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A Time Series of Observations on Red Snapper Larvae from SEAMAP Surveys, 1982–2003: Seasonal Occurrence, Distribution, Abundance, and Size

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Abstract.—Eleven taxa of snappers were found among the 20,301 snapper larvae examined from over 14,000 bongo and neuston samples collected during SEAMAP surveys, 1982 to 2003. During that time series, a total of 639 red snapper *Lutjanus campechanus* larvae were identified in bongo samples and 1053 larvae in neuston samples. Red snapper larvae first appeared in May and were present as late as November. Months of highest occurrence and abundance were July and September when larvae were taken in 12.7% and 11.0% of bongo samples, and in 7.6% and 8.4% of neuston samples. Mean abundance in those months was 1.18 and 0.82 larvae under 10 m^2 of sea surface for bongo samples and 0.36 larvae per 10 min for neuston samples. By November, percent occurrence was less than or equal to 0.2% and mean abundance was less than 0.01 larvae in samples from either gear. Larvae identifiable as red snapper ranged in body length from 2.4 to 19.2 mm (mean = 5.12, median = 4.60) in bongo net samples; and 2.7–24.0 mm (mean = 4.37, median = 4.00) in neuston net samples. Over 95% of larvae in bongo samples were less than or equal to 8.3 mm and in neuston samples were less than or equal to 5.6 mm. Larvae were captured throughout the survey area but were consistently observed in greatest abundance at stations on the mid-continental shelf west of the Mississippi River, especially off western Louisiana and central Texas. This time series of observations is the data set from which annual estimates of larval red snapper abundance were derived for use as a fishery independent index of adult stock size.

Introduction

The Southeast Area Monitoring and Assessment Program (SEAMAP) has supported collection and analysis of ichthyoplankton samples from resource surveys in the Gulf of Mexico (GOM) since 1982 with the goal of producing a long-term database on the early life stages of fishes. Specimens from these collections have been used to describe the larval development of a wide variety of fishes in the western central North Atlantic (Ditty and Shaw 1992, 1993; Ditty et al. 1994; Drass et al. 2000; Richards 2005). Spawning seasonality of Gulf fishes have been inferred from SEAMAP data (Ditty et al. 1988), as well as, the potential 'sources

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and sinks' of recruits to reefs in the northern GOM (Hanisko and Lyczkowski-Shultz 2003). Estimates of abundance of fish eggs and larvae from SEAMAP surveys are being used to assess the impact to Gulf fisheries of entrainment mortality at proposed liquefied natural gas terminals using open rack vaporizers (*www.uscg.mil/hq/g-m/mso/mso5.htm*). Annual indices of larval abundance from SEAMAP surveys are being used in stock assessments of Atlantic bluefin tuna, *Thunnus thynnus* (Scott et al. 1993) and Gulf king mackerel, *Scomberomorus cavalla* (Gledhill and Lyczkowski-Shultz 2000).

Larval indices based on the SEAMAP time series of ichthyoplankton data were examined at recent Southeast Data, Assessment and Review Workshops (SEDAR7 Stock Assessment Report 2004; SEDAR9 Stock Assessment Report 2005; available at *www.sefsc.noaa.gov/sedar/*) for use in stock assessments of red snapper *Lutjanus campechanus*, vermilion snapper *Rhomboplites aurorubens* and gray triggerfish *Balistes capriscus*. A summary of seasonal occurrence, abundance, distribution and size of red snapper larvae collected during twenty-two years of SEAMAP surveys in the GOM is presented in this paper. These are the data from which annual estimates of larval red snapper abundance were derived for use as a fishery independent index of adult stock size (Hanisko et al. 2007, this volume).

Methods and Materials

Surveys and Collections:

SEAMAP resource surveys have been conducted by the National Marine Fisheries Service since 1982 in cooperation with the states of Florida, Alabama, Mississippi, and Louisiana. Plankton sampling is conducted during these surveys at predetermined SEAMAP stations arranged in a fixed, systematic grid across the U.S. Exclusive Economic Zone of the GOM (Figure 1A). Most but not all SEAMAP stations (designated by a unique SEAMAP or 'b' number) are located at ~56 km or ½ degree intervals along this grid. Some SEAMAP stations are located at under 56 km intervals especially along the continental shelf edge, while others have been moved to avoid obstructions, navigational hazards or shallow water. Most SEAMAP plankton samples are taken during both dedicated plankton and shrimp/bottomfish (trawl) surveys but over the years additional samples have been taken using SEAMAP gear and collection methods at locations other than designated SEAMAP stations or outside established SEAMAP surveys, e.g. during Louisiana seasonal trawl surveys, SEAMAP Squid/Butterfish survey, and other serendipitous or special projects.

Although other plankton sampling gear types and mesh sizes have been used over the SEAMAP time series, the gear and methodology considered as standard for SEAMAP surveys are those described in Kramer et al. (1972), Smith and Richardson (1977) and Posgay and Marak (1980). A 61 cm (outside diameter) bongo frame fitted with 0.333 (0.335)† mm mesh netting is fished in a double-oblique tow path from a maximum depth of 200 m or 2–5 m off the bottom at depths less than 200 m. It is assumed that the net does not fish or fishes very little during descent to maximum tow depth because towing cable payout is rapid (~40–50 m/min) while cable retrieval rate is slow (~20 m/min). A mechanical flowmeter is mounted off-center in the mouth of each bongo net to record the volume of water filtered. Volume filtered ranges from ~20–600 m^3 but is typically 30–40 m^3 at the shallowest stations and 300–400 m^3 at the deepest stations. A single or double 2x1 m pipe frame neuston net fitted with 0.947 (0.950)† mm mesh netting is towed at the surface with the frame half-sub-

†Mesh size change in database does not represent an actual change in gear but only a change in the accuracy at which plankton mesh aperture size can be measured by the manufacturer.

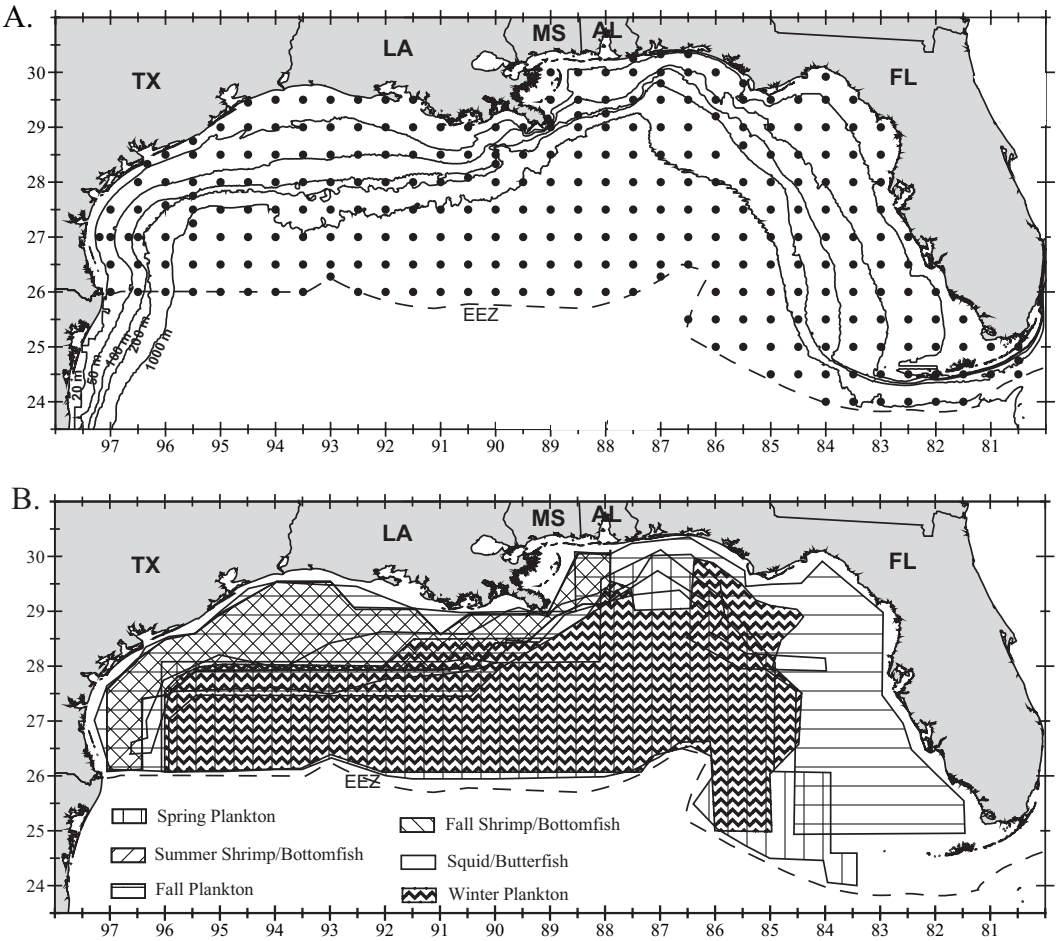

Figure 1. A. Location of SEAMAP stations arranged in a fixed, systematic grid across the Gulf of Mexico. Most but not all stations are located at ~56 km or ½ degree intervals along the grid. B. Generalized areas of the Gulf of Mexico where plankton sampling was conducted during SEAMAP resource surveys.

merged for 10 min. Samples are taken upon arrival on station regardless of time of day. At each station, either a bongo and/or neuston tow are made depending on the specific survey. Samples are routinely preserved in 5–10% formalin and later transferred after 48 h to 95% ethanol for long term storage. During some surveys selected samples are preserved initially in 95% ethanol and within 24–36 h transferred to fresh ethanol.

