LARVAL DISTRIBUTIONS AND RECRUITMENT HYPOTHESES FOR SNAPPERS AND GROUPERS OF THE SOUTH ATLANTIC BIGHT

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Abstract: Present taxonomic status permits discussion of larvae of vermilion snapper (Rhomboplites aurorubens), other snappers combined (Lutjanidae), and all groupers combined (Serranidae, subfamily Epinephelinae). Larvae of these groups together comprise less than 1% of the total larval fish catch from neuston and bongo samplers in shelf waters of the South Atlantic Bight. Larvae of groupers and snappers are most abundant in spring and in summer respectively. Larvae are distributed in outer shelf and upper slope waters, where current is northerly. Northerly current may predominate in affecting larval drift (in which case populations may primarily be recruited from the Caribbean or Gulf of Mexico) or a significant proportion of larvae spawned in the Bight may be retained by currents throughout development to settling.

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Important sport and commercial fisheries for snappers, groupers and porgies (family Sparidae) have been expanding for the past several years in continental shelf waters of the South Atlantic Bight; expansion is continuing at present (Huntsman 1976, Ulrich et al. 1977). Estimated South Carolina commercial landings were some 180,000 kg in 1976, with groupers contributing about 45 percent, snappers 20 percent, and porgies 25 percent (Ulrich et al. 1977). Sport fishery catches for North and South Carolina were estimated at some 725,000 kg for 1973, with groupers contributing some 22 percent, snappers 14 percent and porgies 46 percent (Huntsman 1976). Although number of species contributing to the fishery is high, major species taken are gag (Mycteroperca microlepis), scamp (M. phenax), speckled hind (Epinephelus drummondhayi), red snapper (Lutjanus campechanus), vermilion snapper (Rhomboplites aurorubens) and red porgy (Pagrus pagrus). The fishery is one of the largest of outer continental shelf waters of the South Atlantic Bight and a high priority has been placed on its management by the South Atlantic Regional Fishery Management Council established by the Fishery Conservation and Management Act of 1976.

The wide distribution of species of interest, the currents of the western central Atlantic, and the presence of planktonic larvae in species of families involved complicate descriptions of stocks and recruitment. The major species listed above are all present in the Gulf of Mexico and several are present in the Caribbean Sea. Currents of the western central Atlantic run westward through the Caribbean, swing northward and eastward around the western tip of Cuba, then run north through the Florida Straits toward Cape Hatteras. South Atlantic Bight fish populations thus may be recruited from larvae spawned in the Gulf or Caribbean and transported northward, or from spawning within the South Atlantic Bight. An intermediate condition might also exist, with both indigenous and exogenous spawning contributing to population maintenance. A similar situation exists with Florida spiny lobster populations (Sims and Ingle 1966), and is probably common to all Caribbean fisheries for species with planktonic larvae. Management strategies for South Atlantic Bight populations could be strengthened by further information on recruitment, since protecion of indigenous spawning populations would not be necessary if the bulk of recruitment resulted from spawning in the Gulf or Caribbean. The present paper provides data on distribution and abundance of larvae in the South Atlantic Bight and suggests further research needs.

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MATERIALS AND METHODS

Ichthyoplankton samples were collected from continental shelf and continental slope waters between Cape Fear, North Carolina (latitude 34°00'N) and Cape Canaveral, Florida (latitude 28°30'N). Five cruises were made in 1973 and 1974: Winter 1973 (Feb. 13-March 24)-67 stations; Spring 1973 (May 15-27)-44 stations; Fall 1973 (Oct. 23-Nov. 16)-41 stations; Spring 1974 (April 1-May 9)-55 stations; and Summer 1974 (Aug. 13-Sept. 1)-38 stations. Samples were collected with a 60 cm bongo sampler, towed in a double oblique pattern between surface and bottom or 200 m maximum depth following MARMAP procedures (Powles and Stender 1976), and with a neuston sampler 1.0 m high by 2.0 m wide, towed at the surface at 2.6 m/sec for 10 min. Samples were fixed in 20 percent formalin for 2 min immediately following net washdown, and preserved in 5 percent formalin buffered by saturating with borax. Larval fishes removed from whole plankton samples were identified and enumerated using Wild M-5 dissecting microscopes and were measured to the nearest mm with an ocular micrometer. Volumes strained were calculated from flowmeter readings for the bongo sampler. Catches of both samplers were standardized to number under 100 m² of sea surface area, using formulas given by Powles and Stender (1976). Stations were classed as dawn-dusk (stations sampled within 1 hr on either side of sunrise or sunset), day and night, for examination of diel differences in catches.

