Temporal and spatial spawning patterns of the Atlantic butterfish, *Peprilus triacanthus*, in the South and Middle Atlantic Bights*

Teresa Rotunno
Robert K. Cowen
Marine Sciences Research Center
State University of New York
Stony Brook, New York 11794-5000
E-mail address (for T. Rotunno): trotunno@ccmail.sunysb.edu

Abstract.–Three species of the stromateoid genus *Peprilus* have been found to occur in the northwest Atlantic: *P. triacanthus* (butterfish), *P. burti* (gulf butterfish), *and P. alepidotus* (harvestfish). *Peprilus triacanthus* and *P. alepidotus* reportedly spawn from May through August and June through July, respectively. *Peprilus burti* spawns twice yearly: February through May and September through November. Collections of larvae and juveniles of *Peprilus* spp. from the northern South Atlantic (SAB) and Mid-Atlantic (MAB) Bights during both the spring and summer of 1988 and 1989 suggest that either a combination of species was spawning or that reported spawning dates were suspect. Species identification of *Peprilus* in these collections was determined with morphometric, meristic, and pigment character analyses. Specimens sampled had counts for caudal vertebrae (18–19) and ventral midline melanophores (11–16) consistent with those found for *P. triacanthus* in previous studies. By analyzing otoliths, we estimated larval and juvenile growth rates to be approximately 0.23 mm/day. Backcalculation of hatch dates suggests either two spawning events for *P. triacanthus*, February through mid-April and mid-May through late July, or one extended spawning period beginning in late February and ending in late July. This study reveals that *P. triacanthus* spawns for a much longer period than previously thought. It is possible that *P. triacanthus* spawns during the spring in the SAB and summer in the MAB as a strategy to extend the duration of its spawning period. This strategy is one used by other north-south migrating species and warrants further study.

Manuscript accepted 7 March 1997.
Fishery Bulletin 95:785–799 (1997).

Three species of the stromateoid genus *Peprilus* (order: Perciformes) are reported to occur in the western North Atlantic: butterfish, *P. triacanthus* (Peck), gulf butterfish, *P. burti* (Fowler), and harvestfish, *P. alepidotus* (Linnaeus). Although the ranges of all three species extend along the eastern coast of North America and the West Indies, there is some question as to which species of *Peprilus* are regular residents in the South Atlantic Bight (SAB) and Mid-Atlantic Bight (MAB) regions (Caldwell, 1961; Haedrich, 1967; Horn, 1970; Perschbacher et al., 1979). This question is extended by the suggestion of possible hybridization between *P. triacanthus* and *P. burti* in the northern portion of the SAB (Horn, 1970; Perschbacher et al., 1979).

Reproduction in *P. triacanthus* and *P. burti* is seasonal and apparently associated with annual migration patterns (Horn, 1970). In the summer and fall, *P. triacanthus* migrates northward and inshore, where it reportedly spawns from late May through August, with a peak in June (Horn, 1970). During winter, *P. triacanthus* migrates offshore and becomes horizontally restricted (Horn, 1970). Movement by *P. burti* is somewhat opposite to that of *P. triacanthus*. *Peprilus burti* migrates offshore during late spring through early fall, then onshore towards shallow bays and inlets during the winter and early spring (Horn, 1970). Spawning by *P. burti* is reported to occur during two distinct periods, February through May and September through November (Murphy, 1981). Unlike these other two species, *P. alepidotus* does not exhibit seasonal migration patterns, remaining in shallow waters throughout the year where it spawns during June and July (Horn, 1970).

During the spring and summer seasons of 1988 and 1989, we consistently collected larval and juvenile *Peprilus* from the South Atlantic and Mid-Atlantic Bights. The combination of their location and dates of capture raised the question as to which species were present in our samples. Although most abundant within the MAB region, *P. triacanthus* is reported to spawn during the summer only (Horn, 1970). According to time of capture, the spring-collected larvae in our SAB samples should have been *P. burti* because they were collected before *P. triacanthus* and *P. alepidotus* supposedly begin to spawn (Horn, 1970; Murphy, 1981). However, their occurrence within the South Atlantic and Mid-Atlantic Bights suggests that they were either *P. alepidotus* or *P. triacanthus*. Thus, the overall aim of this study was to identify the species in our samples and to back-

---

* Contribution 1061 of the Marine Sciences Research Center, State University of New York, Stony Brook, New York 11794-5000.

calculate hatching dates by using validated otolith-increment analysis.

Materials and methods

Collections

Peprilus larvae and juveniles were collected during April and May of 1988 and April of 1989 in the northern SAB, offshore of Cape Hatteras, North Carolina, and June–August of 1988 and 1989 in the MAB, from Long Island, New York, to Cape May, New Jersey (Fig. 1; Table 1).

Fish were collected with a 1-m^2 Tucker trawl and a 5-m^2 Frame trawl. The Tucker trawl had three opening-closing 505-µm mesh nets. Five-minute tows were taken at three primary depth intervals: 0–5 m, 5–10 m, and 10–15 m. For the purpose of this study, all depths were combined. The Frame trawl was fitted with a 2-mm mesh net and towed at the surface for 10 minutes. A flowmeter was attached to each net to estimate the volume of water sampled.

Tucker trawl samples were split in half with a Folsom plankton splitter. One half of each sample was preserved in 5% buffered formaldehyde and used for identification and length and body depth measurements. The other half was preserved in 95% ethanol and used for otolith analysis. Frame samples were preserved in 95% ethanol. Samples were sorted in the laboratory with a dissecting microscope for eggs, larvae, and juveniles.

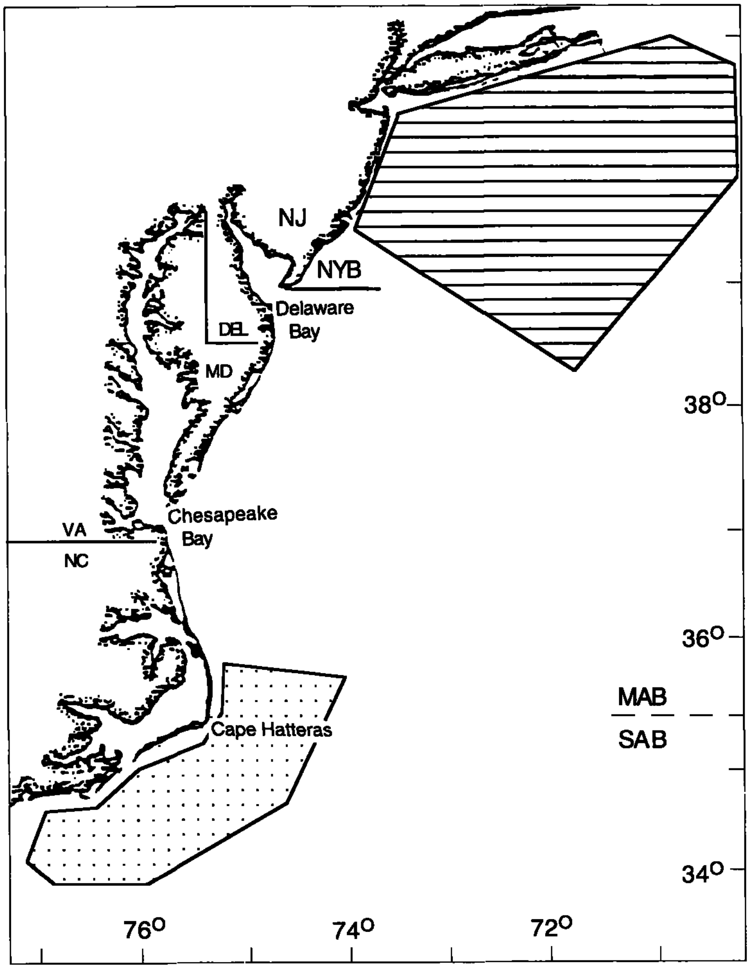

Figure 1

Study area from Cape Hatteras, North Carolina, to Long Island, New York. Dotted and barred areas represent spring and summer sampling areas, respectively.

