ABUNDANCE AND POTENTIAL YIELD OF THE SCALED SARDINE, HARENGULA JAGUANA, AND ASPECTS OF ITS EARLY LIFE HISTORY IN THE EASTERN GULF OF MEXICO¹

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ABSTRACT

Eggs and larvae of the scaled sardine, *Harengula jaguana*, were collected in 1971–74 from the eastern Gulf of Mexico to determine spawning seasons, spawning areas, adult biomass, and fisheries potential. Aspects of the early life history of the species also were studied. Spawning occurred from January to September, but was most intense from May to August, when surface temperatures ranged from 20.8° to 30.7°C and surface salinities were 29.9 to 36.9‰. All spawning occurred between the coast and the 30-m depth contour, mostly within 50 km of the coast. The biomass of scaled sardines, based on annual spawning estimates, apparently increased from 1971 to 1973, the mean estimate for the 3 yr being 184,527 metric tons. Potential yield estimates, based on the 3-yr mean biomass, ranged from 46,000 to 92,000 metric tons. Larval abundance and mortality rates were estimated from 1973 data. More than 99.9% mortality occurred between time of spawning and attainment of 15.5 mm standard length at 20 days of age. Comparisons were made of scaled sardine distribution, abundance, potential yield, and larval mortality with those of other eastern Gulf clupeids.

Scaled sardine, Harengula jaguana Poey, is abundant in coastal waters of the western Atlantic from New Jersey to Santos, Brazil, including the Gulf of Mexico (Berry 1964). It is common from Florida to Brazil (Rivas 1963), but there are no large-scale directed fisheries for the species. Klima (1971) reported it to be an abundant, surface-schooling species that is usually found within the 20-fathom curve in the northeastern Gulf of Mexico. It is one of the most common species in Gulf Coast estuaries (Gunter 1945; Springer and Woodburn 1960; Roessler 1970). Because of its abundance, it is an important latent fishery resource in the Gulf of Mexico and Caribbean region (Reintjes and June 1961; Bullis and Thompson 1970; Klima 1971). Small catches of Harengula spp. totalling 2,189 metric tons in 1974 presently are landed by Cuba, Brazil, and the Dominican Republic (Food and Agriculture Organization 1975). No reported catches are made by the United States, but a small amount, probably less than 500 tons annually, is landed in Florida for bait in commecial and recreational fishing.

Some aspects of the biology of scaled sardines are known. Low (1973) discussed the species and its occurrence in Biscayne Bay, Fla., including food habits and juvenile growth rates. Fecundity, size at maturity, and spawning were reported by Martinez and Houde (1975). Roessler (1970) discussed growth, recruitment, and the relationship of environmental factors to scaled sardine abundance in an Everglades estuary, and Springer and Woodburn (1960) discussed its ecology in Tampa Bay. Eggs and larvae have been described by Matsuura (1972), Houde and Fore (1973), Houde et al. (1974), and Gorbunova and Zvyagina (1975).

Objectives of this study were to estimate scaled sardine biomass and fishery potential in the eastern Gulf of Mexico from the distribution and abundance of its eggs and larvae. Information on the early life history also was obtained. Similar studies on round herring, *Etrumeus teres*, and thread herring, *Opisthonema oglinum*, were recently published (Houde 1976, 1977a, b).

METHODS

Methods to determine scaled sardine biomass and fisheries potential are the same as those used for round herring and thread herring (Houde 1977a, b). Collecting methods were described (Houde 1977a), and summarized station data from

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the 17 ichthyoplankton cruises have been published (Houde and Chitty 1976; Houde et al. 1976). The survey area and its potential sampling stations were illustrated in figure 1 of Houde (1977a, b). Analytical and statistical procedures are based on those discussed by Saville (1964), Ahlstrom (1968), and Smith and Richardson (in press).

RESULTS AND DISCUSSION

Occurrence of Eggs and Larvae

A total of 19,183 scaled sardine eggs and 3,828 larvae were collected during the 17 cruises, in which 867 stations were sampled. Scaled sardines composed 59.8% of all clupeid eggs collected and their larvae composed 13.2% of all clupeid larvae. Scaled sardine eggs made up 6.3% of the total fish eggs from the 867 stations and their larvae constituted 2.7% of the total larval fish catch.

Scaled sardine eggs or larvae were collected on cruises from January through September, but they were most abundant from May through August (Table 1). Stations where they occurred are given in Figure 1. Distribution and abundance of eggs and larvae are illustrated for the May through August cruises (Figures 2-5). Spawning from January to March probably is confined to the southernmost parts of the survey area, since eggs and larvae were collected only at stations south of lat. 26°N on cruises during those months. No eggs were collected where depths exceeded 30 m (Figure 1). Larval distributions were similar to those for eggs, except for a single anomalous occurrence of larvae at a station on the 200-m depth contour (Figures 1, 3). On cruises CL7405 and CL7412 several stations nearer to shore (of only 4-10 m depth) than any on previous cruises were sampled (Figure 5). On cruise CL7412, when intense spawning was taking place, catches of eggs at the nearshore stations exceeded catches at the regular stations. Mean egg abundance under 10 m² at positive stations was 1.85 times greater at the nearshore stations than at the regular stations (158.93 compared with 85.75). Log₁₀ transformed means were tested in a t-test.

	No. of stations		
	with scaled		
Stations	sardine eggs	Log_{10} mean	$Log_{10} S_{\overline{x}}$
Regular	9	1.0056	0.3343
Nearshore	11	1.8118	0.1913
$t_{\rm calc}$ =	= 2.15*	$t_{0.05(2)18} = 1$	2.10

Differences were significant (P < 0.05). Failure to sample nearshore stations on earlier cruises probably resulted in an underestimate of scaled sardine spawning and also an underestimate of adult biomass if egg distribution during cruise CL7412 was representative of earlier cruises.

