REPRODUCTION, GROWTH, AND OTHER ASPECTS OF THE BIOLOGY OF THE GOLD SPOT HERRING, *HERKLOTSICHTHYS QUADRIMACULATUS* (CLUPEIDAE), A RECENT INTRODUCTION TO HAWAII[1]

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ABSTRACT

The gold spot herring, *Herklotsichthys quadrimaculatus*, was introduced to Hawaii by unknown means probably in the early 1970s and apparently spread and increased in abundance very rapidly. On the island of Oahu, it has been regularly present in inshore areas since 1976 and has been most abundant during late spring to early fall. Among adult fishes sampled, females slightly outnumbered males in seine collections by day in shallow water, but males predominated in nighttime collections from deeper water. Both sexes began to mature at 75-80 mm SL and females carried distinct size groups of nearly mature ova by 90 mm SL. Gonad to somatic weight ratios from both sexes indicated a spring-to-fall spawning season with a midsummer peak. Batch fecundity of females was 1,100-6,300. There was no direct evidence of multiple spawning, but secondary size groups of small ova were observed in some females which also carried a distinct batch of larger ova. Holding experiments showed that juveniles deposit daily growth increments on sagittae. Age estimates from increment counts of fish 17-121 mm long indicated that herring metamorphose at about 1 month, mature at 5-6 months, and probably live no more than 1 year. The reproductive life span of females appears long enough to ripen more than one batch of ova.

Only three species of marine clupeid fishes are known to occur in Hawaii. The round herring, *Etrumeus micropus*, and the sprat, *Spratelloides delicatulus*, are both native to the islands, while the Marquesan sardine, *Sardinella marquesensis*, was introduced in the late 1950s in hopes of increasing the supply of baitfish for the local skipjack tuna fishery. The introduction was successful in that *S. marquesensis* reproduced and spread throughout the islands soon afterwards, but the species never became abundant nor contributed significantly to local baitfish catches (Murphy 1960; Hida and Morris 1963).

In 1975, small clupeids began to appear regularly in Kaneohe Bay on the island of Oahu and by 1976 had become very abundant both in the bay and apparently at other areas of Oahu. Because these fishes closely resembled Marquesan sardines and no other similar species was expected to occur in Hawaii, we blithely assumed them to be *S. marquesensis*. Their sudden obvious presence and consistent occurrence in various collections for other purposes prompted us to undertake further sampling in order to investigate their biology in Hawaii.

After the study had been largely completed, careful

examination of a few specimens by W. J. Baldwin of the Hawaii Institute of Marine Biology and subsequent rechecking of our material plus more recent collections showed that we were not dealing with the Marquesan sardine, but rather with the gold spot herring, *Herklotsichthys quadrimaculatus*. No attempts to introduce *H. quadrimaculatus* to Hawaii have been reported and, although its range is uncertain due to probable misidentification in many reports, there is no evidence that it occurs naturally anywhere within ca. 3,500 km of Hawaii. Thus our study became one of an apparently inadvertently introduced species, whose introduction was considerably more successful than the more carefully planned introduction of the Marquesan sardine.

This paper summarizes available data on the introduction and spread of *H. quadrimaculatus*, briefly considers several aspects of its general biology in Hawaii, and presents results of investigations of its reproduction and growth. In the course of the latter we demonstrate that growth increments on otoliths are valid estimates of age in days as has already been shown for several temperate and tropical species including the Hawaiian anchovy or nehu, *Stolephorus purpureus* (Struhsaker and Uchiyama 1976). Although there are few comparable data on other tropical clupeids, some comparisons and contrasts of *H. quadrimaculatus*' life history pattern with those of

other species are possible. Unfortunately, we are only able to speculate about many aspects of the introduction and subsequent spread of this species in Hawaii.

METHODS

Herklotsichthys quadrimaculatus were taken at night with small purse seines in water 12-13 m deep in the southern end of Kaneohe Bay on the island of Oahu. All sets were "blind," i.e., the net was set more or less at random within the general area to be sampled, and no lights were used to attract fish prior to the set. Most herring were taken with a 61 m long by 12 m deep seine of ca. 0.3 mm square mesh. Up to several hundred juveniles and up to 12 adults were taken per set. Between September 1974 and December 1976, 99 sets were made with this net. This series was initially intended to sample the Hawaiian anchovy. Over most of this period, samples were taken at 2-3 wk intervals; the longest interval between sampling was slightly more than a month. Most adult herring were taken with a few exploratory purse seines of a larger (153 m long by 11 m deep), coarser mesh (ca. 25 mm stretch mesh netting); this purse seine was first tested in May 1975 and set at about monthly intervals between December 1975 and December 1976. Other sporadic samples were taken with both nets during 1977-79.

Herklotsichthys quadrimaculatus were found only in shallow water (≤3-4 m) during the day and were collected by a variety of methods from several locations on Oahu. Juveniles were readily captured by small beach seines or cast nets over reef flats in Kaneohe Bay; however, to obtain adults from all seasons of the year, particularly when they were absent from night purse seine collections, we used specimens from beach seining on exposed coasts on the northeast side of Oahu as well as on reef tops in Kaneohe Bay, from baited hook or three-pronged hook "snag" fishing in harbors at Haleiwa and in Kaneohe Bay, and from bait captured in Pearl Harbor by a skipjack tuna vessel.

In addition to our collections for biological analyses, we have also examined specimens caught by others from a wide variety of habitats and locations on Oahu in order to confirm that *H. quadrimaculatus* was present all around the island. We have very few data on the occurrence of *H. quadrimaculatus* elsewhere in the archipelago and thus cannot be certain that our observations apply to all Hawaiian Islands.

Inshore areas in southern Kaneohe Bay were surveyed visually by day, and the presence of gold spot herring schools, their approximate size composition,

and approximate numbers noted. Surveys were made at nearly weekly intervals from June 1978 to September 1979; prior to this time they were made sporadically and unsystematically.

