Larval development, distribution, and abundance of common dolphin, *Coryphaena hippurus*, and pompano dolphin, *C. equiselis* (family: Coryphaenidae), in the northern Gulf of Mexico*

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Abstract.— Dolphinfishes are highly prized commercial and recreational species of worldwide distribution in tropical and subtropical seas, but the development and distribution of their larvae are poorly understood. Common dolphin eggs hatch in about 38 hours at 25°C based on a predictive relationship among egg diameter, water temperature, and development time. Morphometrics are generally greater in pompano dolphin than in common dolphin. Pompano dolphin are deeper–bodied and have a larger eye by 9 mm, and a larger mouth and longer pre-anal length by about 13 mm. Differences in pigment along the caudal peduncle and its finfold separate common dolphin from pompano dolphin <4.0–4.5 mm SL; common dolphin lack pigment in these areas. Number of spines along the outer shelf of the preopercle also separate species although preopercle spines are often difficult to count on larvae not cleared and stained; common dolphin have four spines along the outer preopercular shelf and pompano dolphin have five. Pigmented pelvic fins and bands of pigment laterally on both the body and median fins of common dolphin are diagnostic for separating species >8 mm SL; pompano dolphin lack these characters. Both common dolphin and pompano dolphin larvae usually are found at ≥24°C, ≥33 ppt, and beyond the 50 m isobath. Preflexion larvae (<7.0–7.5 mm SL) were primarily collected in oceanic waters. Both species may spawn year–round, at least in the southern part of the survey area. Larval common dolphin are significantly more abundant than pompano dolphin.

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The dolphinfishes, *Coryphaena hippurus* (common dolphin) and *C. equiselis* (pompano dolphin), are distributed worldwide in tropical and subtropical seas (Briggs, 1960). Highly prized as food, these fishes are important recreational and commercial species, but relatively little is known about their early life stages. Gibbs and Collette (1959) reviewed spawning and adult seasonal distribution for the western North Atlantic Ocean, and Palko et al. (1982) compiled dolphinfish biological data. Aoki and Ueyanagi (1989) discussed larval and early juvenile distribution for the eastern Pacific, and similar information is available for the western Pacific and Indian oceans (Shcherbachev, 1973). Preliminary distribution maps are available for the Gulf of Mexico (Gulf), but associated environmental data are not included (Richards et al., 1984; Kelley et al., 1986). Embryonic development is described for common dolphin (Mito, 1960; Hassler and Rainville, 1975; Hagood and Rothwell[1]) and osteological development for both species (Potthoff, 1980), but descriptive larval morphology is primarily limited to sizes >13 mm SL (Gibbs and Collette, 1959; Shcherbachev, 1973). Okiyama (1988) and Aoki and Ueyanagi (1989) provide information on developmental morphology of Pacific specimens <13 mm SL, but their illustrations are

[1] Hagood, R. W., and G. N. Rothwell. 1979. Sea Grant interim project report—1979. Aquaculture in tropical ocean—*Coryphaena* sp. Oceanic Inst., Makapuu Point, Waimanalo, HI 96795.

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insufficient to examine important details, and Okiyama's study is a general overview of exisitng information. The utility of early life stages of *Coryphaena* in examining previous phylogenetic hypotheses and evolutionary interrelationships of echeneoids (i.e. Coryphaenidae-Rachycentridae-Echeneididae) is discussed by Johnson (1984). Our objectives are 1) to describe and compare early larval development of common dolphin and pompano dolphin using the dynamic approach to larval description (Berry and Richards, 1973) and 2) to describe the spatial and temporal distribution and abundance of early life stages of dolphinfishes in the northern Gulf.

Materials and methods

Seasonal occurrence, distribution, and abundance of dolphinfish larvae were determined primarily from 814 neuston net collections taken during Southeast Area Monitoring and Assessment Program (SEAMAP) ichthyoplankton surveys of the Gulf between 1982 and 1984 (1982–276 stations, 1983–260, 1984–278). These years represent the first time interval for which a complete set of data was currently available. SEAMAP collections were made with an unmetered 1×2 m net (0.947-mm mesh) towed at the surface for 10 minutes at each station. The SEAMAP effort also involved the collection and processing of about 1,819 bongo net stations between 1982 and 1986 (1982–384 stations, 1983–288, 1984–409, 1985–272, and 1986–466) (SEAMAP 1983–1987)[2]. Bongo nets (60-cm net, 0.333-mm mesh) were towed obliquely to the surface from within 5 m of the bottom or from a maximum depth of 200 m. Sampling during April and May was primarily beyond the continental shelf, and that during March and from June to November was primarily over the shelf at stations <180 m depth. No samples were taken during January and February. Tows were made during both day and night depending on when the ship occupied the station. Latitude 24°30'N was the southern boundary of our survey area in the eastern Gulf and latitude 26°00'N the southern boundary of the central and western Gulf (Appendix Fig. 1). These coordinates approximate the U.S. Exclusive Economic Zone (EEZ)/Fishery Conservation Zone (FCZ). Additional information on temporal and spatial coverage of SEAMAP plankton surveys are found in Stuntz et al. (1985), Thompson and Bane (1986, a and b), Thompson et al. (1988), and Sanders et al. (1990).

Ichthyoplankton collections were also examined from riverine/oceanic frontal zones off the Mississippi River delta. These collections were from surface-towed 1×2 m neuston nets (0.947-mm mesh, 10–min. tows, sample n=311) and were obtained from the National Marine Fisheries Service (NMFS), Panama City, Florida (i.e. May 1988 [55 neuston samples]; August 1988 [71]; September 1986 [46], 1987 [68], and 1989 [35]; and December 1988 [36]).

A detailed examination of dolphinfish larvae was made to describe developmental morphology. We examined 25 common dolphin and 19 pompano dolphin larvae between 3.5 and 15.0 mm SL for differences in pigmentation, developmental morphology, and head spination, but only cursorily discuss fin development because of a thorough review of these structures by Potthoff (1980). Body measurements were made to the nearest 0.1 mm with a dissecting scope and ocular micrometer following Hubbs and Lagler (1958) and Richardson and Laroche (1979). We follow Leis and Trnski's (1989) criteria for defining length of preopercular spines, body depth, head length, and eye diameter. We consider notochord length in preflexion and flexion larvae synonymous with standard length (SL) in postflexion larvae and report all lengths as SL unless otherwise noted. Specimens were field-fixed in 10% formalin and later transferred to 70% ethyl alcohol. We used a compound scope to examine origin and location of epithelial spicules and the maxillary spine. Juveniles are those >25 mm, when specimens usually have developed a full complement of rays in all fins and scales (Johnson, 1984). Representative specimens were illustrated with a camera lucida (Figs. 1 and 2). Only three pompano dolphin <4 mm were collected and these were in too poor a condition to illustrate.

Estimates of larval catch (number of larvae/neuston tow) were calculated for each station. Mean catch estimates by month and season were calculated by dividing the sum of larvae (by species) by the total number of stations sampled within each category (month, season, etc.) and multiplying the result by 10 (number of larvae/10 neuston tows). Mean catch more closely reflects the abundance of larvae throughout the area by including total sampling effort in calculations. Catch was combined by month and by season across years. Seasons were defined as follows: spring=March to May; summer=June to August; and fall=September to November (Appendix Fig. 2).

Nonparametric tests were used to evaluate diel, seasonal, and overall differences in catch of common

[2] SEAMAP. 1983–1987. (plankton). ASCII characters. Data for 1982–1986. Fisheries-independent survey data/National Marine Fisheries Service, Southeast Fisheries Center: Gulf States Marine Fisheries Commission, Ocean Springs, MS (producer).

