Comparison of feeding and growth of larval round herring *Etrumeus teres* and gulf menhaden *Brevoortia patronus*

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The round herring *Etrumeus teres* is one of several clupeid fishes, abundant in continental shelf waters of the Gulf of Mexico, that presently is not commercially exploited by the United States, although its sibling species *E. whiteheadi* is a fishery resource for South Africa (Roel and Melo 1990). The potential annual yield of this latent resource is estimated as 3.3×10^4 to 4.2×10^5 metric tons for the eastern Gulf (Houde 1977) and 1.1×10^5 to 1.1×10^6 metric tons for the entire Gulf (Reintjes 1980). Details relevant to the distribution and population dynamics of round herring, including elements of its early life history, are presently sketchy. Houde (1977) reported that round herring in the eastern Gulf of Mexico spawn from mid-October to the end of May between the 30 and 200 m isobaths. He surmised that there is a major spawning area about 150 km west-southwest of Tampa Bay, Florida, and a minor area just north of the Dry Tortugas. Off Texas and Louisiana, spawning occurs from 50 to 200 km offshore and may extend to the edge of the continental shelf (Fore 1971). Round herring and another clupeid, the gulf menhaden *Brevoortia patronus*, are sympatric; the latter spawns in inshore waters of the northern Gulf at least as far offshore as 130 km with a focus of spawning off Mississippi between mid-October and late March (Christmas and Waller 1975).

Differences between adult round herring and gulf menhaden are so obvious that systematists once referred these two species to separate families, Dussumieriidae and Clupeidae (Whitehead 1963), but their larvae are morphologically similar with one major exception, their jaw structure. (The misperception that, unlike other clupeids, round herring larvae do not possess a swimbladder (Fahay 1983) has been perpetuated in the literature.) At hatching larvae of both species are about 3.0 mm notochord length (NL) and are slender and elongate with a straight alimentary canal and a posterior anus (Houde and Fore 1973). Transformation to the juvenile form begins at about 18 mm standard length (SL) (Houde and Fore 1973). Round herring larvae develop teeth on their long, spatulate upper and lower jaws at about 6 mm SL (Houde and Fore 1973); but gulf menhaden do not develop teeth on their shorter, less compressed jaws until they are about 10 mm SL (Hettler 1984).

The diets of the larvae of these species might reflect differences in jaw structure and dentition. In addition, differences in diet quality and quantity may register different growth between these species. While feeding and growth of gulf menhaden larvae are documented (Govoni et al. 1983, Stoecker and Govoni 1984, Warlen 1988), similar information on the early life history of round herring is unavailable. In this paper, we compare the feeding and growth of larval round herring and gulf menhaden.

Materials and methods

Round herring and gulf menhaden larvae used in this study were removed from ichthyoplankton collections obtained during two cruises (December 1980 and February 1981) using MOCNESS gear (multiple opening/closing nets and environmental sensing system). Three stations were occupied, one each at the 18, 91, and 183 m isobaths, along three transects (off Cape San Blas, FL; off the Mississippi Delta, LA; and off Galveston Bay, TX (Sogard et al. 1987)). The objective of the sampling plan was to broadly canvass the continental shelf of the northern Gulf for larval gulf menhaden and two other species (Sogard et al. 1987); larval round herring were collected incidentally. Sampling at three discrete depths (surface, in the middle of the upper mixed layer, and within or below the thermocline) assured the collection of adequate numbers of specimens. In addition, larvae from a single collection taken at the Mississippi River plume front (Govoni et al. 1989) in December 1982 were examined to augment gut content data. Larvae were preserved in 5% formalin for food analysis and in 70% ethanol for growth studies (Table 1). To provide an indication of true dietary differences between species encountering the same food assortment, only those larvae from a single vertically and horizontally discrete collection (Govoni et al. 1986) that produced both species were used for diet comparisons

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Table 1

Time, location, and depth of collection in the northern Gulf of Mexico of round herring *Etrumeus teres* larvae examined for diet composition and growth determination.