Catches of larvae from bongo nets are standardized to account for volume filtered and depth of the sampled water column and expressed as number of larvae under 10 m^2 of sea surface. This is accomplished by dividing the number of larvae of each taxon caught in a sample by the volume of water filtered during the tow; and then multiplying the resultant by the maximum depth of the tow in meters and the factor 10. Catches of larvae from neuston nets are standardized to account for net tow duration and expressed as number of larvae per 10 min tow. During SEAMAP surveys, environmental parameters including temperature, salinity, dissolved oxygen and optical transmission are measured in situ with a SEA-

Table 1. Temporal and spatial coverage of SEAMAP plankton sampling effort during resource surveys in the U.S. Gulf of Mexico, 1982 to 2003. Months in bold account for > 70% of samples taken during the survey. *BN* = bongo net; *NN* = neuston net.

Survey type Number of BN/NN samples	Months	Primary survey area	Time period	% Total BN/NN samples
Winter plankton 332 / 289	**Dec** Jan, Feb	Coastal LA; Shelf edge to U.S. EEZ	1982–1997; 1983 & 1984, 1993 & 1996	4.7 / 3.6
Spring plankton 2196 / 3209	Mar, **Apr**, **May,** Jun	Coastal LA; Shelf edge to U.S. EEZ	1982–1995; 1982 to present	31.1 / 40.3
Summer trawl 1052 / 977	**Jun**, **Jul**	5 to 50 fm, south TX to Mobile Bay	1982 to present	14.9 / 12.3
Squid/butterfish 88 / 85	May, **Aug**	Shelf edge northern Gulf	Aug 1985, May 1986	1.2 / 1.1
Fall plankton 2273 / 2413	Aug, **Sep,** Oct	Coastal & shelf waters, south TX to south FL	1986 to present	32.2 / 30.3
Fall trawl 867 / 762	**Oct**, **Nov,** Dec	5 to 50 fm, south Texas to Mobile Bay	1982 to present	12.3 / 9.6
Other 253 / 221	**Mar**, Apr−Nov	West of Mississippi River off LA	Mostly pre-1986	3.6 / 2.8

BIRD SBE 25 or SBE 911, conductivity temperature depth (CTD) profiler at each station. Although complete CTD profiles of the water column are recorded at sea, only observations from three depth levels; surface, mid and max (near bottom at depths <200 m) were entered in the SEAMAP database. Environmental data from stations where red snapper larvae were captured during SEAMAP surveys in 2000 through 2003 are presented. Dissolved oxygen data were summarized only for surveys in 2001 to 2003 because the oxygen sensor used during the 2000 field season was defective.

Assignment of samples to either day, night or twilight periods for diel comparisons of larval abundance and size followed Seidelmann (1992) and were based on sample date, time and location (coordinates). Nautical twilight, not civil twilight (*www.weather.gov/glossary*) was used as the reference datum for determining which samples had been taken during the transitional period between night and day.

This review of the early life history of red snapper in the GOM is based on over 7,000 bongo and 7,900 neuston collections from SEAMAP plankton sampling during the period 1982 to 2003. The original intent of SEAMAP was to sample both the open (shelf edge to U.S. Exclusive Economic Zone or EEZ) and continental shelf (10–200 m) portions of the Gulf in their entirety at least once during each season. This goal was never achieved and thus the preponderance of SEAMAP plankton samples have been collected during only four annual resource surveys; three in shelf and coastal waters and one in deep Gulf waters (Table 1; Figure 1B).

Two dedicated plankton surveys account for 60–70% of all SEAMAP plankton samples (bongo and neuston combined). The

Spring Plankton survey has been conducted in U.S. EEZ open Gulf waters primarily in April and May since 1982, although in several years during the time series sampling was conducted on the west Florida shelf. The second dedicated plankton survey is the Fall Plankton survey. It has been conducted in coastal and continental shelf waters from south Texas to south Florida as a Gulfwide survey during late August to mid October since 1986. Starting in 1999 the area covered by the Fall Plankton survey was expanded to include stations beyond the continental shelf in the western Gulf. Sampling conducted during a plankton survey of coastal and continental shelf waters of the U.S. GOM during the month of August in 1984 is not considered to be part of the annual SEAMAP Fall Plankton survey. Samples taken during the SEAMAP Summer (mid June through July) and Fall (mid October through November) Shrimp/Bottomfish (trawl) surveys each make up 10–15% of all SEAMAP plankton samples. The area covered by these two surveys includes coastal and continental shelf waters west of 88°W longitude; although during the period 1982–1988, sampling was also irregularly conducted off northwest and western Florida.

Sampling in winter months accounts for less than 5% of all SEAMAP plankton samples. There have been only four winter plankton surveys (1983, 1984, 1993 and 1996) all in open Gulf waters. The exception being the Louisiana seasonal trawl survey of state waters that was conducted typically in December, from 1982 to 1997. Approximately 1% of all SEAMAP plankton samples were taken during a special SEAMAP Squid/Butterfish trawl survey of shelf edge waters in the northern Gulf in August 1985 and May 1986. Additional SEAMAP plankton samples (~3%) were taken prior to 1986 and mostly in the northern Gulf west of the Mississippi River.

Complete descriptions of survey methodologies, data collection and sampling effort by year and survey type can be found in the SEAMAP Environmental and Biological Atlases of the Gulf of Mexico, 1982 to 2001 published by Gulf States Marine Fisheries Commission, Ocean Springs, MS (available at *www.gsmfc.org*).

Sample Processing and Identification of Snapper Larvae:

Plankton samples were sorted for fish eggs and larvae and initial identifications and measurements of larvae were made at the Sea Fisheries Institute, Plankton Sorting and Identification Center (ZSIOP), in Gdynia and Szczecin, Poland. Plankton samples, collected by the Louisiana Department of Wildlife and Fisheries during the period 1989–2002, were processed by Louisiana state biologists. Vials of eggs and identified larvae, plankton displacement volumes, total egg counts; and counts and measurements of identified larvae were sent to the SEAMAP Archive at the Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, St. Petersburg, Florida. These data were entered into the SEAMAP database at the SEAMAP Archive where specimens are curated and loaned to researchers upon request. Data files containing specimen identifications and lengths were sent to the NMFS Mississippi Laboratories where these data were combined with field collection data, edited and maintained in the SEAMAP database. Data are available on request from the SEAMAP Data Manager at the Mississippi Laboratories.

Body length (BL) as defined by Leis and Rennis (1983) was measured to the nearest 0.1 mm with an ocular micrometer fitted to a dissecting microscope. Body length is equivalent to notochord length or standard length depending on the stage of development (Richards 2005). The standard measurement in preflexion and flexion stage larvae is notochord length, i.e. the straight line distance

from the tip of the snout to the posterior tip of the notochord. The standard measurement in postflexion larvae is standard length, i.e. the distance from the tip of the snout along the body midline to a vertical line through the posterior edge of the hypural plate.

In order to assure consistent identifications over the SEAMAP time series, all snapper larvae were examined and identified by ichthyoplankton specialists at the Southeast Fisheries Science Center, Mississippi Laboratories using an identification protocol based on descriptions in Drass et al. (2000) and Lindeman et al. (2005). The level of identification achievable under this protocol depended on the extent of first dorsal fin development, as well as the following morphological traits: presence or absence of melanistic pigment on the throat (sternohyoideus muscle), and on the anterior surface of the visceral mass or gut; and whether preopercular spines or dorsal spines were smooth or serrated (Table 2). Specimens were identified as red snapper only when a minimum of five dorsal spines were present, those spines were smooth, not serrated and melanistic pigmentation on the body and fins matched the description and illustrations of reared and wild caught red snapper larvae in Rabalais et al. (1980), Collins et al. (1980), and Drass et al. (2000).

