

Abstract.—The larval development of red snapper, *Lutjanus campechanus*, is described from reared larvae and from specimens collected in the Gulf of Mexico (GOM). Snapper larvae are pelagic and are characterized by the following features: a deep and compressed, lightly pigmented body; moderately short gut; 24 myomeres; and elongated dorsal and pelvic fins that form early in development. Specimens of *L. campechanus* (1.9 to 26.1 mm) also showed the presence of weak serrations on pelvic-fin spines, absence of serrations on preopercular or dorsal spines, early forming pigment in dorsal and pelvic fins, and notochord flexion between 3.6 and 5.5 mm. Preflexion larvae of the snapper subfamily Lutjaninae in GOM collections cannot be reliably identified to species despite recent larval descriptions. Species-specific differences in number, spacing, and size of melanophores in the postanal ventral series are evident in the youngest larvae of species from the GOM whose development has been described (*Ocyurus chrysurus*, *L. analis*, *L. synagris*, *L. griseus*, *L. campechanus*, and *Rhomboplites aurorubens*) but further evaluation of the utility of these characters is needed. Characteristics that distinguish mid- to late-flexion larvae of these species are compiled in our study and discussed. Among known GOM lutjanine larvae, body depth, pelvic-ray length and serrations on the angle spine of the preopercle can be used in combination with pigmentation to identify larvae to species. Presence of melanistic pigment (and size at first appearance) or absence of melanistic pigment in the following locations are useful characters for larval snapper identification: anterior surface of the visceral mass, ventral to notochord flexure; internal area over the notochord; dorsal midline of caudal peduncle; soft dorsal fin; anal-fin base or membrane; and pelvic fin.

Larval development of red snapper, *Lutjanus campechanus*, and comparisons with co-occurring snapper species

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In the Gulf of Mexico (GOM), the red snapper, *Lutjanus campechanus*, supports lucrative commercial and recreational fisheries that have been under increasingly restrictive regulation since the 1980s (Workman and Foster, 1994; Schirripa and Legault¹). Responsible management decisions should be based on an understanding of all life history stages, but until recently the larval development of only three of the 18 species of snappers found in the GOM were known. Collins et al. (1980) described *L. campechanus* from wild larvae with substantial fin development that allowed identification by meristic counts and Rabalais et al. (1980) described reared red snapper eggs and larvae that developed only until 4 days after hatching. Substantial fin development also allowed identification by meristic counts for larvae of the vermilion snapper, *Rhomboplites aurorubens* (Laroche, 1977), and a third lutjanid, the gray snapper (*L. griseus*), was described by Richards and Saksena (1980)

from reared specimens. More recently, descriptions by Clarke et al., 1997 (*Ocyurus chrysurus*, *L. analis* and *L. synagris*), Riley et al., 1995 (*O. chrysurus*), Leis and Lee, 1994 (*Etelis* spp., *Pristipomoides aquilonaris* and *P. freemani*?) and the summary compilation by Richards et al. (1994) added three genera and four species to the list of known snapper larvae. Our paper describes for the first time the complete sequence of larval development of red snapper from reared specimens and compares the structure and shape of reared and wild larvae. Additionally, we present a summary of developmental characteristics to separate snapper larvae in field collections from the Gulf of Mexico.

¹ Schirripa, M. J., and C. M. Legault. 1997. Status of the red snapper in U.S. waters of the Gulf of Mexico: updated through 1996. Unpublished contribution report MIA-97/98-05, 37 p. Miami Laboratory, Southeast Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA.

Materials and methods

A total of 96 reared larvae, ranging in body length (BL) from 1.9 to 26.1 mm, and a total of 118 wild larvae, ranging from 2.6 to 20.0 mm BL, were used to describe larval development of red snapper. Reared larvae came from the Marine Science Laboratory, University of Texas at Austin, Port Aransas, Texas (TX), and the Claude Peteet Mariculture Center in Gulf Shores, Alabama (AL). Spawning and rearing methods used are described by Riley et al. (1995) at the Texas facility and by Bootes (1998) at the Alabama facility. Notable differences in the rearing methods at the two facilities that could have contributed to different developmental rates include higher salinities in the TX study (33–38 ppt vs. 31–33 ppt), higher temperatures in the AL study (27–32°C vs. 27–28°C) and natural light conditions in the AL study. Several larvae were preserved each day during the Texas rearing study whereas only one larva was preserved each day during the Alabama rearing experiments. Specimens from AL were fixed in 2% formalin and specimens from TX were fixed in 80% ethanol (EtOH) and together formed the developmental series described in our study. Age in days after hatching (DAH) is included in parentheses after BL for reared larvae. In addition, observations on the development of pigment characters were augmented with 96 larvae reared at the Gulf Coast Research Laboratory (GCRL) in Ocean Springs, MS, under conditions similar to the AL study.

Wild red snapper larvae were obtained from plankton samples collected in the GOM by the Southeast Area Monitoring and Assessment Program (SEAMAP) and GCRL. Samples were collected with bongo and neuston nets at stations 56 km apart by using standard SEAMAP collection procedures (Richards, 1984; Richards et al., 1993). Samples were fixed in 10% formalin and transferred to 70% EtOH after 48 h.

All specimens described in our study are considered larvae because they exhibit specializations for pelagic life (head spination, long fin elements) and are pigmented differently than juveniles and adults are pigmented (Leis, 1987; Leis and Trnski, 1989; Leis et al., 1997). Myomere and fin-ray counts were made on the left side of the body. Illustrations were made with a camera lucida. Preserved eggs and larvae were measured to the nearest 0.1 mm with an ocular micrometer fitted to a dissecting microscope. Body length (BL) as defined in Leis and Rennis (1983) is equivalent to notochord length or standard length depending on the stage of development of the larvae. Notochord length is the straight line distance from the tip of the snout to the posterior tip of the notochord and is used as the standard measurement before and during flexion. Standard length is the distance from the tip of the snout along the midline to a vertical line through the posterior edge of the hypural plate. Other common measurements and abbreviations follow Leis and Rennis (1983). Additional abbreviations used here are as follows:

avm = anterior surface of the visceral mass;
 BD = body depth;
 IPo = inner border of the preopercle (=anterior border of some authors);

OPo = outer border of the preopercle (=posterior border of some authors);
 pav = postanal-ventral.

Results

Description of reared larvae

General development (Table 1, Figs. 1–5) Red snapper eggs (AL) were 0.72–0.76 mm in diameter ($n=4$) at one hour after fertilization and contained a single oil globule (diameter 0.11–0.13 mm). Larvae hatched in approximately 24 h and had a large, elongate yolk sac extending anteriorly beyond the head with a single oil globule. The oil globule was the last portion of the yolk to be absorbed at 4 days after hatching (DAH). Body lengths of the youngest larvae measured were 1.9 mm at hatching ($n=1$), 2.5 mm at 12 h ($n=1$), and 2.8 mm at 28 h ($n=1$). The eyes were pigmented and the mouth was functional by the end of 2 DAH when larvae began to swim actively and feed. Larvae were initially elongate (10% BD at 2.9 mm) but became deeper bodied (43% BD at 4.9 mm) and laterally compressed with development. The smallest larvae (2.5–3.1 mm) showed no fin development or spination. Head length increased from 9% BL in preflexion larvae (2.4 mm) to 42% BL in postflexion larvae (7.5 mm). Teeth appeared along the premaxilla and dentary by 3.5 mm. The gut was initially straight but began to coil at 2.4 mm (6 DAH) and was fully coiled by 3.6 mm (9 DAH). Preanal length increased from 38% BL (2.4 mm) in preflexion larvae to 69% BL in postflexion larvae (16.5 mm). Gas bladder inflation occurred at 4 DAH, and in our study the gas bladder was visible in the 2.4-mm (6 DAH) larva. Notochord flexion began at 3.8 mm (12 DAH) and was complete by 5.5 mm (15 DAH). Scales were present on the largest specimen (26.3 mm, 34 DAH).

Spination (Figs. 1–5) All spines described here were easily visible without clearing and staining. Head spination began by 3.0 mm with the development of preopercular spines, with one spine on the inner border of the preopercle (IPo) and two spines (including the angle spine) on the outer border of the preopercle (OPo). At 3.6 mm, there were two spines on the IPo and four spines on the OPo, one above the angle spine and two below. Spines increased to three on the IPo and five on the OPo by 3.8 mm. At 5.6 mm, there were four spines on the IPo and six spines on the OPo, four below and one above the angle. Spines on the IPo increased to six by 12.2 mm, and on the OPo increased to eight with six below and one above the angle. Spines on the preopercle in the two largest specimens were smaller (reduced in size) and more numerous than in smaller specimens. One interopercular spine was observed between the angle spine and the upper OPo spine by 3.5 mm and was present throughout the rest of the series. An opercular spine was present by 4.4 mm and a postcleithral spine was present just above the pectoral-fin base by 9.6 mm. One supracleithral spine formed by 3.6 mm on the 9-DAH specimen and two supracleithral spines were present on the 3.6-mm (10-DAH) specimen. There were three supra-

Table 1
Measurements (mm) of reared larval red snapper. — = not measured owing to damage. TX = Texas; AL = Alabama.

Source	Age (DAH)	Body length (BL)	Head length	% Head length/BL	Preanal length	% Preanal length/BL	Body depth at cleithrum	% Body depth/BL	Eye diameter	% Eye diameter/BL
TX	4-6	1.93	0.48	24.87	0.84	43.52	0.35	18.13	0.21	10.88
TX	1	2.02	0.20	9.90	1.01	50.00	0.56	27.72	—	—
TX	5	2.06	0.42	20.39	0.80	38.83	0.30	14.56	0.18	8.74
TX	4-6	2.07	0.42	20.29	0.83	40.10	0.35	16.91	0.23	11.11
TX	1	2.10	0.24	11.43	0.99	47.14	0.38	18.10	—	—
TX	4-6	2.16	0.51	23.61	1.11	51.39	0.32	14.81	0.21	9.72
AL	6	2.16	0.46	21.30	1.03	47.69	0.39	18.06	0.22	10.19
AL	6	2.16	0.52	24.07	1.05	48.61	0.43	19.91	0.25	11.57
TX	4-6	2.21	0.39	17.65	0.93	42.08	0.35	15.84	0.21	9.50
TX	5	2.24	0.50	22.32	0.90	40.18	0.32	14.29	0.20	8.93
TX	3	2.30	0.39	16.96	0.90	39.13	0.29	12.61	0.20	8.70
AL	6	2.33	0.42	18.03	0.95	40.77	0.37	15.88	0.22	9.44
AL	6	2.34	0.48	20.51	1.08	46.15	0.40	17.09	0.23	9.83
AL	6	2.35	0.46	19.57	1.02	43.40	0.43	18.30	0.25	10.64
TX	1	2.35	0.21	8.94	1.17	49.79	0.51	21.70	—	—
TX	10	2.40	0.59	24.58	0.92	38.33	0.35	14.58	0.24	10.00
TX	4-6	2.40	0.41	17.08	0.99	41.25	0.30	12.50	0.20	8.33
AL	6	2.42	0.49	20.25	1.08	44.63	0.46	19.01	0.25	10.33
TX	1	2.44	0.29	11.89	1.19	48.77	0.42	17.21	—	—
TX	4-6	2.44	0.42	17.21	1.08	44.26	0.33	13.52	0.23	9.43
TX	1	2.44	0.35	14.34	1.17	47.95	0.56	22.95	—	—
TX	4-6	2.44	0.53	21.72	1.14	46.72	0.36	14.75	0.23	9.43
TX	5	2.47	0.53	21.46	0.96	38.87	0.38	15.38	0.23	9.31
TX	1	2.49	0.27	10.84	1.19	47.79	0.42	16.87	—	—
TX	4-6	2.49	0.48	19.28	1.11	44.58	0.36	14.46	0.20	8.03
AL	6	2.53	0.54	21.34	1.11	43.87	0.43	17.00	0.26	10.28
AL	6	2.53	0.51	20.16	1.09	43.08	0.46	18.18	0.25	9.88
TX	3	2.53	0.50	19.76	1.13	44.66	0.32	12.65	0.23	9.09
AL	6	2.53	0.52	20.55	1.08	42.69	0.45	17.79	0.25	9.88
TX	3	2.54	0.44	17.32	0.99	38.98	0.32	12.60	0.21	8.27
TX	1	2.54	0.30	11.81	1.20	47.24	0.44	17.32	—	—
TX	1	2.54	0.33	12.99	1.25	49.21	0.53	20.87	—	—
TX	1	2.54	0.27	10.63	1.22	48.03	0.42	16.54	—	—
TX	1	2.54	0.32	12.60	1.22	48.03	0.53	20.87	—	—
TX	3	2.59	0.41	15.83	1.08	41.70	0.36	13.90	0.21	8.11
TX	4-6	2.59	0.51	19.69	1.11	42.86	0.32	12.36	0.22	8.49
TX	3	2.59	0.35	13.51	1.11	42.86	0.32	12.36	0.18	6.95
TX	3	2.59	0.47	18.15	1.14	44.02	0.29	11.20	0.20	7.72
TX	4-6	2.59	0.49	18.92	1.08	41.70	0.38	14.67	0.21	8.11
TX	4-6	2.59	0.50	19.31	1.16	44.79	0.33	12.74	0.20	7.72
AL	6	2.60	0.55	21.15	1.12	43.08	0.48	18.46	0.25	9.62
AL	7	2.60	0.70	26.92	1.20	46.15	0.60	23.08	0.31	11.92
TX	3	2.63	0.51	19.39	1.26	47.91	0.32	12.17	0.17	6.46
TX	3	2.63	0.51	19.39	1.17	44.49	0.30	11.41	0.23	8.75
TX	4-6	2.63	0.48	18.25	1.08	41.06	0.38	14.45	0.21	7.98
TX	1	2.63	0.29	11.03	1.23	46.77	0.45	17.11	—	—
TX	1	2.63	0.27	10.27	1.19	45.25	0.39	14.83	—	—

continued

Table 1 (continued)