Morphometrics

Determination of a seasonal difference in body size was accomplished by analyzing body depth (BD) and standard length (SL) for all specimens collected. Measurements were made to the nearest 0.1 mm with either a video-enhanced digitizing system (Optical Pattern Recognition System, BIOSONICS, Inc.) or an ocular micrometer. Standard length was measured from tip of the snout to the tip of notochord. Body depth was measured perpendicular to the longitudinal body axis at the anterior margin of the pectoral base (Ditty, 1981).

To examine differences in body depth between spring and summer seasons, linear regressions of body depth on standard length were calculated for Tucker and Frame cruises, 1988 and 1989. Slopes of regression lines were tested for homogeneity. Allometric effects of growth on body depth were examined by calculating regressions of body depth on standard length as a function of standard length.

Meristics

To determine the species composition of the spring- and summer-collected *Peprilus* larvae, two meristic characters were examined: number of caudal vertebrae and number of ventral midline melanophores. Character counts were compared with published data for each of the three possible species (caudal vertebrae: Ditty, 1981; ventral midline melanophores: Ditty and Truesdale, 1983). Subsamples of specimens were either cleared and stained (Taylor, 1967; Wassersug, 1976; Dingerkus and Uhler, 1977; Potthoff, 1984) or x-rayed (Gosline, 1948; Miller and Tucker, 1979; Tucker and LaRoche 1984; Kosenko et al., 1987). Photomicrographs of cleared and stained specimens were taken and slides developed for further

Table 1

List of 1988 and 1989 cruises, sampling dates, number of fish collected, and locations. SAB = South Atlantic Bight; MAB = Mid-Atlantic Bight.

Net	Cruise	Date	No. of fish captured	Location
1988	DEL88-5-2	24 April–1 May	71	SAB
Frame	ATLANTIC TWIN	21 May–23 May	29	SAB
	DEL88-7-1	1 June–3 June	3	MAB
	DEL88-7-2	11 June–16 June	22	MAB
	DEL88-7-3	6 July–9 July	4	MAB
	DEL88-7-4	16 July–22 July	99	MAB
	DEL88-7-5	29 July–2 August	50	MAB
	DEL88-7-6	8 August–12 August	110	MAB
Tucker	DEL88-7-3	6 July–9 July	188	MAB
	DEL88-7-4	16 July–22 July	1,191	MAB
	DEL88-7-5	29 July–2 August	514	MAB
	DEL88-7-6	8 August–12 August	1,063	MAB
1989				
Frame	FE1-89	25 April–29 April	158	SAB
	ONR1-89	30 May–2 June	8	MAB
	ONR2-89	6 June–7 June	4	MAB
	FE2-89	7 July–10 July	2	MAB
	ONR4-89	18 July–2 August	22	MAB
	ONR5-89	14 August–18 August	170	MAB
Tucker	FE1-89	25 April–29 April	201	SAB
	FE2-89	7 July–10 July	445	MAB
	ONR4-89	18 July–2 August	89	MAB
	ONR5-89	14 August–18 August	146	MAB

inspection. Fish were x-rayed with a Kodak Faxitron at settings of 40 kilovolts, 20 milli-amperes and 30 seconds, which gave the best results with Kodak Industry X negatives. These negatives were placed in a Kodak GBX developer and replenisher solution for 2 to 3 minutes, rinsed in water, placed in a Kodak GBX fixer solution for 5 minutes, rinsed for 15 minutes in water, and dried overnight. Caudal vertebrae were counted with the aid of a dissecting scope and included those vertebrae attached to the first fully formed hemal spine and extending to the urostyle (Gosline, 1960).

Caudal vertebrae counts were made for larvae selected to cover the range of sizes (all were larger than 7 mm, the size at which Ditty (1981) found most fish to have adult characters), body depth-standard length ratios (shallow and deep-bodied), and dates of capture (spring and summer) encountered. Caudal vertebrae were counted for a subsample of 34 cleared-and-stained fish and 64 x-rayed fish from the 1988 Frame trawls and 76 x-rayed fish from the 1989 Frame trawls.

Ventral midline melanophores were counted for a subsample of 50 fish (25 from the spring and 25 from the summer) smaller than 4 mm SL (the size at which Ditty based his observations). These fish were randomly chosen from 1989 formalin-preserved collections. Ventral midline melanophores were considered to be those located between the hindgut and notochord tip (Ditty, 1981).

Otolith marking experiment

Otoliths of 22 fish were marked with oxytetracycline hydrochloride (OTC) in August of 1991 to determine if *Peprilus* larvae and juveniles deposit daily rings. Sizes of fish ranged from 10 to 31 mm SL. Fish were acclimated for two days in a five-gallon bucket with built-in screening that allowed water to flow-through the bucket when it was placed in an aerated seawater bath. Fish were fed twice daily with either live *Artemia* nauplii or live field-captured zooplankton during both acclimation and experimental periods. Experimental conditions were maintained as follows: temperature fluctuated between 12°C and 24°C, salinity ranged from 28 to 30‰, pH varied from 7.6 to 8.0 (however, during marking the pH dropped to 6.5 and 6.6), and the photoperiod remained constant at a 14-h light and 10-h dark cycle.

The marking procedure followed those for mass-marking larvae and juveniles (Hettler, 1984; Tsukamoto, 1985; Muth et al., 1988). Briefly, fish were immersed in a 450 mg/L concentration of OTC for a six-hour period. Fish were covered during the marking period to decrease the amount of light because light may interfere with the effectiveness of tetracycline (Secor et al.[1]). While immersed in the marking solution, four fish died. The remaining 18 fish were transferred from the marking solution and placed inside two five-gallon screened buckets. Two additional fish died during the transfer process. Fifteen of the remaining 16 fish survived until the end of the experiment. At four days after marking, four fish were sacrificed. An additional four fish were sacrificed five days after marking. Three fish were sacrificed eight days after marking.

To add a second mark, the remaining four fish were immersed a second time (12 days after the initial marking) and were fed amphipods and brine shrimp that had been immersed in a 450mg/L OTC seawater solution for five hours. These fish were held and fed in a fresh 450 mg/L concentration of OTC for 16 hours. Ten days after the second immersion the remaining four fish were sacrificed.

All specimens were placed in 95% ethanol for preservation. Otoliths were dissected from fish and placed in immersion oil on glass slides. Otoliths were ground with a size-600 carborundem grit and mineral oil slurry. The tetracycline mark was viewed under a Zeiss ultraviolet microscope with a Zeiss FITC acridine-orange excitation filter set. Increments were counted blindly by one reader, a minimum of three times. If the number of increments between counts differed by more than one, the otolith was not used. The number of increments present after the mark was regressed against the number of days since marking; the regression coefficient was compared with unity by using a *t*-test.