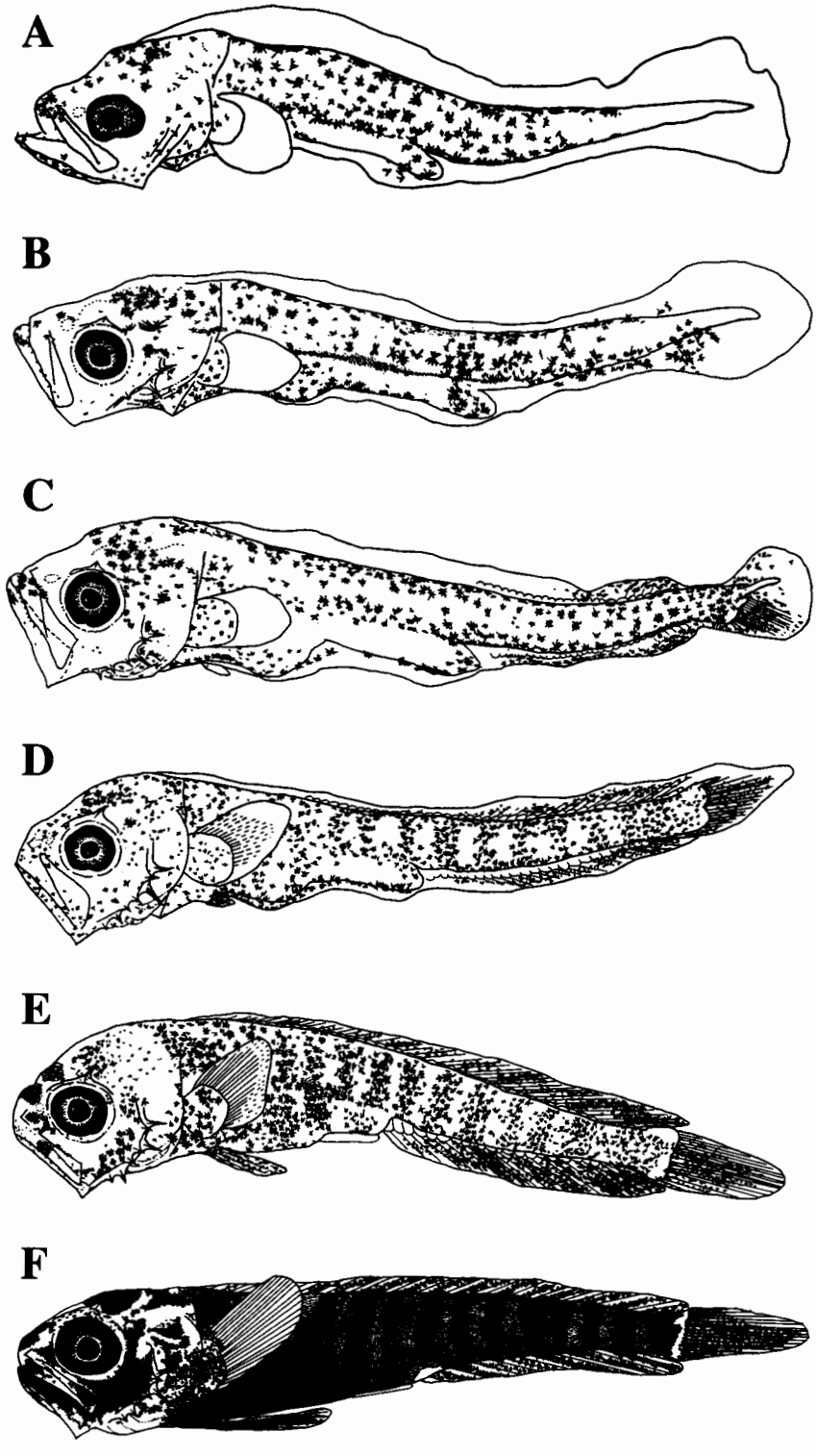

Figure 1

Larval development of common dolphin (*Coryphaena hippurus*) from the northern Gulf of Mexico. (**A**) 3.5 mm, (**B**) 5.0 mm, (**C**) 7.1 mm, (**D**) 9.5 mm, (**E**) 11.0 mm, (**F**) 14.0 mm. All measurements are in standard length (SL).

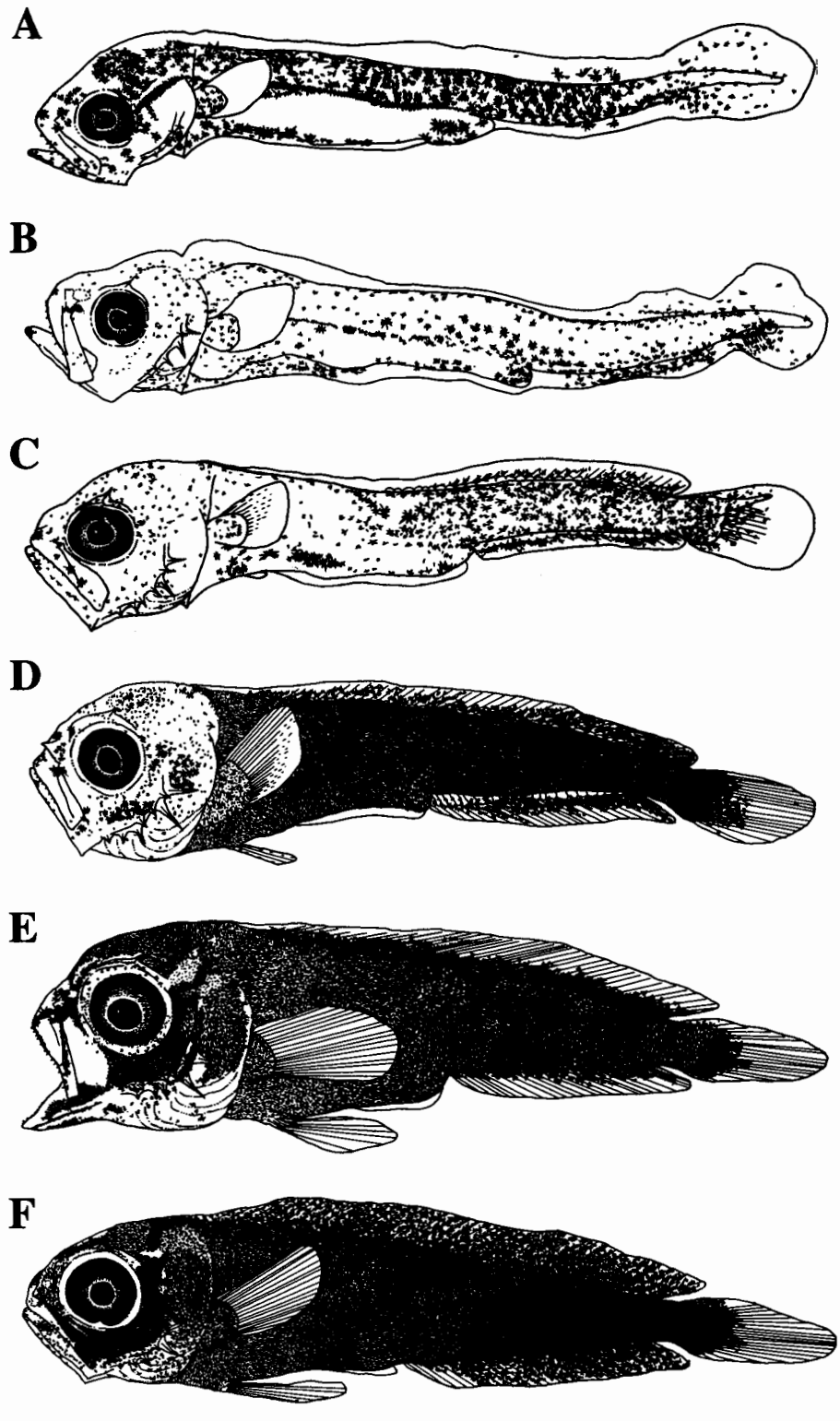

Figure 2

Larval development of pompano dolphin (*Coryphaena equiselis*) from the northern Gulf of Mexico. (**A**) 4.7 mm, (**B**) 5.5 mm, (**C**) 7.5 mm, (**D**) 9.7 mm, (**E**) 11.5 mm, (**F**) 15.0 mm. All measurements are in standard length (SL).

dolphin and pompano dolphin. Only those stations where either of the two species were present were included in analyses. A Kruskal-Wallis test was used to detect differences among groups (α=0.05) and a Tukey-type test to determine if mean differences were significant (Zar, 1984; SAS Institute, 1985). Dolphinfish >25 mm were excluded from analyses.

Temperature and salinity data were taken from the sea surface only. Hydrographic data were multiplied by number of larvae caught (by species) at each station to obtain an overall median and mean. This method gives weight to distribution of larvae rather than distribution of stations. We used a percent cumulative frequency of ≥75% for determining the relationship between distribution of dolphinfish larvae and surface water temperature, salinity, and station depth. Percent frequency indicates the range of hydrographic conditions most often associated with occurrences of larvae. Proc Univariate was used to calculate median, mean, and percent cumulative frequency statistics (SAS Institute, 1985). We divided the continental shelf into approximately equal geographic areas (i.e. into sq. km.) based on depth and designated the inner shelf as <50 m deep, outer shelf waters as those from 50 to 180 m deep, and oceanic waters as those beyond the continental shelf (i.e. >180 m).

