the items contained in more than 5 percent of all stomachs examined, only pteropods and appendicularians were absent in the smaller sardines, but collections from which these occurrences were recorded did not include sardines from the smaller length group.

ASSOCIATED FAUNA

Following is a list of the 35 species of fishes and 5 of invertebrates captured with sardines in the seine. (Some fishes were identified only to family. Question marks denote questionable specific identification; asterisks denote probable predators of sardines.)

FISHES

- Acanthuridae
- *Acanthurus triostegus marquesensis*
- *Aetobatis narinari*
- *Albula vulpes*
- Aulostomidae
- Belonidae
- Blenniidae
- *Bothus leopardus*
- *Caranx ignobilis**
- *Caranx lugubris**
- *Caranx melampygus**
- *Caranx* sp.*
- *Carcharhinus melanopterus*
- *Chanos chanos*
- *Chorinemus sancti-petri**
- *Euthynnus affinis**
- *Gnathanodon speciosus**
- Hemiramphidae
- *Kuhlia sandvicensis* (?)
- Kyphosidae
- *Lutjanus kasmira**
- *Lutjanus vaigiensis**
- Mugillidae
- Myctophidae
- *Neomyxis chaptali*
- *Platycephalus* sp.
- *Polydactylus sexfilis*
- *Scarus* sp.
- *Selar crumenophthalmus*
- *Sphyrna lewini*
- Tetraodontidae
- *Trachinotus bailloni* (?)*
- *Upeneus parvus* (?)
- *Upeneus* sp.

INVERTEBRATES

- Cubomedusae
- Kona crab (Raninidae)
- Lobster (Palinuridae)
- Sea urchins
- Unidentified crab

The list includes two sharks, the blacktip (*Carcharhinus melanopterus*) and the hammerhead (*Sphyrna lewini*), and an eagle ray (*Aetobatis narinari*). Most of the fishes are common inshore, shallow-water inhabitants, but *Euthynnus affinis* and the myctophids are generally inhabitants of waters beyond the immediate vicinity of the shoreline.

Ten of the fishes taken probably prey on the sardine. Predator designations are based on general knowledge of the predacious habits of these species and not from direct observations or from examinations of stomach contents. Except for *E. affinis* and the two species of *Lutjanus,* all are members of the family Carangidae.

The invertebrates captured in the seine were primarily inhabitants of the bottom except, of course, the cubomedusae. These benthic forms were captured as the lead-weighted bottom of the seine was dragged over the substrate.

BEHAVIOR

Like other members of the family Clupeidae, the Marquesan sardine is a schooling species. The size of a school varies from a few individuals to many thousands.

In Taiohae Bay (Fig. 1), large schools often were observed under or near the dock. In response to a disturbing stimulus, such as a passing shadow, they exhibited the characteristic reactions of schooling fish by a unified movement away from the source of disturbance. The sardines under the dock were often in mixed schools with mackerel scad (*Selar crumenophthalmus*) of about the same length. Also, schools of young goatfish (*Upeneus* sp.) sometimes were seen with sardines, but generally the goatfish were near the bottom, whereas the sardines and scad were in midwater.

The sardines proved to be satisfactory as live bait for surface tuna fishing. The major desirable qualities of live bait (such as liveliness, returning to the ship after being thrown overboard, and a silvery or shiny appearance) were common in these fish. When thrown into the water, they made quick dashes in random directions. Then they formed a school and swam toward the vessel. Schools of sardines often were seen leaping out of the water, usually in the vessel's wake, while being pursued by skipjack tuna (*Katsuwonus pelamis*) or by yellowfin tuna (*Thunnus albacares*). Seizure of a sardine in midair by both species was observed several times.

Sometimes mortality of sardines was extremely high when they were confined in baitwells aboard our research vessels. But those that adapted to captivity circled steadily and uniformly within the confined area and were easily induced to feed upon ground flesh of skipjack tuna and bread crumbs. During feeding, the pattern of circular movement became disrupted completely.

On several occasions, sardines in the baitwells were observed to feed on copepods by bending their bodies into the shape of an S, then suddenly extending themselves and lunging forward to engulf the prey. We have observed this same behavior in the nehu (*Stolephorus purpureus*), an engraulid baitfish used by commercial skipjack tuna fishermen in Hawaii. This behavior has also been reported for *Anchoa mitchelli* and *Harengula pensacolae* by Breder and Krumholz (1943) and in larval *Dorosoma petenense* by Gerdes and McConnell (1963).