Otolith ageing

Otolith ageing was performed to determine a length-age relationship for our combined *Peprilus* spp. samples. The presence of daily increments in temperate and tropical water fishes has been noted by Pannella (1971, 1974). Fish fixed and preserved in 95% ethanol and ranging in size from 6 to 28 mm SL were aged from 1988 spring (n=30) and summer (n=33) samples to determine seasonal growth rates. Sagittae and lapilli were removed from each fish following the techniques of Brothers (1984). Otoliths were placed in type-B immersion oil and left to clear for one month. Sagittae were analyzed with a video-enhanced digitizing system (Optical Pattern Recognition System) viewed at 250× with an oil immersion lens.

Increments were counted blindly by one reader a minimum of two times. If counts differed between readings by more than three increments, they were not used. Counts were made along the longest radial axis whenever possible (Brothers, 1980). When otoliths were too thick to see increments clearly, they were ground with size-600 carborundem grit and immersion oil to create thinner sections (Brothers, 1980).

A length-at-age relationship was determined by regressing standard length on age. Because most fish deposit increments on their otoliths either at hatching or yolk-sac absorption (Brothers et al., 1976), a y-intercept of hatch size (1.72 mm; Colton and Honey, 1963) was assigned to the regression. The slope of the spring regression, i.e. growth rate, was compared with the slope of the summer regression by means of a homogeneity of slopes test. To determine date of hatching, an age-on-length relation was first determined. The y-intercept for this equation was determined by the best fit of the data. This regression equation was solved for age by using standard lengths of all 1988 and 1989 Tucker- and Frame-caught fish (size range of 6.0–28.0 mm SL). Hatching dates were backcalculated by subtracting age at capture from the capture date. Hatching date distributions were then plotted to determine spawning date distributions for all 1988 and 1989 Frame-trawl–caught and Tucker-trawl–caught butterfish.

Results

Collection

During 1988, 3,980 *Peprilus* were collected in the Tucker trawl (4 cruises; 196 hauls), and 388 in the Frame trawl (8 cruises; 404 hauls). In 1989, 880 Tucker-trawl–caught (4 cruises; 128 hauls) and 364 Frame-trawl–caught (6 cruises; 158 hauls) *Peprilus* were collected. In 1988, the greatest number of larvae and juveniles were caught in Tucker trawls in the MAB, July (n=1,191; 24.3 per haul) through mid-August (n=1063; 21.7 per haul). There were no Tucker trawl collections during the spring of 1988 in the SAB. The highest numbers of *Peprilus* were collected in 1989 cruises from mid-July through early August in the MAB (n=445; 17.8 per haul). In general, the number of fish collected in the Frame trawl was less than in the Tucker trawl. In the 1988 Frame trawls, *Peprilus* were most numerous during late May (n=29; 1.8 per haul) in the SAB and from mid-July (n=99; 2.0 per haul) through mid-August (n=110; 2.2 per haul) in the MAB. Frame trawls for 1989 had the greatest abundances of larvae during late April (n=158; 4.3 per haul) in the SAB and from mid-July through early August in the MAB (n=170; 4.4 per haul).

---

[1] Secor, D. H., E. D. Houde, and D. M. Monteleone. 1995. Development of otolith-marking methods to estimate survival and growth of early life stages of natural and hatchery-produced striped bass in the Patuxent River in 1991. Maryland Department of Natural Resources, Chesapeake Bay Research and Monitoring Division, CBRM-GRF-94-1, 145 p.

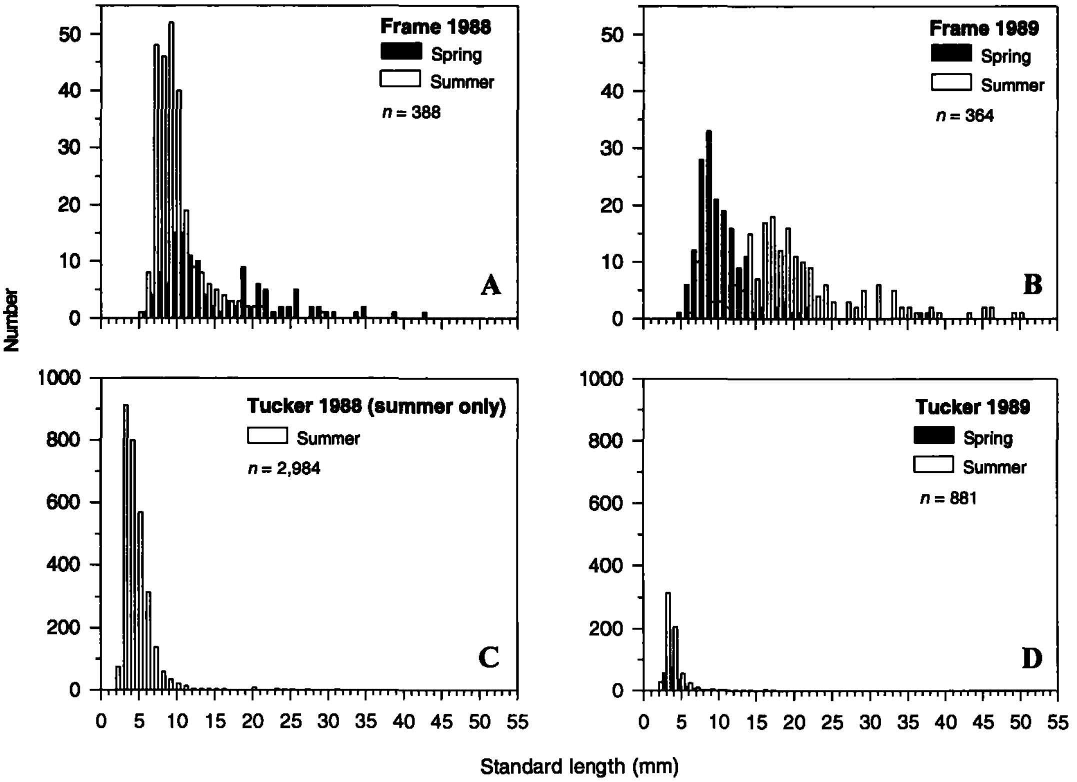

Figure 2

Length-frequency histograms for *Peprilus triacanthus* collected by net during the spring and summer of 1988 and 1989.

Morphometrics

A wide range of sizes of *Peprilus* were collected during both seasons of 1988 and 1989. Because size-frequency distributions had the same mode on all cruises within a season, length frequencies were combined for all fish sampled with a particular gear during each season each year. Spring-collected 1988 fish ranged in size from 6 to 43 mm SL (Frame; Fig. 2A). Similar size distributions of fish were found for the 1989 spring cruises: 4.7 to 37.5 mm SL (Frame; Fig. 2B) and 2 to 6 mm SL (Tucker; Fig. 2D). The 1988 summer trawls collected fish between 5 and 29 mm SL (Frame; Fig. 2A) and 1.3 to 36.0 mm SL (Tucker; Fig. 2C). Summer 1989 fish ranged in size from 6.0 to 50.0 mm SL (Frame; Fig. 2B) and 1.7 to 49.0 mm SL (Tucker; Fig. 2D).

Deep- and shallow-bodied fish were identified from both the spring and summer samples in both years. Fish had BD-SL ratios ranging from 0.119 to 0.750 (Fig. 3, A and B). There was an indication of two modes during both spring and summer of 1989. These BD:SL ranges overlap with ranges reported by Horn (1970) and Ditty (1981) for all species (Table 2). Further analysis of body depth: standard length demonstrated that body depth increases allometrically with respect to standard length up to a size of 10 to 15 mm SL (Fig. 4). Body depth subsequently remained about 50% of length for each year.