Results

Morphology

A continuous median finfold extended posteriorly along the body of early larvae of both species from the posterior midbrain to the cleithral symphysis. Remnants of the finfold were visible ventrally along the hindgut (i.e. preanal finfold) at least through 15 mm. Minute epithelial spicules covered the body of each species by 4 mm and were best observed on the head and larval finfold. Spicules were more easily observed as larvae grew. Yolk-sac larvae <3.5 mm of common dolphin and pompano dolphin had unpigmented eyes. Preflexion larvae (<7.0–7.5 mm) of both species were elongate, with body depth usually ≤20% SL. The body became relatively deeper during flexion (about 7.5–9.0 mm) and pompano dolphin were deeper-bodied than were common dolphin by early postflexion (Table 1). The head was moderately long (i.e. between 20 and 33% SL) in both species and the snout was short and blunt. The eyes were round and larger in pompano dolphin than in common dolphin by early postflexion (Table 1). The mouth was large and oblique; upper jaw length usually ranged from 42 to 45% of head length in postflexion dolphinfish of both species. Pompano dolphin have a larger mouth than do common dolphin by 13 mm (Table 1). The foregut was partially convoluted and had a half-twist in preflexion larvae of both species and a single loop in larger larvae; the hindgut was straight. By 13 mm, however, preanal length was generally greater in pompano dolphin than in common dolphin (Table 1). Preanal length usually ranged from 60 to 65% SL during preflexion, but decreased thereafter to 55–60% SL in both species. The pelvic fins were moderately long (about 15–18% SL; Table 1) and extend to the tips of the pectorals by 12 mm. Myomeres were obscured by heavy

Table 1

Morphometrics of larval common dolphin (*Coryphaena hippurus*) and pompano dolphin (*C. equiselis*) from the northern Gulf of Mexico. Measurements are expressed as % standard length (SL).

SL (mm)	*N*	Preanal length	Head length	Snout length	Orbit diameter	Upper jaw length	Body depth cleithrum	Prepelvic distance	Pelvic length
C. hippurus									
3.5–4.9	5	57.0–65.0	23.0–25.0	4.0–6.0	9.0–10.0	11.0–12.5	16.5–18.5	—	—
5.0–6.9	4	61.0–65.0	24.0–27.0	5.0–6.0	8.0–9.5	9.0–13.0	17.0–22.0	31.0–34.0	bud
7.0–8.9	4	60.0–63.0	23.0–27.0	5.0–6.0	7.0–9.0	9.5–12.0	16.0–20.0	27.0–32.5	bud–3.0
9.0–10.9	3	56.0–59.0	25.0–28.0	5.5–6.0	9.5–11.0	12.0–13.0	19.0–21.0	27.0–30.0	4.5–11.0
11.0–12.9	5	54.0–57.0	24.0–27.0	5.0–6.0	10.0–11.0	11.0–13.0	20.0–23.0	27.0–28.0	11.0–15.0
13.0–14.9	4	54.0–56.5	25.0–28.0	4.0–5.0	11.0–11.5	12.0–12.5	21.0–22.5	26.0–30.0	17.0–18.5
C. equiselis									
3.7–4.9	3	60.0–65.0	23.0–27.5	5.0–6.0	9.5–10.0	11.5–13.0	19.0–21.0	—	—
5.0–6.1	4	60.0–62.0	23.0–24.0	5.0–6.0	8.5–10.0	10.0–13.0	16.0–20.0	—	—
7.5–8.9	2	46.0–47.0	19.0–22.0	4.0–4.5	8.0–9.5	10.0–12.0	16.0–22.0	22.0–24.0	bud–6.0
9.0–10.9	3	56.0–60.0	27.0–30.0	4.5–5.0	12.0–12.0	12.0–15.0	25.0–29.0	30.0–35.0	8.5–14.0
11.0–12.9	4	55.0–60.0	25.0–30.0	4.0–5.0	12.0–14.0	12.0–14.0	27.0–29.0	31.0–35.0	13.0–15.0
13.0–15.0	3	55.0–60.0	27.0–30.0	4.0–5.0	13.0–13.0	13.0–15.0	25.5–28.0	28.0–34.0	16.0–18.5

pigmentation and were difficult to count on dolphinfish larvae; however, a 5.5-mm pompano dolphin had 33 myomeres and a partially cleared 11-mm common dolphin had 30 vertebrae. Only two pompano dolphin between 6.1 and 9.7 mm were collected (7.5 and 8.5 mm) and morphometrics for these larvae were considerably smaller than for the other specimens (Table 1).

Pigmentation

Dolphinfish were heavily pigmented at all sizes, except the caudal peduncle and its finfold in early preflexion larvae of common dolphin which was unpigmented (Fig. 1). In common dolphin <4 mm, the length of the unpigmented portion of the caudal peduncle was 15–20% SL. By 4.5–5.0 mm, however, pigment was present along the caudal peduncle and on the caudal finfold (Fig. 1). Early preflexion pompano dolphin <4 mm had a row of melanophores along the caudal peduncle (both dorsally and ventrally) and pigment was scattered throughout the caudal finfold (Fig. 2). On the head, pigment was scattered externally over the premaxilla, snout, and fore-, mid-, and hind-brain of early larvae of each species. Pigment also was present along the dentary, lower jaw, isthmus, branchiostegal rays, and on the roof of the mouth. On the visceral mass, melanophores were scattered over the foregut and anus of early preflexion larvae of both species but the hindgut was sparsely pigmented laterally (Figs. 1 and 2). Gut pigmentation increased with length. Vertical bands of pigment first formed along the dorsal and anal fins of common dolphin at about 8 mm. These bands of pigment subsequently extended across the body; 12 to 13 poorly formed bands were visible by 10 mm. Vertical bands became more distinct as larvae grew (Fig. 1). Bands of pigment do not form in pompano dolphin, but this species does have a row of enlarged melanophores along the body dorso- and ventro-laterally (adjacent to the dorsal and anal fin bases) by 7.5 mm, which was not present in common dolphin (Figs. 1 and 2).

Pectoral buds were present on early larvae of each species. Pigment was scattered over the pectoral axilla and was heavier on pompano dolphin than on common dolphin of similar length. The proximal portion of the upper pectoral rays of common dolphin was pigmented by 14–15 mm; no pigment was present on the pectoral rays of pompano dolphin. Dorsal- and anal-fin bases were thickening by 5 mm in pompano dolphin and by 6 mm in common dolphin; the anal-fin base developed slightly before that of the dorsal base. Both fin bases and their ray anlagen developed in a posterior to anterior direction. Pelvic-fin buds of common dolphin were present by 6.5 mm and pigmented by 7.5 mm. No pompano dolphin between 6.1 and 7.5 mm were examined, but the pelvic buds were present by 7.5 mm. The pelvic rays of pompano dolphin remained unpigmented at all sizes. Pigment occurred on the developing caudal rays of each species by early flexion. By 10 mm, all but the distal tips of the caudal rays were pigmented in common dolphin; only about the proximal third of each caudal ray was pigmented in pompano dolphin. Differences in caudal-fin pigmentation were more pronounced as larvae grew (Figs. 1 and 2).

Head and body spination

Dolphinfish larvae developed two series of preopercle spines, one series along the posterior margin of the inner shelf and the other along the outer shelf. Number and location of spines along the outer shelf of the preopercle separate larval common dolphin from pompano dolphin. Two spines were present along the margin of both the inner and outer preopercular shelves of 4-mm common dolphin, the largest spines occurring on either side of the angle of the preopercle (Figs. 1 and 2). A third spine was added along both the inner and outer shelf by 7 mm; a fourth spine was added along the outer preopercle by 10.0–10.5 mm. A total of three spines occurred along the inner and four spines along the outer shelf of the preopercle of larval common dolphin (Fig. 1). Arrangement of preopercle spines in larval pompano dolphin <4 mm was similar to that in common dolphin except three rather than two spines were visible along the outer preopercular shelf. A third spine was added along the inner shelf by 7 mm and a fourth and fifth spine along the outer shelf by 9 mm. A total of three spines occurred along the inner and five spines along the outer preopercular shelf of larval pompano dolphin (Fig. 2). Number and placement of preopercle spines were consistent through at least 15 mm in both species. All preopercle spines were simple (Figs. 1 and 2).

Dolphinfish have several spines and ridges on the head. The pterotic area was swollen in both species by 5 mm and a laterally directed spine was present along the supraorbital ridge of each frontal bone of 6-mm pompano dolphin and 7-mm common dolphin (Figs. 1 and 2). The supraorbital ridge of each species usually had a single spine, but some pompano dolphin had two or three spines along the ridge. The swollen pterotics and supraorbital spine were best observed when specimens were viewed dorsally; both features were well developed by 7.5–8.0 mm. The frontal bone was notably thicker above the eye of pompano dolphin, but the supraorbital ridge was less well developed in pompano dolphin than in common dolphin by 9.5 mm. The supraorbital spine(s)

of pompano dolphin were regressing by 11–12 mm. A small spine was present anteriorly along the maxilla of each species by 5 mm (Figs. 1 and 2). The maxillary spine (difficult to locate because of its position and size) pointed dorso-laterally and was slightly better developed in pompano dolphin than in common dolphin of similar size. A posttemporal spine was present in both species by 9 mm and was most easily observed when specimens were viewed dorsally. The anterior portion of the lacrimal bone was prominent in dolphinfish larvae; the lacrimal was more pronounced in pompano than in common dolphin by late flexion (Figs. 1D and 2D).