Identification of larvae of western Atlantic snappers and groupers is complicated by the large number of species present and the similarity of larvae of individual species within groups. The only lutjanid larvae identifiable to species at present are those of vermilion snapper (Laroche 1977), so in this paper other snapper larvae are treated as "Unclassified snappers". Groupers (*Mycteroperca* and *Epinephelus* spp.) constitute the subfamily Epinephelinae of the family Serranidae. At present larvae (described by Presley 1970) are not identifiable below the subfamily level. Of the porgies (family Sparidae) only red porgy are identifiable to species as larvae (Ranzi 1969); literature descriptions of other larval Sparidae are insufficiently detailed for reliable species separation.

The South Atlantic Bight of the United States Atlantic coast extends from Cape Hatteras to Cape Canaveral (Bumpus 1973). Shelf width varies from 70 km off Capes Hatteras and Canaveral to 130 km off Georgia; from northern Florida to North Carolina shelf width averages 90-100 km. Bottom substrate is generally sand, with mud nearshore; patches of rocky bottom ("live" bottom), their extent and distribution incompletely known, occur over the whole shelf. The axis of the northerly-flowing Florida Current (that part of the Gulf Stream system flowing from the Straits of Florida to Cape Hatteras) occurs over the continental slope but the current's influence is felt on the outer part of the continental shelf (Bumpus 1973). Average surface Florida Current velocities south of Cape Hatteras range from 70 km/day (November) to 90 km/day (June), and east of Florida range from 90 km/day (November) to 120 km/day (July) (Emery and Uchupi 1972). On the inner continental shelf low salinities and seasonally fluctuating temperatures are found; from late spring to fall a slow southerly geostrophic surface current is present from Cape Fear to Cape Canaveral (Bumpus 1973). Eddies and meanders of the Florida Current (Bumpus 1973) and wind-driven Ekman transport (Nelson et al. 1977) account for some water transport perpendicular to the axes of these currents and to the coastline. The combination of rocky bottom outcrops and warm Florida Current water year-round permit development on the outer shelf of the warm-water "snapper-grouper" complex.

RESULTS

Two years of ichthyoplankton sampling yielded rather low numbers of larval snappers and groupers (Table 1). The total catch of fish larvae in these 2 years was approximately 100,000 specimens, and the groups of interest here accounted for less than 1 percent of the total catch. Particularly notable are the very low catches of red porgy larvae; this species is abundant in sport and commercial catches of this area. Catches of larvae varied seasonally; highest catches of grouper larvae occurred in spring, of snapper larvae in summer, and of red porgy larvae in winter and spring (Table 2).

Larvae of the 3 major groups were apparently sampled less effectively by the neuston net in daylight than at night, but time of day did not appear to affect bongo net catches appreciably. Most neuston samples containing larvae of unclassified snappers, vermilion snapper and groupers were collected at night (Table 3). No unclassified snapper or grouper larvae were taken by day in the neuston sampler. Bongo samples in which larvae of each of the 3 major groups were present were distributed among the 3 light

	NEUS	TON	BONGO		
	Number Caught	Mean Number Per Station	Number Gaught	Mean Number Per Station	
LUTJANIDAE	135	0.61	103	0.42	
Rhomboplites aurorubens	51	0.23	60	0.24	
Unclassified	84	0.38	43	0.18	
SERRANIDAE	1,354	6.19	1,876	7.65	
Anthiinae	170	0.78	55	0.22	
Epinephelinae	39	0.18	67	0.27	
Liopropominae	1		0		
Serraninae	1,114	5.09	906	3.70	
Unclassified	30	0.14	848	3.46	
SPARIDAE	38	0.17	805	3.29	
Pagrus pagrus	0	0	12	0.05	
Unclassified	38	0.17	793	3.24	
			(89)ª	(0.36)*	
NUMBER OF STATIONS	219		245		

Table 1.	Numbers of larval snappers (Lutjanidae) groupers and sea basses (Serranidae)
	and porgies (Sparidae) taken in neuston and bongo sampler tows in South At-
	Atlantic Bight in 1973 and 1974.

*Excluding single large catch of 704 specimens.

Table 2. Catch by season of larvae of unclassified snappers (Lutjanidae), vermilion snapper (*Rhomboplites aurorubens*), groupers (Epinephelinae) and red porgy (*Pagrus pagrus*) in South Atlantic Bight in 1973 and 1974. N = Neuston; B = Bongo.