Meristics

Ninety-nine percent of the fish collected with the Frame net in 1988 and 1989 had either 18 or 19 caudal vertebrae (of those, approximately 90% had 19 caudal vertebrae; Table 3). Counts of either 18 or 19 caudal vertebrae are consistent with those reported for *P. triacanthus* (Table 3). The number of caudal vertebrae was not related to body depth. According to Ditty and Truesdale (1983), juvenile *P. burti* and *P. alepidotus* have mean body depth-standard length ratios of greater than 0.557 and caudal vertebrae counts of 17–18. However, our findings indicate that fish with high body depth-standard length ratios also had 19 caudal vertebrae.

The fish we sampled had between 8 and 16 ventral midline melanophores. Ditty (1981) reported ranges of 4 to 8 ventral midline melanophores for *P. burti* and 11 to 17 for *P. triacanthus*. Seventy-six percent of our speci-

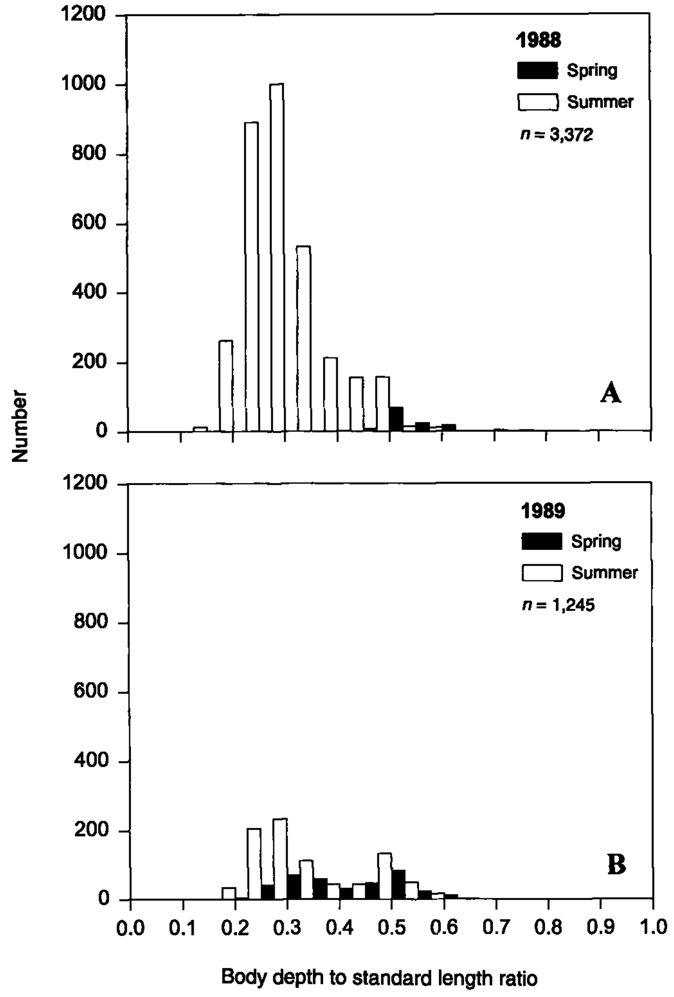

Figure 3

Body depth to standard length-frequency histograms for *Peprilus triacanthus* collected during the spring and summer of 1988 and 1989. Frame- and Tucker-trawl collections were combined.

mens sampled had 11 to 17 ventral midline melanophores, and 94% had 10 to 16 melanophores. These data suggest the presence of *P. triacanthus* in our samples. On further analysis of pigment patterns, we found no difference among specimens (Rotunno, 1992). These data corroborate our caudal vertebral counts.

Otolith marking experiment

Daily increment formation was a valid indicator of age of *Peprilus* spp.. The presence of subdaily increments was also noted in these otoliths. The number of increments observed after the tetracycline mark regressed against the number of days since marking showed a 1:1 correspondence (Fig. 5). A y-intercept value of zero was assigned to the regression. The slope of the regression (0.921) did not differ significantly from unity (t-test: t=0.82, P=0.42).

Growth and hatching date

Spring and summer growth rates were estimated from 1988 collections of *Peprilus* at 0.233 mm/day and 0.219 mm/day, respectively. These growth rates were not significantly different (F=2.071, P=0.155). Therefore, seasons were combined and an overall regression was computed that yielded an average growth rate of 0.225 mm/day (Fig. 6). The regression equation ($Age = 3.433(SL) + 8.270$, r^2=0.93) was used to backcalculate hatching dates from length frequencies. This age-length relation was also applied to 1989 collections for back-calculation purposes.

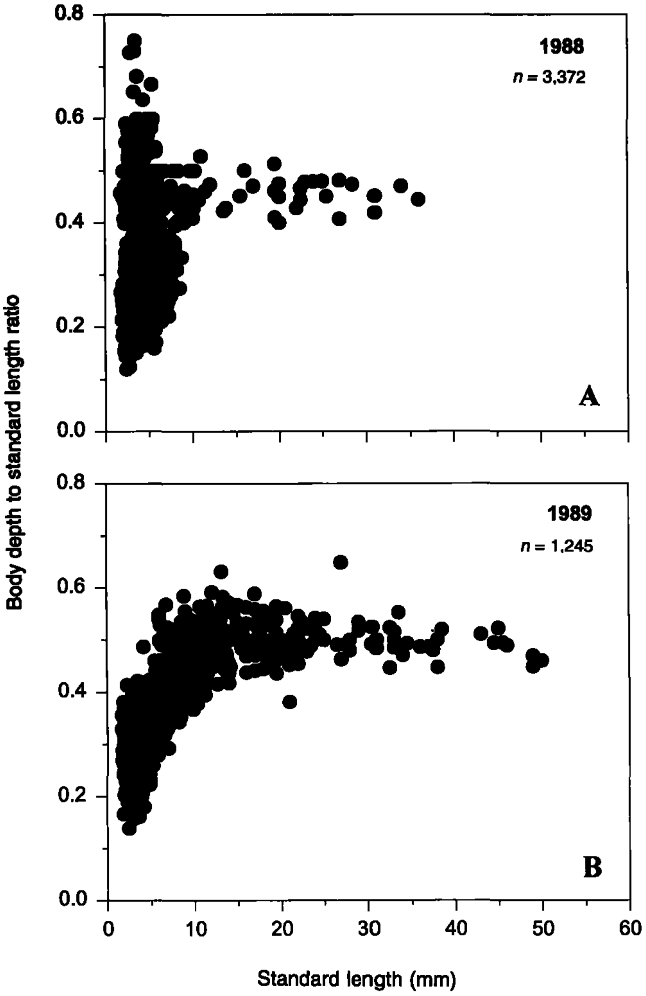

Figure 4

Body depth to standard length versus standard length for *Peprilus triacanthus* collected during the spring and summer of 1988 and 1989. Frame- and Tucker-trawl collections were combined.

Hatching for *P. triacanthus* in our samples occurs from February through at least July and appears to be concentrated in two peaks that occur during early spring and summer (Fig. 7, A and B). The earliest hatching date recorded for fish caught in 1988 was 19 January 1988 and the latest was 22 July 1988. The winter-spring spawning appears to begin in January and continue through late April, with an apparent peak in March in the SAB (Fig. 7A). A decrease in spawning occurs at this time, although some spawning continues at a low level through May (Fig. 7A). Spring-summer spawning occurs during June and July in the MAB with a peak in late June. The relative strength of these two spawnings is not clear because sampling effort was not equivalent during each season.