Most fish were immediately preserved and held in ca. 4% formaldehyde seawater solution. Those fish used for age determination were frozen until otoliths were removed. Standard length (SL) was measured to the nearest mm and wet weight (ww) to the nearest 0.01 g after blotting dry. Dry weight was measured to the nearest 0.01 mg after 24 h at 60°C. Stomach contents of the fish were removed before drying. Sex was determined for all adults and a sample of about 200 juveniles 50-80 mm SL. Rough estimates of stomach fullness and types of prey eaten were recorded from 390 fish. When desired, gonads were dried and weighed separately. The gonad/somatic weight ratio (G/S) was calculated from the dry weight of the gonads and dry weight of the fish excluding gonads (dw_s), rather than total dry weight of the fish including gonads (dw_t).

Portions of the ovaries of mature-sized females from each month's sample were examined, and diameters of several of the largest ova measured to the nearest 0.02 mm with an ocular micrometer. For 20 females with well-developed ova, a section of the ovary containing about 200 ova >0.20 mm was teased apart and all ova >0.20 mm were measured. Preliminary data indicated no differences in ova density or size composition within or between ovaries of the same fish. The examined sections and remaining portions of the ovaries were dried and weighed separately, and the total number of ova in the largest mode was calculated from the weights of the section and remaining ovary and the ova count from the section. For 26 other females with a clearly separated mode of large ova, all ova in that mode were counted from both ovaries.

The growth increments or rings on sagittae of fish less than ca. 50 mm SL faded within a few hours to days after dissection; consequently, counts were made as soon as possible after removal from a fresh or thawed specimen. The sagittae were mounted in glycerine and rings of each counted at least three times under 100-400✕ magnification. Generally otolith rings from fish of this size were easy to discriminate and the repeated counts rarely disagreed; however, if a consistent count could not be made, the data were discarded.

The denser otoliths from fish >50 mm SL were allowed to air dry and then mounted in Euparol[3]. The

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[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

rings became clearer with time; consequently, the otoliths were stored for 2 wk, counted, and then recounted 2 wk later to confirm the first counts. On each occasion, counts were made along the rostral, postrostral, and antirostral axes, when possible. Especially prominent rings were noted and were of great use in tracking and comparing counts of the numerous closely spaced rings of large fish.

To determine if growth increments on the otoliths were formed daily, small metamorphosing herring were captured in Kaneohe Bay and held alive in shaded tanks which received a continuous flow of seawater from the bay at near ambient temperature. A subsample of the collected herring was frozen immediately after capture, and subsamples were removed from the tanks at later dates but at the same time of day (± 1 h) as the original capture. The differences in numbers of rings between fish from the different subsamples were compared with the number of days elapsed. In the first two of these experiments, the fish were fed frozen zooplankton from Kaneohe Bay 3-4 times/wk on an irregular schedule, but in the last two experiments they were fed brine shrimp once or twice daily, 6 d/wk. The fish also probably ate some plankton from the seawater supply to the tanks.

RESULTS

Appearance and General Biology

Catches of the purse seine sets indicated that the gold spot herring first appeared in Kaneohe Bay in mid-1975, but did not begin spawning in the area until 1976. No herring were taken in a total of 25 sets with the small purse seine on 12 dates between September 1974 and July 1975. The first catch was an adult taken on 23 July 1975, and 11 others (66-117 mm SL) plus a 28 mm juvenile were taken in 27 sets on 11 dates between July and December 1975. In the first six months of 1976, 28 sets on 12 dates yielded 65 fully transformed herring 45-120 mm SL—most of them adults. Two of these sets (in March and April) also collected a total of 14 herring just beginning transformation from the larval stage. Catches increased markedly in the second half of the year. A single set taken in late June 1976 took 131 transforming or small juveniles (19-37 mm SL), and almost all subsequent sets with the small purse seine took herring of a wide size range. Two experimental sets with the large seine in May 1975 caught no herring. Adults (up to 120 per set) were taken in subsequent sets in April, May, and October 1976 and June 1977.

There was general agreement between collections made by others in the bay and our visual observations that gold spot herring were not present in the bay prior to mid-1975 and that recruitment of juveniles was not substantial until 1976. Adult or near-adult herring first appeared over reef flats during the day shortly after the first purse seine catches. Although our records do not unequivocally indicate whether or not juveniles were present in 1975, large schools (thousands of individuals) of transforming herring were definitely not observed until 1976. Subsequent to 1976, transforming or small juvenile herring were observed or caught in all months of the year, but were more abundant from June to November or December. In 1976-79, adults were present in catches or observations from March to December, and except for 1979 were present in abundance primarily from May to October. Their presence was, however, sporadic even during the latter months, and in 1979 few were seen or caught at any time.

Our observations in Kaneohe Bay appear to be representative of inshore areas all around the island of Oahu. Casual reports by other scientific personnel as well as by commercial and recreational fishermen indicated that "sardines" appeared and subsequently increased markedly in abundance elsewhere on Oahu at about the same times as in Kaneohe Bay and that subsequently they were most abundant from spring to fall. Unfortunately, we did not obtain any specimens of "sardines" from other areas of Oahu until late 1976, but it is extremely unlikely that the casual observations refer to the Marquesan sardine, the only species with which the gold spot herring might be confused. We have examined specimens taken in 1976-82 from a wide variety of locations on Oahu (from day collections in the surf zone to specimens taken under night lights several km offshore) and found all to be *H. quadrimaculatus*. We find no evidence that, prior to 1975, "sardines" of any sort were ever sufficiently abundant to attract attention, and the most recent specimens of *S. marquesensis* from Oahu were taken in 1968.

During the day, the gold spot herring of all sizes in Kaneohe Bay were mostly found over sand-rubble reef flats 1-2 m deep in fairly clear water or in somewhat deeper water around piers, floating docks, etc. They were absent from these areas at night. Although our nighttime purse seine sampling was inadequate to properly consider dispersion, the catches indicated that juveniles moved into deeper water at night, but tended to remain within a few hundred meters of the reef or shore. Adults were taken routinely up to 1 km away from the nearest shallow water. We have also examined adults taken under

night lights as far as 10 km offshore in water hundreds of meters deep.