Minute teeth were present anteriorly on the upper and lower jaws of each species by 3.8 mm. Number and size of teeth increased with SL. A pair of canine-like teeth were present in 10-mm pompano dolphin and 11-mm common dolphin.

Spatial and temporal distribution

Larval dolphinfish were collected during all months sampled, but small larvae of both species were found primarily during warm months. Preflexion larvae of common dolphin occurred mainly from April through November. One common dolphin larva (7.0 mm) was also collected during December (21, 1983), at a station due south of Caminada Pass, Louisiana (23.5°C, station depth: 531 m). Larval pompano dolphin were collected from March through October; larvae <10 mm were collected through late September. Only one pompano dolphin larva (5 mm) was collected during March (13, 1982; water temperature: 18°C), at a bongo-net station 29 m deep off Caminada Pass, Louisiana. Two pompano dolphin larvae (18.3 and 22.5 mm) were collected during October (14 and 17, 1983), but they were probably spawned during late September.

Larvae of common dolphin and pompano dolphin were collected primarily at water temperatures ≥24°C (90% of larvae) and salinities ≥33 ppt (≥75%) (Table 2, Fig. 3). The pompano dolphin collected during March was the only larva of either species taken at <21°C. Based on water temperatures when common dolphin larvae usually occurred (≥24°C) and using Pauly and Pullin's (1988) relationship between egg diameter and water temperature to predict development time in other marine fishes, we estimate a common dolphin egg of 1.4 mean-mm diameter would hatch in about 38 hours at 25°C and 26 hours at 30°C (Table 3). Few common dolphin larvae and no pompano dolphin were collected at <25 ppt (Table 2; Fig. 3).

Larval dolphinfish of both species were widely distributed in neritic and oceanic waters of the Gulf and most were collected near the surface. Over 90% of common dolphin and about 80% of pompano dolphin occurred over the outer continental shelf and in oceanic waters; preflexion larvae were usually taken in oceanic waters (stations >180 m deep) (Appendix Fig. 3). Overall, larval common dolphin were significantly more abundant than pompano dolphin (Kruskal-Wallis, $P \leq 0.0001$, df= 362; Table 4). Larval common dolphin were also collected at more stations than were pompano dolphin (15.0% versus 5.1% of all stations sampled, respectively; Table 4). Only 3.1% of oblique bongo-net samples (1982–86, n=1819) took common dolphin larvae (no. larvae=83, length=6.5 mm, range=3.2–21.8 mm) and <0.01% captured pompano dolphin (no. larvae=10, $\bar{x}$ length=4.6 mm, range=4.0–8.7 mm).

Differences in catch of common dolphin and pompano dolphin, respectively, were not significant among seasons or between day and night. About 25% of spring and 18% of fall neuston stations collected larval common dolphin, but <9% of those stations sampled during summer (Table 4). Larval pompano dolphin were collected at 7% of spring neuston stations, 2% of summer stations, and 8% of fall stations (Table 4). Only two neuston tows collected >13 larvae of either species; these two tows ac-

Table 2

Summary of hydrographic data for common dolphin (*Coryphaena hippurus*) and pompano dolphin (*C. equiselis*) larvae collected in the northern Gulf of Mexico. Data are from the sea surface only; median values are obtained from the distribution of larvae versus the hydrographic parameter. Bongo and neuston net data are combined. '*N*' is number of larvae used in obtaining median values. Discrepancies in '*N*' result from missing values in the hydrographic data.

	Salinity (ppt)			Water temperature (°C)			Station depth (m)		
	N	Median	Range	*N*	Median	Range	*N*	Median	Range
C. hippurus	537	34.0	18.7–37.8	590	28.0	21.4–32.0	599	195	11–3475
C. equiselis	80	35.1	25.0–37.8	94	27.6	18.0–30.4	94	195	11–3325

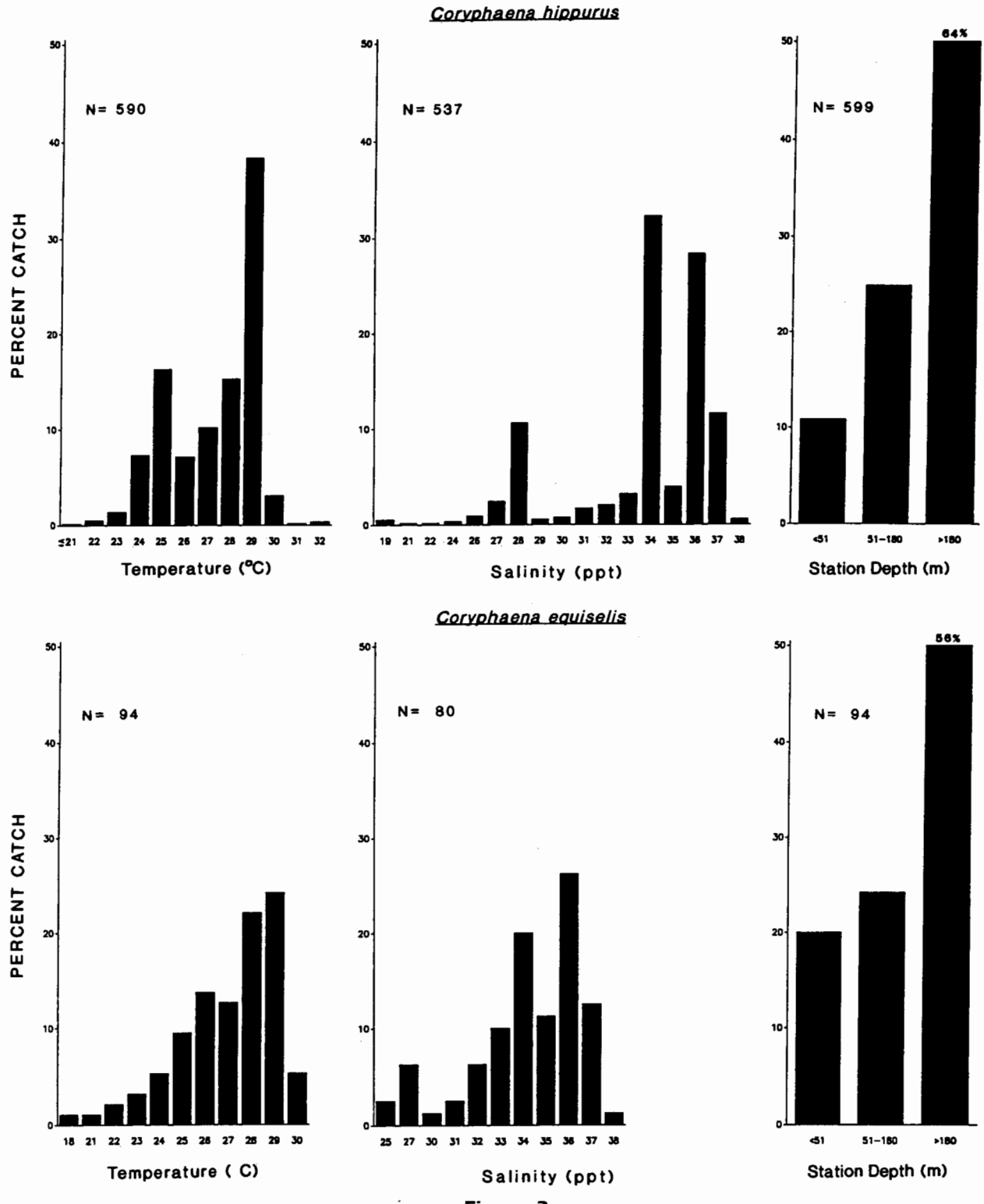

Figure 3

Summary of hydrographic data for larval common dolphin (*Coryphaena hippurus*) and pompano dolphin (*C. equiselis*) in the northern Gulf of Mexico. Data are from both bongo and neuston net tows. Hydrographic values are rounded to the nearest whole number. *N* = number of larvae. Discrepancies in '*N*' among parameters are the result of missing hydrographic data.

Table 3

Egg development time and hatching length (total length:TL) of common dolphin (*Coryphaena hippurus*).

Author	Egg diameter	°C	Hatching Time (hr)	Hatching TL (mm)	Study location
Mito, 1960	1.28–1.62	21–29	48–60	3.95	Japan
Hassler and Rainville, 1975	1.3[1]	27[1]	—	3.0[2]	Atlantic
Hagood and Rothwell	—	26	40	—	Hawaii
(see Footnote 1)	1.35[3]	26[3]	38[3]	—	Hawaii
Soichi, 1978	1.4–1.65	24–25	60	3.8–4.9[2]	Japan
Uchiyama et al., 1986	—	24–25	48–50	4.0–4.6	Hawaii
Lamadrid-Rose and Boehlert, 1988	1.52–1.66	26	54	4.3–5.4[4]	Hawaii
This study	1.4[5]	20	58[5]	—	Gulf of Mexico
		25	38[5]	—	
		30	26[5]	—	

[1] Mean.
[2] One-day-old larva.
[3] *C. equiselis*.
[4] Standard length.
[5] Mean egg diameter and predicted hatching times.