Fish caught in 1989 had a similar spawning pattern to that of fish collected in 1988; the earliest hatching date calculated was 14 February 1989, the latest was 29 July 1989 (Fig. 7B). Spawning peaks occurred in late March to early April in the SAB and early to mid-June in the MAB. There appears to be a reduction in spawning during the month of May along the U.S. Atlantic coast.

Discussion

Peprilus triacanthus is the most common species of *Peprilus* found along the Atlantic coast of the United States. Within the New York Bight, spawning and larval presence for *P. triacanthus* is reported to oc-

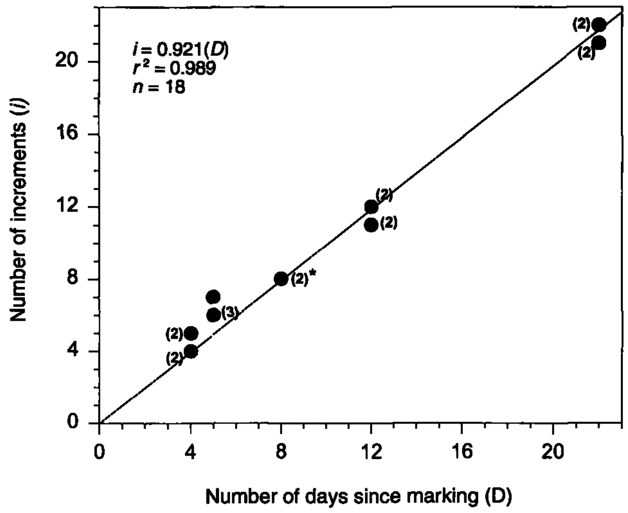

Figure 5

Number of increments observed after oxytetracycline hydrochloride mark versus the number of days since marking for a subsample of 1988 Frame-caught *Peprilus triacanthus.* Numbers in parentheses represent the number of fish. *n = 3, but one otolith was not readable.

Table 2

Body depth-standard length ratios reported by Horn (1970), Ditty and Truesdale (1983), and from our Frame and Tucker trawl surveys.

	Body depth-standard length range	Standard length range (mm)	*n*
Horn (1970)			
P. burti	0.460–0.640	7.80–167.00	232
P. triacanthus	0.364–0.600	10.60–198.00	202
P. alepidotus	0.565–0.877	18.22–222.00	205
Ditty (1981)			
P. burti	0.241–0.579	2.16–19.82	160
P. triacanthus	0.235–0.546	2.04–20.86	159
P. alepidotus	0.205–0.750	1.85–18.92	80
1988 and 1989 Frame and Tucker			
Spring	0.187–0.750	2.01–43.00	496
Summer	0.119–0.727	1.29–50.00	4,121
Spring and Summer	0.119–0.750	1.29–50.00	4,617

cur during summer only (Wilk et al., 1990). Fahay (1975) suggested however, on the basis of the range of larval lengths collected in 1967–68, that spawning of *P. triacanthus* may occur throughout the year in the SAB. The occurrence of larval and pelagic juvenile *Peprilus* within our spring samples collected in the northern SAB suggests two possible scenarios: 1) a species other than the most commonly found *P. triacanthus* spawns within the Atlantic (e.g. *P. burti*) or 2) *P. triacanthus* or *P. alepidotus* has a more protracted spawning season than previously thought. *Peprilus* larvae and juveniles in our samples proved to be *P. triacanthus*; therefore, our results demonstrate an extended spawning period for *P. triacanthus*

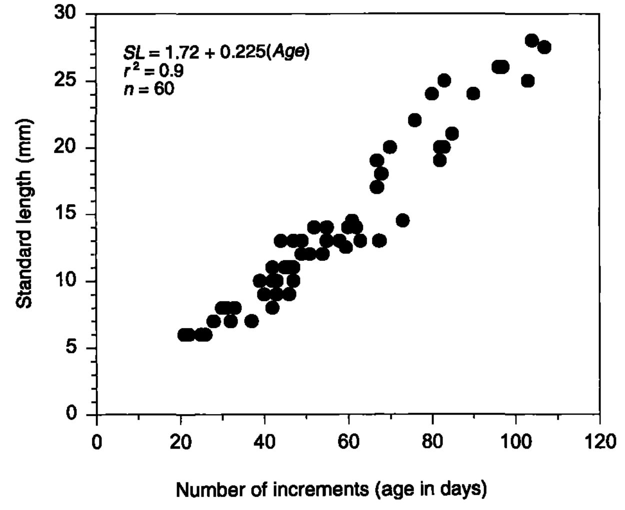

Figure 6

Standard length versus the number of increments for a subsample of 1988 Frame-caught *Peprilus triacanthus*.

Table 3

Vertebral counts for *Peprilus* collected by Collette (1963), Horn (1970), Ditty (1981), and in this study (Frame).

	Standard length (mm) range	16	17	17–18	18	18–19	19	20	*n*
Collette (1963)									
P. burti	—	2	92	0	2	0	0	0	96
P. triacanthus	—	0	4	0	36	0	138	2	180
Horn (1970)									
P. burti	6.0–115.0	5	262	0	6	0	0	0	273
P. triacanthus	6.0–115.0	0	7	0	62	0	208	2	279
P. alepidotus	6.0–115.0	3	176	0	3	0	0	0	182
Ditty (1981)									
P. burti	7.14–14.45	0	13	9	0	0	0	0	22
P. triacanthus	7.14–14.73	0	0	0	1	8	10	0	19
P. alepidotus	7.74–11.01	0	5	0	0	0	0	0	5
Frame									
Spring 1988	8.0–26.0	0	0	0	4	0	48	0	52
Summer 1988	8.0–26.0	0	1	0	6	0	39	0	46
Spring 1989	8.52–37.5	0	0	0	2	0	28	0	30
Summer 1989	8.0–38.0	0	0	0	6	0	39	1	46
Total Frame	8.0–38.0	0	1	0	18	0	154	1	174

in the Atlantic. According to back-calculated hatching dates, *P. triacanthus* spawns from late January through at least July. We did not observe any seasonal differences in body depth. However, geographic differences in body depth need to be further analyzed before discounting the existence of either a polymorphic *P. triacanthus* or a hybrid of *P. triacanthus* and *P. burti*.

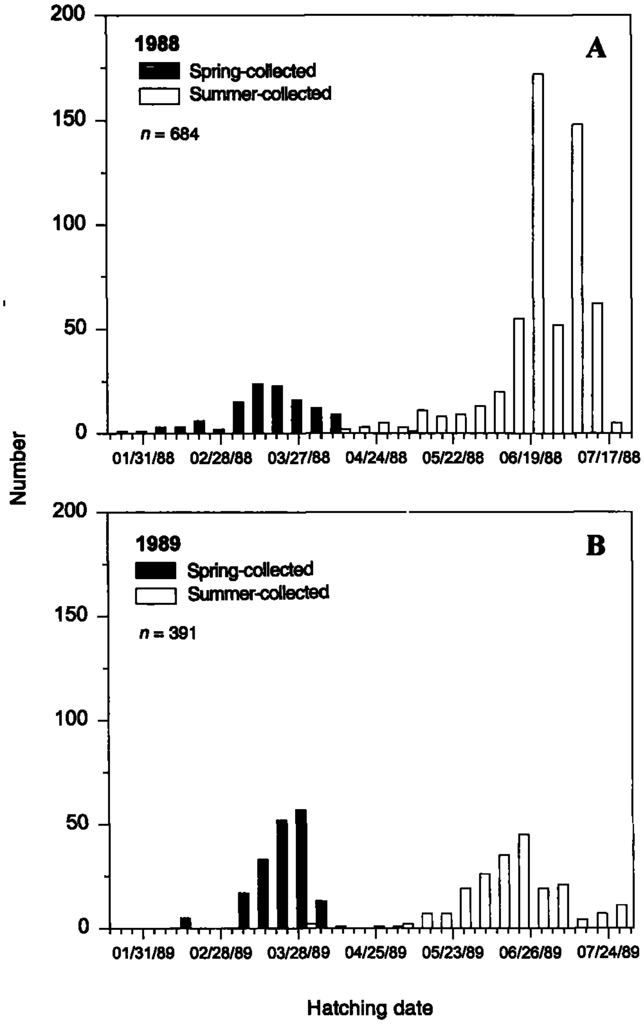

Figure 7

Back-calculated birthdate distributions for all spring and summer samples collected during 1988 and 1989. Frame- and Tucker-trawl samples were combined.