Attempts to attract sardines at night with a 300-watt, 120-volt bulb immersed just below the surface of the water were not successful. Perhaps the light was too intense. As mentioned previously, during darkness, sardines could be attracted to diffused light directed into the water from a floodlight mounted on the bridge of the vessel. The sardines which gathered in the diffused light did not form schools of uniformly oriented individuals. Rather, they appeared to form loose aggregations (as described by Breder, 1959).

PARASITES

An immature trematode belonging to the family Hemiuridae was found in the stomach and the air bladder (a pneumatic duct connects the air bladder to the posterior part of the stomach). This trematode was found occasionally in the intestine also. Of 443 sardines examined, 250 (56.4 percent) were infested.

A camallanid nematode (*Spirocamallanus* sp.) also was found in the intestine of 130 (29.3 percent) of the 443 sardines.

The only other parasite found was a copepod of the family Ergasilidae. It was embedded in the gill filaments of 1 of 458 sardines examined.

SIZE AT MATURITY AND SPAWNING

Ovaries from 208 sardines, 33 to 129 mm standard length, were examined in the laboratory, and the maturity of 1,057 female sardines was determined aboard our research vessels in the Marquesas Islands.

The ovaries of the smallest females were tubular, dark brown, and approximately equal in diameter. The left ovary from the larger females was almost always larger than the right. The surface of the larger ovaries was granular and light brown.

Three types of ova were recognized under the microscope: small, clear cells with the nucleus readily apparent; intermediate cells with a limited amount of yolk and the nucleus visible in some; and large cells, completely filled with granular yolk, in which the nucleus was not visible. The largest ova gave no sign of becoming clear or possessing an oil globule, nor did any ova have the appearance of being resorbed. Small, clear cells were present in all the ovaries. The intermediate ova were not necessarily present when the ovary contained the larger ova.

Four representative frequencies of ova diameters were found (Fig. 5). (Clear ova less than 0.1 mm in diameter were present in all ovaries, but they were not measured.) Sample A is a frequency distribution of ova in which some yolk was present but which had not become completely opaque. In sample B, all of the ova were opaque, and in C, two groups were present —the smaller of intermediate opacity and the larger of complete opacity. Sample D included two groups of opaque ova. The distribution in sample D was believed to represent a condition nearest spawning.

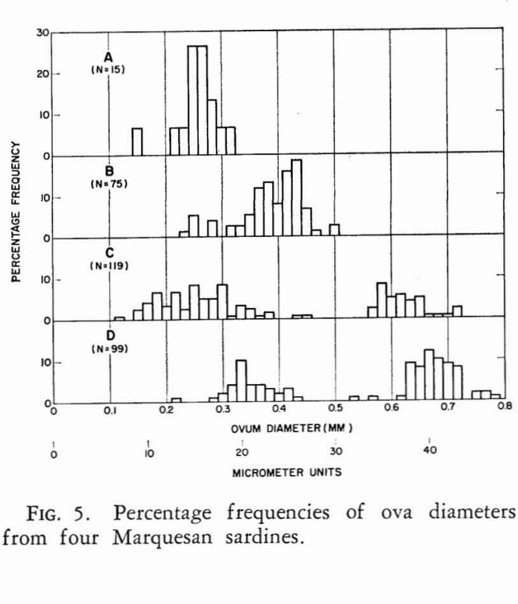

FIG. 5. Percentage frequencies of ova diameters from four Marquesan sardines.

To establish inferences about spawning, the size of the most advanced ova was determined since the ova in the largest modal group would most likely be extruded in a single spawning.

Measurements of ova from the center of the right ovary, the center of the left ovary, and the anterior part of the left ovary were compared to determine whether ova in different portions of the ovaries were different in size. A group comparison (Snedecor, 1956, p. 91) indicated no differences.

Also, to determine the minimum sample size necessary to find a mean expressive of the largest group of ova, a large number of ova were measured from a single ovary. On the basis of Tchebysheff's test for inequality (Mood, 1950, p. 135), the mean from a sample of 25 ova was found to express the true population mean within ± 0.05 mm (95 percent confidence). This accuracy was considered adequate for this study.

The diameters of 25 ova from a center section of the right ovary of 198 sardines were measured. The ovaries of 63 contained only the small, clear cells less than 0.1 mm in diameter.