Table 4

Mean catch (no.larvae/10 neuston tows) of common dolphin (*Coryphaena hippurus*) and pompano dolphin (*C. equiselis*) larvae in the northern Gulf of Mexico by month. Collections for 1982–1984 are throughout the Gulf and those from 1986 to 1989 are primarily around the Mississippi River delta. Mean catch is calculated over all stations sampled by month; months are combined across years. Grand mean catch per 10 tows is calculated by dividing total number of larvae collected by all stations sampled. Numbers in parenthesis are positive catch stations over total stations sampled.

Taxa	N[1]	March	April	May	June	July	August	September	October	November	Grand Total
C. hippurus	517	0.0 (0/13)	3.4 (22/100)	7.6 (58/221)	2.9 (29/208)	0.5 (3/92)	0.5 (13/248)	13.4 (29/163)	3.9 (4/33)	16.7 (2/3)	4.8 (160/1081)
C. equiselis	85	0.8 (1/13)	1.2 (10/100)	0.9 (15/221)	1.0 (8/208)	0.2 (2/92)	<0.1 (1/248)	1.8 (16/163)	0.6 (2/33)	0.0 (0/3)	0.8 (54/1081)

[1] Number of larvae.

counted for about 40% of all common dolphin larvae taken. Both collections occurred off the Mississippi River delta, one during September 1986 (n=161, 195 m station depth) and the other during May 1988 (n=52, 63 m station depth).

Discussion

Early preflexion larvae (<4.0–4.5 mm) of pompano dolphin are separated from those of common dolphin by having melanophores along the caudal peduncle and scattered throughout the caudal finfold (Figs. 1 and 2). Number and placement of spines along the outer shelf of the preopercle also separate species (Table 5). Separation of dolphinfishes is particularly difficult between 4.5 and 8.0 mm because preopercle spines are often difficult to count on larvae not cleared and stained. At >8 mm, common dolphin are more easily separated from pompano dolphin by having pigment on the developing pelvic fins and bands of pigment laterally on the body and median fins (Figs. 1 and 2; Table 5). Differences in caudal-fin pigmentation also separate species by early

Table 5

Characters helpful in separating larvae of common dolphin (*Coryphaena hippurus*) from pompano dolphin (*C. equiselis*).

Species	Pigment			Outer preopercle spines	Meristics	
	Caudal peduncle	Pelvic fins	Vertical bands		Number of vertebrae	Dorsal fin rays
C. hippurus	Absent	Present[2]	Present[2, 3]	4	30–31	58–66
C. equiselis	Present[1]	Absent	Absent	5	33–44	52–59

[1] At <4.0–4.5 mm SL.
[2] At about 8.0 mm SL.
[3] Laterally on body and median fins.

postflexion (Figs. 1 and 2). In general, our findings agree with those of Aoki and Ueyanagi (1989). Lack of pelvic-fin pigment in pompano dolphin is diagnostic for separating the two species when common dolphin lose lateral banding through preservation or specimen deterioration. Although the 8.5-mm common dolphin larva illustrated in Johnson (1984) lacks pelvic pigment, this specimen has bands of pigment laterally on both the body and median fins.

Number of myomeres and dorsal-fin rays separate juvenile and adult common dolphin from pompano dolphin (30 or 31 vertebrae and 58–66 [$\bar{x}$=61] dorsal rays in common dolphin; 33 or 34 vertebrae and 52–59 [$\bar{x}$=55] dorsal rays in pompano dolphin; Collette et al., 1969; Potthoff, 1980). Great care must be taken when counting the most anterior dorsal-fin elements (Gibbs and Collette, 1959), however, because anterior dorsal rays are short and develop late (Potthoff, 1980). Myomeres are difficult to count without clearing and staining larvae because dolphinfish are heavily pigmented.

Early larval development of common dolphin and pompano dolphin from the Gulf is similar to that in the western Pacific Ocean (Aoki and Ueyanagi, 1989). Developmental milestones (e.g. initial formation of dorsal- and anal-fin bases, yolk-sac absorption, and lateral body banding) occur at similar sizes in common dolphin from both the Gulf and western Pacific Ocean. We found yolk-sac absorption in common dolphin complete by about 3.7 mm, as did Aoki and Ueyanagi (1989). Off Japan, however, common dolphin do not complete yolk-sac absorption until about 6 mm TL (Okiyama, 1988). Aoki and Ueyanagi (1989) did not discuss either maxillary or posttemporal spines or the epithelial spicules noted during this study.

Morphometrics are generally greater in pompano dolphin than in common dolphin from the gulf by early postflexion (Table 1). Differences in mean morphometric ratios (expressed as % SL) between species from the Pacific Ocean are significant (Student's *t*-test, α=0.05) for larvae 5–10 mm; relative growth of all body parts measured (except preanal length) were greater in pompano dolphin than in common dolphin (Aoki and Ueyanagi, 1989).

Distribution of dolphinfish larvae (Table 2, Fig. 3), juveniles, and adults is apparently limited by the 20°C isotherm (Gibbs and Collette, 1959). We found larval dolphinfish of both species primarily at temperatures ≥24°C and salinities ≥33 ppt, as did Fahay (1975), Powles (1981), and Aoki and Ueyanagi (1989). On the basis of water temperatures between 25 and 30°C (those when common dolphin larvae primarily occur), we estimate a common dolphin egg would hatch between 26 and 38 hours. Incubation time at 25°C predicted for common dolphin eggs from the Gulf was similar to that of Hagood and Rothwell[1] at 26°C, but less than incubation times predicted by other studies (Table 3).

Location of dolphinfish spawning is poorly documented. We believe that spawning occurs in oceanic waters based on the collection of preflexion larvae of both species at stations primarily beyond the continental shelf (Appendix Fig. 3). In addition, >80% of larvae of each species (Fig. 3) and 85% of stations where larvae occurred were over or beyond the outer continental shelf (Appendix Fig. 2). These findings support information from along the Atlantic coast of the southeastern U. S. that dolphinfish larvae are most abundant near or beyond the 180 m depth contour (Powles, 1981). In the Gulf, larvae of both common and pompano dolphin were collected over a similar median (Table 2), mean, and range of station depths (mean: 815 m for common dolphin and 782 m for pompano dolphin based on our weighted method of calculating these statistics). This similarity between species in distribution of larvae is reinforced by the average depth of stations where larvae were captured. Average station depth of capture was 1198 m for common dolphin (n=216 stations) and 1042 m for pompano dolphin (n=64 stations).

Other studies suggest that common dolphin in the tropical Atlantic (Gibbs and Collette, 1959) and Pacific (Aoki and Ueyanagi, 1989) spawn closer to shore than do pompano dolphin. In the Pacific, mid-oceanic occurrences of common dolphin larvae are limited to waters near islands (Aoki and Ueyanagi, 1989).

Overall, larval common dolphin are significantly more abundant than pompano dolphin in the northern Gulf (Table 4; Appendix Fig. 2) and along the southeastern United States (Fahay, 1975; Powles, 1981). Larvae of both common dolphin and pompano dolphin were particularly abundant around the Mississippi River delta. Higher larval dolphinfish abundances near the delta may reflect the generally higher abundance of fish larvae in the delta area (Ditty, 1986; Govoni et al., 1989; Grimes and Finucane, 1991) as compared to the open Gulf (Richards et al., 1989), or may reflect greater intensity of neuston sampling near the delta rather than the actual distribution of spawning adults. In the Pacific and Indian Oceans, larval pompano dolphin are more abundant than common dolphin (Shcherbachev, 1973; Aoki and Ueyanagi, 1989).

Dolphinfish may spawn year-round in the Gulf, at least in the southern part of the study area where seasonal water temperatures remain above about 24°C. Estimated spawning dates based on collection of preflexion common dolphin support spawning in the northern Gulf from at least April to December (Fig. 4). Peak spawning of common dolphin occurs during spring and early fall based on higher catches of larvae during these seasons, although differences among seasons are not significant. Along the Atlantic coast, eggs have been collected during July and August in the Gulf Stream (Hassler and Rainville, 1975) and larvae and early juveniles year-round along the southeastern United States (Fahay, 1975; Powles and Stender, 1976) and tropical Atlantic (Gibbs and Collette, 1959). Ripe female common dolphin occur in the Gulf Stream off Cape Hatteras (North Carolina) from at least May through July (Schuck, 1951; Rose, 1966), and in the Florida Current from November to July (March spawning peak, Beardsley, 1967). Pompano dolphin spawn in the Gulf from spring through at least early fall (Fig. 4; Gibbs and Collette, 1959). If larval pompano dolphin growth rates are similar to those for common dolphin (about 1 mm/day, Hassler and Rainville, 1975; Uchiyama et al., 1986), the two mid-October collected pompano dolphin larvae (18.3 and 22.5 mm) were spawned during late September. Pompano dolphin spawn year-round in tropical mid-Atlantic and South Atlantic Bight waters based on collection of larvae and juvenile length-frequency data (Potthoff, 1971; Fahay, 1975).