The observed egg and larvae distributions indicate that most adults are located where depth

TABLE 1.—Summarized data on cruises to the eastern Gulf of Mexico, 1971-74, to estimate abundance of scaled sardine eggs and larvae. GE = RV Gerda, 8C = RV Dan Braman, TI = RV Tursiops, 8B = RV Bellows, IS = RV Columbus Iselin, CL = RV Calanus.

		Number of	Positive stations	Positive stations	Mean egg abu	indance under 10 m ²	Mean larvae ab	undance under 10 m ²
Cruise	Dates	stations	for eggs ¹	for larvae ²	All stations	Positive stations	All stations	Positive stations
GE7101 ³	1-8 Feb. 1971	20	1	0	0.64	23.05	0.00	0.00
8C7113								
TI7114	7-18 May 1971	123	2	12	0.78	64.66	6.73	51.52
GE7117	26 June-4 July 1971	27	2	0	1.67	19.95	0.00	0.00
8C7120								
TI7121	7-25 Aug. 1971	146	8	8	0.83	28.09	0.21	4.37
TI7131	5							
8B7132								
GE7127	7-16 Nov. 1971	66	0	0	0.00	_	0.00	_
8B7201								
GE7202	1-11 Feb. 1972	30	0	0	0.00	-	0.00	_
GE7208	1-10 May 1972	30	1	4	1.68	76.21	1.24	11.57
GE7210	12-18 June 1972	13	3	3	35.31	146.94	5.97	22.78
IS7205	9-17 Sept. 1972	34	0	2	0.00		0.16	4.70
IS7209	8-16 Nov, 1972	50	Ó	0	0.00	_	0.00	
IS7303	19-27 Jan, 1973	51	0	1	0.00	_	0.01	0.26
IS7308	9-17 May 1973	49	8	14	14.38	154.16	9.26	38.34
IS7311	27 June-6 July 1973	51	8	6	31.59	174.14	0.59	5.51
IS7313	3-13 Aug. 1973	50	9	11	67.49	747.09	10.86	50.26
IS7320	6-14 Nov. 1973	51	0	0	0.00	_	0.00	
CL7405	28 Feb9 Mar. 1974	36	ō	4	0.00	_	0.39	4.06
CL7412	1-9 May 1974	44	20	23	50.29	125.82	14.45	28.79

¹Positive station is a station at which scaled sardine eggs were collected. ²Positive station is a station at which scaled sardine larvae were collected.

3An ICITA 1-m plankton net was used on this cruise. On all other cruises a 61-cm bongo net was used.



FIGURE 1.—Top. Stations in the survey area where eggs of scaled sardines were collected at least once during 1971–74. Stations where eggs did not occur are indicated by dots. Bottom. Stations in the survey area where larvae of scaled sardines were collected at least once during 1971–74. Stations where larvae did not occur are indicated by dots.

is <20 m and that nearly all are found within the 30-m depth contour. Spawning adults are confined to a band within 85 km of the coast. Klima (1971) reported that scaled sardines in the Gulf of Mexico usually are found within the 20-fathom curve (36.5 m), but he noted occasional occurrence over depths as great as 165 fathoms (302 m). Brazilian scaled sardines also spawned near the coast, within 18.5 km of shore where water depth was <65 m (Matsuura 1972).

There were no areas in the eastern Gulf where consistently high egg or larval catches occurred that would suggest great concentrations of adults. Consistent catches of eggs and larvae between lat. $24^{\circ}45'N$ to $25^{\circ}45'N$ and long. $81^{\circ}30'W$ to $82^{\circ}30'W$, as well as just north of Tampa Bay between lat. $28^{\circ}00'N$ to $28^{\circ}30'N$ and long. $82^{\circ}45'W$ to $83^{\circ}15'W$ did indicate that scaled sardines usually were abundant in those areas.

Mean egg abundances for the 17 cruises ranged from 0.00 to 67.49 under 10 m² of sea surface (Table 1). Considering only positive stations, means ranged from 19.95 to 747.09 under 10 m² (Table 1). Abundances of eggs at stations rarely exceeded 100 under 10 m² of sea surface during 1971 and 1972, but frequently were between 100 and 1,000 under 10 m² during 1973 and 1974 (Figures 2–5). Only once, in August 1973, did abundance of eggs exceed 1,000 under 10 m² (Figure 4).

Cruise means for scaled sardine larval abundances ranged from 0.00 to 14.45 under 10 m² when all stations were considered, and from 0.26 to 51.52 under 10 m² at positive stations (Table 1). At positive stations larval abundances usually ranged from 11 to 100 under 10 m², and exceeded 100 under 10 m² at only eight stations during 1971-74 (Figures 2-5).

Most scaled sardine eggs and larvae were found nearer to shore than those of either thread herring or round herring (Houde 1977a, b). However, there was considerable overlap in areas and seasons of occurrence of thread herring and scaled sardine spawning. Eggs and larvae of scaled sardines and round herring did not occur together because round herring did not spawn in water shallower than 30 m, and most spawning by that species occurred during winter.

Temperature and Salinity Relations

Scaled sardine eggs were collected at surface temperatures from 20.8° to 30.7° C and at surface salinities from 29.92 to 36.88%. Larvae ≤ 5 mm standard length (SL), 5 days or less in age, were taken at surface temperatures from 18.4° to 30.5° C and surface salinities of 27.27 to 36.88%. Vertical sections showing temperature and salinity profiles for cruises during the scaled sardine spawning season indicated that surface temperatures differed from those at 10 m by a maximum of only 1°C, but that a maximum difference of 4°C could occur at 30 m. The difference between the surface and the 30-m depth usually did not exceed 2°C. Salinity differences between the surface and 10 m were always < 0.5% and never exceeded 1.5%



FIGURE 2.—Distribution and abundance of scaled sardine eggs and larvae. Catches are standardized to numbers under 10 m² of sea surface. A, B. Cruise 8C7113–TI7114, May 1971. C, D. Cruise 8C7120–TI7121, August 1971.

between the surface and 30 m. The buoyant eggs and pelagic larvae probably developed at temperatures and salinities similar to those at the sea surface.