Red snapper are among six of the twelve snapper species of the subfamily Lutjaninae found in the GOM whose larvae have been described. Despite these descriptions snapper larvae can be distinguished from each other only after dorsal and pelvic spines have begun to develop using a combination of morphological characters (Lindeman et al. 2005). Red snapper larvae prior to dorsal and pelvic spine formation are generally under 3.5 mm BL and cannot be confidently identified in field collections because of the lack of estab-

Table 2. Key morphological characters used to identify snapper larvae in SEAMAP collections (Lindeman et al. 2005). Melanistic pigmentation on the body and fins of specimens identified as *L. campechanus* matched the description and illustrations of reared red snapper larvae in Drass et al. (2000). shs = sternohyoideus muscle; avm = anterior visceral mass.

Dorsal fin development	Pigment on: throat (shs) and/or gut (avm)	Preopercular spines	Dorsal spines	Identification
little or none	none	smooth		Lutjanidae
little or none	shs	smooth or serrated		*R. aurorubens*
little or none	avm	smooth		*Lutjanus* spp.
2 – 4 spines	none	smooth	smooth	Lutjanidae
2 – 4 spines	shs	serrated	smooth	*R. aurorubens*
2 – 4 spines	avm	smooth	smooth	*Lutjanus* spp.
5 spines	avm	smooth	smooth	*L. campechanus*
≥ 5 spines	shs + avm	serrated	serrated	*R. aurorubens*
≥ 5 spines	avm + shs	smooth	smooth	*L. campechanus*
≥ 5 spines	avm + shs	smooth	serrated	*Lutjanus* spp.

Table 3. Snapper larvae identified to the lowest taxon in SEAMAP ichthyoplankton samples from the Gulf of Mexico, 1982–2003.

Taxon	Number of specimens	% of total
Etelinae	7	<1
Etelis oculatus	10	<1
Lutjanidae	8,516	42
Lutjanus spp.	2,678	13
L. analis	6	<1
L. apodus	1	<1
L. campechanus	1692	8
L. griseus	250	1
L. synagris	173	1
Pristipomoides aquilonaris	2060	10
Rhompoblites aurorubens	4908	24
	$\sum$ = 20,301	

lished characteristics that permit early stage larvae of the lutjanines to be distinguished from each other. The few specimens identifiable as red snapper in SEAMAP collections that were under 3.5 mm BL resulted from variability in size at developmental stage and/or shrinkage during capture and preservation.

The question arises as to the potential for misidentification of red snapper larvae in SEAMAP collections since the larvae of all snappers found in the region have not been described. It is unlikely that this caused extensive misidentification of red snapper larvae considering how much the larvae of species whose larval development has been described differ from each other and red snapper in pigmentation and body shape (Drass et al. 2000). Most of the snappers whose larvae remain undescribed inhabit coral reefs and reef associated ledges as adults, and clear shallow waters or mangrove areas as juveniles (Anderson 2003); biotopes of limited extent in the northern GOM (Parker et al. 1983). No adults or juveniles of the six snapper species whose larvae are undescribed were taken during annual summer and fall SEAMAP shrimp/bottomfish (trawl) surveys from 1982 to 2005 (G. Pellegrin, NOAA/SEFSC Mississippi Laboratories, personal communication). Fewer than five individuals per year of these species were ever observed during ten years of NMFS reef fish video surveys of reef and hard bottom habitat from Brownsville, Texas to the Florida Keys (K. Rademacher, NMFS/SEFSC Mississippi Laboratories, personal communication).

Results

Eleven taxa of snappers were found among the 20,301 snapper larvae examined from over 14,000 bongo and neuston samples collected during SEAMAP surveys from 1982 to 2003 (Table 3). Forty-two per cent of snapper larvae could not be identified beyond the family level and 13% could only be identified to the genus level, *Lutjanus* spp. due to lack of development of distinguishing characters. The annual percentage of *Lutjanus* spp. varied from 6 to 26% over the 22 year time series. The proportion of larvae that could be identified as red snapper varied with size-class (Figure 2). A subset of larval identifications from samples taken in the north-central GOM in June and July best serves to illustrate the relationship between size and achievable identification lev-

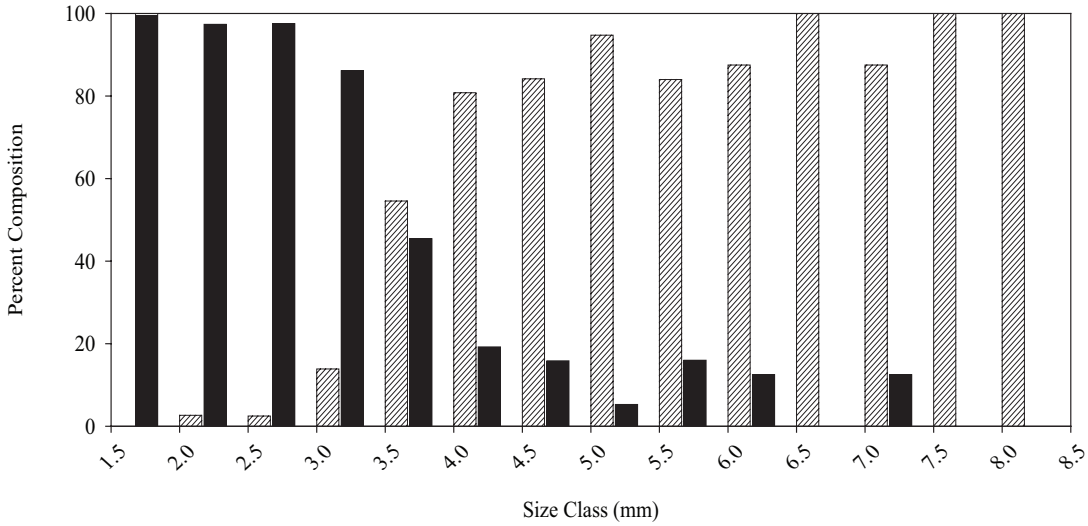

Figure 2. Proportion by size-class of larvae identifiable as *Lutjanus* spp., *n* = 397 (solid bars) and *Lutjanus campechanus, n* = 453 (shaded bars) in June and July SEAMAP plankton samples from the north-central Gulf of Mexico.

el because *L. campechanus* is the dominant species of *Lutjanus* in that region. Slightly over 50% of snapper larvae in the 3.5–3.9 mm BL size-class could be identified as red snapper while all larvae over 4 mm BL were developed enough to be confidently identified as red snapper. Larvae over 4 mm BL identified as *Lutjanus* spp. are the larvae of other species of snappers.

The larvae of red snapper were collected in plankton samples from 95 of 279 state and federal cruises from 1982 through 2003. During that time series a total of 639 red snapper larvae were identified in bongo samples and 1053 larvae in neuston samples from May to November. Months of highest occurrence and abundance with all surveys combined were July and September when larvae were taken in 12.7% and 11.0% of bongo samples; and 7.6% and 8.4% of neuston samples (Table 4). Mean abundance in those months was 1.18 and 0.82 larvae per 10 m^2 for bongo samples, and 0.36 larvae per 10 min for neuston samples. The surveys that accounted for most red snapper larvae were the Summer Shrimp/Bottomfish and Fall Plankton surveys; conducted, principally, in June & July, and September, respectively (Table 5). When captures of red snapper larvae are compared using only samples from the SEAMAP survey area west of 87.75°W longitude, i.e. the survey area common to both these surveys, per cent occurrence and mean abundance were highest in the month of September (Figure 3). The apparent decline in occurrence and abundance of larvae in August may be an artifact of sampling. Only 668 plankton samples were taken during that month over the SEAMAP time series as compared to over 1000 and 3000 samples in July and September, respectively (Table 5). Most of the August samples came from one, Gulfwide survey in 1984. By November red snapper larvae occurred in less than or equal to 0.2% of SEAMAP plankton samples and their mean abundance was less than 0.01 larvae.

Red snapper larvae were captured over a wide range of water depths, 9–2000 m, with mean station depth = 91 m and median depth = 45.5 m during SEAMAP Summer Shrimp/Bottomfish and Fall Plankton sur-

veys. Since depth at capture of red snapper larvae taken in bongo net samples is not known, environmental data from mid and max water column depths only define the range in conditions experienced by red snapper larvae in subsurface waters (Table 6). Surface conditions, however, do reflect the habitat of red snapper larvae captured by SEAMAP neuston nets in the upper 0.5 m of the water column. Average surface environmental conditions indicate that red snapper larvae consistently inhabit warm (mean temperature = 29°C), saline (mean salinity = 34 psu), clear (median optical transmission = 87%) waters. Larvae were taken at stations where minimum oxygen values at mid and near bottom depths were indicative of hypoxia.