Before the appearance of the gold spot herring, the dominant pelagic planktivorous fishes in Kaneohe Bay were the Hawaiian anchovy or nehu (which is the main source of bait for the local skipjack tuna fishery) and the iao, *Pranesus insularum* (Atherinidae). Although the nehu and gold spot herring cooccurred in almost all purse seine catches and adult herring occasionally eat larval or juvenile nehu (see below), there was no evidence that the herring's appearance substantially affected the nehu population. The nighttime areas of highest abundance for the two species appear to be slightly different within the bay, and nehu by day prefer more turbid, brackish areas than do the herring. The iao population, however, appears to have been affected markedly by the herring. Prior to the appearance of herring, iao were regularly present in large numbers over shallow reef flats during the day, but since have been nearly completely replaced by herring in the same situations and are much less frequently seen.

Qualitative examination of stomach contents of gold spot herring showed that they eat a wide variety of zooplankton and indicated that they feed primarily but not exclusively at night. Fish <30 mm SL (116 examined) had eaten small (<1.0 mm) copepods almost exclusively. Those 30-80 mm SL (31 examined) also ate copepods but included larger zooplankton such as decapod zoeae, the pelagic shrimp *Lucifer chacei*, mysids, and small fish larvae. Adult herring (243 examined) ate copepods less frequently and larger zooplankton more frequently than did juveniles and also took considerably larger prey such as chaetognaths, polychaetes, shrimp, and fish (*Pranesus insularum* 23-25 mm SL and *Stolephorus purpureus* 6-31 mm SL). In one late afternoon sample of adults, the stomachs were mostly packed with what appeared to be planulae. Usually, however, both fullness and composition of prey in individual fish were variable even with the same sample; some fish contained several types of prey while others were mainly full of a single type. As with Marichamy's (1970) study of *Herklotsichthys punctatus*, we found no evidence that any sizes of *H. quadrimaculatus* eat phytoplankton. Overall, fresh prey was more frequent in fish caught at night and empty stomachs more so during the day, but fish in both conditions were found in almost every sample examined.

Gold spot herring apparently spawn mostly or entirely outside Kaneohe Bay. No eggs or larvae were found in any plankton tows taken in the bay while adult sardines were present; these tows included eight oblique tows taken during the peak spawning season in the same areas where adults had been collected. The smallest fish collected or observed were 17 mm SL and in the process of transforming from larvae to juveniles.

There were other movements of gold spot herring both within the bay and between the bay and exposed areas. Adult herring on several occasions vanished from all areas of the bay for varying periods and then reappeared with no obvious relation to any environmental factor. What appeared to be the same schools of juveniles were often observed in the same place for several days in a row, but before there was any observable change in size composition, the schools vanished—often to be replaced by another school of obviously different-sized fish. Similarly, the size composition of juveniles from purse seine catches showed no coherent seasonal trend.

Between 17 and ca. 30 mm SL, body depth of the transforming herring obviously increased relatively more rapidly than the standard length. Matsuura (1975) showed that in *Sardinella brasiliensis* the ossification of ventral scales is not completed until a similar size. For 50 gold spot herring 17-29 mm SL, the relationship between SL (mm) and dw_t (g), as determined by linear least squares regression on the logarithms, was

$$dw_t = 1.691 \times 10^{-9} \, SL^{5.200} \quad (r^2 = 0.94).$$

The relationships calculated from data for 60 juveniles 31-79 mm SL and 157 adults 80-128 mm SL were, respectively:

$$dw_t = 8.335 \times 10^{-7} \, SL^{3.377} \quad (r^2 = 0.98),$$

$$dw_t = 3.462 \times 10^{-6} \, SL^{3.044} \quad (r^2 = 0.90).$$

These differed significantly (analysis of covariance, $P < 0.01$) and indicated progressively more nearly isometric growth with increasing size. The equations for somatic weight vs. standard length differed little from those for total dry weight. Somatic weights of adult females tended to be lower than those of similar-sized males, but the difference was not significant. Wet weights of 108 fish 42-121 mm SL were related to standard length by

$$ww = 9.168 \times 10^{-6} \, SL^{3.121} \quad (r^2 = 0.99).$$

The relationship (based on linear least squares regression) between ww and dw_t for 123 fish 42-121 mm SL was

$$dw_t = 0.053 + 0.278 \, ww \quad (r^2 = 0.98).$$

Sex ratio of juveniles 50-80 mm SL did not deviate from 1:1, but there were deviations from 1:1 among larger fish depending upon time of collection. Of 348 adults from open-water night collections, the proportion of males in the total, 86.9% (95% limits: 82-91%), and in all size groups from 85 to 110 mm SL (Fig. 1) differed significantly from that expected for a 1:1 sex ratio. Males made up only 42.6% (95% limits: 37-49%) of the 392 adults from shallow-water day collections; females predominated in all size classes but one and significantly so in two (Fig. 1). The pattern in all large samples was consistent with the trend of the total collection, except for some day samples where the sex ratio was not different from 1:1. For example, a beach seine collection on a reef top in Kaneohe Bay at 1400 h in June 1977 yielded 56 males and 86 females, while a purse seine collection taken at 2000 h on the same date and 1 km away yielded 94 males and 25 females. For both the pooled collections and the above pair of samples alone, there were significant day-night differences in size composition of either sex considered separately or of the total fish collected, but there were no differences between males and females taken at the same time of day (Kolmogorov-Smirnov test, $P <$ or > 0.05, respectively). Among all the specimens examined, several females were larger (up to 128 mm) than the largest male (118 mm).

Although G/S values of 80-90 mm SL fish were higher than those of juveniles, values $>2.5\%$ in males and $>7\%$ in females were found only in fish >90 mm SL. With one exception, the largest ova from females <90 mm SL were <0.6 mm in diameter, while values for larger females ranged up to 0.9 mm. There was no trend in G/S or maximum ova diameter with female length for fish >90 mm SL; even during the spawning season (see below and Figure 3), the G/S ratios of some large females were almost as low as those of juveniles or presumably reproductively inactive females from winter. G/S of females was generally positively correlated with diameter of the largest ova (Fig. 2), but the relationship was highly variable. Fish carrying large numbers of small ova often had the same G/S as others carrying smaller numbers of larger ova.