Relatively few eggs or \leq 5.0-mm larvae occurred where surface temperature was <24.0°C over the 1971-74 period (Figure 6). For eggs, 82.3% of the station occurrences were at surface temperatures above 24°C; for larvae, 71.0% occurred above 24°C. Although spawning occurred over a wide salinity range, 71.0% of the stations with eggs had salinities that exceeded 35.0‰; 62.3% of the stations with \leq 5.0-mm larvae had salinities above 35.0‰.

Matsuura (1972) collected eggs and larvae of Brazilian scaled sardine at temperatures and salinities within the ranges observed for eggs and larvae in the eastern Gulf. Spawning occurred at temperatures and salinities similar to those recorded for thread herring (Houde 1977b). Scaled sardine eggs and larvae were found over slightly wider ranges of temperature and salinity than were thread herring, reflecting the slightly longer spawning season of scaled sardines in the eastern Gulf and their tendency to be most abundant nearer to the coast where temperatures and salinities varied most.

Egg and Larval Abundance in Relation to Zooplankton

There was no apparent relationship between either egg or larval abundance at stations and



FIGURE 3.—Distribution and abundance of scaled sardine eggs and larvae. Catches are standardized to numbers under 10 m² of sea surface. A, B. Cruise GE7208, May 1972. C, D. Cruise GE7210, June 1972.

volume of zooplankton collected in the $333-\mu m$ mesh bongo net in 1972-74. Mean zooplankton volume was 153.4 cm³/1,000 m³ in 1972-74 (Houde and Chitty 1976). Highest abundances of scaled sardine eggs and larvae occurred where zooplankton volumes exceeded 153.4 cm³/1,000 m³ but correlations between zooplankton volume and scaled sardine egg or larval abundance were not significant. Because the $333-\mu m$ mesh did not collect small copepod nauplii, a major food of fish larvae, and because zooplankton was not identified, significant correlations between larvae and zooplankton were unlikely. The relatively high catches of eggs at stations with high zooplankton volumes may have reflected the ability of scaled sardine adults to concentrate in rich zooplankton

areas, rather than indicating that eggs were spawned where food would be abundant for larvae.

Relative Fecundity and Size at Maturity

Mean relative fecundity of scaled sardines is 528.0 ova/g ($S_{\overline{x}} = 26.5 \text{ ova/g}$), based on data from 22 females collected near Miami, Fla., by Martinez and Houde (1975). They found that two modal groups of ova ripened during the spawning season and that both modes apparently were spawned. The relative fecundity estimate here differs slightly from their reported value because they estimated it for female weights minus ovary weights. To determine stock biomass, the best



FIGURE 4.—Distribution and abundance of scaled sardine eggs and larvae. Catches are standardized to numbers under 10 m² of sea surface. A, B. Cruise IS7308, May 1973. C, D. Cruise IS7311, June–July 1973. E, F. Cruise IS7313, August 1973.



FIGURE 5.—Distribution and abundance of scaled sardine eggs and larvae. Catches are standardized to numbers under 10 m² of sea surface. A, B. Cruise CL7412, May 1974.



FIGURE 6.—Percent cumulative frequency distribution of 1971-74 stations where scaled sardine eggs occurred in relation to surface temperatures (A) and to surface salinities (C), and \leq 5.0-mm SL larvae occurred in relation to surface temperatures (B) and surface salinities (D).

relative fecundity estimate is for total weight, including ovary and the estimate given here is based on that criterion. Because relative fecundity did not differ significantly among females from 8.5 to 16.3 cm SL (14.8 to 98.4 g) (Martinez and Houde 1975), the mean value was used in calculating biomass estimates. Mean relative fecundity with 0.95 confidence limits is 528.0 \pm 55.1 ova/g. It seems unlikely that biomass estimating errors greater than \pm 10% could be attributable to errors in fecundity estimates.

Cruise Egg Abundance

The estimated abundances of scaled sardine

eggs, before correction for egg stage duration, within the areas represented by each of the cruises range from 0.00 to 103.39×10^{10} (Table 2). The Table 2 estimates, which represent the number of eggs present on a day during a cruise, were corrected for egg stage duration and then expanded to represent the number of days encompassed by the cruise period (Sette and Ahlstrom 1948; Houde 1977a), before they were used in the biomass estimating procedure.

Time Until Hatching

Egg stage duration is less than 24 h for scaled sardines when temperatures are above 24°C.

TABLE 2.—Abundance estimates of scaled sardine eggs for each cruise. Estimates were obtained using equations (2) and (3) (Houde 1977a) and are not corrected for duration of the egg stage.

Cruise	Area represented by the cruise $(m^2 \times 10^9)$	Positive area ¹ $(m^2 \times 10^9)$	Cruise egg abundance (eggs × 10 ¹⁰)
GE7101	25.79	0.77	0.18
8C7113 and			
TI7114	120.48	18.32	0.94
GE7117	101.10	7.93	1.69
8C7120 and			
TI7121	189.43	13.41	1.57
GE7127, 8B7132			
and TI7131	72.99	0.00	0.00
8B7201 and			
GE7202	148.85	0.00	0.00
GE7208	124.88	27.56	2.51
GE7210	48.43	15.60	17.10
IS7205	104.59	4.88	0.00
IS7209	149.80	0.00	0.00
IS7303	149.80	3.05	0.00
IS7308	151.42	43.38	21.77
IS7311	156.50	25.43	49.44
IS7313	153.18	40.79	103.39
IS7320	153.89	0.00	0.00
CL7405	52.00	5.84	0.00
CL7412	91.33	43.45	45.93

¹Positive area is defined as the area representing stations where either eggs or larvae of scaled sardines were collected.