Table 4. Summary of larval red snapper catches by month during SEAMAP surveys in the Gulf of Mexico, 1982–2003. no. occ. = number of samples with red snapper larvae; FO = frequency of occurrence; CV = coefficient of variation of mean abundance. Abundance in bongo samples = larvae under 10 m^2 sea surface. Abundance in neuston samples = larvae per 10 min.

Bongo samples

Month	No. samples	No. occ.	No. larvae	% FO	Mean abundance ± SE	Max station abundance	Summed abundance	CV
Jan	72	0	-	-	-	-	-	-
Feb	35	0	-	-	-	-	-	-
Mar	185	0	-	-	-	-	-	-
Apr	607	0	-	-	-	-	-	-
May	1410	3	5	0.2	0.02 ± 0.01	10.32	23.21	60
Jun	684	60	91	8.8	0.55 ± 0.10	53.33	374.61	19
Jul	590	75	147	12.7	1.18 ± 0.20	82.61	695.71	17
Aug	337	23	25	6.8	0.44 ± 0.10	13.69	146.94	22
Sep	1749	193	352	11.0	0.82 ± 0.08	43.02	1431.80	10
Oct	684	11	18	1.6	0.14 ± 0.06	28.69	97.07	39
Nov	472	1	1	0.2	0.01 ± 0.01	2.89	2.89	100
Dec	236	0	-	-	-	-	-	-

Neuston samples

Month	No. samples	No. occ.	No. larvae	% FO	Mean abundance ± SE	Max station abundance	Summed abundance	CV
Jan	76	0	-	-	-	-	-	-
Feb	33	0	-	-	-	-	-	-
Mar	50	0	-	-	-	-	-	-
Apr	890	0	-	-	-	-	-	-
May	2136	9	12	0.4	<0.01 ± <0.01	2.00	13.00	35
Jun	768	31	90	4.0	0.12 ± 0.04	30.00	91.82	36
Jul	536	41	185	7.7	0.36 ± 0.13	55.46	194.75	35
Aug	331	22	75	6.7	0.23 ± 0.08	23.80	74.76	37
Sep	1887	159	676	8.4	0.36 ± 0.05	53.00	671.26	15
Oct	658	11	14	1.7	0.02 ± 0.01	1.97	13.42	31
Nov	403	1	1	0.3	<0.01 ± <0.01	1.00	1.00	100
Dec	188	0	-	-	-	-	-	-

Table 5. Summary of larval red snapper catches in bongo and neuston net samples by month and SEAMAP survey type based on all surveys in the Gulf of Mexico, 1982–2003. No. occ. = number of samples with red snapper larvae; FO = frequency of occurrence. Abundance in bongo samples = larvae under 10 m^2 sea surface. Abundance in neuston samples = larvae per 10 min. CV = coefficient of variation of mean abundance. SP = Spring Plankton; SG = Summer Shrimp/Bottomfish; FG = Fall Shrimp/Bottomfish; FP = Fall Plankton; AS and AF = Alabama Summer and Fall Plankton; SQ = Squid/Butterfish. **denotes sampling outside established SEAMAP surveys.

Bongo samples

Month	Survey type	No. samples	No. occ.	No. larvae	% FO	Mean abundance ± SE	Max. station abundance	Summed abundance	CV
Jan	**	72	0	-	-	-	-	-	-
Feb	**	35	0	-	-	-	-	-	-
Mar	**	137	0	-	-	-	-	-	-
Jun	**	50	1	1	2.0	0.07 ± 0.07	3.57	3.57	100
Jul	**	22	1	1	4.6	0.16 ± 0.16	3.48	3.48	100
Aug	**	13	0	-	-	-	-	-	-
Nov	**	31	1	1	3.2	0.09 ± 0.09	2.89	2.89	100
Dec	**	225	0	-	-	-	-	-	-
Mar	SP	48	0	-	-	-	-	-	-
Apr	SP	607	0	-	-	-	-	-	-
May	SP	1394	3	5	0.2	0.02 ± 0.01	10.32	23.21	60
Jun	SP	147	0	-	-	-	-	-	-
Jun	AS	2	0	-	-	-	-	-	-
Jun	SG	485	59	90	12.2	0.77 ± 0.14	53.33	371.04	19
Jul	SG	565	74	146	13.1	1.23 ± 0.21	82.61	692.23	17
May	SQ	16	0	-	-	-	-	-	-
Jul	SQ	3	0	-	-	-	-	-	-
Aug	SQ	69	7	8	10.1	0.88 ± 0.33	13.69	60.53	38
Sept	AF	6	0	-	-	-	-	-	-
Aug	FP	255	16	17	6.3	0.34 ± 0.09	11.43	86.41	27
Sept	FP	1743	193	352	11.1	0.82 ± 0.08	43.02	1431.80	10
Oct	FP	269	6	7	2.2	0.11 ± 0.05	9.09	28.76	46
Oct	FG	415	5	11	1.2	0.16 ± 0.09	28.69	68.31	52
Nov	FG	441	0	-	-	-	-	-	-
Dec	FG	11	0	-	-	-	-	-	-

Mean length and overall size range did not change appreciably over the seven months when red snapper larvae were present in SEAMAP plankton samples (Table 7). There was no indication in monthly size frequency distributions of increasing modal size as the spawning season progressed (Figure 4). Larvae captured in bongo nets ranged from 2.4 to 19.2 mm BL with a mean of 5.1 mm (median = 4.6); size range in neuston samples was 2.7–24.0 mm BL with a mean of 4.4 mm (median = 4.0). Although size range of red snapper larvae captured in bongo and neuston samples was similar, cumulative frequencies indicate that overall, smaller larvae were found in neuston net samples. Ninety-five per cent of larvae captured in neuston samples were less than or

Table 5. (Continued)

Neuston samples

Month	Survey type	No. samples	No. occ.	No. larvae	% FO	Mean abundance ± SE	Max. station abundance	Summed abundance	CV
Jan	**	76	0	-	-	-	-	-	-
Feb	**	33	0	-	-	-	-	-	-
Mar	**	13	0	-	-	-	-	-	-
Apr	**	5	0	-	-	-	-	-	-
May	**	84	0	-	-	-	-	-	-
Jun	**	72	0	-	-	-	-	-	-
Jul	**	3	0	-	-	-	-	-	-
Aug	**	13	0	-	-	-	-	-	-
Nov	**	31	0	-	-	-	-	-	-
Dec	**	180	0	-	-	-	-	-	-
Mar	SP	37	0	-	-	-	-	-	-
Apr	SP	885	0	-	-	-	-	-	-
May	SP	2038	9	12	0.4	0.01 ± <0.01	2.00	13.00	35
Jun	SP	249	3	33	1.2	0.13 ± 0.12	30.00	32.91	91
Jun	AS	4	0	-	-	-	-	-	-
Jun	SG	443	28	57	6.3	0.13 ± 0.03	10.02	58.90	25
Jul	SG	530	41	185	7.7	0.37 ± 0.13	55.46	194.75	34
May	SQ	14	0	-	-	-	-	-	-
Jul	SQ	3	0	-	-	-	-	-	-
Aug	SQ	68	10	59	14.7	0.86 ± 0.39	23.80	58.76	45
Sep	AF	134	0	-	-	-	-	-	-
Oct	AF	18	0	-	-	-	-	-	-
Aug	FP	250	12	16	4.8	0.06 ± 0.02	3.00	16.00	31
Sep	FP	1753	159	676	9.1	0.38 ± 0.06	53.00	671.26	14
Oct	FP	258	3	3	1.2	0.01 ± 0.01	1.00	2.91	57
Oct	FG	382	8	11	2.1	0.03 ± 0.01	1.97	10.50	36
Nov	FG	372	1	1	0.3	<0.01 ± <0.01	1.00	1.00	100
Dec	FG	8	0	-	-	-	-	-	-

equal to 5.6 mm BL while that cumulative percentage of larvae in bongo net samples were less than or equal to 8.3 mm BL. One possible explanation for this observation is differential avoidance of bongo and neuston nets by snapper larvae. The difference between nighttime and daytime catch rates is a measure of sampling gear avoidance with avoidance being directly related to size of larvae (Morse 1989). Not only were red snapper larvae caught more frequently and in greater numbers at night regardless of gear (Table 8), but the night to day ratio of mean abundance (all larvae combined) for neuston samples (13.6) was seven times greater than the ratio (1.9) for bongo samples.