Date	Time	Transect	Water column depth (m)	Sample depth (m)	No. of larvae collected	No. of larvae with food
6 Dec 80[1]	0645	Mississippi Delta	183	1	2	0
8 Dec 80[2]	0013	Cape San Blas	183	1	8	
8 Dec 80[2]	0013	Cape San Blas	183	51	2	
8 Dec 80[1]	0040	Cape San Blas	183	50	6	0
8 Dec 80[1]	0056	Cape San Blas	183	1	10	0
8 Dec 80[1]	0621	Cape San Blas	183	50	3	0
8 Dec 80[2]	1800	Cape San Blas	183	1	20	
8 Dec 80[2]	1800	Cape San Blas	183	102	1	
8 Dec 80[1]	1821	Cape San Blas	183	49	3	0
8 Dec 80[1]	1834	Cape San Blas	183	1	20	1
9 Dec 80[2]	0600	Cape San Blas	91	1	7	
9 Dec 80[2]	0600	Cape San Blas	91	35	1	
9 Dec 80[2]	0600	Cape San Blas	91	74	3	
9 Dec 80[1]	0617	Cape San Blas	91	35	13	0
9 Dec 80[1]	1237	Cape San Blas	91	37	2	0
9 Dec 80[2]	1800	Cape San Blas	91	1	19	0
9 Dec 80[1]	1806	Cape San Blas	91	75	3	0
9 Dec 80[1]	1817	Cape San Blas	91	35	3	0
9 Dec 80[1]	1827	Cape San Blas	91	1	20	4
10 Dec 80[2]	0005	Cape San Blas	91	1	19	
10 Dec 80[2]	0005	Cape San Blas	91	35	1	0
10 Dec 80[2]	0010	Cape San Blas	91	12	4	0
10 Dec 80[1]	0025	Cape San Blas	91	74	6	0
10 Dec 80[1]	0025	Cape San Blas	91	1	1	0
10 Dec 80[1]	0035	Cape San Blas	91	46	16	0
10 Dec 80[1]	0045	Cape San Blas	91	1	11	0
10 Dec 80[1]	1812	Cape San Blas	18	6	2	1
10 Dec 80[1]	1821	Cape San Blas	18	1	17	2
11 Dec 80[1]	0019	Cape San Blas	18	12	11	1
11 Dec 80[1]	0031	Cape San Blas	18	1	3	0
12 Feb 81[2]	1900	Galveston Bay	18	6	2	
13 Feb 81[2]	0600	Galveston Bay	91	35	5	
14 Feb 81[1]	0033	Galveston Bay	91	61	13	1
14 Feb 81[1]	0047	Galveston Bay	91	35	20	1
14 Feb 81[1]	0100	Galveston Bay	91	1	12	0
14 Feb 81[2]	0600	Galveston Bay	91	37	13	
14 Feb 81[1]	0620	Galveston Bay	91	77	8	0
14 Feb 81[1]	0635	Galveston Bay	91	27	20	0
14 Feb 81[1]	0644	Galveston Bay	91	1	20	0
14 Feb 81[1]	1823	Galveston Bay	91	74	20	1
14 Feb 81[1]	1846	Galveston Bay	91	1	20	7
18 Feb 81[1]	0014	Mississippi Delta	91	75	2	0
18 Feb 81[1]	0025	Mississippi Delta	91	1	20	8
18 Feb 81[2]	0600	Mississippi Delta	91	25	20	0
18 Feb 81[1]	0607	Mississippi Delta	91	25	20	2
18 Feb 81[1]	0625	Mississippi Delta	91	1	4	1
18 Feb 81[2]	1800	Mississippi Delta	91	40	8	
10 Dec 82[1]	0830	Mississippi Delta	18	1	88	26

[1]Collections for examination of diet.
[2]Collections for determination of growth.

(Table 1). Adequate numbers of larvae allowed growth comparisons of larvae collected on the Cape San Blas transect in December 1980 and larvae collected on the Mississippi Delta and Galveston Bay transects in February 1981.

Larvae were measured to the nearest 0.1 mm (NL before and SL after the formation of hypural plates). Guts were dissected and all gut contents were excised, identified, and measured. Percent similarity (Schoener 1970) was used to compare the diets of larval round herring and gulf menhaden from single collections.