Source	Age (DAH)	Body length (BL)	Head length	% Head length/BL	Preanal length	% Preanal length/BL	Body depth at cleithrum	% Body depth/BL	Eye diameter	% Eye diameter/BL
TX	10	2.63	0.62	23.57	1.10	41.83	0.40	15.21	0.26	9.89
TX	12	2.65	0.63	23.77	1.22	46.04	0.44	16.60	0.18	6.79
TX	10	2.67	0.63	23.60	1.17	43.82	0.38	14.23	0.27	10.11
TX	4-6	2.68	0.53	19.78	1.13	42.16	0.40	14.93	0.21	7.84
TX	4-6	2.68	0.54	20.15	1.13	42.16	0.36	13.43	0.24	8.96
TX	3	2.68	0.47	17.54	1.08	40.30	0.32	11.94	0.18	6.72
TX	4-6	2.68	0.56	20.90	1.20	44.78	0.35	13.06	0.20	7.46
TX	4-6	2.68	0.54	20.15	1.16	43.28	0.39	14.55	0.23	8.58
TX	1	2.68	0.26	9.70	1.23	45.90	0.51	19.03	—	—
TX	3	2.68	0.51	19.03	1.13	42.16	0.30	11.19	0.21	7.84
TX	4-6	2.68	0.47	17.54	1.10	41.04	0.34	12.69	0.21	7.84
TX	6	2.73	0.60	21.98	1.22	44.69	0.33	12.09	0.23	8.42
TX	3	2.73	0.50	18.32	1.17	42.86	0.33	12.09	0.23	8.42
TX	6	2.73	0.60	21.98	1.20	43.96	0.36	13.19	0.23	8.42
TX	3	2.73	0.48	17.58	1.11	40.66	0.32	11.72	0.23	8.42
TX	10	2.73	0.65	23.81	1.23	45.05	0.41	15.02	0.27	9.89
TX	3	2.73	0.41	15.02	1.31	47.99	0.30	10.99	0.23	8.42
TX	3	2.77	0.51	18.41	1.17	42.24	0.30	10.83	0.21	7.58
TX	5	2.80	0.54	19.29	1.17	41.79	0.30	10.71	0.20	7.14
TX	3	2.82	0.45	15.96	1.17	41.49	0.30	10.64	0.21	7.45
TX	13	2.91	0.83	28.52	1.23	42.27	0.66	22.68	0.36	12.37
TX	3	2.91	0.53	18.21	1.26	43.30	0.30	10.31	0.23	7.90
TX	12	2.99	0.70	23.41	1.37	45.82	0.45	15.05	0.30	10.03
TX	17	3.00	0.77	25.67	1.43	47.67	0.59	19.67	0.30	10.00
TX	12	3.05	0.68	22.30	1.34	43.93	0.48	15.74	0.30	9.84
TX	12	3.11	0.69	22.19	1.28	41.16	0.47	15.11	0.29	9.32
TX	13	3.20	0.81	25.31	1.39	43.44	0.63	19.69	0.33	10.31
TX	13	3.28	0.82	25.00	1.41	42.99	0.53	16.16	0.32	9.76
TX	16	3.30	0.96	29.09	1.49	45.15	0.65	19.70	0.36	10.91
AL	11	3.38	1.06	31.36	1.73	51.18	1.18	34.91	0.43	12.72
TX	16	3.42	0.96	28.07	1.59	46.49	0.72	21.05	0.31	9.06
AL	9	3.51	1.06	30.20	1.68	47.86	1.03	29.34	0.41	11.68
AL	10	3.51	1.06	30.20	1.70	48.43	1.01	28.77	0.41	11.68
TX	13	3.52	0.95	26.99	1.68	47.73	0.68	19.32	0.33	9.38
AL	12	3.64	1.22	33.52	1.93	53.02	1.41	38.74	0.52	14.29
TX	16	3.65	1.08	29.59	1.70	46.58	1.00	27.40	0.41	11.23
TX	16	3.80	1.16	30.53	1.82	47.89	1.00	26.32	0.50	13.16
AL	13	4.42	1.73	39.14	2.50	56.56	1.80	40.72	0.62	14.03
AL	14	4.81	1.74	36.17	2.68	55.72	2.07	43.04	0.66	13.72
AL	15	5.27	2.07	39.28	3.01	57.12	2.16	40.99	0.75	14.23
AL	16	5.40	1.97	36.48	3.15	58.33	2.16	40.00	0.75	13.89
AL	19	7.54	3.15	41.78	4.70	62.33	2.91	38.59	1.03	13.66
AL	17	9.49	3.42	36.04	5.58	58.80	3.42	36.04	1.35	14.23
AL	26	12.20	4.23	34.67	7.74	63.44	4.23	34.67	1.53	12.54
AL	21	15.34	5.20	33.90	9.23	60.17	5.59	36.44	1.95	12.71
AL	33	16.50	6.63	40.18	11.44	69.33	6.76	40.97	2.47	14.97
AL	35	18.10	6.37	35.19	11.57	63.92	6.89	38.07	2.47	13.65
AL	26	20.50	7.02	34.24	13.00	63.41	7.28	35.51	2.60	12.68
AL	34	26.10	9.62	36.86	16.90	64.75	9.62	36.86	3.25	12.45

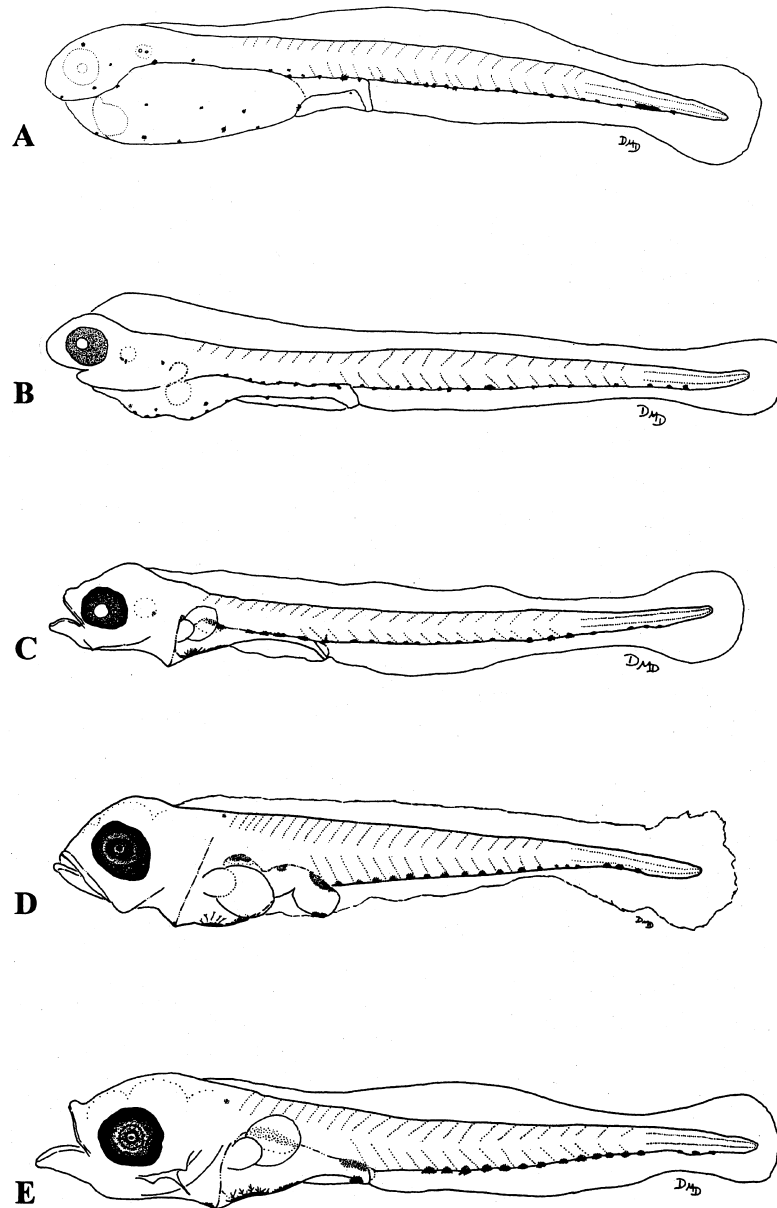
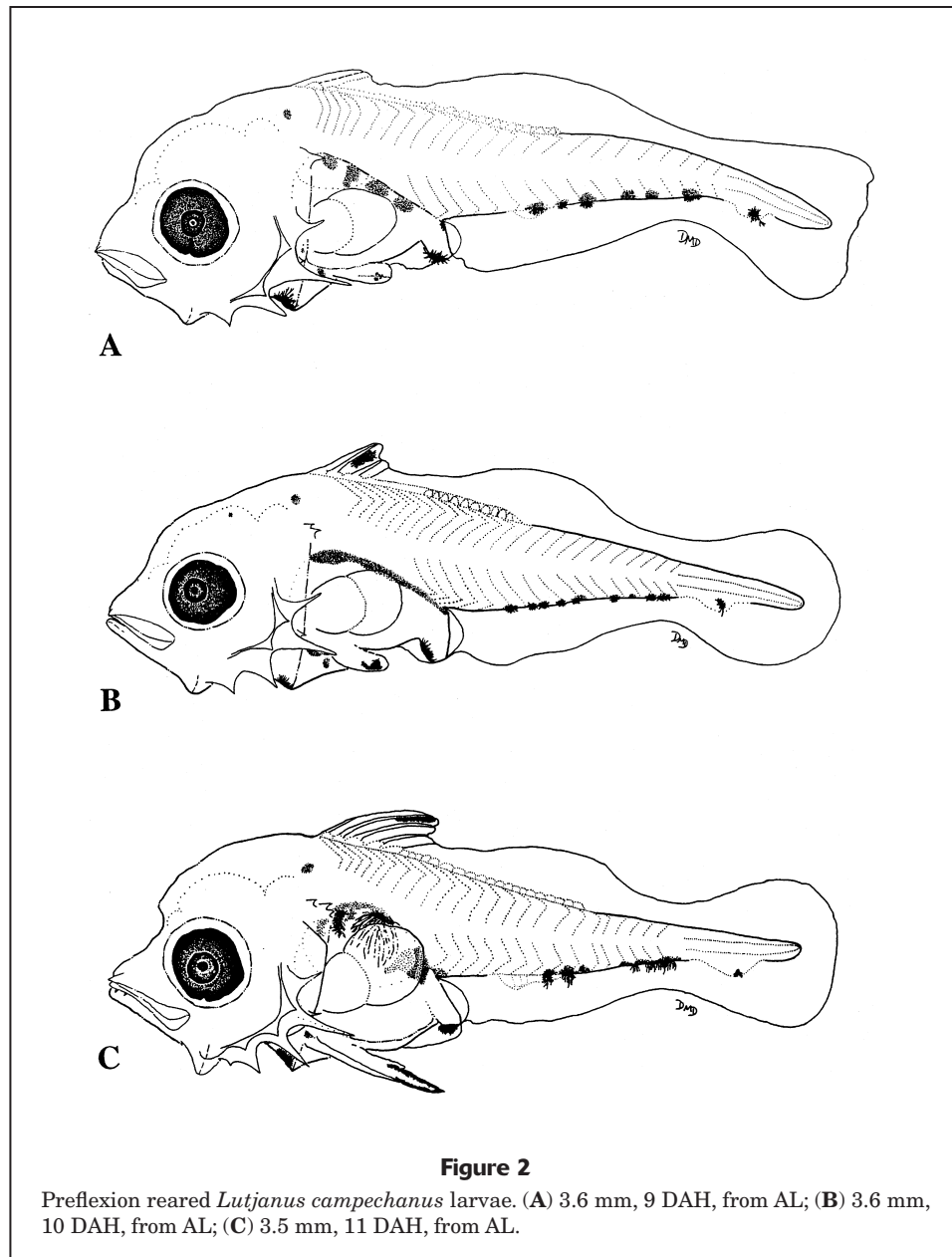