Capture locations and mean station abundances of red snapper larvae taken during four ongoing SEAMAP surveys and one special project survey yielded a generalized depiction of seasonal distribution of red snapper larvae in the Gulf of Mexico (Figures 5–9). Larvae were captured in the months of May and June during the SEAMAP Spring Plankton survey that is conducted in Gulf waters primarily beyond the continental shelf (Figure 5). The greatest number of captures and

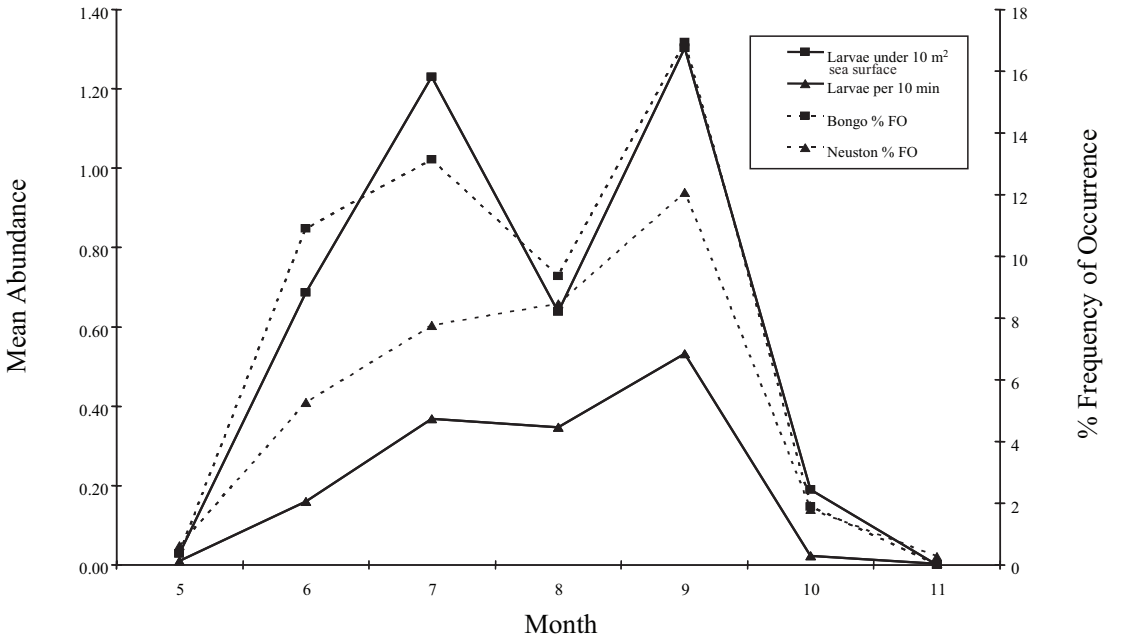

Figure 3. Monthly mean abundance and percent frequency of occurrence (FO) of red snapper larvae in SEAMAP bongo (□) and neuston (Δ) samples west of 87.75°W longitude in the Gulf of Mexico.

highest mean station abundances during this survey were observed in the westernmost region of the survey area, although larvae also were taken at stations in the north-central and extreme southeastern corner of the survey area. Predictably, occurrence and abundance of larvae was much greater during the summer Shrimp/Bottomfish survey of continental shelf waters conducted mainly from Mobile Bay to south Texas in mid June through July (Figure 6). Most occurrences and highest mean station abundances were observed off central and western Louisiana where water depths ranged from 50 to 100 m. Red snapper larvae were also consistently taken off south Texas, Mississippi and Alabama but mean abundances east of the Mississippi River were lower than west of the River. Mean station abundances were higher during the Gulfwide SEAMAP Fall (late August to mid October) Plankton survey then during the summer survey (Figure 7). Larvae were concentrated in the same general area as the summer survey but mean station abundances were markedly higher from 50 to beyond 100 m depth off central and south Texas during the fall than the summer survey. The Fall Plankton survey is the only survey that has, since 1986, consistently covered the eastern Gulf on the continental shelf off northwest and west Florida. Red snapper larvae occurred there much less frequently and in lower numbers than in the western Gulf. The Squid/Butterfish trawl survey was conducted as a SEAMAP special project for only two years but the coverage of that survey, along the continental shelf edge and during the month of August, added observations in an area and time that is underrepresented in the established surveys (Figure 8). No red snapper larvae were captured in May 1986 in collections made predominantly around the mouth of the Mississippi River. There were few captures of red snapper larvae in August 1985 despite extensive sampling along the 100–200 m contours over the northern Gulf from south Texas to

Table 6. Summary of environmental data gathered at stations where *Lutjanus campechanus* were caught during SEAMAP Summer Shrimp/Bottomfish (SG) and Fall Plankton (FP) surveys, 2000 to 2003. Measurements were taken at three levels in the water column; surface (surf); middle of water column (mid); and maximum sampling depth (max). Water temperature (temp) was measured in °C; salinity (sal) in psu; dissolved oxygen (oxy) in mg/l; and optical transmission (trans) in %. *Oxygen data from 2001 to 2003 surveys only.

	N	Mean	Std. Dev.	Median	Min	Max
SG surf temp	42	29.36	0.97	29.41	27.10	31.03
FP surf temp	92	29.20	0.71	29.35	25.40	30.25
SG mid temp	41	27.21	2.55	27.66	18.47	30.43
FP mid temp	92	26.50	3.62	28.47	17.79	30.09
SG max temp	41	23.94	3.15	23.97	15.36	28.92
FP max temp	92	22.28	4.64	22.63	13.30	29.73
SG surf sal	41	32.53	2.78	33.43	24.18	35.74
FP surf sal	92	34.67	2.16	35.49	27.15	36.57
SG mid sal	41	34.75	2.21	35.31	25.46	36.90
FP mid sal	91	35.65	1.67	36.36	27.66	36.65
SG max sal	41	35.70	1.20	36.06	30.02	36.90
FP max sal	91	35.99	1.11	36.39	30.06	36.57
SG surf oxy*	27	5.66	0.45	5.70	4.70	6.70
FP surf oxy*	65	6.07	0.19	6.10	5.50	6.60
SG mid oxy*	27	5.62	0.91	5.70	2.30	6.90
FP mid oxy*	65	5.82	0.86	6.00	2.50	7.30
SG max oxy*	27	3.92	1.52	4.00	1.10	6.70
FP max oxy*	65	4.56	0.99	4.40	1.90	6.70
SG surf trans	37	81.76	14.09	86.45	24.67	90.27
FP surf trans	70	86.37	2.66	87.12	74.72	88.69
SG mid trans	37	83.04	14.29	87.31	24.57	91.24
FP mid trans	70	85.45	5.29	87.04	59.27	88.50
SG max trans	37	55.64	19.84	61.34	5.99	82.04
FP max trans	70	73.97	11.50	75.81	37.26	88.80

Table 7. Size of red snapper larvae by month captured in SEAMAP bongo and neuston net samples. BL = body length; *N* = number of larvae measured.

	May	Jun	Jul	Aug	Sep	Oct	Nov
BL (mm)			Bongo				
Mean	4.7	5.1	5.2	5.3	5.1	5.0	4.8
Median	4.5	4.6	4.5	4.8	4.7	4.2	-
Range	3.8–6.5	3.3–10.0	2.4–19.2	3.6–10.2	3.1–18.2	3.5–8.1	-
95% Quantile	6.5	8.0	10.7	8.7	8.2	8.1	-
N	5	89	147	25	352	18	1
BL (mm)			Neuston				
Mean	4.7	5.0	5.1	4.3	4.1	4.3	4.8
Median	4.5	4.3	4.2	4.1	4.0	4.2	-
Range	3.1–6.5	3.3–21.0	3.1–24.0	3.4–12.6	2.7–10.5	3.4–5.0	-
95% Quantile	6.5	6.3	10.9	5.6	5.2	5.0	-
N	14	90	158	73	622	14	1