In Figure 6, the standard length of a sardine is plotted against the mean diameter of the largest group of ova in its ovary. The curvilinear expression

$$Y = 102.5 - 70e^{-13.1X},$$

where $Y =$ standard length in millimeters and $X =$ mean diameter of the largest group of ova in millimeters, was calculated from the data. If sexual maturity in female sardines is defined as that stage where yolk begins to be added to the ovum when the ovum is about 0.1 mm in diameter, then the smallest size at maturity of the female Marquesan sardine is estimated as about 84 mm standard length.

This estimate was similar to results from judgments of maturity made aboard our research

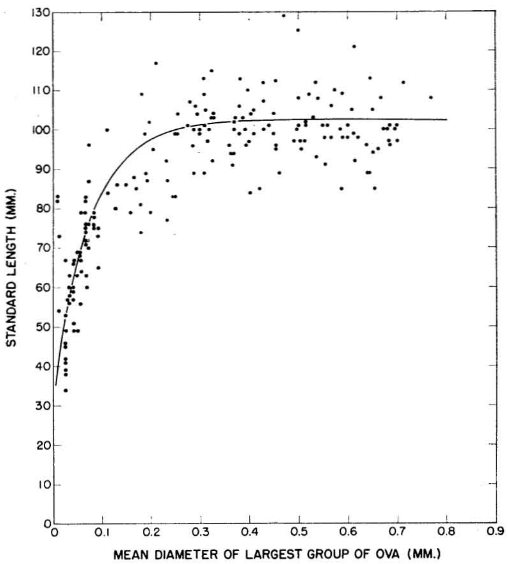

FIG. 6. Relationship between standard length and mean diameter of the largest group of ova of 198 Marquesan sardines.

vessels while capturing bait in the Marquesas Islands. Female sardines were judged on shipboard to be in one of the following four stages of maturity: *Immature,* ovary small, threadlike; *developing,* ovary enlarged, no ova visible; *ripe,* ovary large, turgid, ova visible to naked eye; *spent,* ovary highly vascular and flaccid. The smallest ripe or spent sardines in the latter two categories were 85 and 84 mm fork length (79 and 78 mm standard length), respectively (Table 5).

To estimate the spawning period, females with ova diameters of 0.1 to 0.6 mm and greater than 0.6 mm were grouped into 2-month periods of capture (Table 6). Females with the largest ova were present in all the periods for which samples were available. Female sardines judged to be ripe and spent also were found in all of the sampling periods. The Marquesan sardine is therefore believed to spawn throughout the year. Evidence of any seasonal preponderance of spawning was not found. The data in Table 6 show no significant heterogeneity (Snedecor, 1956, p. 225).

The presence of more than one group of maturing ova in the Marquesan sardines suggests multiple spawning. Inferences on spawning frequency within a specific period based on such evidence are questionable, however (MacGregor, 1957).

TABLE 5

SIZE FREQUENCY OF FEMALE MARQUESAN SARDINES WITH OVARIES IN FOUR STAGES OF MATURITY

FORK LENGTH (mm)	STAGE OF MATURITY			
	IMMATURE	DEVELOPING	RIPE	SPENT
50–54	1	0	0	0
55–59	5	0	0	0
60–64	2	0	0	0
65–69	4	0	0	0
70–74	19	1	0	0
75–79	39	1	0	0
80–84	72	2	0	1
85–89	102	12	3	2
90–94	66	23	10	5
95–99	47	30	11	22
100–104	28	78	74	17
105–109	5	46	65	31
110–114	3	47	61	19
115–119	0	24	27	2
120–124	0	9	13	5
125–129	0	6	10	0
130–135	0	6	1	0
Totals	393	285	275	104

FECUNDITY

Six ovaries were selected for an estimation of fecundity. The selection was not random since an attempt was made to obtain as broad a range of fish sizes as possible. A count was made of ova which were classed as intermediate or larger, since many of the small, clear cells

TABLE 6

PERCENTAGE OF FEMALE MARQUESAN SARDINES WITH OVA 0.1–0.6 MM AND WITH OVA LARGER THAN 0.6 MM IN DIAMETER DURING DIFFERENT 2-MONTH PERIODS

MONTHS	MEAN OVA DIAMETER		NUMBER OF FISH
	0.1–0.6 mm %	$>$ 0.6 mm %	
Jan.–Feb.	86	14	49
March–April	87	13	23
May–June	80	20	39
July–Aug.	—	—	0
Sept.–Oct.	75	25	12
Nov.–Dec.	56	44	9

could not be separated from the ovarian tissue. In ovaries with two size groups of ova, estimates of the number in the larger modal group were used. These figures were plotted against the standard length of the fish (Fig. 7). From these data, it was estimated that between 1,000 and 8,000 ova are released in a single spawning.