Group	Gear	Winter 1973 (Feb Mar.)	Spring 1973 (May)	Fall 1973 (Oct Nov.)	Spring 1974 (Apr May)	Summer 1974	Total
Lutjanidae Unclassified	N	1	0	3	13	26	43
	В	0	1	4	7	72	84
Rhomboplites aurorubens	Ν	0	1	9	0	50	60
	в	0	0	8	0	43	51
Epinephelinae	N	1	0	3	63	0	67
	в	0	13	0	18	8	39
Pagrus pagrus	N	3	0	0	9	0	12
	в	0	0	0	0	0	0

phases (day, night, and dawn-dusk) essentially in the same proportions as total number of samples (Table 3). Of the 4 neuston samples in which red porgy larvae occurred, 1 was collected during daylight, 1 at night, 1 at dawn and one at dusk. Mean standard length of bongo-caught larvae did not differ significantly between the 3 light phases, with 1 exception. Vermilion snapper larvae captured with the bongo net during dawn and dusk were significantly smaller (SL = 3.46 mm) than day-caught larvae (SL = 4.24 mm) (t-test, p < 0.005). Mean standard lengths of bongo-caught larval groupers and

	Stations Sampled		Stations With Unclassified Snappers		Stations With Vermilion Snappers		Stations With Groupers	
	N	(%)	N	(%)	N	(%)	N	(%)
Neuston								
Night	29	(31.2)	7	(87.5)	2	(66.7)	6	(85.7)
Day	43	(46.2)	0	(0.0)	1	(33.3)	0	(0.0)
Dawn-Dusk	21	(22.6)	1	(12.5)	0	(0.0)	1	(14.3)
Total	93	(100.0)	8	(100.0)	3	(100.0)	7	(100.0)
Bongo								
Night	22	(27.5)	7	(24.1)	4	(30.8)	5	(25.0)
Day	38	(47.5)	17	(58.7)	7	(53.8)	12	(60.0)
Dawn-Dusk	20	(25.0)	5	(17.2)	2	(15.4)	3	(15.0)
Total	80	(100.0)	29	(100.0)	13	(100.0)	20	(100.0)

Table 3. Day, night, and dawn-dusk catches of larvae of unclassified snappers, vermilion snapper and groupers in bongo and neuston samples from 1974 cruises.

unclassified snappers did not differ significantly between the 3 light phases, and mean standard lengths of bongo-caught larval vermilion snapper did not differ significantly between day and night or between night and dawn-dusk.

Distribution patterns for each of the 3 major groups in bongo samples for the season of peak larval abundance (spring, 1974 for groupers; summer, 1974 for vermilion snapper and unclassified snappers) were generally similar (Fig. 1). Larvae were found throughout the north-south extent of the South Atlantic Bight, except for vermilion snapper, which were not caught on the southernmost line of stations off Cape Canaveral. All were present in waters of the middle and outer continental shelf and upper continental slope (bottom depth > 20 m), and were absent from inner shelf waters (bottom depth < 20 m). Larvae of vermilion snapper and unclassified snappers were present somewhat further inshore than larval groupers. Relatively high standardized catches were found



Fig. 1. Distribution of larval snappers and groupers from bongo samples during season of maximum larval abundance. A. Groupers (Epinephelinae), spring, 1974. B. Unclassified snappers (excluding vermilion snappers), summer, 1974. C. Vermilion snapper, summer, 1974.

at groups of stations randomly distributed through the study area. Similar distribution patterns were found in neuston catches of these 3 groups for the same seasons; however, catches were more widely scattered mainly due to the absence of larvae from day neuston tows. Distribution patterns were similar for other seasons in which larvae were present, although catches were less widespread. Red porgy larvae were taken on 4 neuston stations (1 in 1973, 3 in 1974) at mid-shelf (bottom depths 16-24 m) between northern Georgia and Cape Fear.

Standard length (SL) ranges and distributions for the total neuston and bongo catches of the 3 major groups were similar (Fig. 2). Larger larvae were taken in the



Fig. 2. Standard length frequency distributions of larval groupers (Epinephelinae), unclassified snappers (Lutjanidae) and vermilion snapper (Rhomboplites aurorubens) from neuston and bongo samples.

neuston net than in the bongo net. Mean SL of neuston-caught larvae was significantly greater (t-test, p < 0.01 for all 3 groups) than mean SL of bongo-caught larvae in all 3 groups. Minimum SL of bongo-caught larvae was less than that for neuston-caught larvae for all groups. Red porgy larvae collected ranged from 6-22 mm SL.