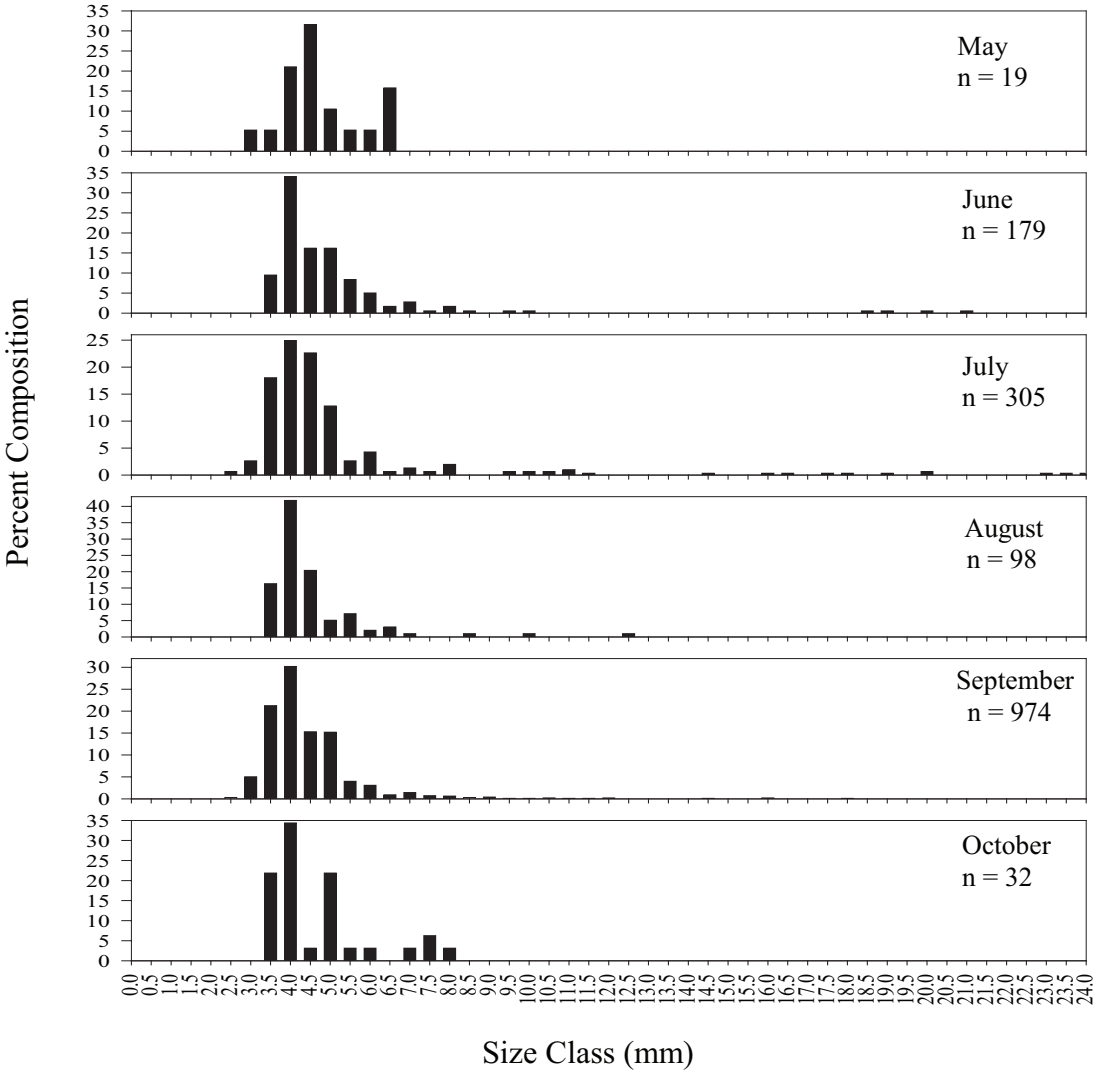

Figure 4. Monthly size frequency distributions of red snapper larvae in SEAMAP plankton samples. *N* = number of larvae measured. Individual y-axes are not to same scale.

midway down the west Florida shelf. Red snapper larvae were rarely taken during the Fall Shrimp/Bottomfish survey of continental shelf waters conducted mainly from Mobile Bay to south Texas in mid October through November (Figure 9). All captures were made in October except for two specimens taken in November; all captures were made in the western Gulf, and except for one, west of 94° west longitude.

Discussion

Temporal and spatial coverage of SEAMAP surveys for the most part encompass times and areas of known red snapper spawning (Collins et al. 1996, 2001; Woods 2003). The presence of red snapper larvae in SEAMAP plankton collections indicates continuous spawning within the spawning season, April–May and September–October, as determined from examination of adult go-

Table 8. Mean abundance and percent occurrence of red snapper larvae captured in bongo and neuston samples from day, night and twilight periods during SEAMAP Summer Shrimp/Bottom-fish and Fall Plankton surveys, 1982–2003. Bongo abundance = larvae under 10 m^2 sea surface; neuston abundance = larvae per 10 min.

	Bongo			Neuston		
	Day	Night	Twilight	Day	Night	Twilight
Mean abundance	0.60	1.13	0.53	0.05	0.68	0.12
Percent occurrence	8.8	13.8	7.3	2.7	15.4	3.3
No. samples	1785	1218	314	1732	1201	301

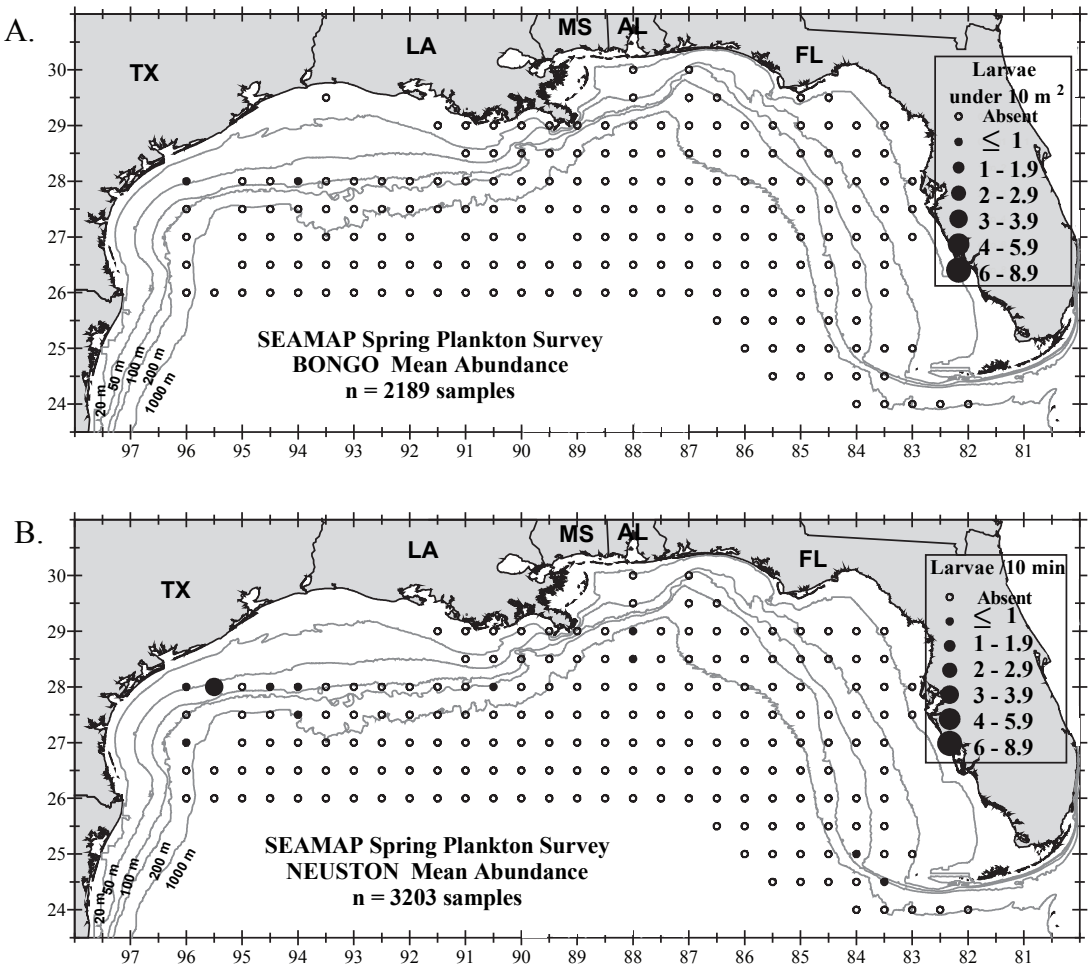

Figure 5. Mean abundance of red snapper larvae in bongo (A) and neuston (B) net samples during SEAMAP Spring Plankton surveys, 1982–2003. Abundance in bongo samples = larvae under 10 m^2 sea surface. Abundance in neuston samples = larvae per 10 min.