Figure 1

Preflexion larvae of reared *Lutjanus campechanus*: (A) 2.5 mm, 1 DAH, from TX; (B) 2.6 mm, 3 DAH, from TX; (C) 2.8 mm, 5 DAH, from TX; (D). 2.4 mm, 6 DAH, from AL; (E) 3.1 mm, 12 DAH, from TX.

cleithral spines on the 3.5-mm (11-DAH) specimen and by 4.9 mm (14 DAH), four supracleithral spines were present. A posttemporal spine had developed by 3.8 mm (12 DAH), and by 5.5 mm (15 DAH) there were two posttemporal spines. A supraocular ridge formed by 3.8 mm and one spine developed on the ridge by 4.4 mm (13 DAH). Two, three, and four additional spines were present on the supraocular ridge by 4.9 mm (14 DAH), 5.6 mm (16 DAH), and 9.6 mm (17 DAH), respectively.

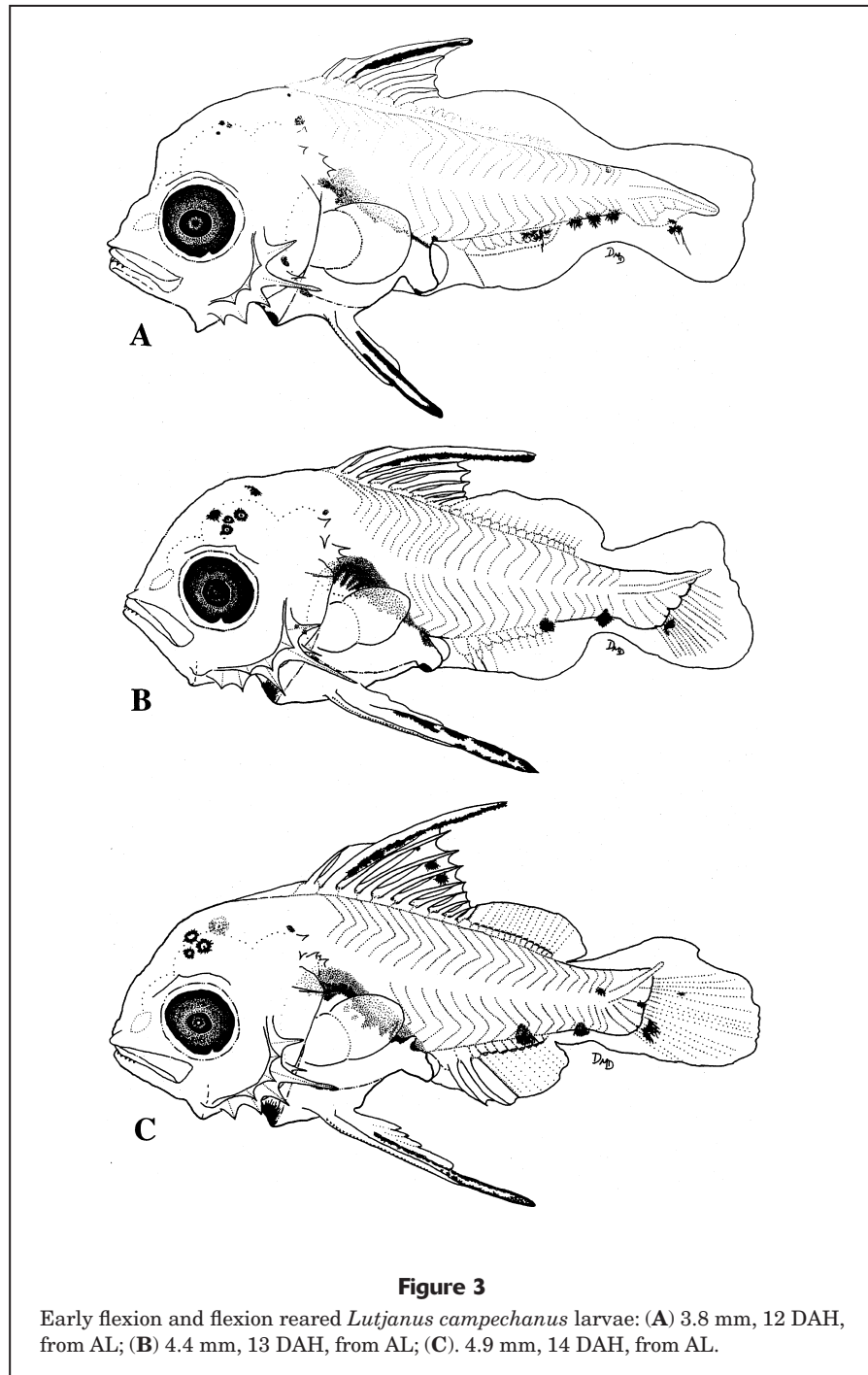
Fin development (Table 2, Figs. 1–5) Sequence of fin-ray formation can be characterized either by initial or completed development of fin elements. The order of development, based on initial development as reported by Potthoff et al. (1988), for red snapper is first dorsal, then pelvic, caudal, second dorsal, anal, pectoral. Order by completed development as reported by Johnson (1984) for lutjanids in general is first dorsal, then pelvic, second dorsal, anal, pectoral. Elements of the dorsal and pelvic fins began forming



at >3.6 mm between 9 and 11 DAH. The second spine of the dorsal fin was first to develop followed by the third, then the first and fourth spines. Development of the remaining dorsal-fin elements proceeded posteriorly; the tenth dorsal spine initially formed as a raylike element. Fine serrations were present on the leading edge of the pelvic spine at 3.8 mm (12 DAH). Anal-fin development began by 3.6 mm (11 DAH) and by 3.8 mm (12 DAH) the first anal spine began to form. Development of the remaining anal-fin elements proceeded posteriorly; the third anal spine initially forming as a raylike element. All fin spines were V-shaped in cross section. Caudal rays were first noticeable at 4.4 mm (13 DAH) and pectoral-fin rays began forming at 5.5 mm (15 DAH). By 9.6 mm (17 DAH), all elements in the dorsal,

pelvic, and anal fins were formed. Formation of pectoral rays and both principal and procurrent rays of the caudal fin was completed by 12.2 mm.

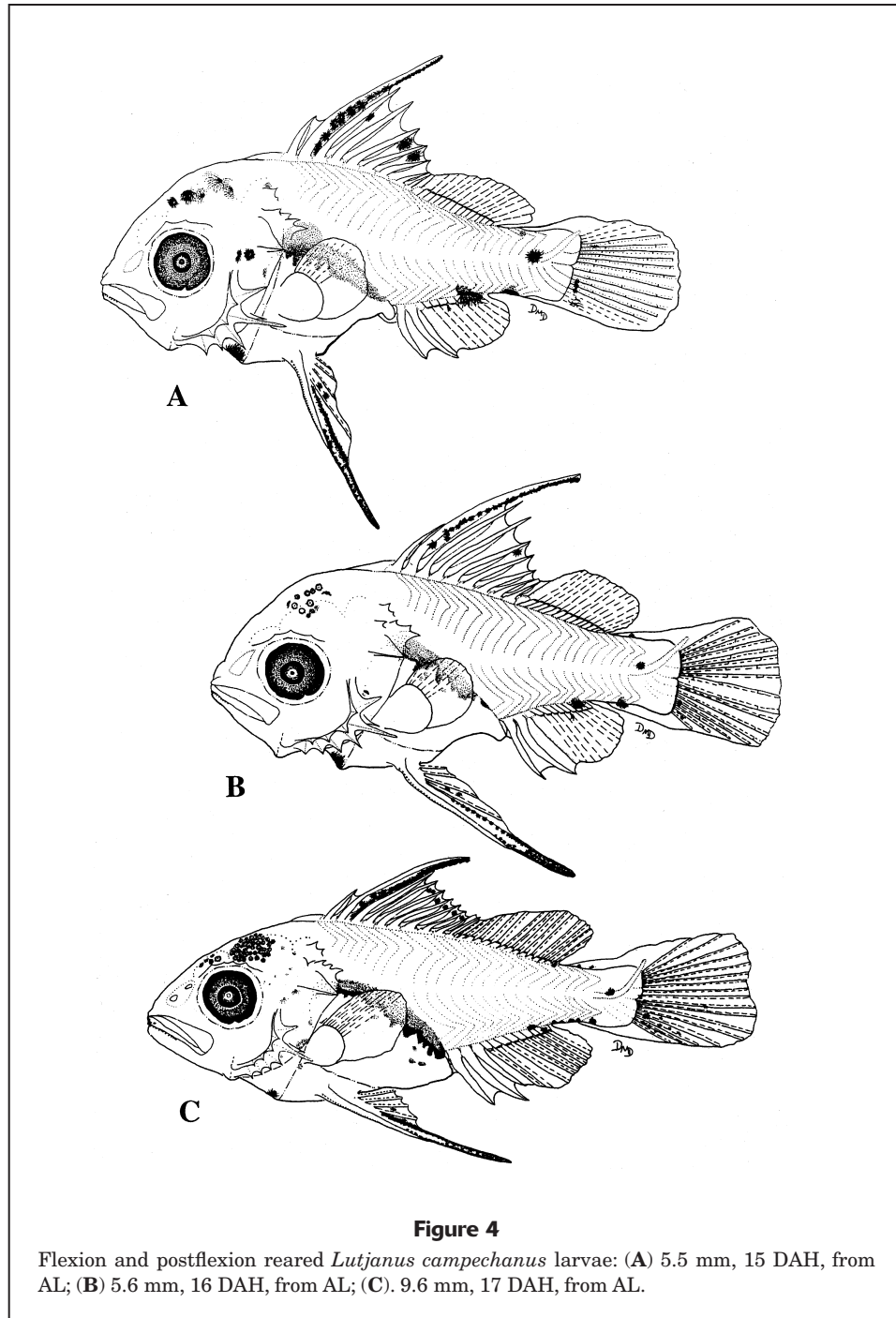
Pigmentation (Figs. 1–5) Head Small melanophores were scattered over the head of day-old yolk sac larvae at 2.5 mm. These melanophores were not present in 3 DAH larvae but small melanophores were present in the otic capsule of 2.6- and 2.8-mm larvae (3 and 5 DAH). A melanophore appeared over the midbrain at 3.6 mm and with development, both internal and external head pigment increased until at 9.6 mm, most of the surface of the head above the midbrain was covered with small melanophores. Pigment on the surface of the head over the forebrain was



present by 9.6 mm, and by 12.2 mm the forebrain region was covered with many small melanophores. An internal nape melanophore was present at 3.1 mm and persisted until overlying tissue obscured it. Pigment did not appear on the operculum until 5.5 mm, and by 9.6 mm additional small melanophores were present dorsal to the operculum pigment and posterior to the orbit. Pigment first appeared on the tip of the premaxilla at 9.6 mm and increased over the snout and on the lower jaw by 12.2 mm. The head