We found no significant diel differences in catch of larvae for either species as did Fahay (1975). Eldridge et al. (1977), however, found both common dolphin and pompano dolphin significantly more abundant at night, and that catch of larval common dolphin increased with concentration of *Sargassum*. Larval common dolphin <10 mm are more common in subsurface (i.e. depths of 20–30 m) than in surface tows during both day and night (Aoki and Ueyanagi, 1989). Larval pompano dolphin <10 mm are more frequently collected in subsurface tows during the day only; larvae >10 mm are more common near the surface during the night (Aoki and Ueyanagi, 1989).

New information on the larval morphology of pompano dolphin from this study corroborates Johnson's (1984) hypothesis of a relationship between Coryphaenidae and Rachycentridae rather than that previously hypothesized between Rachycentridae and Echeneididae. Larvae of dolphinfishes and cobia share similar patterns of head spination: laterally swollen pterotics; a single, simple spine on the supraorbital ridge of each frontal bone (except in *C. equiselis* which may have multiple spines along the ridge); a small posttemporal spine; and both dolphinfish and cobia have 3 or 4 spines along the inner shelf and 4 or 5 spines along the outer shelf of the preopercle with the largest spines on either side of the preopercular angle (Johnson, 1984; Ditty and Shaw, 1992; this study). Dolphinfishes have a small maxillary spine that cobia lack (Ditty and Shaw, 1992; this study), but no spine on the supracleithrum found in cobia (Dawson, 1971; Ditty and Shaw, 1992; this study). *Echeneis* lack head spines. Larval dolphinfishes and cobia also lack large hooked teeth anteriorly on the dentary found in *Echeneis* (Johnson, 1984; Leis and Trnski, 1989). Dolphinfishes differ from cobia by lacking dorsal and anal spines and by having more vertebrae (30–34 in dolphinfishes versus 25 in cobia). Dolphinfishes also have 50+ soft dorsal rays, whereas cobia have 27–33 (Ditty and Shaw, 1992).

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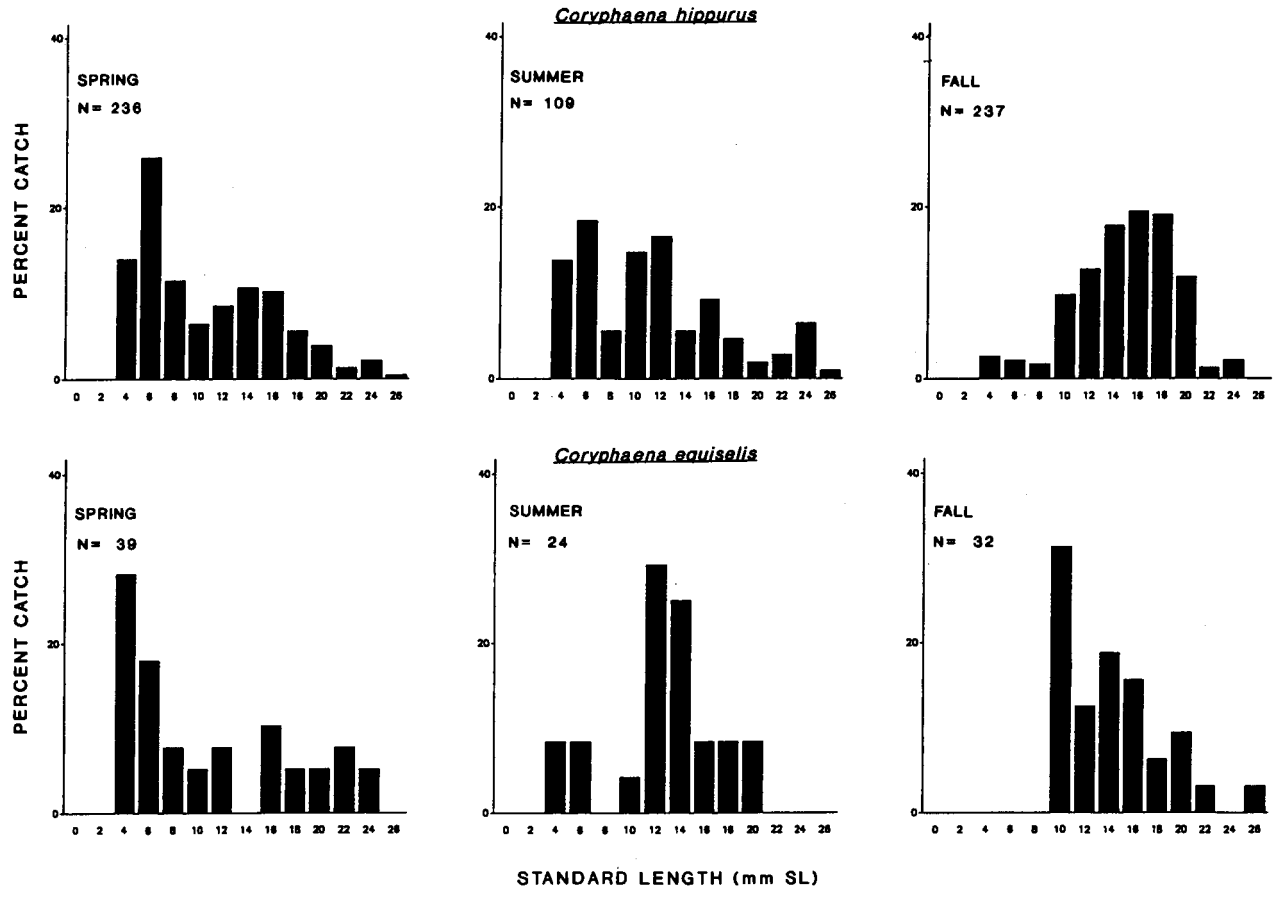


Figure 4

Length-frequency distribution of larval common dolphin (*Coryphaena hippurus*) and pompano dolphin (*C. equiselis*) in the northern Gulf of Mexico by season. Catches are from both bongo and neuston net tows; seasons are combined across years. Spring: March–May, Summer: June–August, Fall: September–November. Length categories are combined by 2-mm intervals; ≥0.5–mm increments are rounded to the nearest whole number. N = number of larvae.

copy of the English translation of Aoki and Ueyanagi (1989). We also thank Cathy Grouchy for illustrating the larvae.

Literature cited

Aoki, M., and S. Ueyanagi.
1989. Larval morphology and distribution of the dolphin-fishes, *Coryphaena hippurus* and *C. equiselis* (Coryphaenidae). Tokai Univ. Proc., Oceanogr. Sec., No. 28, p. 157–174. [In Japanese.]

Beardsley, G. L.
1967. Age, growth, and reproduction of the dolphin, *Coryphaena hippurus*, in the straits of Florida. Copeia 1967:441–451.

Berry, F. H., and W. J. Richards.
1973. Characters useful to the study of larval fishes. Mid. Atl. Coast. Fish. Cent. Tech. Pap. 1:48–65.

Briggs, J. C.
1960. Fishes of worldwide (circumtropical) distribution. Copeia 1960(3):171–180.

Collette, B. B., R. H. Gibbs, and G. E. Clipper.
1969. Vertebral numbers and identification of the two species of dolphin (*Coryphaena*). Copeia 1969(3):630–631.

Dawson, C. E.
1971. Occurrence and description of prejuvenile and early juvenile Gulf of Mexico cobia, *Rachycentron canadum*. Copeia (1):65–71.

Ditty, J. G.
1986. Ichthyoplankton in neritic waters of the northern Gulf of Mexico off Louisiana: composition, relative abundance, and seasonality. Fish. Bull. 84: 935–946.

Ditty, J. G., and R. F. Shaw.
1992. Larval development, distribution, and ecology of cobia, *Rachycentron canadum* (Family:

Rachycentridae), in the northern Gulf of Mexico. Fish. Bull. 90:668–677.

Eldridge, P. J., F. H. Berry, and M. C. Miller III.
1977. Test results of the Boothbay neuston net related to net length, diurnal period, and other variables. S. Car. Mar. Resour. Cent. Tech. Rep. No. 18, 22 p.

Fahay, M. P.
1975. An annotated list of larval and juvenile fishes captured with surface-towed meter net in the South Atlantic Bight during four RV *Dolphin* cruises between May 1967 and February 1968. NOAA Tech. Rep., NMFS SSRF-685, 39 p.