SIZE AND SEX COMPOSITION

The percentage occurrences of size groups of sardines captured in 10 bays of the Marquesas are presented in Figure 8. A comparison of the size compositions from the three bays on the south side of Nuku Hiva is of interest: Tai Oa, the westernmost; Taiohae, in the center; and Taipi, the easternmost. Significant numbers of small fish were taken only at Tai Oa. An explanation may be that ova and larvae are carried to the west by prevailing currents of the area, and the juveniles, returning toward the land, find the westernmost bay first. The picture is somewhat similar in the three bays, Hakaehu, Atiheu, and Anaho, on the north side of Nuku Hiva; the largest proportion of small fish was taken in Hakaehu, the westernmost bay.

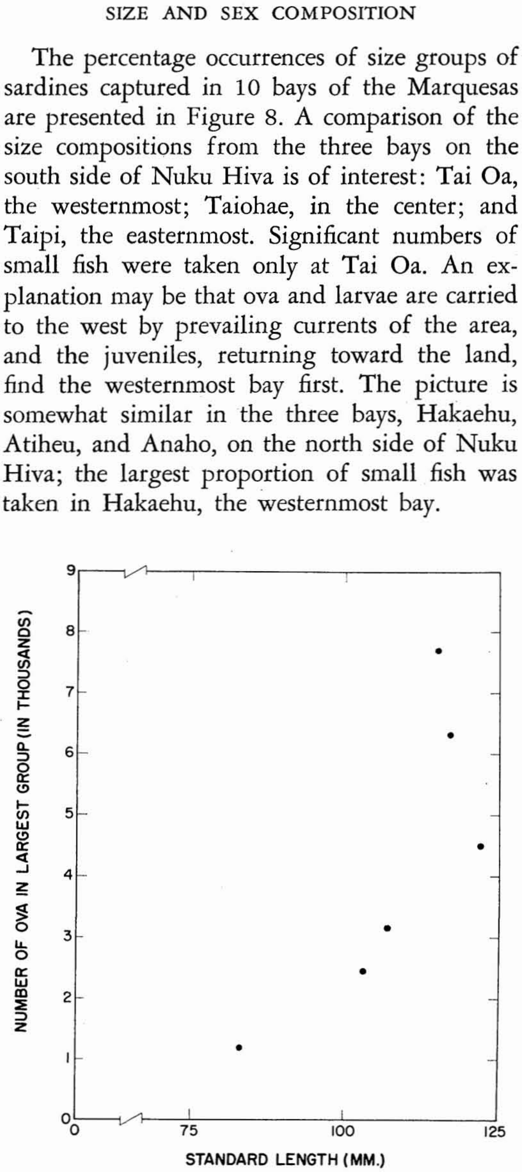

FIG. 7. Relationship between number of ova in the largest modal group and the standard length of six Marquesan sardines.

Frequencies of the fork lengths of samples taken at Taiohae, where most of the sardine samples were obtained, are presented for each sex in Figure 9. Two conclusions can be drawn: (1) Growth cannot be deduced from a study of the progression of modes in the length-frequency distributions. This statement is consistent with the conclusion that spawning occurs throughout the year. (2) The mean length of females in most of the samples is greater than that of males. Greater average sizes of females suggest that females grow faster than males. Faster growth of females has been noted in other clupeids (Ben-Tuvia, 1960*a*) also.

Of the sardines examined grossly during the cruises to the Marquesas, 2,286 were sufficiently developed so that their sex could be determined. Of these, 1,237 (54 percent) were males. The number of males was significantly greater than that of females (chi-square = 15.5; $p < 0.0001$). Predominance of one sex (not always males) is common in other clupeids (Ben-Tuvia, 1960*b*; Matthews, 1960; Nair, 1960; Postel, 1960; Soerjodinoto, 1960) and is often associated with size and season (Ben-Tuvia, 1960*a*; de Jager, 1960; Nair, 1960).