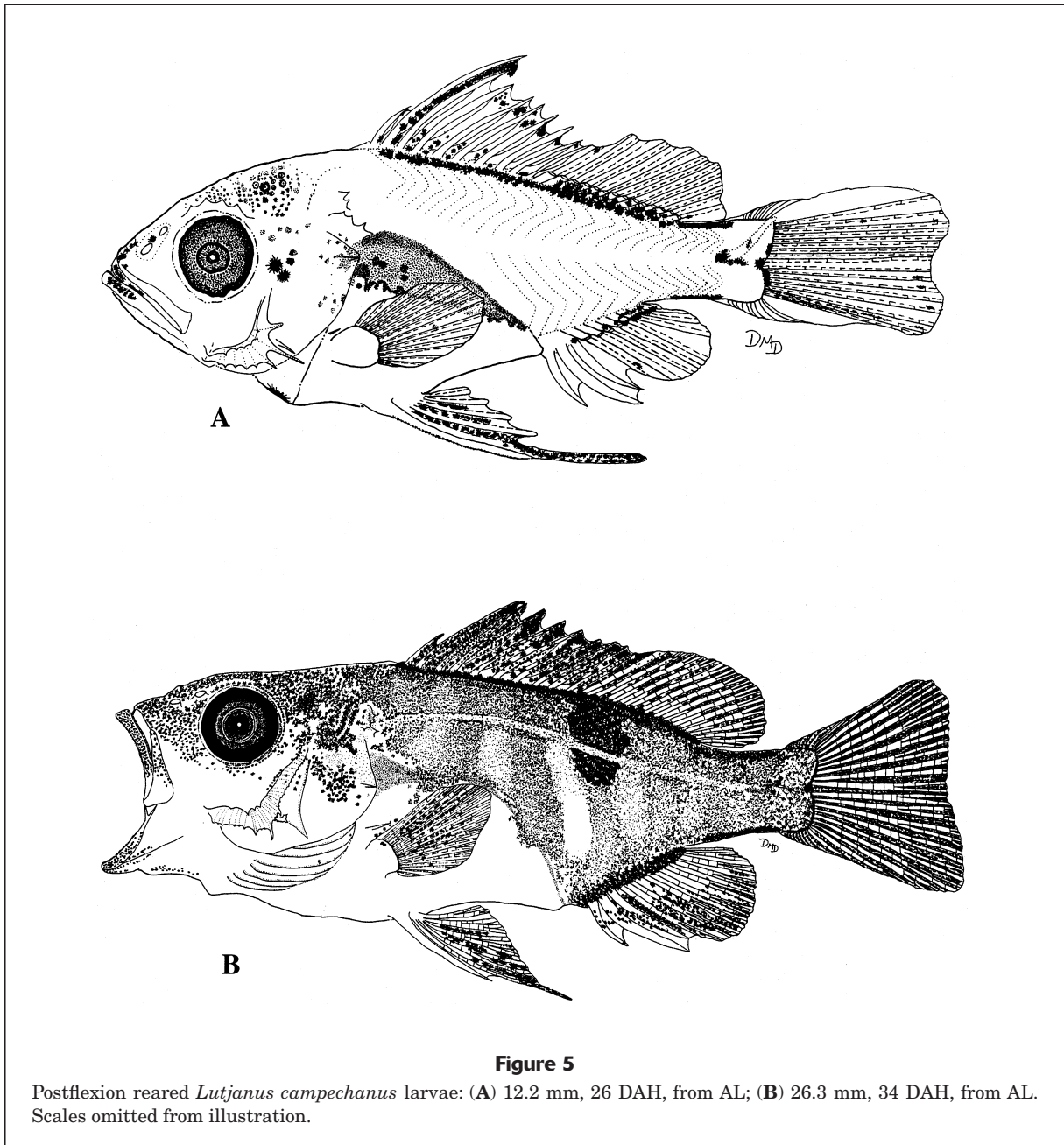
region and jaws of the 26.3-mm specimen were densely covered with pigment. A melanophore lying just anterior to the cleithral symphysis first appeared by 2.4 mm (6 DAH) and remained visible throughout the developmental series until becoming obscured by tissue in fish larger than 12.0 mm.

Body Numerous melanophores were scattered over the yolk sac and dorsal surface of the gut in the smallest larvae. The number of melanophores over the gut and



gas bladder increased until 3.6 mm when this pigment appeared as a solid melanistic patch. Pigment on the ventral surface of the trunk (between the cleithrum and the anus) consisted of one or two melanophores that were present until the pelvic fin bud emerged. As the pelvic fin developed, this pigment migrated internally to a position anterodorsal to the insertion of the pelvic fin and remained discernible through the body wall of specimens up to 4.9 mm. One melanophore was also present on the

ventral surface of the hindgut just anterior to the anus over the size range of 2.4 mm to 4.4 mm. A melanophore was present in the peritoneum on the anterior surface of the visceral mass (avm) at the level of the pectoral-fin base and was visible through the operculum in the 3.6-, 3.8-, 4.4-, and 5.6-mm specimens. This melanophore was more easily observed when the operculum was lifted. Additional data from larvae ($n=96$) raised at GCRL showed that the avm melanophore was first present in larvae as small as



3.4 mm (preflexion) and was found in all specimens ≥ 3.6 mm. When present, this spot lies above the internal melanophore that is located anterodorsal to the insertion of the developing pelvic fin.

Melanophores that form a postanal ventral (pav) series on the tail were most numerous (18–20) in the smallest larvae and decreased in number with development. The pav series is further characterized by the presence of a gap posteriorly and by the presence of one to four melanophores (typically three) located after the gap in the hypural area. As flexion began (3.8 mm), three melanophores were present on the caudal peduncle, but these melanophores coalesced to form a single ventral spot on

the caudal peduncle in postflexion larvae up to 9.6 mm. In larger larvae, additional melanophores lined the entire ventral edge of the caudal peduncle. At the beginning of flexion, one to three melanophores were present over the ventral edge of the hypural plate anlagen. As flexion progressed, this pigment bent up with the hypural elements and came to lie at the base of the ventral caudal rays. A melanophore at the flexure of the notochord on the caudal peduncle first appeared in the 4.9-mm larva. It remained prominent until extensive surface pigment on the body obscured it in the largest specimen. Dorsal pigment on the caudal peduncle appeared in the 3.8-mm early flexion larva in the form of a single internal melanophore. This

Table 2

Meristics and spine lengths of reared larval red snapper. nd = not developed, i = incipient ray(s) or spine(s). AL = Alabama; TX = Texas. P₂ = pelvic fin.

Source	Body length (BL)	Dorsal fin spines and rays	2nd dorsal spine length	% 2nd dorsal spine length/BL	3rd dorsal spine length	% 3rd dorsal spine length/BL	P ₂ spine length	% P ₂ spine length/BL	P ₂ ray length	% P ₂ ray length/BL	Anal fin spines and rays
AL	3.57	ii	nd	nd	nd	nd	bud	nd	bud	nd	nd
AL	3.57	Iii	0.32	8.96	0.21	5.88	bud	nd	bud	nd	nd
AL	3.57	IIIii	0.53	14.85	0.38	10.64	0.24	6.72	0.45	12.61	nd
TX	3.65	III	0.36	9.86	0.21	5.75	0.26	7.12	0.42	11.51	nd
AL	3.76	Vii	0.89	23.67	0.60	15.96	0.55	14.63	0.86	22.87	i
TX	3.80	IIIi	0.54	14.21	0.29	7.63	0.27	7.11	0.50	13.16	nd
AL	4.40	VIIi	1.45	32.95	0.91	20.68	1.05	23.86	1.64	37.27	Iii
AL	4.85	IXi,(14i)	1.75	36.08	1.06	21.86	1.22	25.15	1.82	37.53	II,(9i)
AL	5.47	IXi,(14i)	1.85	33.82	1.32	24.13	1.32	24.13	2.16	39.49	II,(9i)
AL	5.64	IXi,(14i)	2.16	38.30	1.42	25.18	1.37	24.29	2.09	37.06	II,(10i)
AL	7.54	IXi,(14i)	2.49	33.02	1.74	23.08	2.11	27.98	3.02	40.05	III,8
AL	9.59	X,15	2.91	30.34	2.02	21.06	2.07	21.58	3.10	32.33	III,9
AL	12.20	X,14	3.15	25.82	2.44	20.00	2.82	23.11	3.38	27.70	III,8
AL	15.34	X,14	3.71	24.19	3.06	19.95	2.96	19.30	4.61	30.05	III,9
AL	16.50	X,13	3.76	22.79	3.24	19.64	3.71	22.48	4.95	30.00	III,8
AL	18.10	IXi,14	3.71	20.50	3.20	17.68	3.10	17.13	12.87	71.10	III,9
AL	20.50	X,14	4.42	21.56	3.90	19.02	4.51	22.00	2.91	14.20	III,9
AL	26.10	X,14	4.56	17.47	4.47	17.13	4.32	16.55	6.75	25.86	III,8

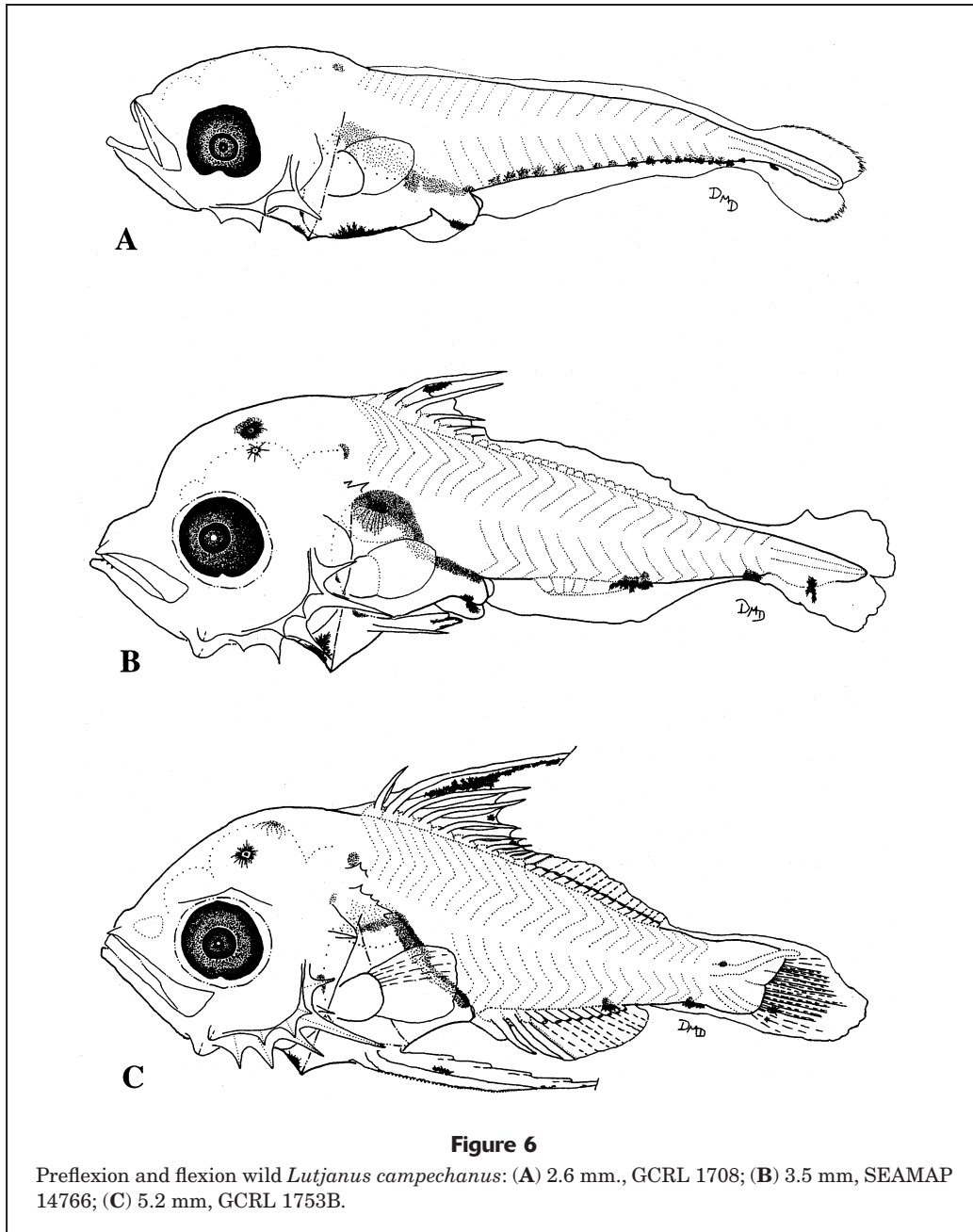
pigment was absent in the next two larvae in the series (4.4 and 4.9 mm) but it was present in the remaining larvae of the series. Additional melanophores were added until the entire dorsal surface of the caudal peduncle was lined with pigment by 12.2 mm.