Sagittal otoliths were removed from larvae, cleaned in distilled water, and mounted on glass microscope slides with clear acrylic resin; no griding or sectioning was necessary to resolve daily growth increments. Otoliths of round herring were semi-opaque and similar to those of gulf menhaden. Presumed daily increments were clearly discernable as bipartite structures consisting of adjoining incremental and discontinuous zones (Campana and Neilson 1985).

In describing the growth of larval round herring, we did not experimentally verify that their first otolith increment appeared 5 days after hatching or that subsequent increments were added daily as Warlen (1988) has done for gulf menhaden. We assumed that initial and subsequent increment deposition in round herring was similar to gulf menhaden. This assumption is justified, in part, by similarities in the period of some key developmental events. Incubation takes 36 hours at 20.5°C for round herring (O'Toole and King 1974), and 40–42 hours at 19–20°C for gulf menhaden (Hettler 1984). Complete adsorption of the yolk occurs in 4 days for round her-

ing reared in the laboratory at 24–26°C (Miller et al. 1979), as well as for gulf menhaden reared at 18–22°C (Hettler 1984). Further, we used alternative empirical methods to support our assumption that otolith growth increment formation occurs daily (Hales 1987). By comparing the width of marginal increments with the width of the proximal completely-formed increment, we determined the percentage of larvae with partially-formed or completely-formed marginal increments over a 24-hour period (8–10 December 1981; Table 1). The frequency of increment formation was inferred from these percentages and from the relationship of otolith radius and larval length.

The Laird version of the Gompertz growth model was used to describe growth from the logarithm of length and the estimated age of larvae (Zweifel and Lasker 1976). Growth curves of round herring and gulf menhaden larvae were compared by using the predictive, resampling method described by Kappenman (1981). Data for gulf menhaden growth were taken from Warlen (1988) for comparisons with the growth of round herring.

Results

Distribution and co-occurrence

In all, 419 round herring larvae were identified in the present collections, four fewer than gulf menhaden (Sogard et al. 1987). Collections of the larvae of both species indicate that they co-occur infrequently. Round herring and gulf menhaden larvae occurred together at 15 of 45 locations where collections produced either species. Larval round herring were collected most frequently throughout the water column at the offshore stations in water 91 m deep, although one of the largest single collections was made at 18 m (Table 1). Larval gulf menhaden were collected mostly inshore at the 18 m stations along each transect. The larvae of these species co-occurred mainly at the 91 m stations along each transect.

Diet comparisons

Only 56 round herring larvae had food in their guts. Larval round herring had eaten primarily copepod nauplii, copepodites, and adults, with pteropods (mainly *Limacina trochiformis*), tintinnids, invertebrate eggs, and *Eucalanus* spp. nauplii contributing lesser percentages (Table 2). *Eucalanus* nauplii were considered a discrete food organism separate from other copepod nauplii, because its form and size differed markedly; *Eucalanus* spp. nauplii have long, paddle-like appendages and are more than three times larger than the other copepod nauplii observed in the guts of larvae.

Table 2

The diet composition of 56 round herring *Etrumeus teres* larvae in the northern Gulf of Mexico.

	Percent frequency of occurrence	Percent total no.
Centric diatoms	1.8	1.3
Tintinnids	3.6	5.2
Pteropods	8.9	6.5
Pelecypods	1.8	1.3
Unidentified copepod nauplii	25.0	36.4
Unidentified *Eucalanus* nauplius	3.6	3.9
Copepodid and adult copepods	21.4	16.9
Calanoid copepodites and adults	5.4	3.9
Harpacticoid copepodites and adults	1.8	1.3
Cyclopoid copepodites and adults	16.1	11.7
Invertebrate eggs	10.7	11.7

Table 3

Comparison of the percent frequency of occurrence of food organisms in the diet of 26 larval round herring and gulf menhaden larvae collected simultaneously in the northern Gulf of Mexico.