The possibility that females approaching their spawning period attract males was examined. Under this hypothesis, females in samples containing a greater number of males should have ova in advanced stages of development, and females in samples containing a greater number of females should not. Sexual maturity in single-school samples indicated that this possibility was unlikely. Ripe females occurred just as frequently in samples with a higher percentage of females as in those with a higher percentage of males.

DISTRIBUTION AND ABUNDANCE

During January and February 1957, visual surveys were made of eight bays in the Marquesas Islands. The total estimated quantity of sardines observed was slightly over 1,774 buckets (about 6,200 kg). The localities and the quantities of sardines seen are summarized in Table 2.

The visual survey method of determining the presence and quantity of sardines in shallow water had some obvious defects, the most ap-

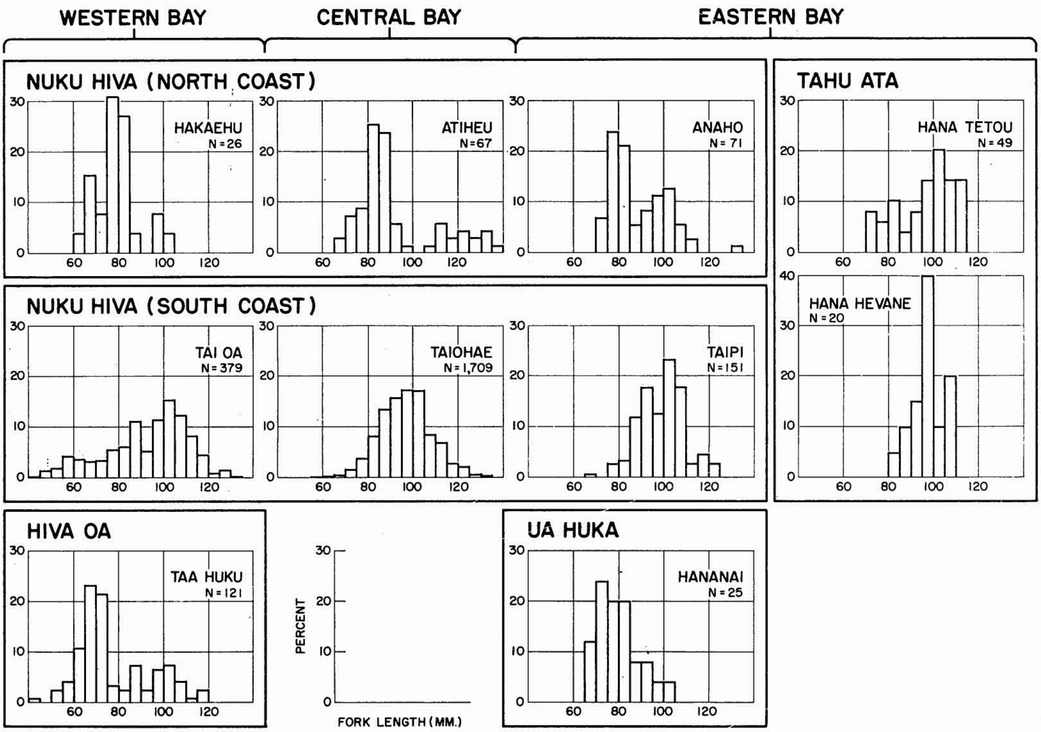

FIG. 8. Percentage occurrences of size groups of Marquesan sardines captured at 10 localities.

parent of which was the possibility that some unknown portion of the sardines in a given bay was in deeper water below the range of visibility. Another factor which may have greatly influenced the quantity of sardines seen during the surveys of the bays was the turbidity of the water. Two of the bays of the island of Nuku Hiva—Taipi and Tai Oa—receive relatively large amounts of fresh water discharged by rivers entering them. A development of brackish-water phytoplankton there rendered effective visual surveys impossible. Bays with water of intermediate turbidity were Taa Huku on Hiva Oa, and Vai Take and Hananai on Ua Huka, where the survey results were probably underestimates. Bays where clear water permitted the most reliable estimates of the quantity of sardines in shallow water were Taiohae and Anaho on Nuku Hiva, and Hana Tetou and Hana Hevane on Tahu Ata.

The relationship of the sardines captured with a lift net in relatively deep waters (12 meters) at night to those caught with a seine in shallow water (3 meters or less) during day is unknown. Comparison of the lengths of the fish taken by the two methods did not reveal any difference.