Fins Melanophores were present on the pelvic fin bud at its emergence in the 3.6-mm (9 DAH) specimen. This pigment became concentrated on the first ray and in the membrane between the first and second rays as fin elements developed. Melanophores appeared on the membrane between the second and third rays by 5.5 mm and continued to increase until pigment was present between the first four pelvic rays by 12.2 mm. Pigment appeared in the dorsal-fin membrane behind the second dorsal spine by 3.6 mm (10 DAH) and continued to increase as that spine grew, so that pigment extended out along the entire length of the spine. At 4.9 mm, additional melanophores were present near the distal margin of the dorsal-fin membrane between the third and fourth, fourth and fifth, and fifth and sixth spines. This latter condition was not consistent over the series; the 5.5-mm specimen had pigment between the third and fourth, fifth and sixth, sixth and seventh spines, whereas the 5.6-mm specimen had pigment only between the fifth and sixth spines. As seen in the largest specimens of the series, pigment eventually developed in the membrane between all of the dorsal spines but pigment was consistently most extensive behind the second dorsal spine. By 12.2 mm, melanophores appeared

in the proximal region of the fin membrane at the base of the spines. One melanophore was present at the base of the last dorsal ray by 9.6 mm, and by 12.2 mm pigment covered the entire base of the dorsal fin. As the anal fin formed, one to four melanophores from the pav series persisted over the posterior pterygiophores. At sizes larger than 9.6 mm, additional melanophores began to form on the anal fin base, and by 12.2 mm the pterygiophores of the last six rays were pigmented and eventually the entire anal-fin base was covered. The distal region of the anal fin and the pectoral fin were extensively pigmented in the 26.3-mm specimen. Pigment on the caudal-fin rays first developed on the ventralmost rays and subsequently near the posterior margin of the fin until in the 26.3-mm specimen, the membrane between the rays was pigmented from the base out to the edge of the fin.

Comparison of reared and wild larvae

Reared and wild red snapper larvae were examined and compared to determine variability and usefulness of various developmental characters (Figs. 1–6; Tables 1–4). Field-collected larvae were identified as red snapper by the presence of morphological and pigmentational features described in Collins et al. (1980) and Richards et al. (1994), as well as by their general resemblance to the reared larvae described in our study. All wild larvae were collected in shelf waters in the northcentral GOM, where



relatively few species of lutjanids (larvae or adults) occur in abundance [SEAMAP Atlas 1985–1995 (Thompson et al., 1988; Sanders et al., 1990a, 1990b, 1991a, 1991b, 1992; Donaldson et al. 1993, 1994, 1996, 1997a, 1997b); longline data, (Jones²); video data, (Gledhill³)].

² Jones, L. M. 1998. Personal commun. Mississippi Laboratories, Southeast Fisheries Science Center, National Marine Fisheries Service, PO Drawer 1207, Pascagoula, MS 39568-1207.

³ Gledhill, C. T. 1998. Personal commun. Mississippi Laboratories, Southeast Fisheries Science Center, National Marine Fisheries Service, PO Drawer 1207, Pascagoula, MS 39568-1207.

There were no notable or consistent differences between laboratory-reared and field-caught red snapper larvae in pigmentation, development or morphometry at similar stages of development. Presence of avm pigment, number of pav spots, and arrangement of median fin pigment among wild larvae matched the appearance of these features in reared larvae at about the same stage of development (Figs. 2–6). Differences in size at stage of development that were evident were probably caused by net-related shrinkage or abrasion, or by both (Theilacker, 1980). We observed no consistent differences in pigment that could have been caused by rearing conditions. Median fin element development in wild red snapper larvae appeared at smaller sizes

Table 3

Measurements (mm) of wild larval red snapper. — = not measure owing to damage. GCRL = Gulf Coast Research Laboratory; SEAMAP = Southeast Area Monitoring and Assessment Program.

Source	Body length (BL)	Head length	% Head length/BL	Prealanal length	% Preanal length/BL	Body depth at cleithrum	% Body depth/BL	Orbit diameter	% Orbit diameter/BL
GCRL	2.60	0.79	30.38	1.39	53.46	0.77	29.62	0.34	13.08
GCRL	2.60	0.75	28.85	1.36	52.31	0.66	25.38	0.30	11.54
GCRL	2.60	0.77	29.62	1.27	48.85	0.79	30.38	0.34	13.08
GCRL	2.73	0.79	28.94	1.30	47.62	0.74	27.11	0.29	10.62
GCRL	2.73	0.84	30.77	1.44	52.75	0.79	28.94	0.36	13.19
GCRL	2.86	0.72	25.17	1.25	43.71	0.77	26.92	0.31	10.84
GCRL	2.86	0.77	26.92	1.44	50.35	0.72	25.17	0.34	11.89
SEAMAP	2.86	1.27	44.41	1.41	49.30	1.18	41.26	0.47	16.43
GCRL	2.99	0.89	29.77	1.46	48.83	0.82	27.42	0.43	14.38
GCRL	2.99	0.91	30.43	1.61	53.85	0.89	29.77	0.36	12.04
GCRL	2.99	0.99	33.11	1.74	58.19	1.08	36.12	0.38	12.71
SEAMAP	2.99	1.08	36.12	1.63	54.52	0.98	32.78	0.38	12.71
SEAMAP	2.99	1.10	36.79	1.56	52.17	1.15	38.46	0.41	13.71
SEAMAP	2.99	1.37	45.82	1.97	65.89	1.32	44.15	0.46	15.38
GCRL	3.12	0.85	27.24	1.46	46.79	0.89	28.53	0.33	10.58
GCRL	3.12	0.91	29.17	1.56	50.00	0.86	27.56	0.41	13.14
GCRL	3.12	0.98	31.41	1.56	50.00	0.89	28.53	0.38	12.18
GCRL	3.12	0.89	28.53	1.42	45.51	0.86	27.56	0.31	9.94
SEAMAP	3.12	1.08	34.62	1.63	52.24	0.96	30.77	0.41	13.14
SEAMAP	3.12	1.13	36.22	1.50	48.08	1.18	37.82	0.47	15.06
SEAMAP	3.12	1.27	40.71	1.65	52.88	1.13	36.22	0.52	16.67
GCRL	3.25	1.13	34.77	1.61	49.54	1.01	31.08	0.38	11.69
GCRL	3.25	0.89	27.38	1.55	47.69	0.89	27.38	0.38	11.69
GCRL	3.25	1.13	34.77	1.79	55.08	1.22	37.54	0.42	12.92
SEAMAP	3.25	1.27	39.08	1.69	52.00	1.13	34.77	0.47	14.46
GCRL	3.38	0.91	26.92	1.61	47.63	1.03	30.47	0.36	10.65
GCRL	3.38	0.94	27.81	1.49	44.08	0.91	26.92	0.36	10.65
GCRL	3.38	1.20	35.50	1.68	49.70	1.03	30.47	0.41	12.13
SEAMAP	3.38	0.98	28.99	1.51	44.67	1.13	33.43	0.41	12.13
SEAMAP	3.38	1.15	34.02	1.58	46.75	1.15	34.02	0.43	12.72
SEAMAP	3.38	1.13	33.43	1.70	50.30	1.22	36.09	0.38	11.24
SEAMAP	3.38	1.27	37.57	1.75	51.78	1.25	36.98	0.48	14.20
SEAMAP	3.38	1.41	41.72	1.83	54.14	1.41	41.72	0.45	13.31
SEAMAP	3.38	1.41	41.72	1.93	57.10	1.36	40.24	0.52	15.38
GCRL	3.51	1.13	32.19	1.75	49.86	0.98	27.92	0.43	12.25
GCRL	3.51	1.22	34.76	1.83	52.14	1.13	32.19	0.38	10.83
GCRL	3.51	1.15	32.76	1.85	52.71	1.20	34.19	0.43	12.25
SEAMAP	3.51	1.25	35.61	—	—	1.20	34.19	0.41	11.68
SEAMAP	3.51	1.22	34.76	1.69	48.15	1.22	34.76	0.47	13.39
SEAMAP	3.51	1.41	40.17	1.93	54.99	1.36	38.75	0.52	14.81
SEAMAP	3.51	1.41	40.17	2.07	58.97	1.41	40.17	0.47	13.39
GCRL	3.64	0.79	21.70	1.44	39.56	0.86	23.63	0.38	10.44
GCRL	3.64	1.10	30.22	1.75	48.08	1.08	29.67	0.43	11.81
GCRL	3.64	1.10	30.22	1.75	48.08	1.13	31.04	0.41	11.26
SEAMAP	3.64	1.32	36.26	1.88	51.65	1.27	34.89	0.47	12.91
SEAMAP	3.64	1.50	41.21	1.97	54.12	1.50	41.21	0.52	14.29

continued

Table 3 (continued)

Source	Body length (BL)	Head length	% Head length/BL	Preanal length	% Preanal length/BL	Body depth at cleithrum	% Body depth/BL	Orbit diameter	% Orbit diameter/BL
SEAMAP	3.64	1.27	34.89	1.83	50.27	1.22	33.52	0.52	14.29
GCRL	3.77	1.18	31.30	1.80	47.75	1.15	30.50	0.43	11.41
GCRL	3.77	1.03	27.32	1.74	46.15	1.18	31.30	0.42	11.14
GCRL	3.77	1.13	29.97	1.83	48.54	1.13	29.97	0.47	12.47
GCRL	3.77	1.27	33.69	1.87	49.60	1.22	32.36	0.46	12.20
SEAMAP	3.77	1.66	44.03	2.28	60.48	1.56	41.38	0.53	14.06
SEAMAP	3.77	1.20	31.83	1.73	45.89	1.42	37.67	0.58	15.38
SEAMAP	3.77	1.56	41.38	2.11	55.97	1.49	39.52	0.55	14.59
SEAMAP	3.77	1.41	37.40	1.88	49.87	1.46	38.73	0.56	14.85
SEAMAP	3.77	1.41	37.40	2.02	53.58	1.50	39.79	0.52	13.79
SEAMAP	3.77	1.65	43.77	2.21	58.62	1.55	41.11	0.52	13.79
SEAMAP	3.81	1.55	40.68	2.21	58.01	1.41	37.01	0.52	13.65
SEAMAP	3.84	1.50	39.06	2.12	55.21	1.46	38.02	0.47	12.24
SEAMAP	3.90	1.36	34.87	1.97	50.51	1.46	37.44	0.47	12.05
GCRL	3.90	1.46	37.44	2.16	55.38	1.46	37.44	0.56	14.36
SEAMAP	3.90	1.32	33.85	1.93	49.49	1.36	34.87	0.56	14.36
SEAMAP	3.90	1.46	37.44	2.07	53.08	1.55	39.74	0.52	13.33
SEAMAP	3.90	1.41	36.15	2.02	51.79	1.55	39.74	0.52	13.33
GCRL	4.03	1.36	33.75	1.97	48.88	1.27	31.51	0.52	12.90
SEAMAP	4.03	1.32	32.75	2.11	52.36	1.44	35.73	0.43	10.67
GCRL	4.03	1.41	34.99	2.16	53.60	1.46	36.23	0.52	12.90
SEAMAP	4.03	1.50	37.22	2.12	52.61	1.55	38.46	0.56	13.90
SEAMAP	4.03	1.60	39.70	2.21	54.84	1.55	38.46	0.61	15.14
SEAMAP	4.03	1.50	37.22	2.07	51.36	1.46	36.23	0.56	13.90
SEAMAP	4.03	1.56	38.71	2.23	55.33	1.63	40.45	0.60	14.89
GCRL	4.16	1.27	30.53	2.02	48.56	1.22	29.33	0.47	11.30
GCRL	4.16	1.20	28.85	1.63	39.18	1.10	26.44	0.41	9.86
GCRL	4.16	1.41	33.89	2.21	53.13	1.50	36.06	0.52	12.50
GCRL	4.16	1.60	38.46	2.26	54.33	1.50	36.06	0.56	13.46
SEAMAP	4.16	1.55	37.26	2.16	51.92	1.60	38.46	0.56	13.46
SEAMAP	4.16	1.55	37.26	2.30	55.29	1.69	40.63	0.56	13.46
SEAMAP	4.16	1.65	39.66	2.30	55.29	1.55	37.26	0.56	13.46
SEAMAP	4.16	1.65	39.66	2.16	51.92	1.65	39.66	0.56	13.46
SEAMAP	4.29	1.50	34.97	2.07	48.25	1.41	32.87	0.52	12.12
SEAMAP	4.29	1.65	38.46	2.35	54.78	1.65	38.46	0.56	13.05
GCRL	4.29	1.50	34.97	2.30	53.61	1.46	34.03	0.56	13.05
SEAMAP	4.42	1.50	33.94	2.26	51.13	1.50	33.94	0.51	11.54
SEAMAP	4.42	1.60	36.20	2.07	46.83	1.65	37.33	0.56	12.67
SEAMAP	4.42	1.79	40.50	2.49	56.33	1.79	40.50	0.56	12.67
SEAMAP	4.42	1.50	33.94	2.44	55.20	1.69	38.24	0.61	13.80
GCRL	4.42	1.79	40.50	2.54	57.47	1.79	40.50	0.71	16.06
SEAMAP	4.55	1.55	34.07	2.44	53.63	1.65	36.26	0.52	11.43
SEAMAP	4.55	1.55	34.07	2.35	51.65	1.74	38.24	0.61	13.41
GCRL	4.55	1.79	39.34	2.49	54.73	1.74	38.24	0.66	14.51
SEAMAP	4.55	1.88	41.32	2.54	55.82	2.02	44.40	0.66	14.51
GCRL	4.68	1.65	35.26	2.54	54.27	1.74	37.18	0.56	11.97
GCRL	4.68	1.55	33.12	2.44	52.14	1.69	36.11	0.61	13.03
SEAMAP	4.68	1.69	36.11	2.44	52.14	1.65	35.26	0.56	11.97

continued

Table 3 (continued)