	Percent frequency of occurrence	
Food organism	Round herring	Gulf menhaden
Tintinnid	3.8	4.2
Pteropods	19.2	2.1
Unidentified copepod nauplii	7.7	5.3
Unidentified *Eucalanus* nauplius	3.8	5.3
Unidentified copepodites and adult copepods	15.4	31.6
Calanoid copepodites and adults	3.8	33.7
Harpacticoid copepodites and adults	3.8	0
Cyclopoid copepodites and adults	30.8	11.6
Invertebrate eggs	11.5	6.3

The width of food organisms ranged from 40 to 280 μm, a width range comparable to that found for gulf menhaden (Govoni et al. 1983).

Of the 88 round herring larvae collected simultaneously with gulf menhaden, 26 had food in their guts. There were differences in the gut contents of these 26 round herring and 26 randomly selected gulf menhaden larvae collected simultaneously (Table 3). Larval round herring had eaten cylopoid copepods (*Oncaea* spp. and *Corycaeus* spp.) and pteropods more frequently, but calanoid copepodites and adult copepods less frequently, than had larval gulf menhaden. Percent similarity of the diets of these larvae was 52.2, a value that indicates marginal overlap in diet (Schoener 1970).

Growth comparisons

Marginal growth increments seemed to form from evening through early morning (Table 4). The allometric relationship ($\log_{10}$ radius = 0.126 $\log_{10}$SL + 1.413; r^2 0.91) between otolith radius and standard length of 131 larvae also suggested a daily periodicity in otolith increment formation (Hales 1987).

Estimates of the length at hatching ($L_{(0)}$) for gulf menhaden provided by the Laird-Gompertz model 3.4 mm SL (Fig. 1; Table 5), closely approximate the length-at-hatching of larvae incubated in the laboratory at a temperature of 20°C, 2.6–3.0 mm SL (Hettler 1984). Estimates of $L_{(0)}$ for round herring, about 1.2 mm SL, however, are considerably lower than the lengths reported for larvae hatched in the laboratory: 3.8–4.0 mm body length from eggs collected in the South Atlantic and incubated at 20.5°C (O'Toole and King 1974) and 6.0 mm SL from eggs collected in the Pacific and incubated at 24–26°C (Miller et al. 1979). If the interval from hatching to deposition of the first growth increment is shorter in reality than the assumed 5 days, the Laird Gompertz growth curve would shift to the left, yielding a greater value for $L_{(0)}$, but the form of the growth curve, i.e., the growth rate, would remain the same.

Round herring grew faster than gulf menhaden through the first 20–40 days; gulf menhaden exhibited faster growth than round herring thereafter (Fig. 2). The fastest growth rate (≈0.85 mm/day) for round herring larvae occurred at about 15 days. Average growth rates through 27 days for December 1980 were 0.71 and 0.46 mm/day for round herring and gulf menhaden; average rates through 50 days in February 1981 were 0.45 and 0.34 mm/day. Annual differences in larval gulf menhaden growth are discussed in Warlen (1988).

Table 4

Percentage of round herring larvae with partially formed (narrow) or completed (wide) marginal otolith growth increments collected at three different times of day.

Time of capture (h)	No. of fish	Percentage	
		Partially formed	Completed
1800	9	22	78
2400	10	40	60
0600	6	100	0