Most of the seining for sardines was done at Taiohae, Nuku Hiva. The sardines were used as live bait for surface tuna fishing in Marquesan waters (some were taken to Hawaii for transplantation). Records of catch and effort for sardines in the bay from January 24, 1957, to June 12, 1958 (Table 7), show that during the latter part of this period, the availability of sardines in shallow waters of Taiohae Bay was considerably reduced.

From May 13, 1958, through June 12, 1958, a shore party was stationed at Taiohae, and 24 visual surveys of its shallow waters (Fig. 1) were made. The estimated visible population ranged from 2 to 53 buckets per day and averaged 22 buckets per day.

The crew of our research vessel attempted to catch bait in Taiohae on eight days during this same period. The catches ranged from nil to 60 buckets and averaged 27 buckets per day. On no occasion was the crew able to catch a sufficient quantity of sardines at Taiohae to satisfy

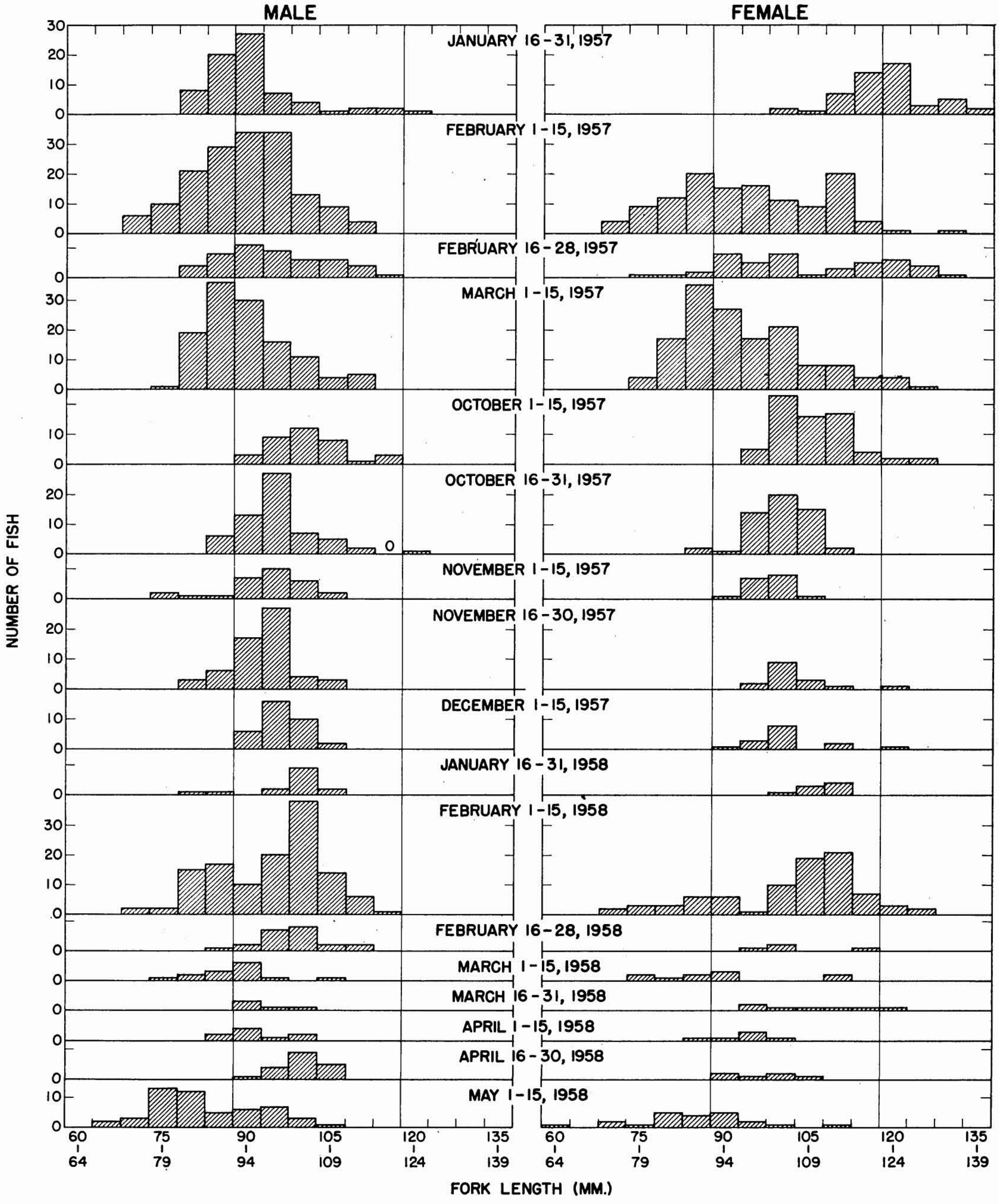

FIG. 9. Fork length frequencies of Marquesan sardines from Taiohae Bay, Nuku Hiva.

fully the requirement for live bait for the type of fishing practiced.