Source	Body length (BL)	Head length	% Head length/BL	Preanal length	% Preanal length/BL	Body depth at cleithrum	% Body depth/BL	Orbit diameter	% Orbit diameter/BL
SEAMAP	4.68	1.83	39.10	2.59	55.34	1.79	38.25	0.66	14.10
SEAMAP	4.81	1.69	35.14	2.44	50.73	1.74	36.17	0.56	11.64
SEAMAP	4.81	1.97	40.96	2.82	58.63	1.97	40.96	0.71	14.76
SEAMAP	4.81	1.93	40.12	2.77	57.59	1.97	40.96	0.56	11.64
SEAMAP	4.94	1.93	39.07	2.63	53.24	1.93	39.07	0.66	13.36
SEAMAP	4.94	1.97	39.88	2.73	55.26	2.12	42.91	0.71	14.37
GCRL	5.07	1.79	35.31	2.68	52.86	1.79	35.31	0.71	14.00
SEAMAP	5.07	1.88	37.08	2.73	53.85	1.88	37.08	0.61	12.03
SEAMAP	5.07	1.65	32.54	2.44	48.13	2.02	39.84	0.61	12.03
SEAMAP	5.07	1.93	38.07	2.73	53.85	1.79	35.31	0.71	14.00
GCRL	5.20	1.74	33.46	2.73	52.50	1.83	35.19	0.66	12.69
SEAMAP	5.20	1.93	37.12	2.77	53.27	1.93	37.12	0.71	13.65
SEAMAP	5.20	1.88	36.15	2.82	54.23	2.02	38.85	0.71	13.65
GCRL	5.46	1.97	36.08	3.01	55.13	1.97	36.08	0.71	13.00
SEAMAP	5.46	2.35	43.04	3.29	60.26	2.21	40.48	0.71	13.00
GCRL	5.46	1.88	34.43	3.15	57.69	2.16	39.56	0.61	11.17
SEAMAP	5.46	2.12	38.83	3.10	56.78	2.12	38.83	0.71	13.00
GCRL	5.59	1.97	35.24	3.15	56.35	2.16	38.64	0.71	12.70
SEAMAP	5.59	2.16	38.64	3.10	55.46	2.21	39.53	0.80	14.31
SEAMAP	5.85	1.97	33.68	3.10	52.99	2.54	43.42	0.71	12.14
GCRL	6.37	2.26	35.48	3.57	56.04	2.26	35.48	0.85	13.34
GCRL	9.49	3.85	40.57	5.67	59.75	3.57	37.62	1.36	14.33
SEAMAP	10.01	4.03	40.26	5.85	58.44	3.48	34.77	1.32	13.19
SEAMAP	20.02	7.15	35.71	12.09	60.39	7.02	35.06	2.60	12.99

(2.9 mm) than in reared larvae, whereas fin pigmentation seemingly appeared later in development (Tables 1–4). Comparisons of the ratios of head length, preanal length, body depth, and orbit diameter to body length indicated that development in the laboratory resulted in larvae that mirrored development in the wild.

Discussion

The larvae of as many as eighteen species of snappers in three subfamilies can occur in the western Central Atlantic which includes the Gulf of Mexico and Caribbean Sea. The early life stages of the subfamily Apsilinae are mostly unknown but the low number of dorsal soft rays (10, rarely 9) should separate late-stage larvae and juveniles of *Apsilus dentatus* from larvae of species in the other two subfamilies (Leis et al., 1997; Leis and Lee, 1994; Richards et al., 1994). Eteline snappers are represented by four species in GOM collections, *Etelis oculatus* and three species of *Pristipomoides*. The larvae of these taxa should be separable from lutjanine larvae by body shape and spine structure because eteline larvae are slender bodied and have weaker median fin spines (Leis and Lee, 1994; Richards et al., 1994). The lower dorsal count of etelines (21) will

also distinguish larvae from lutjanines (22–24) in specimens whose total dorsal elements can be counted (Leis and Lee, 1994; Richards et al., 1994). The majority of snappers (13 species) found in the area belong to the subfamily Lutjaninae (Richards et al., 1994). Distinguishing the lutjanine larvae from each other is difficult despite published larval descriptions for six taxa: *Rhomboplites aurorubens* (Laroche, 1977); *Lutjanus griseus* (Richards and Saksena, 1980); *Ocyurus chrysurus* (Riley et al., 1995; Clarke et al., 1997); *L. synagris* (Clarke et al., 1997); *L. analis* (Clarke et al., 1997); and *L. campechanus* (Rabalais et al., 1980; Collins et al., 1980; and our study). We undertook a synthesis of these published descriptions and illustrations to better evaluate the usefulness of various characters in distinguishing the larvae of lutjanine species occurring in the Gulf of Mexico (Table 5).

Our tabulated character list is not exhaustive and represents only those features for which known GOM lutjanine larvae appear to differ. Dorsal-fin meristics can be used to narrow the possible choices among species once total fin element number is established and even before spines and rays are completely differentiated. Only four species have 22 or 23 total dorsal elements and of these, *R. aurorubens* is the only species with 12 dorsal spines; the other three usually have 10 spines. Body shape may also

Table 4

Meristics and spine lengths of wild larval red snapper. nd = not developed, — = not measured owing to damage, i = incipient ray(s) or spine(s), P₂ = pelvic fin. SEAMAP = Southeast Area Monitoring and Assessment Program; GCRL = Gulf Coast Research Laboratory.

Source	Body length (BL)	Dorsal fin spines and rays	2nd dorsal spine length	2nd dorsal spine length/BL	3rd dorsal spine length	3rd dorsal spine length/BL	P ₂ spine length	P ₂ spine length/BL	P ₂ ray length	P ₂ ray length/BL	Anal fin spines and rays
SEAMAP	2.86	II	0.30	10.49	0.24	8.39	bud	nd	bud	nd	anlage
SEAMAP	2.99	i	0.09	3.01	nd	nd	bud	nd	bud	nd	nd
SEAMAP	2.99	IIi	0.44	14.72	0.36	12.04	0.21	7.02	0.29	9.70	anlage
SEAMAP	2.99	IVi	0.58	19.40	0.38	12.71	0.26	8.70	0.26	8.70	anlage
SEAMAP	3.12	ii	0.17	5.45	0.12	3.85	bud	nd	bud	nd	nd
SEAMAP	3.12	IIIi	0.44	14.10	0.36	11.54	0.23	7.37	0.23	7.37	anlage
SEAMAP	3.12	IVi	0.54	17.31	0.39	12.50	0.32	10.26	0.38	12.18	anlage
GCRL	3.25	IIIi	0.29	8.92	0.18	5.54	bud	nd	bud	nd	anlage
SEAMAP	3.25	IIIi	0.48	14.77	0.36	11.08	0.26	8.00	0.38	11.69	anlage
SEAMAP	3.38	IIi	0.38	11.24	0.32	9.47	0.18	5.33	0.38	11.24	anlage
SEAMAP	3.38	IIIi	0.50	14.79	0.41	12.13	0.19	5.62	0.26	7.69	anlage
SEAMAP	3.38	IVii	0.53	15.68	0.36	10.65	0.22	6.51	0.26	7.69	anlage
SEAMAP	3.38	IVii	0.55	16.27	0.38	11.24	0.26	7.69	0.31	9.17	anlage
SEAMAP	3.38	V	0.66	19.53	0.42	12.43	0.42	12.43	0.47	13.91	anlage
SEAMAP	3.38	Vi	0.80	23.67	0.52	15.38	0.52	15.38	0.61	18.05	anlage
GCRL	3.51	IIIi	0.29	8.26	0.22	6.27	1.06	30.20	0.58	16.52	na
SEAMAP	3.51	IIIi	0.38	10.83	0.24	6.84	0.19	5.41	0.19	5.41	anlage
SEAMAP	3.51	IIIii	0.55	15.67	0.36	10.26	0.29	8.26	0.34	9.69	anlage
SEAMAP	3.51	V	0.61	17.38	0.56	15.95	0.38	10.83	0.52	14.81	anlage
SEAMAP	3.51	VIi	0.99	28.21	0.61	17.38	0.33	9.40	0.56	15.95	i
SEAMAP	3.64	IIIii	0.66	18.13	0.38	10.44	0.56	15.38	—	—	anlage
SEAMAP	3.64	Vi	0.72	19.78	0.48	13.19	0.50	13.74	0.50	13.74	anlage
SEAMAP	3.64	VI	0.55	15.11	0.38	10.44	0.26	7.14	0.34	9.34	anlage
GCRL	3.77	II	0.20	5.31	0.17	4.51	bud	nd	bud	nd	nd
GCRL	3.77	IIi	0.31	8.22	0.24	6.37	bud	nd	bud	nd	nd
GCRL	3.77	IIIi	0.24	6.37	0.17	4.51	bud	nd	bud	nd	anlage
GCRL	3.77	IVi	0.36	9.55	0.29	7.69	bud	nd	bud	nd	anlage
SEAMAP	3.77	Vi	1.08	28.65	0.70	18.57	0.70	18.57	0.89	23.61	anlage
SEAMAP	3.77	VI	0.87	23.08	0.53	14.06	0.53	14.06	0.56	14.85	anlage
SEAMAP	3.77	VI	0.94	24.93	0.67	17.77	—	—	—	—	anlage
SEAMAP	3.77	VIi	0.82	21.75	0.55	14.59	0.48	12.73	0.50	13.26	anlage
SEAMAP	3.77	VIi	1.08	28.65	0.65	17.24	0.70	18.57	0.79	20.95	anlage
SEAMAP	3.77	VIi	1.18	31.30	0.75	19.89	0.80	21.22	0.99	26.26	ii
SEAMAP	3.81	Vi	0.56	14.70	0.47	12.34	0.21	5.51	0.68	17.85	anlage
SEAMAP	3.84	Vi	0.71	18.49	0.42	10.94	0.47	12.24	0.66	17.19	anlage
SEAMAP	3.90	IVii	0.82	21.03	0.53	13.59	0.55	14.10	0.77	19.74	anlage
GCRL	3.90	Vi	0.72	18.46	0.46	11.79	0.43	11.03	0.43	11.03	anlage
SEAMAP	3.90	Vii	0.89	22.82	0.50	12.82	0.60	15.38	0.63	16.15	anlage
SEAMAP	3.90	VIi	1.03	26.41	0.61	15.64	0.65	16.67	0.70	17.95	anlage
SEAMAP	3.90	VIi	1.03	26.41	0.71	18.21	0.71	18.21	0.89	22.82	i
GCRL	4.03	IVi	0.54	13.40	0.35	8.68	0.30	7.44	0.57	14.14	anlage
SEAMAP	4.03	IVii	0.68	16.87	0.44	10.92	0.29	7.20	0.60	14.89	anlage
GCRL	4.03	Vi	0.66	16.38	0.48	11.91	0.50	12.41	0.57	14.14	anlage
SEAMAP	4.03	Vi	0.94	23.33	0.56	13.90	0.66	16.38	1.03	25.56	anlage
SEAMAP	4.03	VIi	1.03	25.56	0.65	16.13	0.62	15.38	0.82	20.35	anlage

continued

Table 4 (continued)