Seasonal differences in G/S ratios of both males and females (Fig. 3) indicated that the principal spawning season is May-July and that at least some fish are fully mature or nearly so between March and October. Ova with yolk were not found in several of the females from August to October and in none of the 13 from November and December; yolked ova were present in all females examined from March through July. The few or no data from November to February do not preclude some spawning during the entire year, and, in fact, recently transformed juveniles about 1-mo-old (see below) were observed
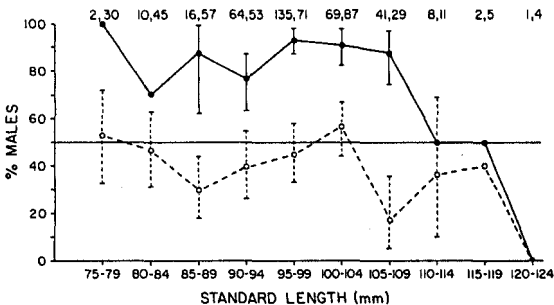

FIGURE 1.—Percentages of males among different size groups of *Herklotsichthys quadrimaculatus* for night (solid circles and lines) and day (open circles, dashed lines) collections, Kaneohe Bay, Oahu. Vertical lines indicate 95% confidence limits for observed proportions; for seven points represented by 10 or fewer fish, the limits, which included 50% (light horizontal line) were omitted for clarity. Pairs of numbers at the top represent numbers of fish of each size group examined; night collections on the left, day on the right.

Reproduction

The G/S ratios (Fig. 2) indicated that both sexes begin to mature at about 75-80 mm SL, and both the G/S and maximum ova diameters indicated that females continue to grow while ova are maturing.
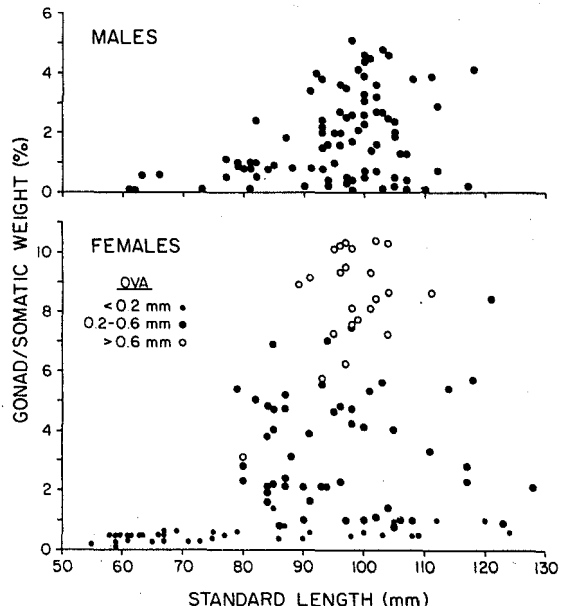

FIGURE 2.—Relationship between gonad/somatic weight and size of male and female *Herklotsichthys quadrimaculatus* collected in Kaneohe Bay, Oahu.
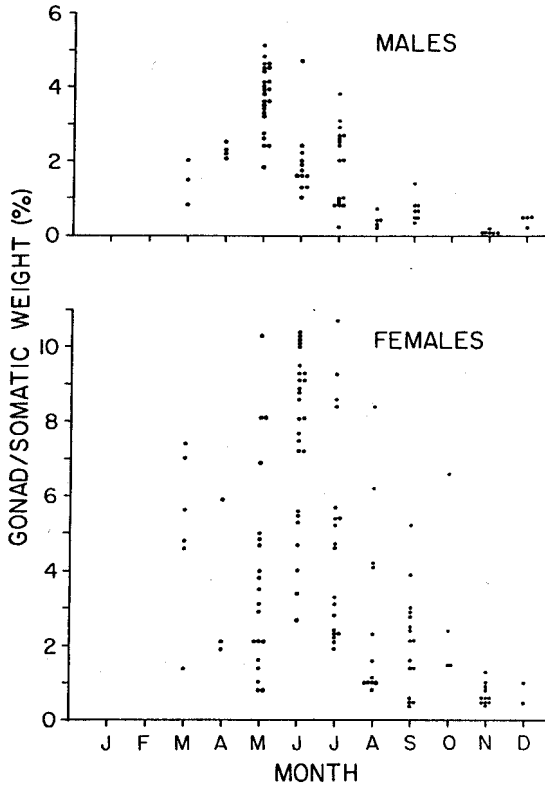
FIGURE 3.—Relationship between gonad/somatic weight and month of capture for adult (>80 mm SL) male and female *Herklotsichthys quadrimaculatus*, Kaneohe Bay, Oahu.

quesan sardine (see their figure 5). In addition to transparent ova less than ca. 0.10-0.15 mm in diameter, the ovaries of most adult female herring also contained partially yolked, semi-opaque ova ca. 0.16-0.30 mm and completely yolked, opaque ova >0.30-0.35 mm. Distinctly separated size-frequency modes of opaque ova were found from 0.30-0.40 mm to 0.60-0.90 mm. No larger, hydrated ova were found. The small, partially yolked ova were usually continuous with the smaller transparent ova; but in some fish, they formed a partially separated mode—often with opaque ova at the large end. Such modes, which were never completely separated from the smaller ova, were found in fish both with and without a separate mode of larger, opaque ova. Although a few females without a separate advanced mode had somewhat flaccid ovaries, we found no atretic ova nor any other evidence that these or any of the fish had already spawned. There was no indication of synchronous spawning or any short-term cycle; the large samples from the middle of the spawning season included females with ova in a wide range of sizes and stages of development.