Distribution of larvae in the South Atlantic Bight was similar for different size classes. For bongo-caught unclassified snapper larvae (Fig. 3), small specimens (2-3 mm SL) and



Fig. 3. Distribution of bongo sampler-caught larvae of unclassified snappers (excluding vermilion snapper) by size classes.

larger specimens (4-5 mm SL) were distributed in a pattern similar to that for all larvae combined, i.e. in mid and outer continental shelf waters and upper slope waters throughout the north-south extent of the survey area. Similarly, bongo-caught larval groupers and vermilion snapper of different SL classes were distributed essentially in the same pattern as all larvae of these fishes combined. Neuston net catches of larvae of each group were scattered; however, in all 3 groups small larvae (2-3 mm SL) were caught only in continental slope waters, while larger larvae (> 4 mm SL) were caught in both slope and shelf waters.

Changes in SL distributions of bongo-caught larvae over the 5 weeks required to make a cruise were investigated (Fig. 4). Mean SL of unclassified snapper larvae was not significantly different in the 3 periods into which the summer 1974 cruise was divided (t-test, p > 0.05). Similarly, mean SL of grouper larvae did not change significantly during the spring 1974 cruise (p > 0.05). Mean SL of vermilion snapper larvae increased significantly (p < 0.05) from the third to the fourth week of August 1974, and no larvae were taken during the last 2 days of August.

DISCUSSION

The small number of snapper and grouper larvae taken suggests that use of egg and larval surveys to assess population biomass in these groups may not be feasible. Such estimates have been made for large spawning populations of pelagic fishes in the California Current (e.g. Smith 1972) and Gulf of Mexico (Houde 1977), but it is perhaps not surprising that the procedure may not be practical in a fish assemblage of high



Fig. 4. Standard length frequency distributions of larval groupers (Epinephelinae), unclassified snappers (Lutjanidae) and vermilion snapper (Rhomboplites aurorubens) by periods within total duration of a sampling cruise (bongo samples).

species diversity, where individual species biomass is a relatively small proportion of the total. Other kinds of fishes (e.g. herring-like fishes, family Clupeidae; spot, *Leiostomus xanthurus;* hakes, *Urophycis* spp.; and mullet *Mugil* spp.) form a much larger proportion of South Atlantic Bight ichthyoplankton than do snappers and groupers (Powles and Stender 1976).

Data on seasonality in catches of larval snappers and groupers agree well with published information on spawning in these fishes. Vermilion snapper spawn from May-September off North and South Carolina, and summer spawning is apparently the rule among western Atlantic Lutjanidae (Grimes 1976). Lutjanus campechanus, the red snapper, spawns July-October with a peak in September in the Gulf of Mexico (Beaumariage and Bullock 1976). Snapper larvae were most abundant during summer in the present study. Red grouper (Epinephelus morio) spawn mainly in April and May (Moe 1969), while gag are in spawning condition January-March (Beaumariage and Bullock 1976) in the Gulf of Mexico. Catches of larval groupers were highest in spring in the present study. Peak spawning of red porgy occurs in March and April off North Carolina (Manooch 1976); the few larvae found in this study were caught in February-March 1973 and April-May 1974. The increase in mean SL during August 1974, suggests that vermilion snapper spawned during early August 1974, but not during late August or early September. This may be indicative of pulsed spawning within the overall spawning season; Grimes (1976) suggests that multiple spawning during the spawning season may occur in this species. The data are not numerous and further information will be required to substantiate these observations.

No day neuston catches of snapper and grouper larvae, except for 1 catch of vermilion snapper, were made. Low or zero catches of larvae in daylight neuston tows are characteristic of several other kinds of fish in our area, e.g. frigate mackerels (Auxis spp.), gobies (family Gobiidae) and eels (order Anguilliformes) (Eldridge et al. 1977). This diel difference for snapper and grouper larvae is probably due to daylight absence of larvae from the sea surface layer rather than to diel changes in visually-cued net avoidance, since bongo net catches differed little with time of day. Water-column sampling gear is thus preferable to neuston sampling gear for routine surveys for snapper and grouper larvae, since neuston gear is effective only for part of the 24 hr period. With 1 exception, mean SL of bongo-caught larvae did not change with time of day, suggesting that midwater collecting gear will collect samples unbiased with respect to size of larvae throughout the 24 hr period.

Larger larvae of all groups were sampled by the neuston net than by the bongo net. The larger minimum size taken by the neuston net is probably due to extrusion of small larvae through its larger meshes. The larger mean size is probably due to the larger mouth size and higher towing speed of the neuston net. Escapement by larvae tends to increase with larval length, and escapement decreases with increasing mouth size and towing speed of towed samplers (Barkley 1972). Thus, larger, faster-towed samplers than the bongo may be necessary for sampling larger-sized larvae of these groups.