Source	Body length (BL)	Dorsal fin spines and rays	2nd dorsal spine length	2nd dorsal spine length/BL	3rd dorsal spine length	3rd dorsal spine length/BL	P ₂ spine length	P ₂ spine length/BL	P ₂ ray length	P ₂ ray length/BL	Anal fin spines and rays
SEAMAP	4.03	Viii	0.85	21.09	0.49	12.16	0.52	12.90	0.80	19.85	anlage
SEAMAP	4.03	Viii	1.22	30.27	0.77	19.11	0.94	23.33	1.22	30.27	i
GCRL	4.16	Vii	0.53	12.74	0.33	7.93	0.26	6.25	0.33	7.93	anlage
GCRL	4.16	Vi	0.62	14.90	0.47	11.30	0.45	10.82	0.45	10.82	anlage
GCRL	4.16	Vi	0.82	19.71	0.50	12.02	0.46	11.06	0.55	13.22	anlage
GCRL	4.16	Vi	0.70	16.83	0.43	10.34	0.31	7.45	0.53	12.74	anlage
SEAMAP	4.16	Vi	1.13	27.16	0.38	9.13	0.75	18.03	0.89	21.39	ii,(9i)
SEAMAP	4.16	Vi	1.27	30.53	0.85	20.43	0.94	22.60	0.85	20.43	anlage
SEAMAP	4.16	Viii,(16i)	1.13	27.16	0.80	19.23	0.80	19.23	0.99	23.80	anlage
SEAMAP	4.16	Viii,(15i)	1.32	31.73	0.85	20.43	0.42	10.10	0.75	18.03	ii,(9i)
SEAMAP	4.29	Vi	0.82	19.11	0.67	15.62	0.54	12.59	0.72	16.78	anlage
SEAMAP	4.29	Vii	0.94	21.91	0.66	15.38	0.75	17.48	0.80	18.65	anlage
GCRL	4.29	Vi	0.86	20.05	0.58	13.52	0.53	12.35	0.79	18.41	anlage
SEAMAP	4.42	Vi	0.94	21.27	0.52	11.76	0.56	12.67	0.71	16.06	anlage
SEAMAP	4.42	Vi,(17i)	1.25	28.28	0.82	18.55	0.72	16.29	0.96	21.72	ii,(9i)
SEAMAP	4.42	Vii,(16i)	1.18	26.70	0.79	17.87	—	—	—	—	II,(9i)
SEAMAP	4.42	Viii	0.33	7.47	0.89	20.14	1.03	23.30	1.32	29.86	II
GCRL	4.42	Viii,(13i)	1.44	32.58	0.96	21.72	1.15	26.02	1.49	33.71	ii,(8i)
SEAMAP	4.55	Vi	1.00	21.98	0.65	14.29	0.77	16.92	0.78	17.14	anlage
SEAMAP	4.55	Vii	1.13	24.84	0.71	15.60	0.56	12.31	1.03	22.64	i
SEAMAP	4.55	Viii	1.65	36.26	0.80	17.58	0.38	8.35	1.41	30.99	II,(8i)
GCRL	4.55	Viii,(14i)	1.04	22.86	0.69	15.16	0.93	20.44	1.41	30.99	ii,(9i)
SEAMAP	4.68	IXi,(14i)	1.74	37.18	1.08	23.08	1.20	25.64	1.46	31.20	II,(8i)
GCRL	4.68	Vi	0.98	20.94	0.46	9.83	0.62	13.25	0.77	16.45	anlage
GCRL	4.68	Vi,(16i)	0.98	20.94	0.65	13.89	0.91	19.44	0.98	20.94	ii
SEAMAP	4.68	Viii,(15i)	1.55	33.12	0.94	20.09	1.03	22.01	1.34	28.63	ii,(9i)
SEAMAP	4.81	IXi,(14i)	1.60	33.26	0.94	19.54	1.20	24.95	1.78	37.01	ii,(9i)
SEAMAP	4.81	Vi,(15i)	1.18	24.53	0.80	16.63	0.94	19.54	1.08	22.45	ii,(9i)
SEAMAP	4.81	Viii,(14i)	0.61	12.68	0.89	18.50	0.24	4.99	1.22	25.36	ii,(8i)
SEAMAP	4.94	IXi,(14i)	0.94	19.03	1.08	21.86	1.36	27.53	1.83	37.04	II,(9i)
SEAMAP	4.94	Viii	1.46	29.55	0.94	19.03	1.03	20.85	1.60	32.39	ii,(10i)
GCRL	5.07	Vii,(16i)	1.20	23.67	0.79	15.58	0.93	18.34	0.82	16.17	ii,(9i)
SEAMAP	5.07	Viii,(13i)	1.27	25.05	0.89	17.55	0.99	19.53	1.13	22.29	ii,(9i)
SEAMAP	5.07	Viii	1.55	30.57	1.03	20.32	1.18	23.27	1.70	33.53	II,(8i)
SEAMAP	5.07	Viii,(14i)	1.66	32.74	1.01	19.92	1.08	21.30	1.75	34.52	II,(8i)
SEAMAP	5.20	IXi,(14i)	1.74	33.46	0.99	19.04	1.27	24.42	1.32	25.38	II,(8i)
GCRL	5.20	Viii,(15i)	1.32	25.38	0.84	16.15	0.86	16.54	1.42	27.31	II,(9i)
SEAMAP	5.20	Viii,(14i)	1.54	29.62	0.94	18.08	1.08	20.77	1.39	26.73	II,(8i)
SEAMAP	5.46	IXi,(14i)	1.88	34.43	1.13	20.70	1.36	24.91	1.32	24.18	II,(8i)
SEAMAP	5.46	Vii,(15i)	1.58	28.94	1.06	19.41	1.22	22.34	1.89	34.62	II,(8i)
GCRL	5.46	Vii,(15i)	1.39	25.46	0.89	16.30	0.94	17.22	1.15	21.06	II,(9i)
GCRL	5.46	Viii,(15i)	1.10	20.15	0.91	16.67	0.74	13.55	0.74	13.55	II,(9i)
SEAMAP	5.59	IX,(15i)	1.92	34.35	1.32	23.61	1.61	28.80	2.04	36.49	II,(8i)
GCRL	5.59	Viii,(14i)	2.96	52.95	1.06	18.96	1.15	20.57	1.49	26.65	II,(9i)
SEAMAP	5.85	IXi,(14i)	1.74	29.74	1.32	22.56	1.46	24.96	1.97	33.68	II,(8i)
GCRL	6.37	IXi,(14i)	1.61	25.27	1.13	17.74	0.89	13.97	1.37	21.51	II,(9i)
GCRL	9.49	X,14	3.20	33.72	1.74	18.34	1.79	18.86	0.80	8.43	III,8
SEAMAP	10.01	X,14	2.96	29.57	2.26	22.58	2.87	28.67	3.85	38.46	III,9
SEAMAP	20.02	X,14	6.63	33.12	3.64	18.18	2.73	13.64	5.20	25.97	III,9

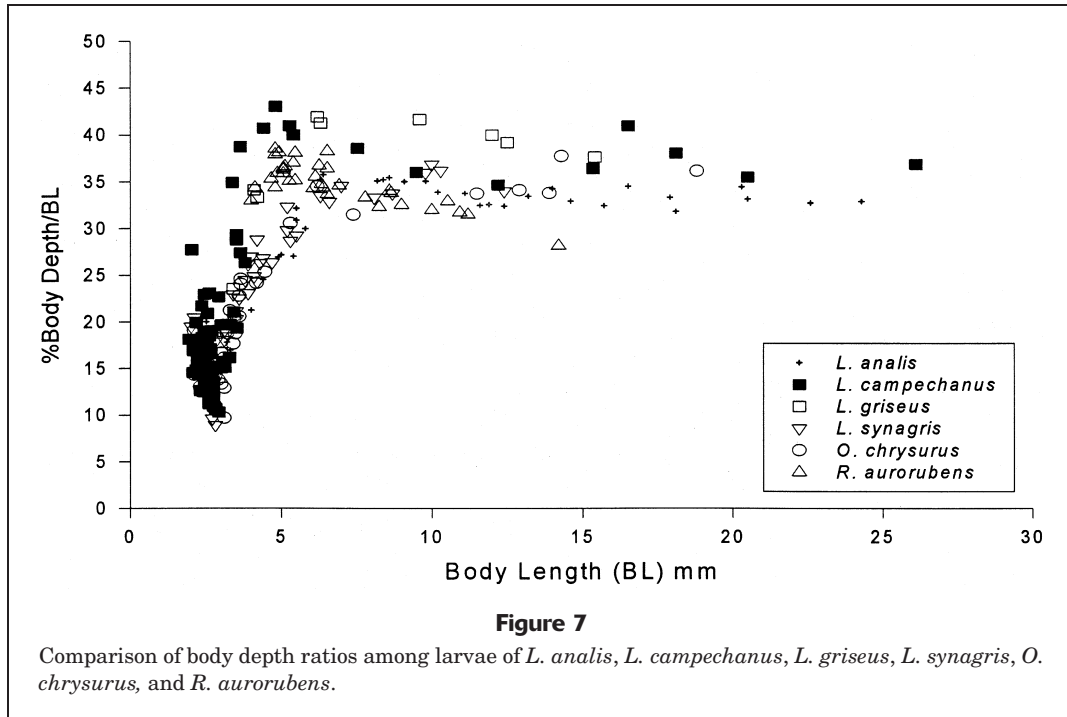
Table 5

Morphological comparison of *Rhomboplites aurorubens*, *Ocyurus chrysurus*, and *Lutjanus* spp. larvae based on presence (+), absence (–), and specimen size (BL in mm) at the first noted appearance of selected characters from published descriptions and illustrations. Abbreviations: D = dorsal; D₂ = soft dorsal fin; BD = body depth; sp = spine; a = anterior; p = posterior; P₂ = pelvic fin; Pr An sp = preopercular angle spine; avm = anterior visceral mass; pav = postanal ventral melanophore series; nv = not visible in published illustrations; ? = no published illustrations. “Spots” refer to melanophores. Dorsal fin counts in parentheses are rare values (Richards et al., 1994).

	Dorsal-fin count	BD to BL ratio	P ₂ ray length	Avm pigment	Pr An sp serrations	D sp serrations	No. of pav spots in preflexion	Enlarged pav spot in preflexion	Gap in pav series in preflexion
<i>R. aurorubens</i>	XII,(10)11(12)	35% at 4.0	=P ₂ sp	–	+	+	8–18	–	–
<i>L. apodus</i>	X,14	?	?	?	?	?	?	?	?
<i>L. cyanopterus</i>	X,14	?	?	?	?	?	?	?	?
<i>L. griseus</i>	X,14	34% at 4.2	=P ₂ sp	nv	–	+	23–27	–	–
<i>L. jocu</i>	X,(13)14	?	?	?	?	?	?	?	?
<i>L. mahogani</i>	X,(11)12	?	?	?	?	?	?	?	?
<i>O. chrysurus</i>	(IX)X(XI),12-13(14)	26% at 4.5	2×P ₂ sp	3.3–4.0	–	+	13–19	–	–
<i>L. synagris</i>	X,12(13)	29% at 4.6	2×P ₂ sp	3.3–4.0	–	+	15–25	+	–
<i>L. analis</i>	X(XI),(13)14	23% at 4.6	2×P ₂ sp	3.3–4.0	–	+	13–23	+	+
<i>L. buccanella</i>	X,14	?	?	?	?	?	?	?	?
<i>L. campechanus</i>	(IX)X,(13)14(15)	36% at 4.2	2×P ₂ sp	3.4	–	–	8–22	–	+
<i>L. purpureus</i>	(IX)X,(13)14(15)	?	?	?	?	?	?	?	?
<i>L. vivanus</i>	X(XI),(13)14	?	?	?	?	?	?	?	?