Species identification

According to the reported ranges of body depth-standard length ratios (Horn, 1970; Ditty and Truesdale, 1983), our larval specimens could have been any one of the Atlantic or Gulf coast species of *Peprilus*. However, two points must be considered when interpreting these data. First, we found a strong allometric relation between body depth and standard length for individuals smaller than 15 mm SL. Because the collections of Horn (1970) include fish ranging in size from 6 to 222 mm SL, this allometric relation could have confounded his conclusions. Ditty and Truesdale (1983), however, apparently recognized this problem and therefore presented their data by size class. Second, our other analyses (caudal vertebrae and melanophore counts) supported the contention that *P. triacanthus* was the dominant species of *Peprilus* in our samples. Our sample was predominantly composed of individuals with 19 caudal vertebrae, which was consistent with findings of previous authors for *P. triacanthus* (Collette, 1963; Horn, 1970; Ditty and Truesdale, 1983). The ventral midline melanophore counts were also similar to those used for *P. triacanthus* by Ditty (1981).

The overall results of the above morphometric, meristic, and pigment analyses lead us to conclude that *P. triacanthus* is the dominant and probably the only species of *Peprilus* collected in our samples. The two most definitive characters for identification were the number of caudal vertebrae and ventral midline melanophores.

Age and growth

Ages of larval and juvenile *P. triacanthus* can be determined by counting otolith increments. Validation was necessary because of the prevalence of subdaily increments in this species. Secondary nuclei (multinucleation) were also noted in *Peprilus otoliths*. The cause and timing of the formation of secondary nuclei are not presently understood (Campana and Neilson, 1985), although these secondary nuclei have been demonstrated to form during metamorphosis in bluefish (Hare and Cowen, 1994). Secondary nuclei, in butterfish otoliths, do not seem to follow a consistent pattern in the development of the fish; we found that two sagittal bones from one fish frequently contained differing numbers of secondary nuclei. Although secondary nuclei may form during metamorphosis (Campana and Neilson, 1985; Hare and Cowen, 1994), we found secondary nuclei in larvae that were several millimeters smaller than the size at which metamorphosis occurs (16 mm).

Larval and early juvenile *P. triacanthus* from 6.0 to 28.0 mm SL grew at a rate of 0.227 mm/day. Although ages of young butterfish have not been recorded previously, Colton and Honey (1963) gave sizes of *P. triacanthus* from hatching to six days of age. Based on their estimates, growth rates ranged from 0.01 to 0.55 mm/day and decreased with the age of the fish. Specimens of young *P. burti* have been aged with modal length-frequency analysis; growth rates of *P. burti* ranged from 0.25 to 0.56 mm/day (Murphy and Chittenden, 1990). *Peprilus burti* may be expected to have a higher growth rate than *P. triacanthus* owing to the fact that it spawns in warmer waters of the Gulf of Mexico.

Our analysis of hatching-date distributions demonstrated that *P. triacanthus* has a more extensive spawning season than previously reported. Their spawning effort seems to be focused into two cohorts (spring: February–March; and summer: June–July) although evidence is presented that suggests at least some fish spawn during the interim period between seasonal peaks (i.e. late April to early June). Kawahara[2] speculated that *P. triacanthus* may begin spawning in April. It should be noted that Kawahara (1977) based his spawning estimate on adult growth rates, which are higher than our estimate for larvae and juveniles and, therefore, would have underestimated the spawning duration.

A bimodal hatching-date distribution in *P. triacanthus* is similar to that reported for another north-south migrating species within the western Atlantic, the bluefish, *Pomatomus saltatrix* (Kendall and Walford, 1979; Nyman and Conover, 1988). However, Hare and Cowen (1993) and Smith et al. (1994) have proposed that *P. saltatrix* spawns continually during its north-south migration and that the apparent bimodal hatching date distribution may result from advective processes acting on the larval distributions and from sampling artifact.

The presence of an apparent bimodal spawning in *P. triacanthus*, with spring and summer peaks, may be an artifact of our sampling. Because we did not sample from April to June in each year and because our sampling locations were spatially distinct between spring and summer, it is possible that we did not collect larvae spawned during May and early June. However, we could have collected older fish in our samples that were spawned early in June. Data collected monthly by the National Marine Fisheries Services (NMFS) as part of their Monitoring, Assessment, and Prediction (MARMAP) surveys suggest that larvae are indeed present from April to August in the MAB, thus it is likely that spawning occurs continually (Fig. 8). Moreover, MARMAP data indicate a northward progression of larvae from near Cape Hatteras during March or April (or both) into the entire MAB by mid-summer and until October. This spatio-temporal pattern is consistent with the possibility of spawning associated with a seasonal northward migration of adult *P. triacanthus*. Horn (1970) has speculated that butterfish movements are highly influenced by temperature (and salinity to a lesser degree). Temperature-related movements by butterfish (and bluefish) would correspond with the observed northward progression of young larvae from the SAB in the spring into the MAB in the summer in association with seasonal warming. The extent of north-south migration by *P. triacanthus*, however, requires further study.

In conclusion, this study adds to our current knowledge of the early life history and spawning seasonality of butterfish, *P. triacanthus*. Our finding of a more protracted spawning season and of a seasonal difference between spawning locations should be of value in reassessing management plans for this species. Current management plans are based on conclusions that *P. triacanthus* spawns during summer months only. The apparent similarity of spawning periodicity of butterfish to that of bluefish (Cowen et al., 1993; Hare and Cowen, 1994, Smith et al., 1994) suggests

---

[2] Kawahara, S. 1977. Age and growth of butterfish, *Peprilus triacanthus* (Peck), in ICNAF Subarea 5 and Statistical Area 6. ICNAF Res. Doc. 77/VI/27. June 1977 Annual Meeting. Far Seas Fishery Laboratory, Shimizu, Japan.