In the 46 females (80-121 mm SL) with a separate advanced mode, the batch fecundity or number of ova in that mode ranged from 1,155 to 6,296 (Fig. 4). The relationships of batch fecundity to length or weight as determined by least squares linear regression were

$$F = 7,518.0 + 110.8 \; SL \; (mm) \qquad (r^2 = 0.84),$$
$$F = 172.0 + 218.4 \; ww \; (g) \qquad (r^2 = 0.79),$$
$$F = -10.2 + 795.6 \; dw_t \; (g) \qquad (r^2 = 0.80),$$
$$F = 21.8 + 842.1 \; dw_s \; (g) \qquad (r^2 = 0.77).$$

Fecundity was clearly correlated with some measure of size, but not very precisely with any of them. The appropriate equations predicted relative fecundities

in Kaneohe Bay in all months. The juveniles, however, were decidedly more abundant and more frequently recorded during the summer and fall as would be predicted by a summer peak in spawning.

Our findings on ova development and size frequency in the gold spot herring are essentially the same as those of Nakamura and Wilson (1970) for the Mar-
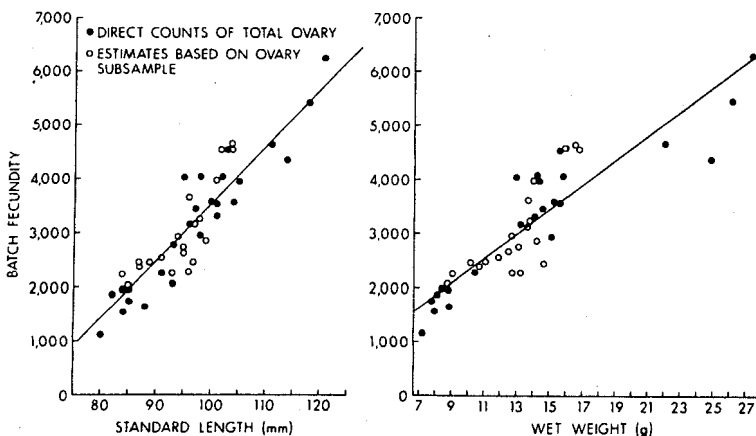

FIGURE 4.—Relationship between batch fecundity and length and wet weight of female *Herklotsichthys quadrimaculatus*, Kaneohe Bay, Oahu. Straight lines are drawn from regression equations (see text).

of 225-242 ova/g *ww* and 791-794 ova/g *dw$_t$* for the observed ranges of fish weights, while actual values ranged from 160-311 ova/g *ww* and 502-1,102 ova/g *dw$_t$*. There was no trend between relative fecundity and size.

Age and Growth

The holding experiments (Fig. 5, Table 1) provided strong evidence that growth increments on the otoliths are deposited daily. In the first experiment, there was a wide range of size and otolith ring counts in the initial and subsequent subsamples. Probably because of this, the increase in average number of rings agreed closely with the numbers of days elapsed for only two of the subsamples; otherwise, only a general trend for increase in average ring count was evident. In the second experiment, the fish were smaller and consisted primarily of two distinct groups separated by 3 mm SL and five otolith rings. These two groups were apparent in all the subsamples, and the increase for each in number of rings corresponded closely with the number of days elapsed. Since each group was about equally represented, the average difference in number of rings for the whole experiment also correlated closely with the number of days.

Both the fish and their otoliths grew faster in the third and fourth experiments, probably due to the higher feeding rate. The distance between rings was markedly greater and counts much easier to make than in the first two experiments. Fish in the initial subsample for the third experiment had a wide range of sizes and ring numbers, but a single group of fish with 26 rings dominated the initial subsample (16 of 41 fish). This group was apparent in most of the rest of the subsamples. The increase in number of rings in this group and differences in means for the subsamples corresponded closely with number of days. The results of the fourth experiment were similar. The subsample which deviated most from the predicted increase had a much narrower range of ring counts and was apparently made up mostly of the younger fish in the experiment.

Initial collections for the third and fourth experiments were made on consecutive days (31 July and 1 August 1979) from the same location and from what appeared to be the same school of transforming juveniles. In the initial subsample for the third experiment, the dominant group had 26 rings, while in that for the fourth, 13 of 39 had 27 rings (Fig. 5). Similarly, the lowest number of rings in the initial subsample for the third experiment was 23 (5 fish), and that for the fourth experiment was 24 (6 fish).
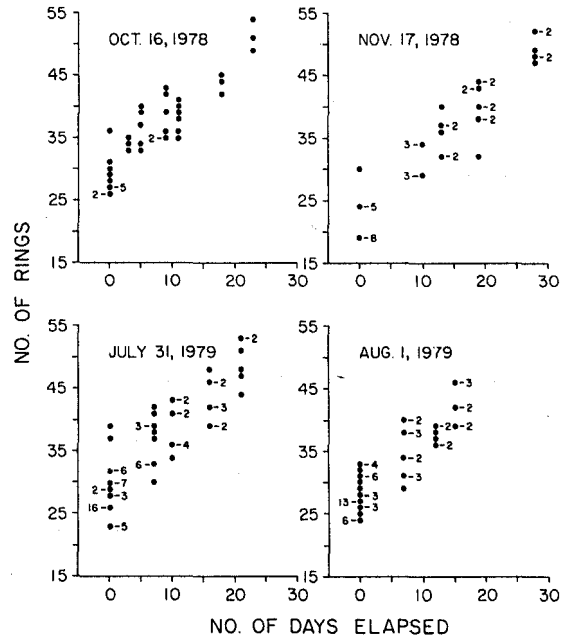

FIGURE 5.—Relationship between number of otolith rings and elapsed time for subsamples of juvenile *Herklotsichthys quadrimaculatus* from holding experiments started on four dates, 1978-79 (see text for details). Numbers of specimens are given for points representing more than one fish per subsample.

TABLE 1.—Number of days elapsed and mean increase in the number of otolith rings in subsamples of *Herklotsichthys quadrimaculatus* from holding experiments started on four different dates, 1978-79, at Kaneohe Bay, Oahu, Hawaii.