Gibbs, R. H., Jr., and B. B. Collette.
1959. On the identification, distribution, and biology of the dolphins, *Coryphaena hippurus* and *C. equiselis*. Bull. Mar. Sci. 9(2):117–152.

Govoni, J. J., D. E. Hoss, and D. R. Colby.
1989. The spatial distribution of larval fishes about the Mississippi River plume. Limnol. Oceanogr. 34(1):178–187.

Grimes, C. B., and J. H. Finucane.
1991. Spatial distribution and abundance of larval and juvenile fish, chlorophyll and macrozooplankton around the Mississippi River discharge plume, and the role of the plume in fish recruitment. Mar. Ecol. Prog. Ser. 75:109–119.

Hassler, W. W., and R. P. Rainville.
1975. Techniques for hatching and rearing dolphin, *Coryphaena hippurus*, through larval and juvenile stages. Univ. N. Carolina Sea Grant Prog., UNC-SG-75–31, 17 p.

Hubbs, C. L., and K. F. Lagler.
1958. The fishes of the Great Lakes region. Univ. Mich. Press, Ann Arbor, 213 p.

Johnson, G. D.
1984. Percoidei: development and relationships, p. 464–498. *In* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall Jr., and S. L. Richardson (eds.), Ontogeny and systematics of fishes, p. 464–498. Am. Soc. Ichthy. Herp., Spec. Publ. No. 1.

Kelley, S., T. Potthoff, W. J. Richards, L. Ejsymont, and J. V. Gartner.
1986. SEAMAP 1983—Ichthyoplankton. Larval distribution and abundance of Engraulidae, Carangidae, Clupeidae, Lutjanidae, Serranidae, Sciaenidae, Coryphaenidae, Istiophoridae, Xiphiidae, and Scombridae in the Gulf of Mexico. NOAA Tech. Mem., NMFS-SEFC-167, no pagination.

Lamadrid-Rose, Y., and G. W. Boehlert.
1988. Effects of cold shock on egg, larval, and juvenile stages of tropical fishes: potential impacts of ocean thermal energy conversion. Mar. Environ. Res. 25:175–193.

Leis, J. M., and T. Trnski.
1989. The larvae of Indo-Pacific shorefishes. Univ. Hawaii Press, Honolulu, 371 p.

Mito, S.
1960. Egg development and hatched larvae of the common dolphin-fish *Coryphaena hippurus* Linne. Bull. Jap. Soc. Sci. Fish. 26:223–226.

Okiyama, M.
1988. An atlas of the early stage fishes in Japan. Tokai Univ. Press, Tokyo, p. 481–483.

Palko, B. J., G. L. Beardsley, and W. J. Richards.
1982. Synopsis of the biological data on dolphinfishes, *Coryphaena hippurus* Linnaeus and *Coryphaena equiselis* Linnaeus. NOAA Tech. Rep., NMFS Circ. 443, 28 p.

Pauly, D., and R. S. V. Pullin.
1988. Hatching time in spherical, pelagic, marine fish eggs in response to temperature and egg size. Environ. Biol. Fish. 22(4):261–271.

Potthoff, T.
1971. Observations on two species of dolphin (*Coryphaena*) from the tropical mid-Atlantic. Fish. Bull. 69:877–879.

1980. Development and structure of fins and fin supports in dolphin fishes *Coryphaena hippurus* and *Coryphaena equiselis* (Coryphaenidae). Fish. Bull. 78:277–312.

Powles, H.
1981. Distribution and movements of neustonic young of estuarine dependent (*Mugil* spp., *Pomatomus saltatrix*) and estuarine independent (*Coryphaena* spp.) fishes off the southeastern United States. Rapp. P.-v. Reun. Cons. int. Explor. Mer 178:207–209.

Powles, H., and B. W. Stender.
1976. Observations on composition, seasonality and distribution of ichthyoplankton from MARMAP cruises in the South Atlantic Bight in 1973. South Car. Mar. Res. Cent. Tech. Rep. Ser. No. 11, 47 p.

Richardson, S. L., and W. A. Laroche.
1979. Development and occurrence of larvae and juveniles of the rockfishes *Sebastes crameri*, *Sebastes pinniger*, and *Sebastes helvomaculatus* (Family Scorpaenidae) off Oregon. Fish. Bull. 77:1–46.

Richards, W. J., T. Potthoff, S. Kelley, M. F. McGowan, L. Ejsymont, J. H. Power, and R. M. Olvera L.
1984. SEAMAP 1982—Ichthyoplankton. Larval distribution and abundance of Engraulidae, Carangidae, Clupeidae, Lutjanidae, Serranidae, Coryphaenidae, Istiophoridae, Xiphiidae, and Scombridae in the Gulf of Mexico. NOAA Tech. Mem., NMFS-SEFC-144, no pagination.

Richards, W. J., T. Leming, M. F. McGowan, J. T. Lamkin, and S. Kelley-Fraga.
1989. Distribution of fish larvae in relation to hydrographic features of the Loop Current boundary in the Gulf of Mexico. Rapp. P. v. Reun. Cons. int. Explor. Mer 191:161–176.

Rose, C. D.
1966. The biology and catch distribution of the dolphin *Coryphaena hippurus* (Linnaeus) in North Carolina waters. Ph.D. diss., N. Carolina State Univ., Raleigh, 153 p.

Sanders, N., Jr., T. Van Devender, and P. A. Thompson.
1990. SEAMAP environmental and biological atlas of the Gulf of Mexico, 1986. Gulf States Marine Fish. Comm., Ocean Springs, MS, No. 20, 328 p.

SAS Institute, Inc.
1985. SAS User's Guide: Statistics, 1985 ed. SAS Institute, Cary, NC, 584 p.

Schuck, H. A.
1951. Notes on the dolphin (*Coryphaena hippurus*) in North Carolina waters. Copeia 1951(1): 35–39.

Shcherbachev, Y. N.
1973. The biology and distribution of the dolphins (Pisces, Coryphaenidae). J. Ichthyol. 13:182–191.

Soichi, M.
1978. Spawning behavior of the dolphin, *Coryphaena hippurus*, in the aquarium and its eggs and larvae. Jap. J. Ichthyol. 24:290–294. [In Jap., Engl. summ.]

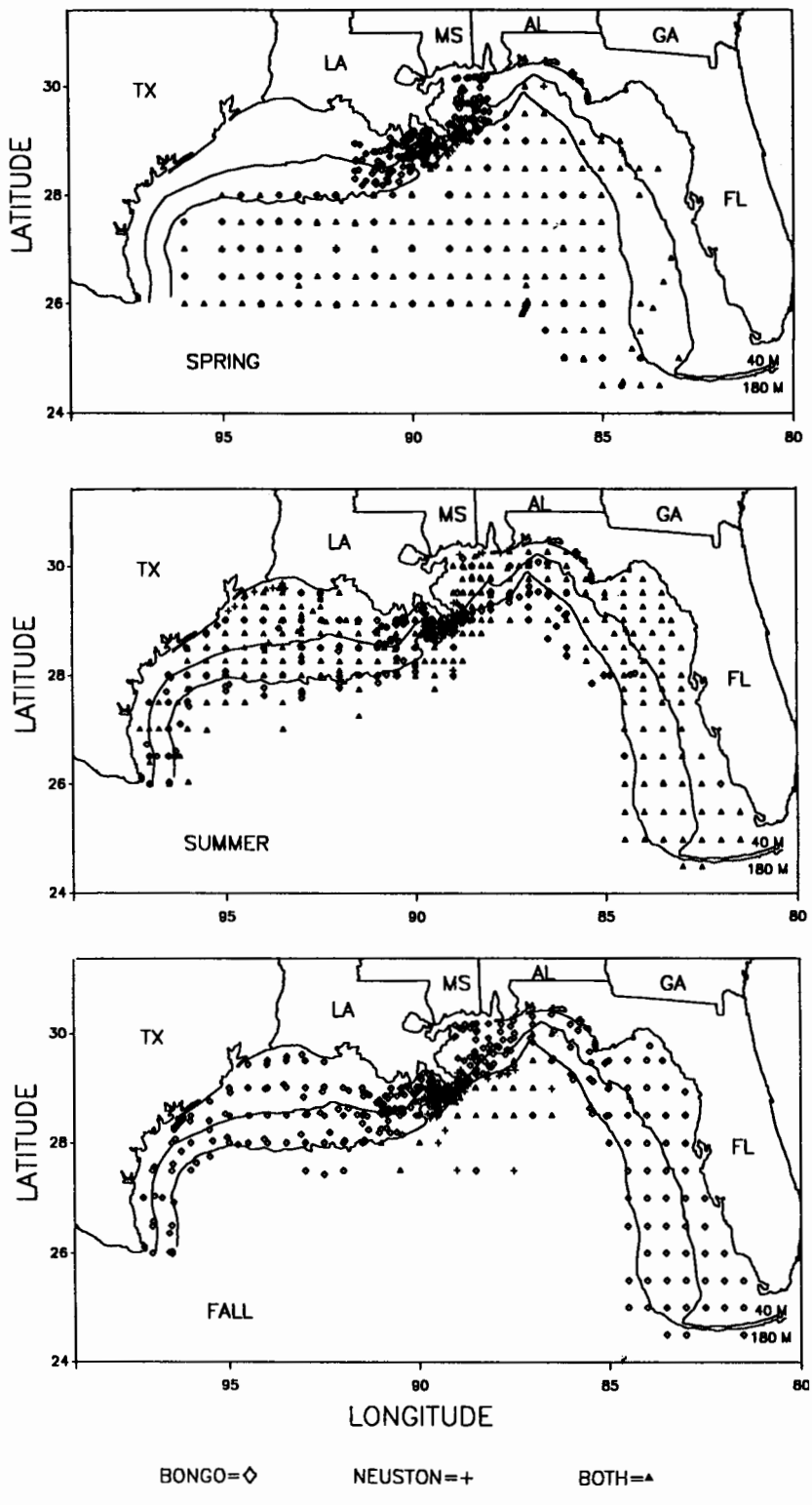
Stuntz, W. E., C. E. Bryan, K. Savastano, R. S. Waller, and P. A. Thompson.
1985. SEAMAP environmental and biological atlas of the Gulf of Mexico, 1982. Gulf States Marine Fish. Comm., Ocean Springs, MS, No. 12, 145 p.