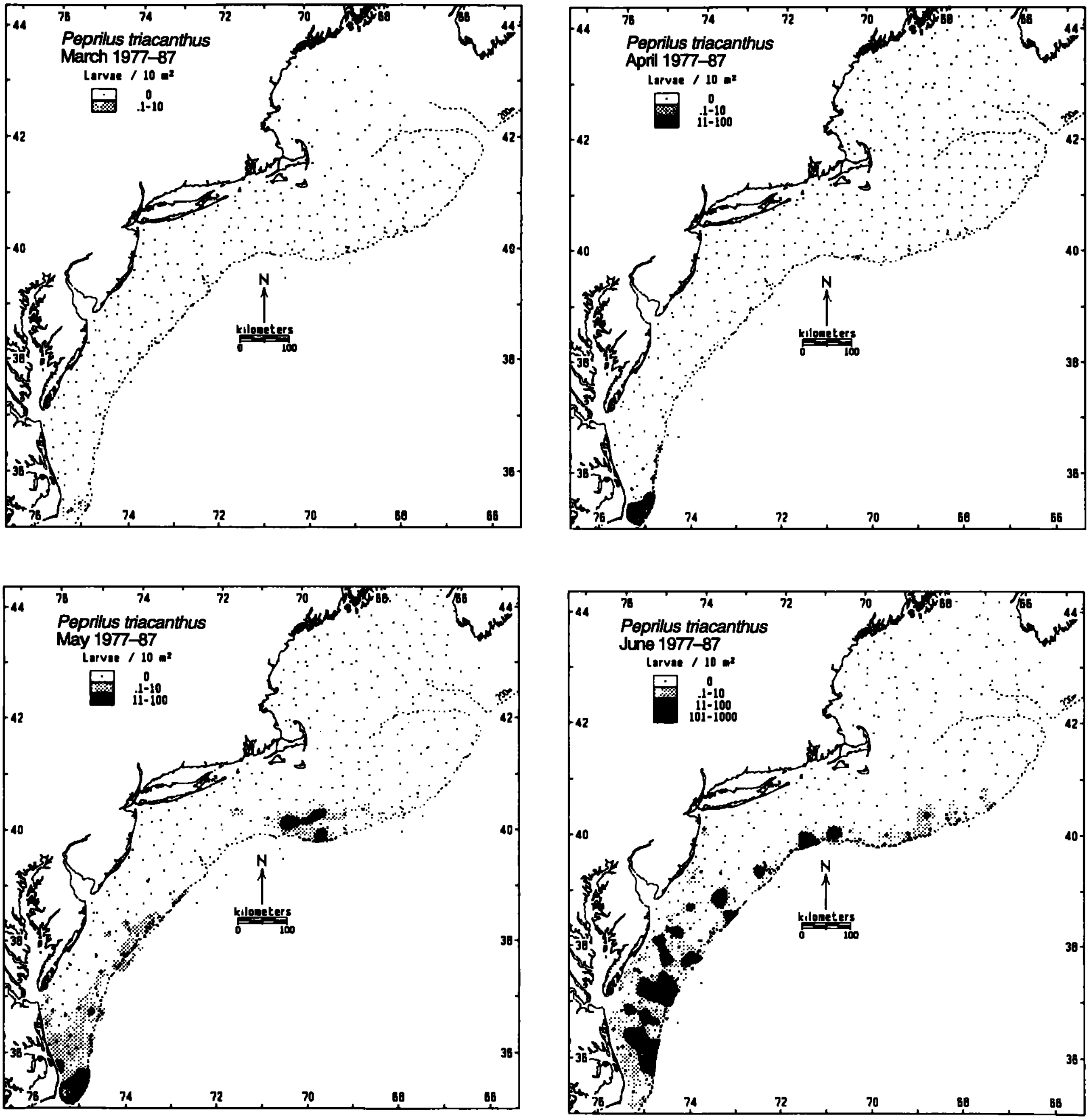

Figure 8

MARMAP monthly averaged collections (March through October) of larval *Peprilus triacanthus* during the years (1977–87).

that a possible adaptive strategy may be shared by these two seasonally migrating pelagic species. Perhaps with closer inspection, other seasonally migrating species may be found that share this spawning strategy (Hare and Cowen, 1996). Further study into the basis of this pattern is warranted.

Acknowledgments

We would like to thank all the people who assisted during the cruises and in the laboratory. In addition, comments on earlier drafts were provided by Jeff Buckel, Dave Conover, Steve Morgan, Michael Murphy,

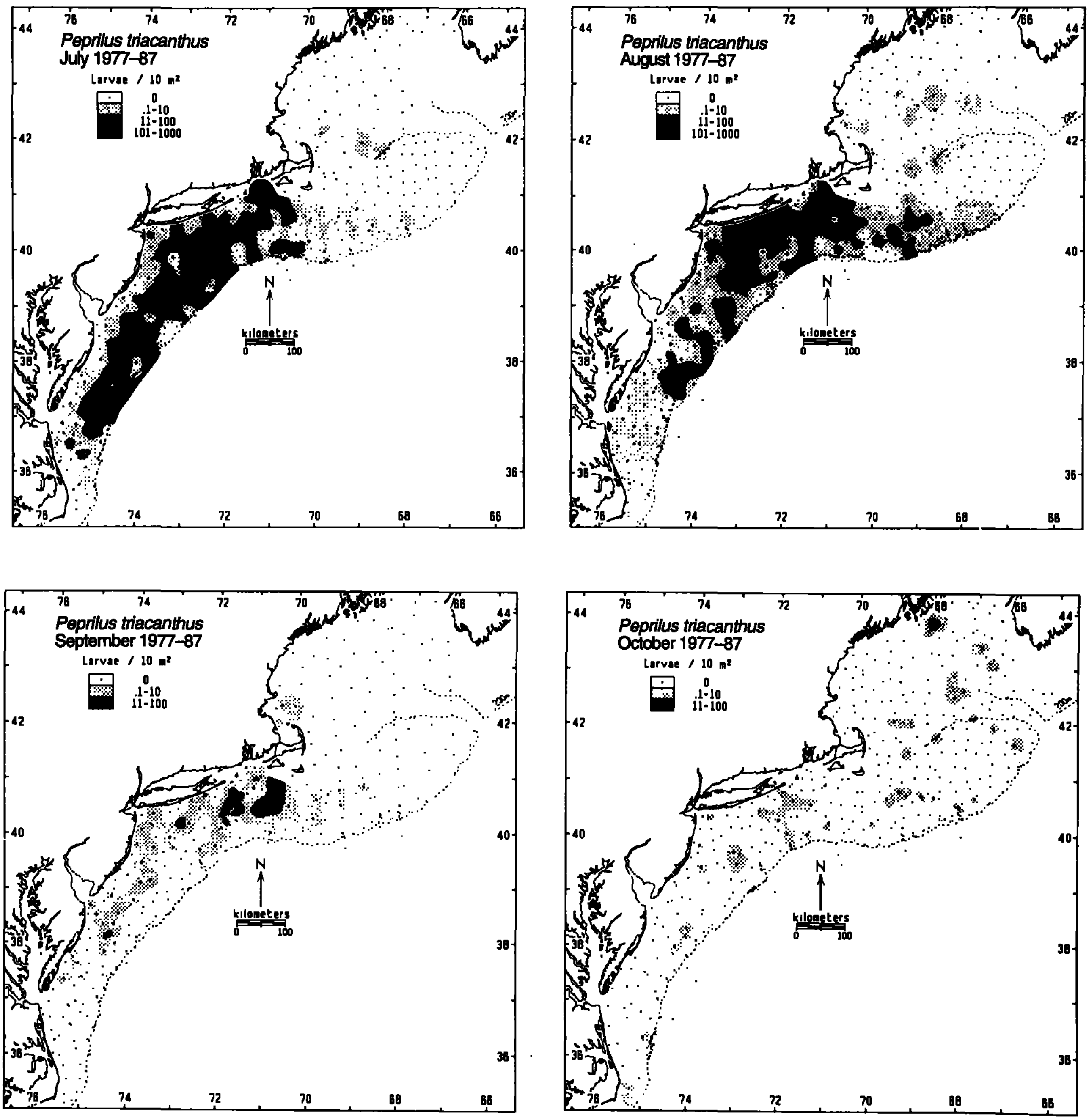

Figure 8 (continued)

and two anonymous reviewers. Jon Hare provided help with all phases of larval identification and otolith analysis. Mike Fahay generously provided Figure 8. This work is a result of research sponsored by the NOAA Office of Sea Grant, U.S. Department of Commerce, under Grants #NA86AA-D-SG045 and #NA90AA-D-SG078 to the New York Sea Grant Institute.