Starting date/ No. days elapsed	No. in subsample (Size range, mm SL)	Increase in mean increment count
16 October 1978		
0	12 (19.5-25.0)	0
3	3 (22.0-22.5)	5.6
5	5 (22.5-25.0)	8.2
9	6 (22.0-25.0)	9.9
11	6 (22.0-27.0)	9.8
18	3 (24.0-30.0)	15.4
23	3 (26.5-28.0)	22.9
17 November 1978		
0	14 (17.0-21.5)	0
10	6 (20.0-23.0)	9.9
13	6 (22.0-24.0)	14.1
19	9 (22.0-23.5)	18.7
28	6 (23.0-28.0)	27.8
31 July 1979		
0	41 (19.5-24.0)	0
7	14 (22.0-25.0)	7.9
10	9 (23.0-25.0)	10.6
16	8 (23.0-26.0)	14.9
21	6 (24.0-26.0)	21.3
1 August 1979		
0	39 (20.5-23.5)	0
7	11 (21.0-23.0)	7.8
12	6 (21.0-23.0)	9.5
15	7 (21.0-23.5)	14.9

Two fish in the initial subsample for the third experiment had higher counts than the maximum for the

fourth, 33 (4 fish), but the next highest value for the third was 32 (6 fish).

Although growth increments appear to be deposited daily, the age at deposition of the first ring is unknown because newly hatched gold spot herring were not available. Brothers et al. (1976) found that the northern anchovy, *Engraulis mordax*, deposits the first ring at 5 d and the grunion, *Leuristhes tenuis*, at 1 d after hatching. The otolith "age" or number of rings in the gold spot herring is probably only a few days less than the actual age, and the error for the former is substantial only for the youngest fish.

The ring counts from 106 gold spot herring 17-121 mm SL (Fig. 6) indicate that the smallest individuals were about 1-mo-old, both sexes mature at about 5-6 mo, and the largest fish was probably about 1-yr-old. Variability was high in length of fishes estimated to be older than 6 mo. There was no definite difference between males and females except that several females were both older and larger than any males.

Data suggest at least two growth cycles or stanzas. A two-cycle Gompertz-type model from Zweifel and Lasker (1976) was fitted to the data by a nonlinear least squares iteration. The equation was

$$L_t = 8.07e^{1.48\left(1-e^{-0.037A}\right)+1.37\left(1-e^{-0.013B}\right)}$$

where $A = \text{Min}(t, 59.6)$ and $B = \text{Max}(t - 59.6, 0)$ and t is the estimated age in days. The curve describes the data quite well for the fish < 80 mm, and the length at the break value for the two cycles of the curve, 59.6 d, is about 30 mm—identical to the size at which transformation appeared complete and subsequent growth more nearly isometric. The model predicts a length at time infinity of 119 mm—about the size of the largest male but well below that of the largest female. This indicates that the growth pattern for males is similar to that of juveniles, but a different curve or perhaps a third stanza may be required to describe the growth of females after maturity.
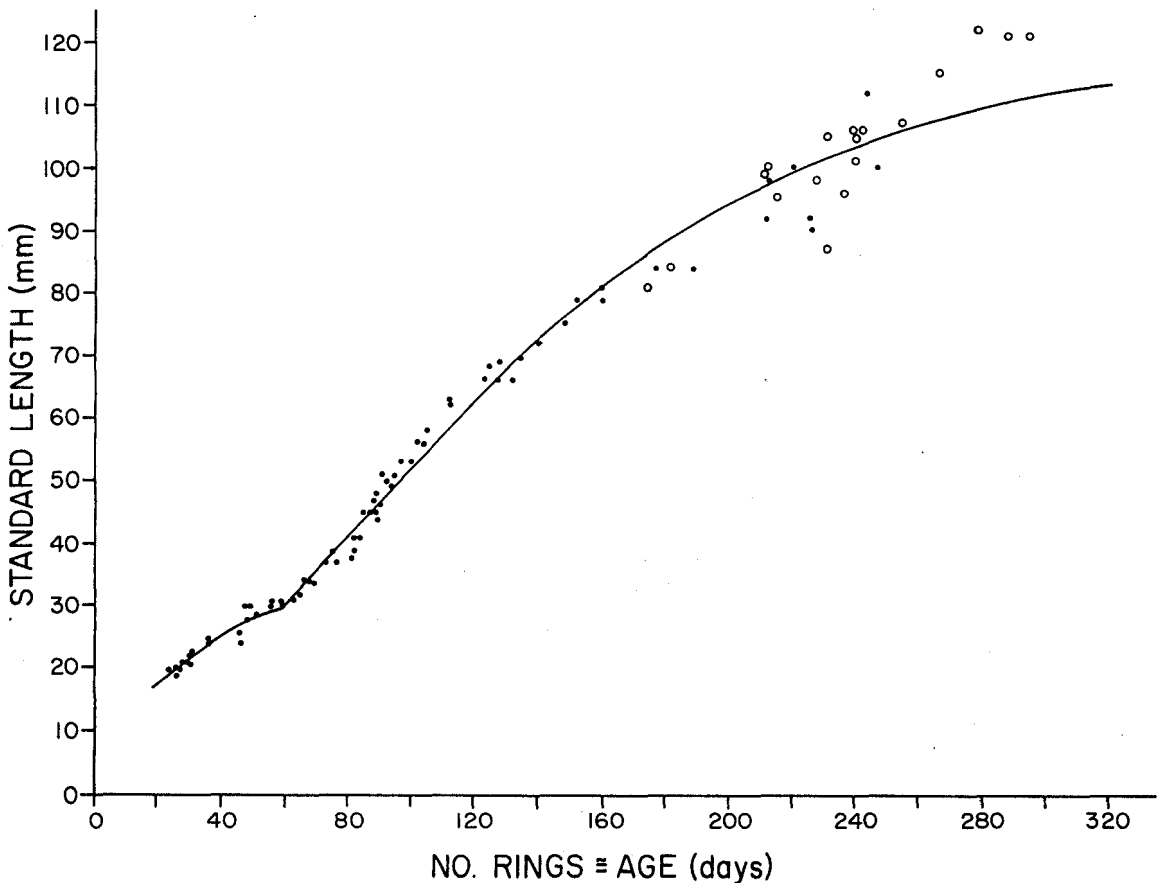

FIGURE 6.—Relationship between standard length and number of otolith rings or approximate age in days for 106 *Herklotsichthys quadrimaculatus* collected off Oahu, Hawaii. Females are indicated by open circles; solid circles represent juveniles (<80 mm SL) and males. Curve is drawn from a two-cycle growth model fitted to the data (see text).