Distributions of larvae of the 3 major groups studied were generally similar to those of adults in the South Atlantic Bight. Information from fishermen and MARMAP surveys suggests that snappers and groupers are most abundant at depths greater than 37 m in our area, i.e. on approximately the outer third of the continental shelf. The similarity in distribution between different size classes of bongo-caught larvae suggests that there is no net movement of larvae with growth, on either seaward-shoreward or north-south axes. Data on neuston-caught larvae, more scattered, suggest spawning offshore and shoreward movement with growth. The reason for the discrepancy between bongo and neuston observations is presently unknown.

Published information and our data suggest that spawning of snappers and groupers occurs within the South Atlantic Bight but, if northerly current is the dominant factor affecting larval drift, most larvae spawned within the Bight may be lost through drift. However, present current information is insufficiently detailed for definitive conclusions. Although information on age and growth of snapper and grouper larvae is not available, estimating age at length is possible from development rates of other perciform species, e.g. Bairdiella chrysura (Kuntz 1914) and Cynoscion regalis (Welsh and Breder 1923). If information from these other species is applicable, 2-3 mm larvae are probably some 4 days post-spawning. Surface velocities in the Florida Current in spring and summer are 90-120 km/day (Emery and Uchupi 1972). Taking 100 km/day as an approximate average, a 4-day-old larva would have drifted 400 km from its spawning site. The northsouth extent of the South Atlantic Bight is some 740 km. Thus, at least those small larvae in the northern part of our area were probably spawned within the Bight. Benthic snapper juveniles as small as 11 mm SL (Lutianus griseus, Starck and Schroeder 1971) and red grouper as small as 23 mm SL (Moe 1969) have been taken. Age of these benthic juveniles must be greater than 10 days. In 10 days, drift at 100 km/day would be 1,000 km, or greater than the length of the South Atlantic Bight. Thus, if one-way drift at this velocity were occurring, all larvae spawned in the Bight would have drifted past Cape Hatteras to the north and been lost from Bight populations; populations to the south would then be the only source of recruiment to Bight populations. The velocity given is, however, that of the axis of the Florida Current off the shelf, and northerly surface currents over the shelf are probably slower. Also, as noted, southerly flow may occur within the distribution limits of larvae on the shelf.

Spawning seasonality, larval distribution patterns, and seasonal current changes suggest that recruitment pathways for snappers may be different from those for groupers in the South Atlantic Bight. Snappers spawn in summer and larvae occur over the outer two-thirds of the outer shelf and over the upper slope. In August-September most of the shelf is subject to southerly surface water drift (Bumpus 1973), so retention of larvae in an eddy-like current system (northerly over the slope, southerly over the shelf) may be significant. Groupers, on the other hand, spawn in spring and larvae occur on the outer one-third of the shelf and on the upper slope. Surface water drift is northerly over the outer two-thirds of the shelf in April, but in May southerly surface flow affects most of the shelf (Bumpus 1973). Thus grouper larvae may be primarily subject to northerly flow early in the spawning period (April) and to an eddy-like circulation later (May). More precise information on grouper spawning chronology and seasonal current shifts would improve the grouper larval drift picture.

Further information is required for drawing a more detailed picture of larval drift pathways to populations comprising the snapper-grouper complex. The following kinds of information are suggested:

1. Taxonomic--identification of larvae to species level; identification of eggs, not presently possible, would be desirable at least for major species.

2. Ingress/egress-data on water transport and number of larvae present, integrated over the spawning season at northern (Cape Hatteras) and southern (Florida Straits) extremes of the South Atlantic Bight.

3. South Atlantic Bight currents-detailed information on velocity and transport on the shelf and upper slope.

4. Egg and larval production within the Bight.

5. Age and growth of larvae.

These data might be summarized in a generalized larval drift model, which could be used to simulate changes under varying conditions, e.g. reduced spawning within the Bight (which could result from reduction of spawning stocks through excessive fishing) or reduced contribution of larvae from southern populations (representing excessive spawning stock reduction in the Caribbean and Gulf of Mexico). Such a model might have general application to many fisheries on isolated populations affected by unidirectional currents (e.g. Caribbean island fisheries).

Recruitment to snapper-grouper fisheries of the region may depend on other factors as well as abundance of larvae available to settle. Suitable habitat for juveniles and adults is limited, and habitat availability might limit recruitment independent of numbers of larvae present. Survival of early benthic juveniles may also affect final recruitment to fisheries.

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