Newly fertilized eggs were collected only at night in the Gulf of Mexico surveys and only advanced embryos usually were present from midday to late afternoon. Similar observations were made for scaled sardine eggs collected near Miami and used in laboratory rearing experiments (Houde and Palko 1970; Houde et al. 1974). The estimated peak spawning time is 2200 h.

Egg abundance was underestimated on most cruises because hatching time was less than 1 day. All cruise abundances were adjusted by dividing them by the estimated mean egg stage duration (Table 3) before annual spawning estimates were made.

Adjusting Cruise Egg Abundance Estimates for Area

Some cruises did not completely cover the area within the 30-m depth contour of the eastern Gulf where scaled sardines spawned. Egg abundance estimates for those cruises were adjusted by dividing the cruise abundance estimate (Table 2) by

TABLE 3.—Assigned egg stage durations of scaled sardine eggs for each cruise in which they occurred, 1971-73.

Cruise	Egg stage duration (days)	Cruise	Egg stage duration (days)
GE7101	1.17	GE7208	0.84
8C7113		GE7210	0.80
TI7114	0.84	IS7308	0.84
GE7117	0.80	157311	0.80
8C7120		IS7313	0.80
T17121	0.80	-	

an adjustment factor, the proportion of the spawning area represented by the cruise. Egg abundance estimates were adjusted for cruises GE7117, 8C7120-TI7121, GE7208, and GE7210. Area adjustment factors were: GE7117-0.394; 8C7120-TI7121-0.746; GE7208-0.644; and GE7210-0.574. Cruise IS7205, in which scaled sardine larvae but no eggs were taken, also did not encompass the entire spawning area. Larval abundance estimates were adjusted for that cruise by its area factor, 0.750. Cruise egg abundance estimates from Table 2, after adjustment, were: GE7117-4.29 \times 10¹⁰; 8C7120-TI7121-2.10 \times 10¹⁰; GE7208-3.90 \times 10¹⁰; and GE7210-29.79 \times 10¹⁰.

Annual Spawning and Biomass Estimates

Method I

Estimates of total annual spawning by scaled sardines were obtained after egg stage duration and area factor corrections had been made on daily spawning estimates using the Sette and Ahlstrom (1948) method and procedures described by Houde (1977a). They were: 44.106×10^{11} eggs in 1971, 391.357×10^{11} eggs in 1972, and $1,025.834 \times 10^{11}$ eggs in 1973 (Table 4). No estimate was obtained in 1974 because the entire season was not surveyed, but the abundance of eggs from cruise CL7412 (Table 2) suggested that annual spawning was high in that year.

Estimated biomasses increased from 16,708 metric tons in 1971 to 148,255 metric tons in 1972, and to 388,610 metric tons in 1973 (Table 4). Variance estimates for each year's spawning (Table 4) were used to place 0.95 confidence intervals on biomass estimates. These ranged from 0 to 56,210 metric tons in 1971, 0 to 327,130 metric tons in 1972, and 300,965 to 476,271 metric tons in 1973. The mean of the three annual biomass estimates was 184,527 metric tons. The 1972 estimate may be unreliable because of poor area coverage and curtailment of cruise GE7210 due to a hurricane, but the low 1971 estimate probably is accurate because area coverage was good on cruises during the peak spawning period.

A severe red tide in 1971 occurred during spring and summer along the Florida coast of the Gulf of Mexico (Steidinger and Ingle 1972), and it may have caused a high mortality of adult scaled sardines. Dead scaled sardines were observed in red tide areas during cruise GE7117. It is also possible

TABLE 4.—Annual spawning and biomass estimates for scaled sardines from the eastern Gulf of Mexico during
1971, 1972, and 1973 spawning seasons. Estimates are based on the Sette and Ahlstrom (1948) technique. Details
of the estimating procedure are given in Houde (1977_{B}) .

Year	Cruise	Daily spawning estimate (eggs × 10 ¹¹)	Days represented by cruise	Eggs spawned during cruise period (× 10 ¹¹)	Variance estimates on spawned eggs (× 10 ²⁴)	Adult biomass (metric tons)
1971	GE7101 8C7113	0.015	51.5	0.773	0.134	
	TI7114	0.112	74.5	8.344	1.950	
	GE7117 8C7120	0.541	44.5	24.074	22.959	
	TI7121	0.263	41.5	10.915	2.121	
Annual total				44.106	27.164	16,708
1972	8B7201					
	GE7202	0.000	50.0	0.000	_	
	GE7208	0.468	65.0	30.420	22.664	
	GE7210	3.721	97.0	360.937	534.743	
Annual total				391.357	557.407	148,255
1973	IS7303	0.000	63.5	0.000		
	IS7308	2.613	79.5	207.734	56.388	
	IS7311	6.180	43.5	268.830	42.829	
	IS7313	12.924	42.5	549.270	34.628	
Annual total				1,025.834	133.845	388,610

that few adult scaled sardines were killed, but that they did not spawn during red tides or that spawned eggs experienced high mortality. Failure to spawn or unusual egg mortality could have caused biomass to be underestimated in that year.

Effects on biomass estimates of area adjustments for the four cruises that did not completely cover the scaled sardine spawning area were important. Unadjusted biomass in 1971 was only 10,100 metric tons, 60.5% of the adjusted estimate; in 1972 it was 85,964 metric tons, 58.0% of the adjusted estimate.

Method II

Biomass estimates, using Simpson's (1959) method in a modified form (Houde 1977a), were calculated (Table 5). Mean biomass estimated for the 3 yr was 146,595 metric tons.