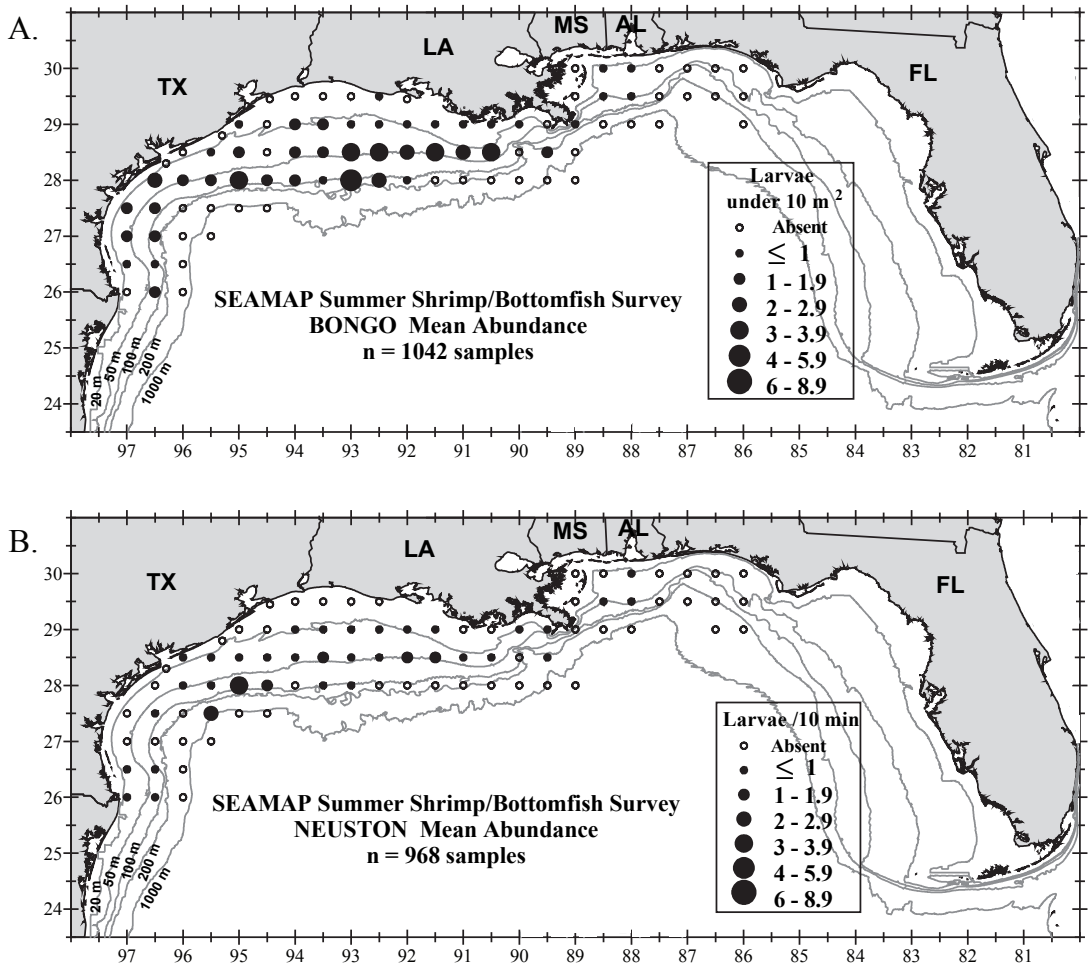

Figure 6. Mean abundance of red snapper larvae in bongo (A) and neuston (B) net samples during SEAMAP Summer Shrimp/Bottomfish surveys, 1982–2003. Abundance in bongo samples = larvae under 10 m^2 sea surface. Abundance in neuston samples = larvae per 10 min.

nads (Collins et al. 2001). The sharp drop in number of red snapper larvae caught in October may be indicative of abrupt termination of spawning in this species as was suggested by Woods (2003) based on the low incidence during the spawning season of red snapper ovaries exhibiting more than 50% atresia. It is likely that larvae were not found in SEAMAP samples from April because most sampling during the springtime survey is conducted in deep Gulf waters far from red snapper spawning sites. Station depths and bottom temperatures where red snapper larvae were captured during SEAMAP surveys agree with observed depths and temperatures at locations where spawning female red snapper were found (Collins et al. 2001). Furthermore, the consistent presence of red snapper larvae in samples taken between the 100 and 200 m contour in both the western and eastern Gulf supports the contention of Collins et al. (2001) that red snapper may spawn over a wide depth range, i.e. from mid-shelf to the continental slope. Settlement of juvenile red snapper has been reported on the outer continental shelf in the northwestern Gulf

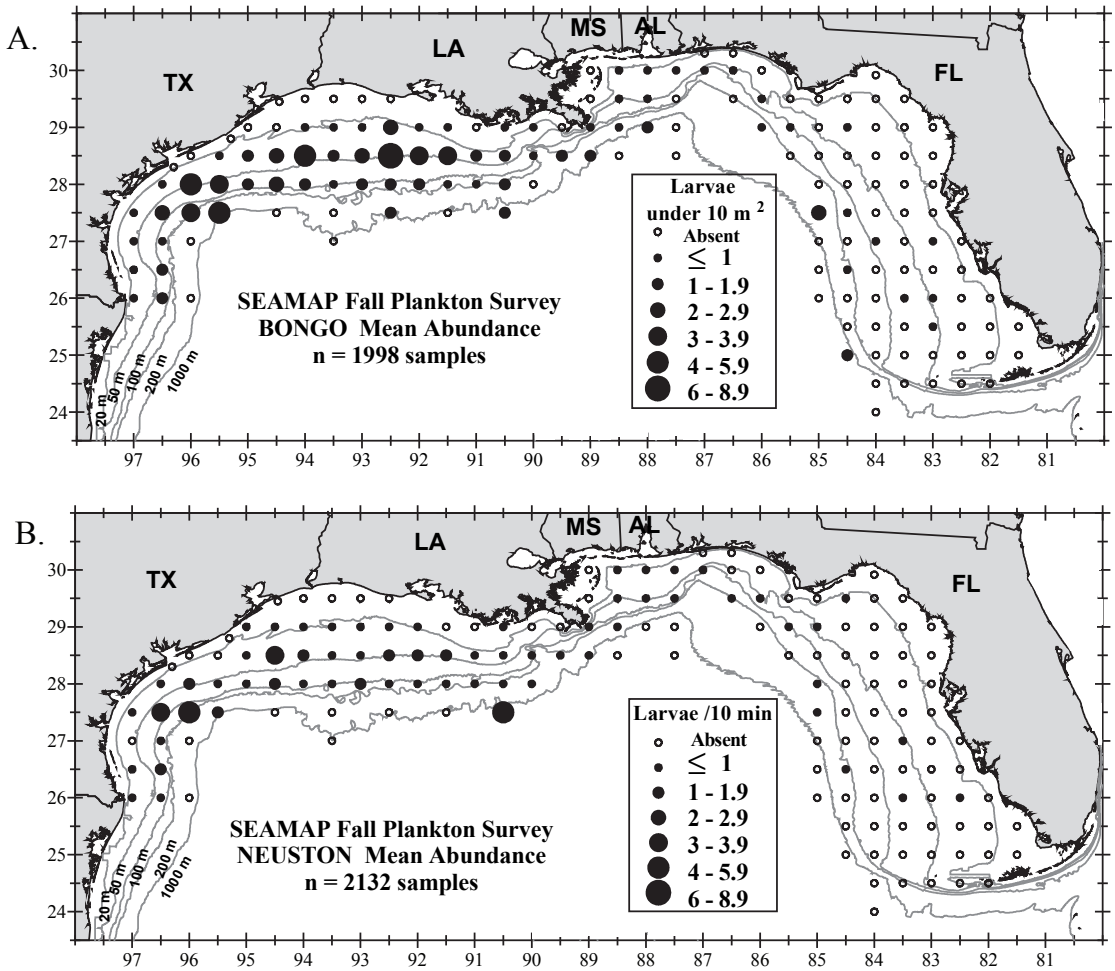

Figure 7. Mean abundance of red snapper larvae in bongo (A) and neuston (B) net samples during SEAMAP Fall Plankton surveys, 1986–2003. Abundance in bongo samples = larvae under 10 m^2 sea surface. Abundance in neuston samples = larvae per 10 min.

from June through October (Holt and Arnold 1982).

Data from SEAMAP samples present little information on vertical distribution of red snapper larvae, other than they are slightly more common below than at the surface. Recently, a critical need has arisen for information on vertical distribution of fish larvae, especially in the northern Gulf of Mexico, so that submerged warming water intakes at Liquefied Natural Gas (LNG) facilities might be placed at depths where entrainment of fish larvae would be minimized. There is some evidence that snapper larvae are vertically stratified in shelf waters less than 55 m in depth. Lutjanid larvae (not identified beyond the family level) captured at three discrete depths in coastal waters off east Louisiana, Mississippi and Alabama during September 1984, 1986 & 1987 were, in general, captured more frequently and in greater numbers at depths of 5 and 11 m than at 1 m (Lyczkowski-Shultz, J., NMFS Mississippi Laboratories, unpublished data).