Thompson, P. A., and N. Bane.
1986a. SEAMAP environmental and biological atlas of the Gulf of Mexico, 1983. Gulf States Marine Fish. Comm., Ocean Springs, MS, No. 13, 179 p.
1986b. SEAMAP environmental and biological atlas of the Gulf of Mexico, 1984. Gulf States Marine Fish. Comm., Ocean Springs, MS, No. 15, 171 p.

Thompson, P. A., T. Van Devender, and N. J. Sanders Jr.
1988. SEAMAP environmental and biological atlas of the Gulf of Mexico, 1985. Gulf States Marine Fish. Comm., Ocean Springs, MS, No. 17, 338 p.

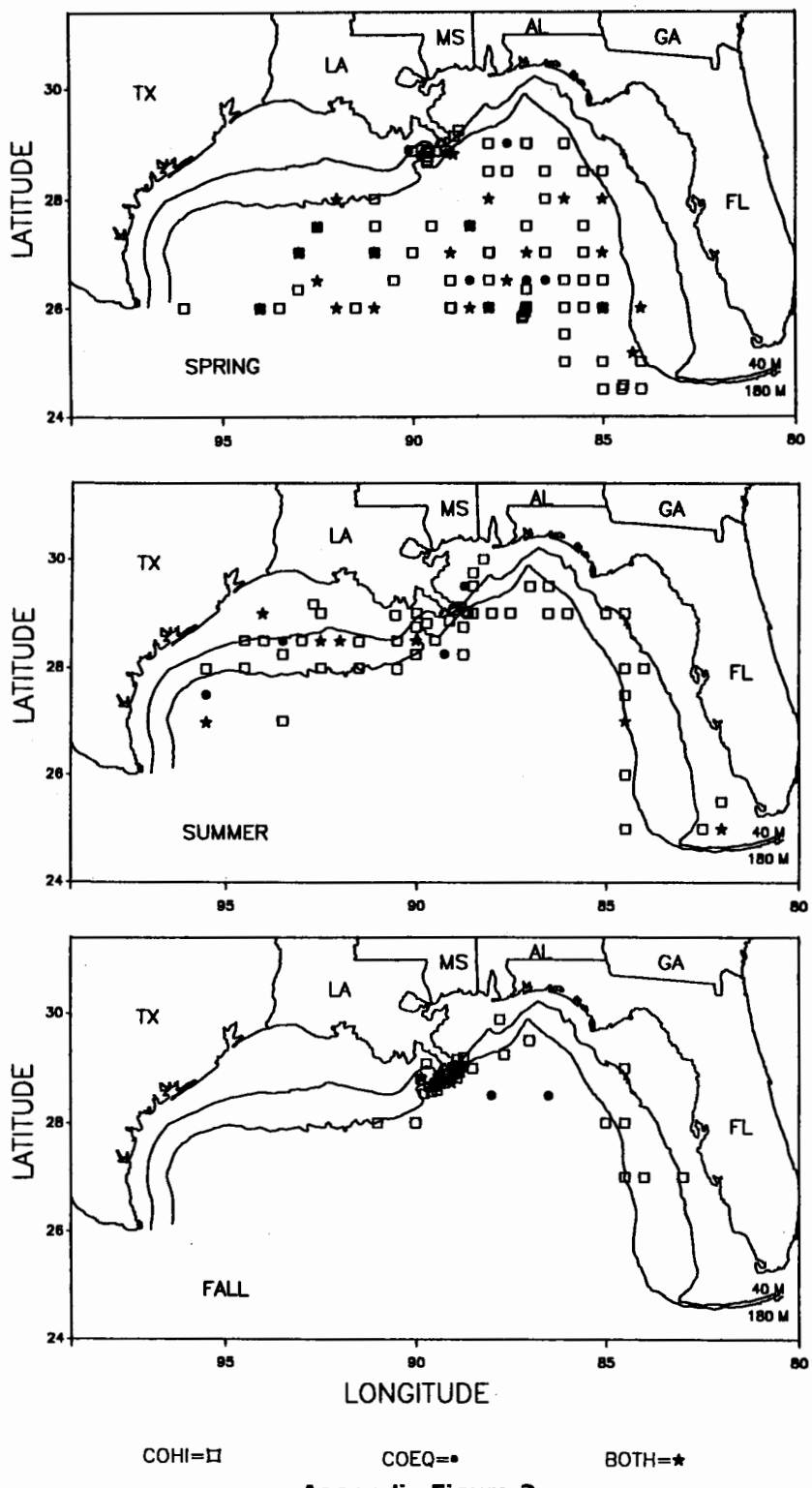
Uchiyama, J. H., R. K. Burch, and S. A. Kraul Jr.
1986. Growth of dolphins, *Coryphaena hippurus* and *C. equiselis*, in Hawaiian waters as determined by daily increment on otoliths. Fish. Bull. 84:186–191.

Zar, J. H.
1984. Biostatistical analysis. Second ed., Prentice-Hall, Inc., NJ, 718 p.



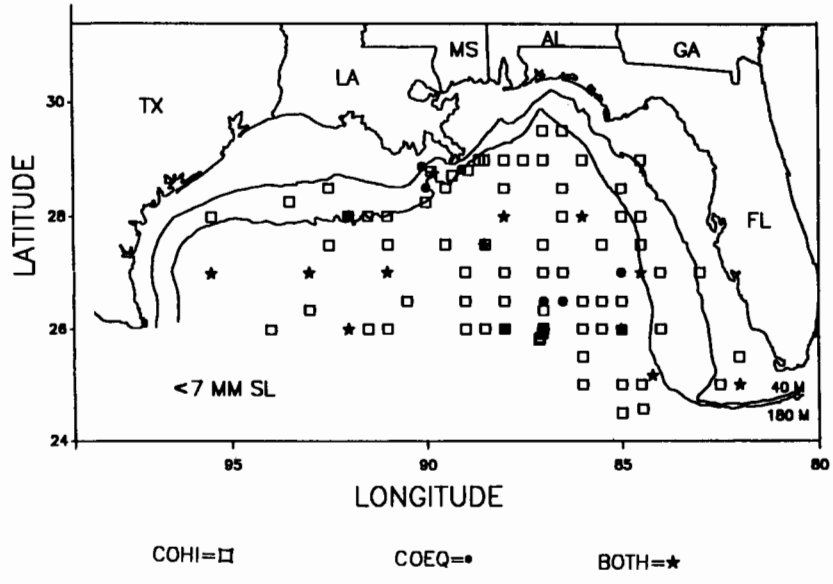
Appendix Figure 1

Distribution of sampling by season for the northern Gulf of Mexico. Seasons are combined across years. Spring (March-May), summer (June-August), fall (September–November).



Appendix Figure 2

Distribution of common dolphin (*Coryphaena hippurus*) and pompano dolphin (*C. equiselis*) larvae in the northern Gulf of Mexico by season. Seasons are combined across years. Catches are from both bongo and neuston net tows. Spring (March–May), summer (June–August), fall (September–November).



Appendix Figure 3

Distribution of early larval (<7.0 mm) common dolphin (*Coryphaena hippurus* [COHI]) and pompano dolphin (*C. equiselis* [COEQ]) in the northern Gulf of Mexico. Both bongo and neuston net tows are used in determining early larval distribution. Data are combined across seasons and years.