Most Probable Biomass

Scaled sardines as small as 8.0 cm SL are mature (Martinez and Houde 1975), and estimates of adult biomass from egg and larvae surveys probably include most of the stock, juvenile weights being relatively insignificant. Biomass estimates ranged from 16,000 to nearly 400,000 metric tons and stock apparently increased from 1971 to 1973. The evidence from cruise CL7412 indicated that spawning increased nearer to shore than measured at regular survey stations. This suggests that biomasses were underestimated, perhaps by as much as 30%. If so, then biomass may have ranged from 23,000 to 571,000 metric tons during 1971–73, the mean being 265,000

TABLE 5.—Annual spawning and biomass estimates for scaled sardines from the eastern Gulf of Mexico during 1971, 1972, and 1973. Estimates are based on the method described by Simpson (1959).

Year	Cruise	Daily spawning estimate (eggs × 10 ¹¹)	Annual spawning estimate (eggs × 10 ¹¹)	Adult biomass (metric tons)
1971	GE7101	0.015		
	8C7113			
	TI7114	0.112		
	GE7117	0.541		
	8C7120			
	TI7121	0.263		
			42.981	16,282
1972	8B7201			
	GE7202	0.000		
	GE7208	0.468		
	GE7210	3.721		
			245.940	93,168
1973	IS7303	0.000	-	
	IS7308	2.613		
	IS7311	6,180		
	IS7313	12.924		
			872.000	330,334

metric tons. Despite variability in estimates, it is clear that the eastern Gulf scaled sardine stock was less than 700,000 metric tons between 1971 and 1973, and it apparently was less than 100,000 metric tons in 1971.

Comparison of Scaled Sardine Biomass With That of Other Clupeids

Biomass of scaled sardines in the eastern Gulf of Mexico is similar to that reported for round herring and thread herring (Houde 1977a, b). Mean biomass of round herring was estimated to be approximately 400,000 metric tons, mostly distributed between the 30- and 200-m depth contours, while thread herring mean biomass was about 250,000 metric tons, much of it occurring in the same areas as scaled sardine, although

many thread herring also occurred farther offshore (Houde 1977b). In aggregate the three species totalled approximately 850,000 metric tons. The menhaden (*Brevoortia* spp.) resource apparently is small in the survey area, since relatively few eggs and larvae were collected (Houde et al. 1976). No estimate of Spanish sardine (Sardinella spp.) biomass was obtained, but its eggs and larvae were abundant (Houde et al. 1976). Its biomass may be as great as that for thread herring, i.e., 250,000 metric tons. If true, then aggregate adult biomass of unfished clupeids exceeds 1 million metric tons. The contention that large potential fisheries exist in the eastern Gulf of Mexico is supported by the estimated biomasses. However, none of the individual species appears to represent a resource as large as that of Gulf menhaden, B. patronus, which presently yields about 500,000 metric tons annually to the northern Gulf fishery.

Concentration of Biomass

Scaled sardine eggs and larvae occurred in most of the 76 \times 10⁹ m² area between the coast and 30-m depth contour, except for approximately 15 to 20×10^9 m² in the northeastern part of the survey area (Figure 1). During the spawning season, adult scaled sardines were assumed to occur in 60×10^9 m² of the eastern Gulf. Concentration of biomass, assuming an even distribution, based on the annual biomass estimates from Method I (Table 4) and their 0.95 confidence limits were: 1971, 0 to 9.4 kg/ha; 1972, 0 to 54.5 kg/ha; and 1973, 50.2 to 79.4 kg/ha. Mean biomass concentrations were: 1971, 2.8 kg/ha; 1972, 24.7 kg/ ha; and 1973, 64.8 kg/ha. Estimated scaled sardine biomasses under a hectare of sea surface are similar to those of thread herring but less than those of round herring (Houde 1977a, b).

Potential Yield to a Fishery

Estimates of annual yield varied greatly from year to year, reflecting the biomass fluctuations (Table 6). The estimator $C_{max} = XMB_0$ was used to predict potential maximum sustainable yield (Alverson and Pereyra 1969; Gulland 1971, 1972). X is assumed to equal 0.5 and B_0 is the virgin biomass. M, the natural mortality coefficient, was allowed to vary from 0.5 to 1.0, values that are probable for scaled sardines. The range of potential yields over the 3-yr period was 4,177 to

TABLE 6.—Range of potential yield estimates for eastern Gulf of Mexico scaled sardines, based on biomass estimates in 1971, 1972, and 1973 by the Sette and Ahlstrom (1948) method. Yields are predicted at three possible values of M, the natural mortality coefficient. Biomass estimates were obtained from values in Table 4.

Year	Biomass estimate (metric	Estimated potential annual yields (metric tons) for given values of M				
	tons)	M=0.50	M=0.75	M=1.0		
1971	16,708	4,177	6,266	8,354		
1972	148,255	37,064	55,596	74,128		
1973	388,610	97,153	145,729	194,305		
Mean of						
3 yr	184,527	46,132	69,198	92,264		

194,305 metric tons (Table 6). Based on mean biomass estimates for 1971–73, potential yield was between 46,132 and 92,264 metric tons. If scaled sardines were evenly distributed over the $60 \times 10^9 \text{ m}^2$ where they occur in the eastern Gulf, harvestable annual yield, based on 1971–73 mean biomass, is 7.7 to 15.4 kg/ha.

Comparison of Potential Yield With That of Other Clupeids

Potential yield of scaled sardines is slightly less than that estimated for thread herring and less than that for round herring (Houde 1977a, b). Using mean annual biomass estimates by Method I, and the value 1.0 for M, potential maximum sustainable yields are: scaled sardines—92,264 metric tons; thread herring—120,598 metric tons; and round herring—212,238 metric tons. Total potential for the three species is 425,100 metric tons. If Spanish sardines are as abundant as thread herring, they could contribute another 120,000 metric tons raising the aggregate potential yield to 545,100 metric tons.