Avoidance of SEAMAP bongo and, especially, neuston nets was clearly evident

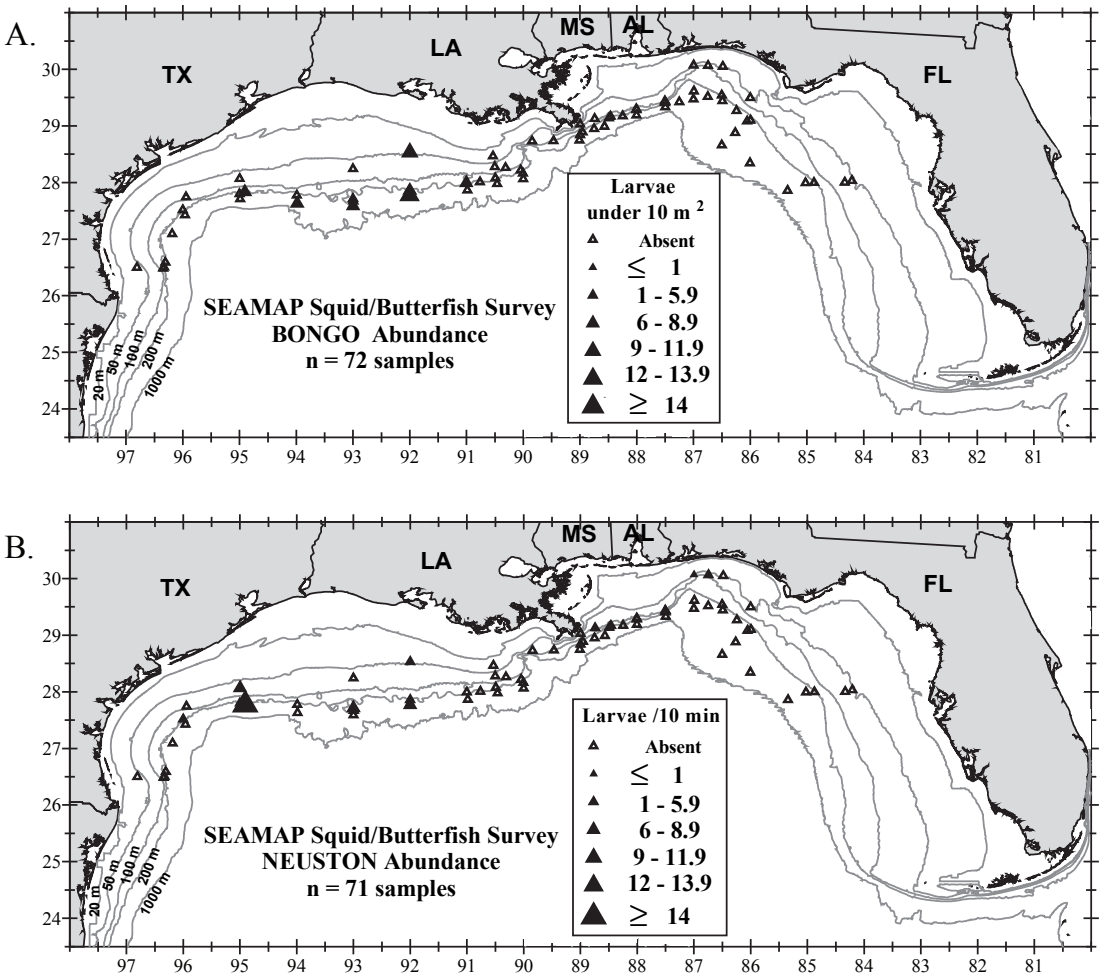

Figure 8. Station abundance of red snapper larvae in bongo net (A) and neuston (B) net samples during the SEAMAP Squid/Butterfish survey in August 1985. Abundance in bongo samples = larvae under 10 m^2 sea surface. Abundance in neuston samples = larvae per 10 min.

among red snapper larvae over 5 mm BL. Relatively few specimens greater than 6 mm BL were ever captured in plankton samples even though settlement from the planktonic to the benthic habitat first occurs at 16–19 mm and 26–30 d (Szedlmayer and Conti 1999; Rooker et al. 2004). Another reason why few postlarval and juvenile red snapper were taken in plankton samples may have been because the area within a few meters of the bottom is not effectively sampled using SEAMAP methods. If presettlement snappers become concentrated in the lower reaches of the water column they would not be susceptible to capture by bongo nets. Regardless of the cause (avoidance or undersampled habitat), the near absence of larvae from over half the expected planktonic size range and duration in SEAMAP samples preclude the use of these data to generate meaningful estimates of larval mortality rates. Unfortunately, actual not relative estimates of natural mortality are needed to effectively assess the impact of larval mortality caused by entrainment in LNG facilities in terms of loss to red snapper fisheries in the Gulf of Mexico. The inabil-

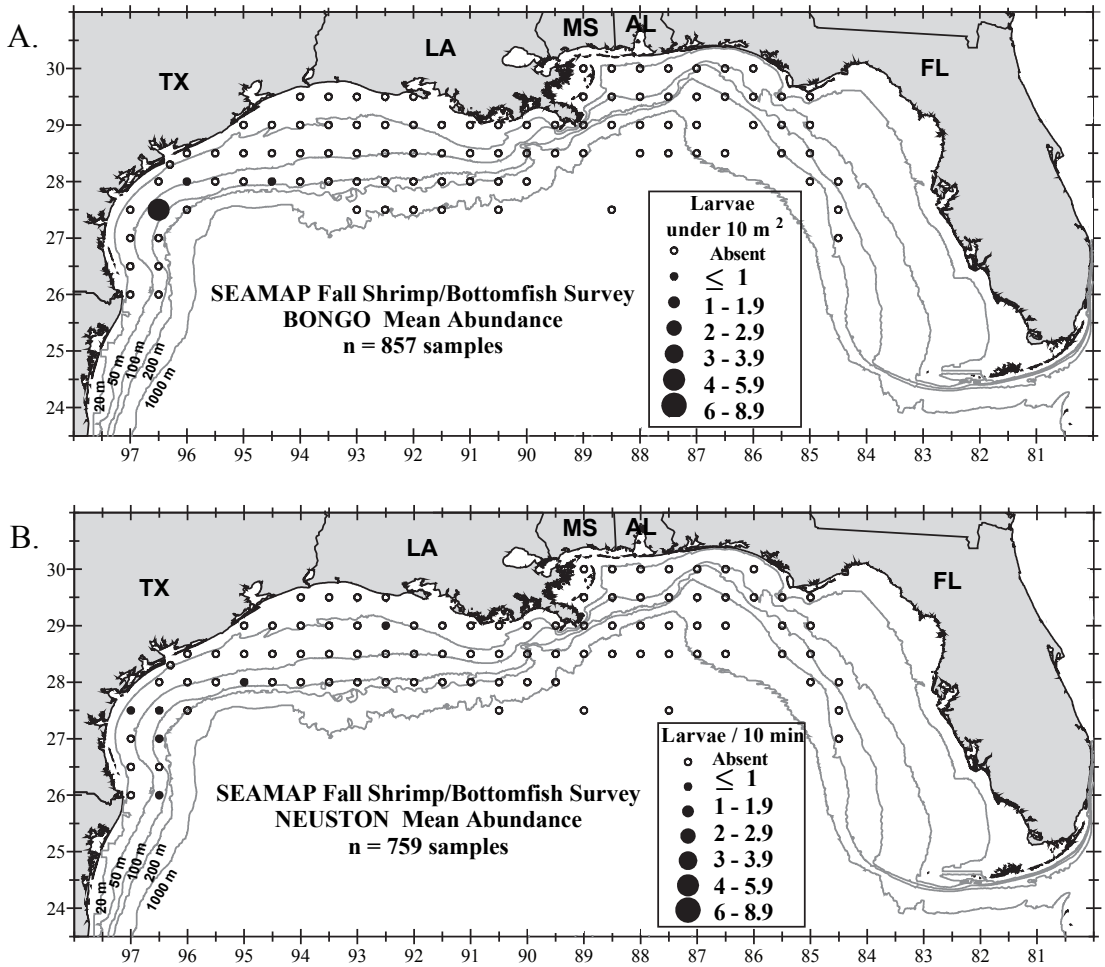

Figure 9. Mean abundance of red snapper larvae in bongo net (A) and neuston (B) net samples during SEAMAP Fall Shrimp/Bottomfish surveys, 1982–2003. Abundance in bongo samples = larvae under 10 m^2 sea surface. Abundance in neuston samples = larvae per 10 min.

ity to identify all snapper larvae in SEAMAP plankton samples, and the truncated size distribution of the catch results in underestimation of occurrence and abundance of red snapper larvae. Despite the shortcomings, these data represent the most comprehensive description of distribution and seasonal abundance of red snapper larvae available for the Gulf of Mexico. Ongoing SEAMAP resource surveys provide a reliable, albeit relative, measure of annual abundance of red snapper larvae over the size range caught, retained and identifiable in bongo and neuston nets.

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