Literature cited

Brothers, E. B.

1980. Methodological approaches to the examination of otoliths in aging studies. *In* R. C. Summerfelt and G. E. Hall (eds.), Age and growth of fish, p. 319–330. Iowa State Univ. Press, Des Moines, IA.

1984. Otolith studies. *In* Moser et al. (eds.), Ontogeny and systematics of fishes, p. 50–57. Spec. Publ. Am. Soc. Ichthyol. Herp. 1.

Brothers, E. B., C. P. Mathews, and R. Lasker.
1976. Daily growth increments in otoliths from larval and adult fishes. Fish. Bull. 74(1):1–557.

Caldwell, D. K.
1961. Populations of butterfish, *Poronotus triacanthus* (Peck), with systematic comments. Bull. S. Cal. Acad. Sci. 60:19–31.

Campana, S. E., and J. D. Nielson.
1985. Microstructure of fish otoliths. Can. J. Fish. Aquat. Sci. 42:1014–1033.

Collette, B. B.
1963. The systematic status of the Gulf of Mexico butterfish, *Poronotus burti* (Fowler). Copeia 1963(3):582–583.

Colton, J. B, Jr., and K. A. Honey.
1963. The eggs and larval stages of the butterfish, *Poronotus triacanthus*. Copeia 1963(2):447–450.

Cowen, R. K., J. A. Hare, and M. P. Fahay.
1993. Beyond hydrography: Can physical process explain larval fish assemblages within the Mid-Atlantic Bight? Mar. Ecol. Prog. Ser. 53(2):567–587.

Dingerkus, G., and L. D. Uhler.
1977. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. Stain Tech. 52(4):229–232.

Ditty, J. G.
1981. Comparative morphological development of *Peprilus burti*, *Peprilus triacanthus*, and *Peprilus paru* (Pisces: Stromateidae) from the Western North Atlantic. M.S. thesis, Louisiana State Univ., Baton Rouge, LA, 39 p.

Ditty, J. G., and F. M. Truesdale.
1983. Comparative larval development of *Peprilus burti*, *Peprilus triacanthus*, and *Peprilus paru* (Pisces: Stromateidae) from the Western North Atlantic. Copeia 1983(2): 397–406.

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. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-685, 39 p.

Gosline, W.A.
1948. Some possible uses of x-rays in ichthyology and fishery research. Copeia 1948(1):58–61.
1960. Contributions toward a classification of modern isospondylous fishes. Bull. Br. Mus. (Nat. Hist.) Zool. 6:327–365.

Haedrich, R. L.
1967. The stromateoid fishes: systematics and a classification. Bull. Mus. Comp. Zool. 135(2):31–139.

Hare, J. A., and R. K. Cowen.
1993. Ecological and evolutionary implications of the larval transport and reproductive strategy of bluefish *Pomatomus saltatrix*. Mar. Ecol. Prog. Ser. 98:1–16.
1994. Ontogeny and otolith microstructure of bluefish *Pomatomus saltatrix* (Pisces: Pomatomidae). Mar. Biol. (Berl.) 118:541–550.
1996. Transport mechanisms of larval and pelagic juvenile bluefish *(Pomatomus saltatrix)* from the South Atlantic Bight spawning grounds to the Middle Atlantic Bight nursery habitats. Limnol. Oceanogr. 41:1264–1280.

Hettler, W. F.
1984. Marking otoliths by immersion of marine fish larvae in tetracycline. Trans. Am. Fish. Soc. 113:370–373.

Horn, M. H.
1970. Systematics and biology of the stromateoid fishes of the genus *Peprilus*. Bull. Mus. Comp. Zool. 140(5):165–262.

Kendall, A. W., Jr., and L. A. Walford.
1979. Sources and distribution of bluefish, *Pomatomus saltatrix*, larvae and juveniles off the east coast of the United States. Fish. Bull. 84:91–103.

Kosenko, N. A., L. A. Nikolaychuk, and A. A. Vronskly.
1987. Applications of electroradiography to studies of skeletons of fishes. J. Ichthyol.. 27(1):126–128.

Miller, J. M., and R. W. Tucker Jr.
1979. X-radiography of larval and juvenile fishes. Copeia 1979(3):535–538.

Murphy, M. D.
1981. Aspects of the life history of the Gulf butterfish, *Peprilus burti*. M.S. thesis, Texas A&M Univ., Galveston, TX, 76 p.

Murphy, M. D., and M. E. Chittenden Jr.
1990. Reproduction, age and growth, and movements of the Gulf butterfish, *Peprilus burti*. Fish. Bull. 89:101–116.

Muth, R. T., T. P. Nesler, and A. F. Wasowicz.
1988. Marking cyprinid larvae with tetracycline. Am. Fish. Soc. Symp. 5: 89–95.

Nyman, R. M., and D. O. Conover.
1988. The relation between spawning season and the recruitment of young-of-the-year bluefish, *Pomatomus saltatrix*, to New York. Fish. Bull. 6(2):237–250.

Pannella, G.
1971. Fish otoliths: daily growth layers and periodical patterns. Science (Washington, D.C.) 173:1124–1127.
1974. Otolith growth patterns: an aid in age determination in temperate and tropical fishes. *In* T. Bagenal (ed.), Ageing of fish, p. 28–39. Unwin Bros. Ltd., London.

Perschbacher, P. W., K. J. Sulak , and F. J. Schwartz.
1979. Invasion of the Atlantic by *Peprilus burti* (Pisces: Stromateoidae) and possible implications. Copeia 1979:538–541.

Potthoff, T.
1984. Clearing and staining techniques. *In* Moser et al. (eds.), Ontogeny and systematics of fishes, p. 35–37. Spec. Publ. Am. Soc. Ichthyol. Herp. 1.

Rotunno, T. K.
1992. Species identification and temporal spawning patterns of butterfish, *Peprilus* spp., in the south and mid-Atlantic Bights. M.S. thesis, State Univ. New York, Stony Brook., NY, 77 p.

Smith, W., P. Berrien, and T. Potthoff.
1994. Spawning patterns of bluefish, *Pomatomus saltatrix*, in the northeast continental shelf ecosystem. Bull. Mar. Sci. 54:8–16.

Taylor, W. R.
1967. An enzyme method of clearing and staining small vertebrates. Proc. U.S. Natl. Mus. 122(3596):1–17.

Tsukamoto, K.
1985. Mass-marking of Ayu eggs and larvae by tetracycline tagging of otoliths. Bull. Jap. Soc. Sci. Fish. 51(6):903–911.

Tucker, J. W., and J. L. Laroche.
1984. Radiographic techniques in studies of young fishes. *In* H. G. Moser et al. (eds). Ontogeny and systematics of fishes, p. 37–39. Spec. Publ. Am. Soc. Ichthyol. Herp. 1.

Wassersug, R. J.
1976. A procedure for differential staining of cartilage and bone in whole formalin-fixed vertebrates. Stain Tech. 51(2):131–134.

Wilk, S. J., W. W. Morse, and L. L. Stehlik.
1990. Annual cycles of gonad-somatic indices as indicators of spawning activity for selected species of finfish collected from the New ork Bight. Fish. Bull. 88: 775–786.