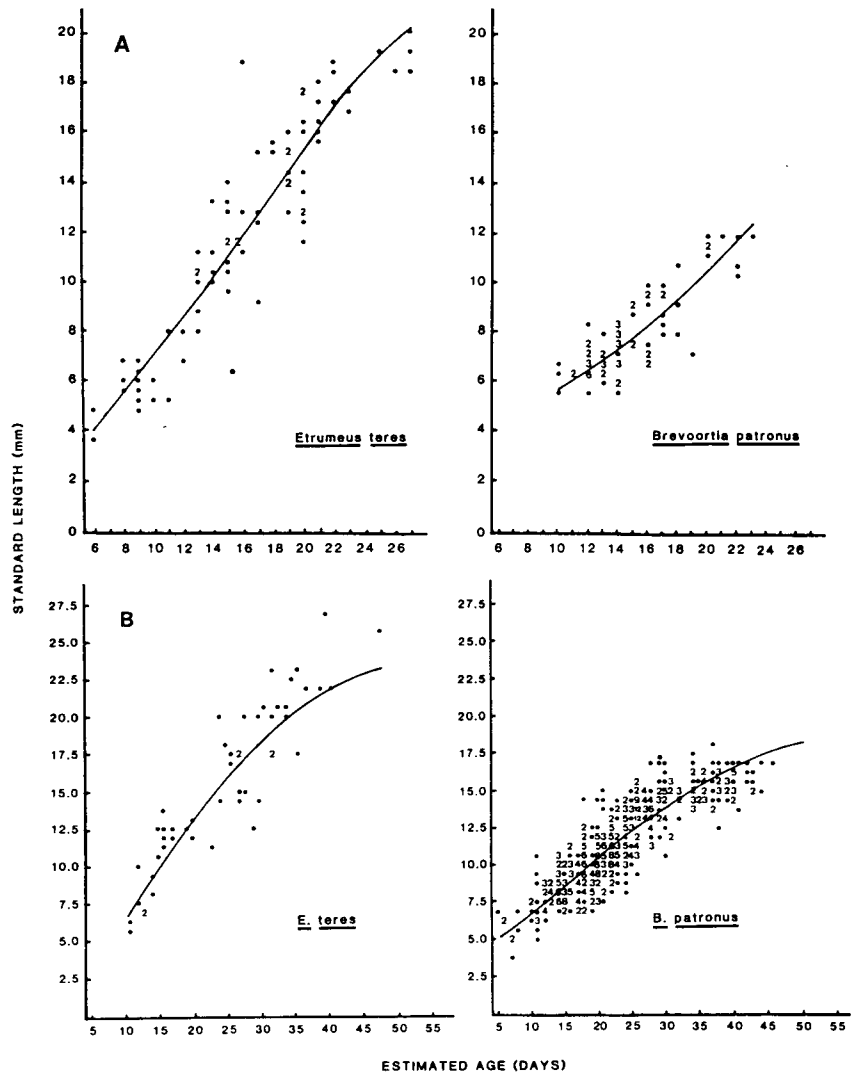

Figure 1

Growth of larval round herring *Etrumeus teres* and gulf menhaden *Brevoortia patronus* collected in December 1980 (A) and February 1981 (B) in the northern Gulf of Mexico. The log form of the Laird-Gompertz model was used to describe the growth of both species (numbers indicate location of coincident data points).

Table 5

Estimates of Laird-Gompertz growth model parameters* and mean age (d) and SL (mm) for larval round herring and gulf menhaden collected in the northern Gulf of Mexico during December 1980 and February 1981.

Date		Number of observations	Growth model parameters $L_{(0)}$	$A_{(0)}$	α	Mean estimated age (d)	Mean SL (mm)
December 1980	Round herring	81	1.184 (0.310)	0.259 (0.055)	0.081 (0.015)	16.025 (0.590)	12.056 (0.501)
	Gulf menhaden	80	3.418 (0.995)	0.056 (0.037)	<0.001 (0.407)	14.862 (0.337)	8.034 (0.191)
February 1981	Round herring	50	1.240 (0.710)	0.232 (0.089)	0.077 (0.018)	25.200 (1.318)	15.620 (28.871)
	Gulf menhaden	561	3.401 (0.246)	0.087 (0.009)	0.045 (0.005)	23.401 (0.333)	11.493 (0.121)

* $L_{(0)}$ = length at hatching, $A_{(0)}$ = specific growth rate at hatching, α = exponential decay of the specific growth rate. Values in parentheses are asymptotic standard errors.

In two comparisons, the growth curves of these species differed, i.e., the sum of squares of the differences between observed and predicted lengths was greater when data for the two species were pooled than when the data were considered separately. In the comparison of larvae collected in December 1980, the sum of squares of deviations was 6.327 for pooled data and 2.736 for data considered separately (total observations = 161). In the comparison of larvae collected in February 1981, from two transects, the sum of squares of deviations was 13.255 for pooled data and 10.477 for data considered separately (total observations = 611).