DISCUSSION

The gold spot herring is an "annual" species which grows rapidly, but matures at an early age while small, and rarely lives more than a few months thereafter beyond maturity. Reproduction probably occurs all year, but there is a definite peak in the summer. Less extensive data on what is probably the same species[4] in the Marshall Islands (Hida and Uchiyama 1977) indicate the same life history pattern. Although seasonal changes in abundance and size composition observed in Kaneohe Bay were in part due to movements in and out of the bay, they correlate generally with the reproductive season and the 1-yr life cycle and are probably indicative of changes in the general population.

Few comparable data exist on other *Herklotsichthys* spp. or the closely related *Sardinella* spp. Maximum size in many, e.g., *H. punctatus* (Marichamy 1974) and *S. marquesensis* (Nakamura and Wilson 1970), is about the same as in *H. quadrimaculatus. Sardinella jussieui* (= *S. gibbosa*) and *S. brachysoma* (= *S. albella*) also appear to have a maximum age of about 1 yr (Nair 1960; Okera 1974). Other aspects of the life history of these small species may prove to be similar to those of *H. quadrimaculatus*. Within the tropics (and often cooccurring geographically with small clupeid species) some *Sardinella* spp., e.g., *S. longiceps* (Nair 1960; Ritterbush 1974) and *S. aurita* (Postel 1960), grow more than twice the length of *H. quadrimaculatus*, live for several years, and may reproduce more than one season. Such species are qualitatively more similar to the *Sardinops* spp. from higher latitudes than to the small tropical species. Following the arguments of Murphy (1968) and Leggett and Carscadden (1978), this indicates that reproductive success is more consistent in the smaller species and that even within the tropics, the basic population regulatory mechanisms of closely related species may be qualitatively different.

Data on ova development and fecundity of other species are also limited. The gold spot herring is very similar in these respects to *S. marquesensis* (Nakamura and Wilson 1970). Relative fecundity of *S. aurita* and *S. maderensis* (calculated from the respective data of Kwan-Ming 1960 and Ben-Tuvia 1960) is comparable with that of *H. quadrimaculatus*, but because of their larger size, batch fecundity in these species is much higher. *Sardinella longiceps*, however, is not only larger than *H. quadrimaculatus*, but has considerably higher relative fecundity (940-2,090 ova/g, calculated from Ritterbush 1974). These differences again indicate that reproductive success of the large species is lower or less predictable than in the small, less fecund species.

Neither our results nor those of Leary et al. (1975) on the Hawaiian anchovy offer any unequivocal evidence that these tropical clupeoids ever ripen and spawn more than one batch of eggs. The age-length data (Fig. 6) indicate that 90 mm SL gold spot herring, some of which appeared ready to spawn, are only about 1-mo older than clearly immature fish 75-80 mm SL and that females live 3-4 mo longer after reaching 90 mm SL. Thus the herring appear capable of spawning several times during their reproductive life span, but we have no evidence that they actually do so. The wide range in maximum size of ova found in herring >90 mm SL could result either from multiple spawning or variation in the size and age at which females begin to ripen ova for a single spawning. The absence of spent females indicates a single spawning and high mortality of spawners; however, no females with hydrated ova were observed either. Since spawning appears to occur away from the areas where we made our collections, it is possible that both hydration and recovery from spawning are so rapid that there is no trace of either in fishes about to leave for or just returned from spawning.

Our results, as well as those of the great majority of studies on clupeoid fishes in which appropriate data have been examined and presented, show that sex ratio of fish caught by a given gear and at a given time frequently deviates from 1:1. Assuming the actual sex ratio of adult gold spot herring is 1:1, the day-night differences in sex ratio indicate that males are more likely to move offshore at night and perhaps to remain there during the day. Such behavior is most likely related to spawning. The gold spot herring, like most other clupeoids, probably spawns at night, and Hunter and Goldberg (1980) have presented evidence that spawning schools of pelagic clupeoids are dominated by males.

Like many other clupeids, female gold spot herring appear to reach sizes larger than the largest male. Although there may be sexual differences in growth, our data indicate that female herring reach larger sizes because they live longer. If spawning incurs increased mortality due to either energy requirements or exposure to predation, the males may not live as long because they spawn more frequently than do females.

Discussion of the introduction and spread of *H. quadrimaculatus* in Hawaii is limited because we do

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[4]Hida and Uchiyama identified their specimens as *H. punctatus*. W. J. Baldwin of the Hawaii Institute of Marine Biology has, however, examined numerous specimens collected from the Marshalls during Hida and Uchiyama's study and found them all to be *H. quadrimaculatus*.

not know (and probably never will) precisely when and how the species was introduced. Nevertheless, some speculations based on available data and very likely possibilities seem justified. First, it is almost certain that *H. quadrimaculatus* was not inadvertently introduced along with the *S. marquesensis* in the late 1950s. The former species is not known to occur in the Marquesas Islands, and the extensive study of Nakamura and Wilson (1970) would have likely detected it if it were actually present. The absence of any "sardines" generally and in our Kaneohe Bay samples prior to 1975, as well as the very rapid increase in abundance of *H. quadrimaculatus* between 1975 and 1976, both indicate that this species had probably not been in Hawaii very long before we collected our first specimens. Finally, the number of individuals released in Hawaii was almost certainly less than the 144,000 fish released when the Marquesan sardine was introduced (Hida and Morris 1963).

If the above speculation is close to the truth, *H. quadrimaculatus* appears to have increased from a small group of individuals to a widespread and very abundant species within a span of 2-3 yr. Even allowing for multiple spawnings per lifetime in females, the fecundity of *H. quadrimaculatus* is so low that survival from egg to adult during this period must have been extremely high. Since the population appears to have remained relatively stable since about 1976, some mechanism must have acted to lower survival rates. The most likely regulatory mechanism would be the increasing abundance of the gold spot herring themselves, i.e., intraspecific competition at some point in the life cycle. It is also possible that local predators have responded to the herring as a new resource and are presently regulating abundance.