	Spot ventral to notochord flexure	Internal spots over notochord	Dorsal midline caudal pigment	D ₂ pigment	Anal-fin pigment base and membrane	Pelvic-fin pigment during flexion	Data sources
<i>R. aurorubens</i>	–	–	4.5	nv	5.1/nv	membrane ray 1	1,2,3
<i>L. apodus</i>	?	?	?	?	?	?	
<i>L. cyanopterus</i>	?	?	?	?	?	?	
<i>L. griseus</i>	–	–	–	by 9.6	by 6.2/by 7.1	spine+ray tips (?)	2,4
<i>L. jocu</i>	?	?	?	?	?	?	
<i>L. mahogani</i>	?	?	?	?	?	?	
<i>O. chrysurus</i>	–	6.3	6.3	11.5	5.3/6.3	membrane all rays	5,6
<i>L. synagris</i>	–	6.2	6.2	6.2	4.7/9.8	membrane ray 1	6
<i>L. analis</i>	5.8	–	8.1	11.5	6.2/16	membrane ray 1	6
<i>L. buccanella</i>	?	?	?	?	?	?	
<i>L. campechanus</i>	–	–	3.8 or 5.5	12.2	3.8/12.2	membrane ray 1	2,7,8
<i>L. purpureus</i>	?	?	?	?	?	?	
<i>L. vivanus</i>	?	?	?	?	?	?	

¹ Laroche (1977).² Richards et al. (1994).³ Comyns, B.H., and J. Lyczkowski-Shultz. 1993. Spawning and early life history of snappers in the northcentral Gulf of Mexico. Final Report, MARFIN grant NA17FF0382-01, NMFS Southeast Regional Office, St. Petersburg, FL 33701.⁴ Richards and Saksena (1980).⁵ Riley et al. (1995).⁶ Clarke et al. (1997).⁷ Collins et al. (1980).⁸ Our study.



provide important diagnostic characters. Flexion larvae of *O. chrysurus*, *L. analis*, and *L. synagris* are shallow-bodied ranging from 23% to 29% of body length (Fig. 7), whereas body depth in flexion larvae of *L. campechanus*, *L. griseus*, and *R. aurorubens* is from 34% to 36% of body length. The approximately equal length of the longest pelvic-fin ray and pelvic spine helps distinguish *R. aurorubens* and *L. griseus* from *O. chrysurus*, *L. synagris*, *L. analis*, and *L. campechanus* larvae in which the longest pelvic ray is nearly twice the length of the pelvic spine.

Small preflexion larvae of *L. campechanus* can be consistently distinguished from larvae of *R. aurorubens* in northcentral GOM waters by the presence of the avm melanophore. This character first appeared in reared specimens at 3.4 mm but would be seen in somewhat smaller wild specimens because of the shrinkage experienced by net-captured larvae (Theilacker, 1980). Larvae of *O. chrysurus*, *L. synagris*, and *L. analis* also develop avm pigment at BLs between ~3 and 4 mm. The presence or absence of this character in *L. griseus* larvae could not be ascertained from published illustrations (Richards and Saksena, 1980), but avm pigment was present in all specimens of *L. griseus* that we examined. The presence of serrations on the angle spine of the preopercle in *R. aurorubens* larvae at sizes >3.4 mm distinguishes them from *O. chrysurus* and all *Lutjanus* larvae currently known in the GOM. Snapper larvae may develop serrations on the median fin spines to some degree or another, but at least three species of lutjanine snappers (*Hoplopagrus gunteri*, *L. novemfasciatus*, and *L. peru*) from the Pacific do not develop serrations on any fin spines (Brogan, 1996; Watson and Brogan, 1996). Larvae of the six species compared in Table 5 develop serrations on the pelvic spine and all species,

except *L. campechanus*, develop serrations on dorsal-fin spines. Although not shown in the illustrations of Richards and Saksena (1980), the larvae of *L. griseus* do develop pronounced serrations on both dorsal and pelvic spines (Clarke et al., 1997; Richards et al., 1994). The relative size and extent of these serrations vary among species; *R. aurorubens* has the stoutest serrations among snapper larvae on both the leading and trailing edges of the spines (Laroche, 1977).

The postanal series of melanophores (pav) along the ventral midline is characteristic of many percoid larvae, including those of snappers. In snapper larvae, postanal pigmentation decreases dramatically during the flexion stage. Despite the dynamic nature of this pigment during development and the considerable overlap in number of pav melanophores among preflexion larvae (Table 5), Clarke et al. (1997) suggested that the "usual" number (not overall range) of pav melanophores would distinguish the larvae of *L. synagris* and *L. analis* from each other. Yolksac and preflexion larvae of these two species are further distinguished from other known lutjanine larvae by the presence of an enlarged melanophore in the pav series (Clarke et al., 1997). An additional pav-related character that differs among known lutjanine larvae is the gap in the pav series posteriorly, as seen in *R. aurorubens*, *L. campechanus*, and *L. analis*. The pav series of melanophores in *L. griseus*, *O. chrysurus*, and *L. synagris* is continuous in preflexion larvae.

Pigmentation associated with the notochord can be used to distinguish the larvae of *O. chrysurus*, *L. synagris*, and *L. analis* from other described GOM lutjanine larvae (Table 5). Although pigment overlying the point of notochord flexure develops by ~6 mm in all described GOM

lutjanine larvae, only *L. analis* simultaneously acquires pigment ventral to notochord flexure. Only the larvae of *O. chrysurus* and *L. synagris* develop internal melanophores over the notochord. Both species first acquire this pigment by ~6 mm but it becomes more extensive with development in *O. chrysurus* than in *L. synagris*. Pigment on the dorsal midline of the caudal peduncle develops in all lutjanine larvae except *L. griseus*. There is some interspecific variation in the size when this pigment first develops (Table 5). *Rhomboplites aurorubens* larvae as small as 4.5 mm have dorsal pigment on the caudal peduncle (Richards et al., 1994) and this pigment does not develop in *L. analis* larvae until ~8 mm. A single melanophore first appeared on the dorsal midline of the caudal peduncle in the 3.8-mm *L. campechanus* of our series. It was not present in the next two specimens but was present in the 5.5-mm specimen and all subsequent larvae.

Interspecific differences among known lutjanine larvae are apparent in the amount, location, and size at first appearance of dorsal-fin pigment. Pigment in the spinous dorsal fin first appears in the membrane behind the second spine in *L. campechanus*, *O. chrysurus*, *L. synagris*, and *L. analis*. Additional melanophores develop posteriorly behind successive spines in *L. synagris* throughout flexion, whereas in the other three species, pigment develops posteriorly behind successive spines only in late flexion or after flexion. It appears from the illustrations of Clarke et al. (1997) that although pigment between the first and second spines is present in *L. synagris* from 4.7 to 6.2 mm, it is consistently present only in *O. chrysurus* larvae from preflexion onward. Spinous dorsal-fin pigment in *L. griseus* differs notably from the other species of lutjanines; melanophores first form low in the fin at the base of the second or third spines, or at the base of both, and as development proceeds, melanophores are added distally (farther out onto the fin) and posteriorly. Pigment was present between the second and third dorsal-fin spines in the few *R. aurorubens* larvae that had intact dorsal-fin membranes. Dorsal-fin pigment was not indicated in illustrations by Laroche (1977), probably because these specimens did not have intact fin membranes. Among known GOM lutjanine larvae, only *L. synagris* larvae develop pigment in the second (soft) dorsal fin before ray formation is complete, at ~6 mm. In larvae of the remaining species, pigment in the second dorsal-fin first appears at larger sizes when fin ray development is well advanced (Table 5).

Anal- and pelvic-fin pigmentation is also useful in separating the larvae of GOM lutjanines. Pigment on the anal-fin base develops in all six species whose larvae have been described and of these, *L. campechanus* larvae develop this pigment at the smallest size, <4 mm (Table 5). There are greater differences among larvae in size at first appearance of pigment in the anal-fin membrane than in the anal base. *Lutjanus campechanus* and *L. analis* larvae can be distinguished from the other described larvae by later development of anal-fin pigment at sizes ≥ 12 mm (Table 5). Pigment on the pelvic fin bud has been indicated in all illustrated lutjanine larvae except *L. griseus*. It is likely that this exception is due, not to true absence of this fea-

ture in *L. griseus*, but to the limited number of larvae in the described series (Richards and Saksena, 1980). The 4.2-mm *L. griseus* larva illustrated by these authors had pigment at the distal tips of the pelvic fin, but this pigment was not present in larger larvae of the series or in the 7.1-mm specimen illustrated in Richards et al. (1994). Pelvic-fin pigment distinguishes *O. chrysurus* and *L. griseus* from other lutjanine larvae once the spine and first ray are formed. From illustrations in Clarke et al. (1997), it appears that starting in the preflexion stage, *O. chrysurus* larvae have pigment throughout the pelvic-fin membrane and not just around the first fin ray as in *L. campechanus*, *L. synagris*, and *L. analis*. The unique condition of pelvic-fin pigmentation that characterizes *L. griseus* is the "candycane stripe" pattern of melanophores that overlay the pelvic spine. Pigment on the pelvic spine is present in *L. griseus* larvae as small as 4.2 mm and the striped pattern is evident by at least 6.2 mm (Richards and Saksena, 1980).

In Table 9 of their recent publication, Clarke et al. (1997) provided a summary of distinguishing characters for the known larvae and juveniles of western Central Atlantic lutjanine snappers. We have noted some discrepancies in that summary that may cause confusion for those attempting to identify lutjanine snapper larvae from our area. In Table 9, the "usual" number of pav melanophores listed for *L. campechanus* was given as 16–18. The modal number of pav spots among preflexion *L. campechanus* larvae (2.2–3.8 mm BL; $n=70$) from the GCRL rearings was 15, and 50 specimens had 14 to 19 pav spots. Also in Table 9, for the character "serrations on dorsal and pelvic fin spines," the entry for *L. campechanus* states, "on anterior spine margin only." Larvae of *L. campechanus* develop serrations on the anterior margin of the pelvic spine only, not on the dorsal spines (Collins et al., 1980; Potthoff et al., 1988). Clarke et al. (1997) also note that *L. griseus* larvae develop internal melanophores ventral to the point of notochord flexure (their character "O"). This feature is not visible in any of the published illustrations of *L. griseus* larvae or in specimens we have examined. Finally, information in Table 9 that pertains to character "P"—"internal melanophores on antero-ventral surface of gut (peritoneum) dorsal to pelvic bone" noted as being absent in four species—was clearly present in the *R. aurorubens* and *L. campechanus* larvae that we examined and is visible in illustrations of *L. analis* and *O. chrysurus* in Clarke et al. (1997).

The descriptions of larval lutjanine snapper development now available will allow scientists to identify mid- to late-flexion and postflexion larvae of the most common lutjanids in the Gulf of Mexico. In an examination of over 1500 snapper larvae from Gulfwide collections in 1992 and 1993, we found that the larvae of *R. aurorubens*, *L. campechanus*, and *P. aquilonaris* made up 23%, 13%, and 13% of all snapper larvae captured, respectively. Other identified taxa consisted of *Lutjanus* spp. (3%), *L. griseus* (<1%), and *L. synagris* (<1%). However, 47% of snapper larvae in these collections, typically <3.5–4.0 mm in length, could not be identified beyond the family level because diagnostic characters are present only after flexion has begun.

Closer scrutiny of characters, such as the number of pav spots, the enlarged pav spot, and the gap in the pav series, may allow identification of preflexion and early flexion snapper larvae, if not to a single species, at least to a reduced number of possibilities. Of course, larvae of the remaining snapper species need to be described before all small "undifferentiated snapper larvae" can be reliably and consistently identified to the species level. Investigation of additional characters among preflexion larvae such as the presence and location of other chromatophores, may yield further useful species-specific traits (Riley et al., 1995). Initial observations of *L. campechanus* show yellow chromatophores in similar locations (head and gut area) as those reported for *O. chrysurus* (Riley et al., 1995). Among larger *L. campechanus* specimens, additional chromatophores were present in locations not noted for *O. chrysurus* larvae. More specific comparisons will have to await a larger sample size to determine variability in numbers of chromatophores and size at development. Additionally, biochemical techniques are currently being investigated for the purpose of species-specific identification of snapper larvae (Chow et al., 1993; Sarver et al., 1996; Schultz et al., 1996). Initial results seem to indicate that no single technique will distinguish between all species in the subfamily Lutjaninae. Use of these biochemical assay methods for routine identification of snapper larvae may not be feasible for specimens taken during broadscale surveys. Yet a positive species identification of subsamples of field-caught snapper larvae with biochemical methods may lead to recognition of morphological features that have been previously overlooked and determination of the error rate of morphologically based identifications.

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