Potential yields were estimated for adult stock. If a significant biomass of harvestable juveniles is present, they could contribute to the yield. For scaled sardines, and probably round herring (Houde 1977a), small size at first maturity makes it unlikely that a significant, unestimated juvenile biomass is present, but the large size at first maturity of thread herring (Prest³) and Spanish sardines (Varea Rivero 1967) indicates that a significant unestimated biomass of juveniles may be present.

³Prest, K. W., Jr. 1971. Fundamentals of sexual maturation, spawning, and fecundity of thread herring (*Opisthonema oglinum*) in the eastern Gulf of Mexico. Unpubl. manuscr., Natl. Mar. Fish. Serv., NOAA, St. Petersburg Beach, Fla.

Larval Abundance

Larval abundance varied annually and seasonally (Table 7; Figure 7); the greatest abundances being observed in 1973 and 1974 cruises. Abundance estimates for cruises in which larvae occurred, ranged from 0.20 to 16.63×10^{10} larvae. Estimated annual abundances of larvae were low in 1971 and 1972, but increased in 1973 (Figure 8). No annual estimates were available for 1974, but the great abundance of larvae from cruise CL7412 (Figure 7) suggests that more larvae were present in that year than in any previous year. The increases in larval abundance between 1971 and 1974 are further evidence that spawning intensity increased during the period.

Some scaled sardines as long as 30 mm SL were collected but few larvae longer than 20 mm were taken, and only larvae from 1.1 to 20.0 mm are included in the length-frequency distributions. Most larvae of 1.1 to 3.0 mm were distorted from collection and preservation. Scaled sardine larvae are 2.4 mm at hatching, but within 15 h their length increases to more than 4.0 mm, mostly due to straightening of the body axis rather than true growth (Houde et al. 1974). The most abundant larvae were 2.1 to 4.0 mm in 1972–74, but were larger in 1971 (Figure 7) when towing speed was faster (Houde 1977a) and mesh escapement by small larvae may have been greater.

The ratio of night-caught to day-caught scaled sardine larvae increased slowly as larvae increased in length. No larvae longer than 18.0 mm were sampled during daylight hours. An exponential model $R = 0.7999e^{0.0550X}$ was fitted to the data (Figure 9), where R is the ratio of night-caught to day-caught larvae and X is standard length. It provided the correction factor R, by which daytime catches were adjusted to obtain abundance estimates of larvae by 2-mm length classes in each station area (equation 11, Houde 1977a).

An exponential decrease in abundance of larvae was observed in 1973 (Figure 8) and the larval mortality rate was estimated from these data. Larvae longer than 3.0 mm were assumed to be fully vulnerable to the sampling gear. Abundances (Figure 8) were previously corrected for daytime avoidance. An exponential function was fitted to the data, and the instantaneous rate of decline in abundance per millimeter increase in length was estimated for larvae from 3.1 to 20.0 mm SL. The instantaneous coefficient, Z =0.3829, is a measure of larval mortality, if gear

TABLE 7.—Abundance estimates of scaled sardine larvae for each cruise. Estimates include larvae in all size classes and were obtained using equations (2) and (3) (Houde 1977a).

Cruise	Area represented by the cruise (m² ×10º)	Positive area ¹ (m ² \times 10 ⁹)	Cruise larvae abundance ² (larvae × 10 ¹⁰)
GE7101	25.79	0.77	0.00
8C7113 and			
TI7114	120.48	18.32	8.11
GE7117	101.10	7.93	0.00
8C7120 and			
TI7121	189.43	13.41	0.39
GE7127, TI7131			
and 8B7132	72.99	0.00	0.00
8B7201 and			
GE7202	148.85	0.00	0.00
GE7208	124.88	27.56	1.85
GE7210	48.43	15.60	2.89
IS7205	104.59	4.88	0.17
IS7209	149.80	0.00	0.00
IS7303	149.80	3.05	0.01
IS7308	151.42	43.38	14.02
IS7311	156.50	25.43	0.92
IS7313	153.18	40.79	16.63
IS7320	153.89	0.00	0.00
CL7405	52.00	5.84	0.20
CL7412	91.33	43.45	13.19

¹Positive area is defined as the area representing stations where either eggs or larvae of scaled sardines were collected.

²Values are not adjusted for cruises that did not encompass the entire area, nor have estimates been corrected to account for gear avoidance by larvae at stations sampled in daylight.

avoidance was not too great for larval length classes in the analysis. The 0.95 confidence limits on Z are $Z \pm 0.0833$. The observed coefficient corresponds to a 31.8% decrease in larval abundance per millimeter increase in length. Although mortality was not estimated for 1972 larvae, the high estimated abundance of larvae longer than 10 mm (Figure 8) indicates that survival may have been relatively good in that year.

Mortality relative to age of larvae was determined assuming an exponential model of growth for scaled sardine larvae, based on evidence from laboratory rearing experiments. Mean daily growth increments of scaled sardine larvae reared at temperatures above 26°C exceeded 0.5 mm, and frequently were in the range of 0.7 to 1.0 mm (Houde and Palko 1970; Saksena and Houde 1972; Saksena et al. 1972). Methods to estimate age at length and mortality have been reported (Houde 1977a).

Mean egg stage duration for scaled sardine is about 0.81 day. In 1973 the nonfully vulnerable length classes were 1.1 to 3.0 mm. Duration of that larval stage is from 1.0 to 3.0 days based on laboratory experiments (Saksena and Houde 1972; Houde et al. 1974).

An example of duration-corrected abundance data at estimated mean ages for eggs and larvae up to 20.0 mm in 1973 is given in Table 8. In this example the mean daily growth increment was



FIGURE 7.—Length-frequency distributions of scaled sardine larvae for 1971-74 cruises to the eastern Gulf of Mexico. Frequencies are expressed as estimated abundance of larvae in each length class within the area represented by the cruise. No adjustments for abundance have been made for cruises that did not cover the entire area where scaled sardine larvae might occur.