The known differences between *Herklotsichthys quadrimaculatus* and *Sardinella marquesensis* seem unlikely to account for the former's greater success in Hawaii; to the contrary, the two species are very similar in morphology and ecology. Berry and Whitehead (1968) noted that in several respects *S. marquesensis* is more similar to the *Herklotsichthys* spp. than are other *Sardinella* spp. Fresh specimens of *H. quadrimaculatus* can be distinguished from *S. marquesensis* by the gold spots on the operculae; otherwise, close examination of the second supramaxilla, the imbedded portions of the body scales or the posterior anal rays (see Berry and Whitehead 1968) are required to separate the two species unequivocally. *Sardinella marquesensis* has higher gill raker counts than *H. quadrimaculatus*, but Nakamura and Wilson's (1970) diet data from the Marquesas indicate that, unlike most other *Sardinella*

spp., *S. marquesensis* eats very little phytoplankton and, in fact, eats zooplankton equivalent to those recorded for *H. quadrimaculatus* in Hawaii. Other features of the life history of *S. marquesensis* considered by Nakamura and Wilson are almost identical to those of *H. quadrimaculatus*. Investigation of the physiology and larval ecology of the two species and, if still possible, of the ecology of *S. marquesensis* in Hawaii might better account for the greater success of *H. quadrimaculatus* in Hawaii and might also be pertinent to the broader problem of factors limiting natural distributions.

ACKNOWLEDGMENTS

LITERATURE CITED

BEN-TUVIA, A.
    1960. Synopsis of the systematics and biology of *Sardinella maderensis* (Lowe). *In* H. Rosa, Jr., and G. Murphy (editors), Proceedings of the World Science Meeting on Biology of Sardines and Related Species, Vol. 2, p. 497-519. FAO, Rome.
BERRY, F. H., AND P. J. P. WHITEHEAD.
    1968. A new species of sardine (*Sardinella*, Clupeidae) from the Marquesas Islands. Proc. Biol. Soc. Wash. 81:209-221.
BROTHERS, E. B., C. P. MATHEWS, AND R. LASKER.
    1976. Daily growth increments in otoliths from larval and adult fishes. Fish. Bull., U.S. 74:1-8.
HIDA, T. S., AND R. A. MORRIS.
    1963. Preliminary report on the Marquesan sardine, *Harengula vittata*, in Hawaii. Pac. Sci. 17:431-437.
HIDA, T. S., AND J. H. UCHIYAMA.
    1977. Biology of the baitfishes *Herklotsichthys punctatus* and *Pranesus pinguis* in Majuro, Marshall Islands. *In* R. S. Shomura (editor), Collection of tuna baitfish papers, p. 63-68. U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 408.
HUNTER, J. R., AND S. R. GOLDBERG.
    1980. Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 77:641-652.
KWAN-MING, L.
    1960. Synopsis on the biology of *Sardinella* in the tropical eastern Indo-Pacific area. *In* H. Rosa, Jr., and G. Murphy (editors), Proceedings of the World Science Meeting on Biology of Sardines and Related Species, Vol. 2, p. 175-

212. FAO, Rome.

LEARY, D. F., G. I. MURPHY, AND M. MILLER.
1975. Fecundity and length at first spawning of the Hawaiian anchovy, or nehu (*Stolephorus purpureus* Fowler) in Kaneohe Bay, Oahu. Pac. Sci. 29:171-180.

LEGGETT, W. C., AND J. E. CARSCADDEN.
1978. Latitudinal variation in reproductive characteristics of American shad (*Alosa sapidissima*): Evidence for population specific life history strategies in fish. J. Fish. Res. Board Can. 35:1469-1478.

MARICHAMY, R.
1970. Food and feeding habits of the spotted herring, *Herklotsichthys punctatus* (Ruppell) from the Andaman Sea. Indian J. Fish. 17:159-168.
1974. A note on the length-weight relationship and relative condition in *Herklotsichthys punctatus* (Ruppel). Indian J. Fish. 21:582-584.

MATSUURA, Y.
1975. A study of the life history of Brazilian sardine, *Sardinella brasiliensis*. III. Development of sardine larvae. Bol. Inst. Oceanogr., S. Paulo 24:17-29.

MURPHY, G. I.
1960. Introduction of the Marquesan sardine, *Harengula vittata* (Cuvier and Valenciennes), to Hawaiian waters. Pac. Sci. 14:185-187.
1968. Pattern in life history and environment. Am. Nat. 102:391-403.

NAIR, R. V.
1960. Synopsis on the biology and fishery of the Indian sardines. *In* H. Rosa, Jr., and G. Murphy (editors), Proceedings of the World Science Meeting on Biology of Sardines and Related Species, Vol. 2, p. 329-414. FAO, Rome.

NAKAMURA, E. L., AND R. C. WILSON.
1970. The biology of the Marquesan sardine, *Sardinella marquesensis*. Pac. Sci. 24:359-376.

OKERA, W.
1974. Morphometrics, 'condition' and gonad development of the East African *Sardinella gibbosa* (Bleeker) and *Sardinella albella* (Valenciennes). J. Fish. Biol. 6:801-812.

POSTEL, E.
1960. Rapport sur la sardinelle (*Sardinella aurita* Valenciennes) (Atlantique Africain). *In* H. Rosa, Jr., and G. Murphy (editors), Proceedings of the World Science Meeting on Biology of Sardines and Related Species, Vol. 2, p. 55-95. FAO, Rome.

RITTERBUSH, S. W.
1974. Certain aspects of the population biology of the Bali Strait lemuru fishery. M.S. Thesis, Univ. Hawaii, Honolulu, 50 p.

STRUHSAKER, P., AND J. H. UCHIYAMA.
1976. Age and growth of the nehu, *Stolephorus purpureus* (Pisces: Engraulidae), from the Hawaiian Islands as indicated by daily growth increments of sagittae. Fish. Bull., U.S. 74:9-17.

ZWEIFEL, J. R., AND R. LASKER.
1976. Prehatch and posthatch growth of fishes—A general model. Fish. Bull., U.S. 74:609-621.