On January 24, 1957, a population of 1,200 buckets of sardines was estimated to be present in Taiohae Bay (Table 2). On June 9, 1958, the last visual survey in Taiohae gave an estimate of 32 buckets of sardines. This apparent reduction in the population was believed to have resulted from our catches in the bay. To our knowledge, no other fishing mortality was

TABLE 7

RECORD OF MARQUESAN SARDINE CATCHES BY SEINING IN TAIOHAE BAY FROM JANUARY 24, 1957 TO JUNE 12, 1958 (No sets in April–September 1957)

MONTH AND YEAR	CATCH (BUCKETS)	EFFORT (SETS)	CATCH PER EFFORT
1957			
January	76	6	12.7
February	340	22	15.5
March	414	14	29.6
October	206	9	22.9
November	233	9	25.9
December	100	3	33.3
1958			
January	102	8	12.8
February	311	27	11.5
March	73	21	3.5
April	144	14	10.3
May	196	29	6.8
June	1	2	0.5
Total	2,196	164	—

inflicted on them during this period. Thus, replenishment of sardines by recruitment and growth in Taiohae Bay appears to be inadequate to provide sufficient live bait on a sustained basis for a commercial live-bait tuna vessel like those operating from ports in southern California.

SUMMARY

1. Data on the biology of the Marquesan sardine obtained on cruises of Bureau of Commercial Fisheries research vessels to the Marquesas Islands and from samples examined at the Biological Laboratory, Honolulu, form the basis of this report.

2. Data were obtained in the field by visual surveys during daylight and by fishing for live bait during both day and night. In the laboratory, morphological measurements and counts were taken, stomach contents were examined, and ovaries were examined for spawning and fecundity studies.

3. Ventral scute count ranged from 27 to 31, dorsal fin rays from 15 to 18, anal fin rays from 17 to 20, pectoral fin rays from 13 to 15, pelvic fin rays from 7 to 9, transverse scales from 9½ to 12½, longitudinal scales from 37 to 47, and vertebrae from 41 to 43. Gill raker count and its variation increased with sardine size. Scales from most parts of the body had a single continuous transverse groove and several interrupted grooves.

4. Sardines were found in a variety of habitats but mostly in bays where the water was clear to slightly turbid, clear-green to brownish-green, and where the substrate was composed of sand, rock, coral rubble, or a combination of these materials. Crustaceans and molluscs were the major constituents of plankton in sardine habitats. Plankton composition did not vary among three seasons.

5. The food of sardines consisted primarily of copepods. The composition of the sardine stomach contents and plankton samples was very similar. Food varied little with season and with sardine size.

6. The fishes and invertebrates taken with sardines in seine hauls included 10 probable predators, all of which, with the exception of *Euthynnus affinis* and 2 species of *Lutjanus*, belong to the family Carangidae.

7. The occurrence of sardines in mixed schools, their satisfactory behavior as live bait for tuna fishing, their behavior in captivity, their feeding activity, and their attraction to diffused light were noted.

8. Hemiurid trematodes and camallanid nematodes were found in the digestive systems of 56.4 and 29.3 percent of the sardines, respectively. An ergasilid copepod was embedded in the gills of a single sardine.

9. No evidence was uncovered of seasonal periodicity of spawning; some females with ova of the largest size were found in all months. The size at maturity was estimated at a standard length of about 84 mm.

10. The number of ova spawned at one time by a Marquesan sardine was estimated as between 1,000 and 8,000.

11. Sardine samples from single schools taken at Taiohae Bay yielded the following conclusions: Growth could not be ascertained from progression of modes in length distributions; the mean length of females in a single school was greater than the mean length of males. An unbalanced sex ratio favored the males (54 percent).

12. The supply of sardines in the Marquesas Islands is inadequate to sustain commercial live-

bait tuna vessels like those operating from California ports.

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