FIGURE 8.—Length-frequency distribution of annual larval abundance estimates for scaled sardine larvae collected in the eastern Gulf of Mexico, 1971–73. Frequencies in each 1-mm length class are expressed as estimated annual abundance and have been corrected for daytime avoidance. A fitted exponential function for 1973 data provides an estimate of the instantaneous coefficient of decline in abundance by length.

set at 0.8 mm and nonfully vulnerable larval stage duration was 1.0 day. I believe that those values are the best estimates for scaled sardine larvae, but other values also were assigned from which both mean ages and duration-corrected abundances were generated. Duration-corrected abundances (Table 8) were regressed on mean ages in an exponential regression to estimate the instantaneous mortality coefficient (Z) for age in days.

Mortality coefficients were calculated for various combinations of mean daily growth increments and durations of the nonfully vulnerable larval stage for 1973 data (Table 9). Possible values of the mortality coefficient, Z, range from 0.1822 to 0.3471, which correspond to daily percentage losses of 16.7 to 29.3%. For data from Table 8, where mean daily growth increment was 0.8 mm and nonfully vulnerable larval stage



FIGURE 9.—Night to day ratios of sums of catches, standardized to numbers under 10 m² of sea surface, for scaled sardine larvae collected in 1971–74 in the eastern Gulf of Mexico. The ratios were calculated for larvae within each 2-mm length class from 1.1 to 19.0 mm SL. A fitted exponential regression describes the relationship. Larval abundance estimates for each length class at stations occupied during daylight were corrected by the appropriate ratio factor for each length class to account for daytime avoidance.

TABLE 8.—An example of data from 1973 used to obtain stage duration, mean age, and duration-corrected abundance of scaled sardine eggs and larvae. Duration-corrected abundances were subsequently regressed on mean ages to obtain mortality rates (Table 9). Abundance estimates in the second column of the Table were previously corrected for daytime avoidance. In this example, the mean daily growth increment (\bar{b}) was set at 0.80. The nonfully vulnerable size classes were 1.1 to 3.0 mm. Calculating procedures were given in Houde (1977a), equations (12) to (16). The regression for these data is presented as Figure 10.

Stage	Abundance (no. × 1011)	Duration (days)	Mean age (days)	Duration-corrected abundance (no. × 10 ¹¹)
Eggs	827.54	0.81	0.41	1,025.83
1.1- 3.0 mm	43.27	1.00	1.33	43.27
3.1- 4.0	46.63	2.89	3.21	16.14
4.1- 5.0	45.49	2.25	6.06	20.23
5.1- 6.0	14.71	1.84	8.33	7.99
6.1- 7.0	13.20	1.56	10.22	8.47
7.1- 8.0	7.25	1.35	11.84	5.36
8.1- 9.0	4.52	1.19	13.26	3.79
9.1-10.0	1.45	1.07	14.52	1.35
10.1-11.0	0.84	0.97	15.66	0.87
11.1-12.0	1.65	0.88	16.69	1.87
12.1-13.0	1.24	0.81	17.63	1.52
13.1-14.0	0.83	0.75	18.50	1.11
14.1-15.0	1.56	0.70	19.31	2.23
15.1-16.0	0.61	0.66	20.07	0.93
16.1-17.0	0.05	0.62	20.78	0.09
17.1-18.0	0.39	0.58	21.44	0.68
18.119.0	0.00	0.55	22.07	_
19.1-20.0	0.04	0.52	22.67	0.07

duration was 1.0 day, the estimated mortality coefficient is Z = 0.2835, corresponding to a 24.7% daily loss rate (Figure 10). The most probable scaled sardine mortality estimate for abundance at age data, $Z = 0.2835 \pm 0.0754$ at the 0.95 confidence level, is similar to those for thread

TABLE 9.—Summary of mortality estimates for scaled sardine larvae from the eastern Gulf of Mexico, 1973. Estimates were obtained from the exponential regression of egg and larvae abundances on mean age. Instantaneous growth and mortality coefficients were calculated for various possible combinations of mean daily growth increment and duration of the nonfully vulnerable larval stages. Egg stage duration was assigned the value 0.81 days. Nonfully vulnerable larval lengths were 1.1 to 3.0 mm SL. Explanation of the estimating method is given in equations (12) to (16) of Houde (1977a).

Mean daily growth increment, b (mm)	Instantaneous growth coefficient, g	Nonfully vulnerable larvae duration (days)	Instantaneous mortality coefficient, Z	Y-axis intercept, N_0 (no. $\times 10^{11}$)	Daily mortality rate 1 - exp(-Z)
0.5	0.0552	1.0	0.1842	97.32	0.1683
0.6	0.0662	1.0	0.2179	116.45	0.1958
0.7	0.0772	1.0	0.2509	136.44	0.2220
0.8	0.0883	1.0	0.2835	157.36	0.2469
0.9	0.0993	1.0	0.3156	179.28	0.2706
1.0	0.1103	1.0	0.3471	202.26	0.2933
0.5	0.0552	3.0	0.1822	131.23	0.1665
0.6	0.0662	3.0	0.2146	164.36	0.1932
0.7	0.0772	3.0	0.2461	200.90	0.2182
0.8	0.0883	3.0	0.2767	240.98	0.2417
0.9	0.0993	3.0	0.3065	284.66	0.2640
1.0	0.1103	3.0	0.3353	332.06	0.2849

herring (Z = 0.2124 in 1971 and Z = 0.2564 in 1973), but higher than those for round herring: Z = 0.1317 in 1971–72 and Z = 0.1286 in 1972–73 (Houde 1977a, b).