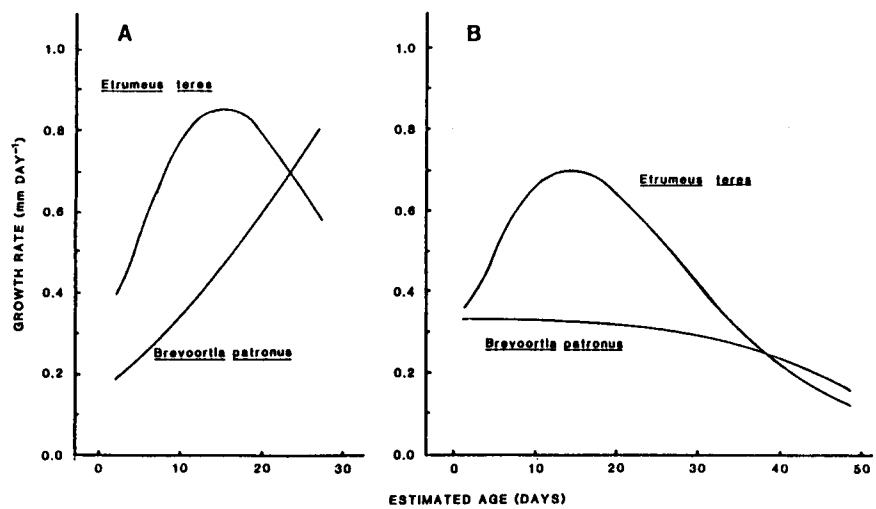

Figure 2

Age-specific growth rates of larval round herring *Etrumeus teres* and gulf menhaden *Brevoortia patronus* collected in December 1980 (A) and February 1981 (B) in the northern Gulf of Mexico. Specific growth rates-at-age were derived from the log form of the Laird-Gompertz growth model parameters.

Discussion

The large, spatulate, and toothed jaws of larval round herring might enable them to eat larger food organisms than gulf menhaden, but while the diets of larval round herring and gulf menhaden differed, the width of food organisms coincided. Diets, then, do not directly reflect differences in jaw structure and dentition. The pteropods eaten by both species were *Limacina trochiformis*, the cyclopoid copepods were primarily of the genera *Oncaea* and *Corycaeus*, and the calanoid copepods were primarily of the genera *Paracalanus* and *Acartia*. Round herring larvae ate more pteropods and cyclopoid copepods, but fewer calanoid copepods than did gulf menhaden larvae.

The more offshore distribution of larval round herring in the central and western northern Gulf of Mexico (Shaw and Drullinger 1990; present data) may explain differences in diet and growth. All of the food organisms eaten by larval round herring and gulf menhaden are broadly distributed in continental shelf waters, but some of the copepods have different patterns of distribution across the shelf in the northern

Gulf of Mexico (Ortner et al. 1989). *Acartia*, for example, occurs in greater abundance inshore, in less saline waters, whereas *Oncaea* and *Corycaeus* are more abundant in water of traditional salinities offshore (Ortner et al. 1989). Prior experience and learning can influence the capture efficiency, food selection, and ingestion rates of larval fishes (see review in Stoecker and Govoni 1984); and because larval round herring occupy more offshore waters, they may be conditioned to feed preferentially on the cyclopoids *Oncaea* and *Corycaeus*.

The difference in larval growth between these two species may reflect differences in the physical environment where these larvae grow. Offshore water in the northern Gulf of Mexico is typically warmer than inshore water during the winter. Inshore–offshore gradients in average water column temperature among the three stations along the three transects were 19.2 to 20.7 to 22.1°C for the Cape San Blas transect in December 1980; 16.1 to 15.0 to 18.1, 16.9 to 19.5 to 19.8, and 12.9 to 18.5 to 19.0°C for the Mississippi Delta, Cape San Blas, and Galveston Bay transects in February 1981. Temperature differences of this magnitude can account for intraspecific differences in growth rates among larval fish (Jones 1986, Warlen 1988) as seen here in the slower growth of round herring larvae in the cooler water of February 1981. The faster, early growth of round herring larvae, overall, probably results from the warmer waters of its offshore occurrence.

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