The y-axis intercepts (N_0) of the regressions in Table 9 also estimate the number of eggs spawned in 1973. Their values are lower than those calculated by the Sette and Ahlstrom (1948) method for 1973 (Table 4), which is considered the best estimate of annual spawning. A higher than expected mortality rate of eggs or nonfully vulnerable larvae may have caused the discrepancy (Figure 10). Larval mortality, considering only fully vulnerable stages, may be lower than that for the entire egg-larval stage. For data from Table 8 and Figure 10, the mortality coefficient for fully vulnerable 3.1- to 20.0-mm larvae is Z = 0.2458, a daily loss rate of 21.8%.

The numbers of probable survivors at hatching, 5.5 mm, and 15.5 mm were estimated in 1973 for three instantaneous growth rates that likely encompass the true rate for scaled sardine larvae (Table 10). Initial egg abundance was the 1973 estimate from Table 4. The estimated number alive at each stage was calculated from the parameters of the exponential functions (Table 9) and from the estimated age in days at each stage (Table 8).

Mortality was high during the egg and larval stages. An apparent mortality of 85 to 91% occurred between spawning and hatching (Table 10). Less than 2% survived to 5.5 mm, when larvae would have been feeding for 2 days at 26° to 28°C (Houde et al. 1974). More than 99.9% mortality had occurred by 15.5 mm, when larvae were beginning to transform to juveniles. At the most probable growth rate, g = 0.0883, only 5 larvae/



FIGURE 10.—Estimated abundance of egg and larval stages of scaled sardines in the eastern Gulf of Mexico in 1973. Abundance is expressed as a function of estimated age. A fitted exponential function gives an estimate of the instantaneous rate of decline in abundance for eggs and larvae up to 23 days of age. The symbol enclosed in the circle represents the nonfully vulnerable 1.1- to 3.0-mm length classes and was not included in the regression estimate of instantaneous decline.

10,000 spawned eggs were estimated to have survived to 15.5 mm and 20 days of age in 1973.

for 1.1 to 3.0	mm larvae. Tł	•	vned eggs was l	based on the es	of the nonfully vi timate in Table 4. data.		-	
Instantaneous growth	Number of spawned	Instantaneous mortality	Number	Percent	Number of	Percent	Number of	Percent mortality to

TABLE 10.--Estimated numbers and percentages of survivors of scaled sardines at hatching, 5.5 mm SL, and 15.5 mm SL in 1973.

Instantaneous growth coefficient, g	Number of spawned eggs (×10 ¹¹)	Instantaneous mortality coefficient, Z	Number hatching (×10 ¹¹)	Percent mortality ¹ to hatching	Number of 5.5-mm larvae (×10 ¹¹)	Percent mortality to 5.5 mm	Number of 15.5-mm larvae (×10 ¹¹)	Percent mortality to 15.5 mm
0.0662	1,025.83	0.2179	97.61	90.5	11.82	98.8	0.39	99.96
0.0883	1,025.83	0.2835	125.07	87.8	14.83	98.6	0.53	99.95
0.1103	1,025.83	0.3471	152.69	85.1	17.63	98.3	0.68	99.93

¹Hatching assumed to occur at 0.81 day.

Estimated survival of scaled sardines at hatching and 5.5 mm was lower than that for thread herring or round herring (Houde 1977a, b). In 1973 scaled sardines apparently experienced high mortality during embryonic and young larval stages, which quickly reduced the initial number of eggs to relatively few larvae. Thread herring and scaled sardine mortality rates may be similar for larvae in the fully vulnerable length classes. Round herring larvae had a lower estimated mortality rate than either scaled sardines or thread herring. But, the probable slower growth rate of round herring larvae at cooler temperatures (Houde 1977a) caused estimated numbers at 15.5 mm to be only 40 to 120 survivors/10,000 spawned eggs, which was comparable with the thread herring estimate of 60 to 200 survivors/ 10,000 eggs, but higher than the 5 survivors/ 10,000 eggs estimated for scaled sardines.

SUMMARY

1. Scaled sardines spawned from January to September in the eastern Gulf of Mexico, with most spawning occurring during spring and summer. They spawned in waters <30 m deep, mostly within 50 km of the coast.

2. Eggs were collected where surface temperatures ranged from 20.8° to 30.7° C and surface salinities were 29.9 to 36.9° . Larvae $\leq 5.0 \text{ mm SL}$ were collected at surface temperatures from 18.4° to 30.5° C and at surface salinities of 27.3 to 36.9° . Most eggs and ≤ 5.0 -mm larvae occurred where surface temperature exceeded 24°C and surface salinity was above 35° .

3. Estimates of annual spawning increased in each year, 1971-73. Biomass estimates increased from 16,000 to 390,000 metric tons during those years. The mean biomass estimate for the 3-yr period was 184,527 metric tons. Concentrations of adult biomass between the coast and the 30-m depth contour were: 1971-2.8 kg/ha; 1972-24.7 kg/ha; 1973-64.8 kg/ha. 4. Estimated annual potential yields to a fishery were: 1971—4,177 to 8,354 metric tons; 1972— 37,064 to 74,128 metric tons; 1973—97,153 to 194,305 metric tons. Potential yield, based on the 3-yr mean biomass estimate, was between 46,132 and 92,264 metric tons, or 7.7 to 15.4 kg/ha.

5. Larvae were more abundant in 1973 than in 1971 or 1972. Larval mortality, relative to length and to estimated ages, was estimated for 1973 data. For length, the instantaneous coefficient was Z = 0.3829, corresponding to a 31.8% decrease in larval abundance per millimeter increase in length. For age, the most probable estimate is Z = 0.2835, which corresponds to a 24.7% daily loss rate.

6. It is probable that more than 99.9% mortality occurred between spawning and the 15.5-mm stage in 1973. Only 5 larvae/10,000 spawned eggs were estimated to have survived to 15.5 mm at 20 days of age in that year.

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