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Spring and Summer Larval Fish Assemblages in the Surf Zone and Nearshore off Northern New Jersey, USA

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Abstract Larval fish use of surf zone and nearshore habitats at northern latitudes has received little attention. Consequently, potential impacts of beach nourishment and other forms of disturbance are not well understood. This study, on a northwestern Atlantic coastline spanning May through July over 4 years, demonstrates that recently hatched larvae are common in both surf zone and nearshore habitats. Taxonomic compositions of surf zone and nearshore assemblages were similar to each other and those from an adjacent estuary. An influence of upwelling events was apparent in coincident changes in abundance and/or size of several species in the surf zone. Other changes over the late spring–summer transition, including buoyancy-driven flows from the Hudson River plume, demonstrate the dynamic nature of larval fish assemblages in the New York Bight area.

Keywords Ichthyoplankton · Environmental monitoring · Seasonality

Introduction

Sandy-shore ecosystems are extensively altered world-wide and may be threatened with rising sea levels, yet we know little of how they function (Ross 1983; Brown and Mclachlan 2002; Finkl et al. 2006; McLachlan and Brown 2006; Schlacher et al. 2008). For instance, their role as larval fish habitat is poorly understood, in part, because the turbulent shallow surf zone environment is difficult to sample using traditional methods (Borges et al. 2007; Strydom 2007). In contrast to ecological characterizations of larval fish assemblages in coral reef (e.g., Mora and Sale 2002; DeMartini and Friedlander 2004), rocky reef (e.g., Borges et al. 2007; Marliave 1986), shelf/bay (e.g., Cowen et al. 1993; McBride and Able 1994; Jessop et al. 2007), and estuarine (Allen and Barker 1990; Able and Fahay 1998; Witting et al. 1999) environments, far less is known about the larval fish composition of shallow nearshore and surf zones. Studies of surf zone larval fish ecology are restricted in geographic scope, primarily to South Africa (Whitfield 1989; Cowley et al. 2001; Harris et al. 2001; Watt-Pringle and Strydom 2003), Mauritius (Sato et al. 2008), and Japan (Senta and Kinoshita 1985; Suda et al. 2002), and studies in the USA are limited to the Gulf of Mexico (Ruple 1984; Sanvicente-Añorve et al. 1998).

The role of surf zone habitat for fish larvae in the northeastern United States is currently not well known, but has ecological and management consequences. For instance, larval estuarine-dependent fish may accumulate in surf zones while in transit from offshore spawning grounds to estuaries (Boehlert and Mundy 1988; Strydom 2003). Although sandy shorelines are commonly affected by disturbances such as coastal development and beach nourishment, the lack of information concerning the dependence of larval fish on surf zones affects efforts to

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minimize potential impacts from these projects as well as develop appropriate monitoring practices. For instance, understanding temporal patterns of surf zone habitat use is necessary for natural resource managers to evaluate project schedules and the appropriateness of monitoring practices. Setting priorities for habitat conservation also requires knowledge of species that utilize surf zone and nearshore areas during early life stages.

This study was conducted as part of a broader investigation of the potential impacts of beach nourishment in northern New Jersey on environmental factors such as suspended sediments (Wilber et al. 2006) and biotic resources that include benthic infauna, fish abundance, and food habits (Burlas et al. 2001) and surf zone fish distribution patterns (Wilber et al. 2003a, b). This study provides a new understanding of surf zone and shallow nearshore larval fish assemblages in the region and focuses on temporal and spatial patterns of distribution, abundance, size, stage, and species composition for May–July sampling from 1995 through 1999.

Materials and Methods

Site Description

The study area is located on a 15-km stretch of beach on the coast of New Jersey in the Middle Atlantic Bight (Fig. 1). The beaches in this region are typically high-energy, exposed and steeply sloped. Wave heights average 0.3 to 1.2 m with a period of 5 to 9 s and a tidal range of approximately 1.4 m. The beach is divided at regular intervals by groin structures (Nordstrom et al. 1977). Manasquan and Shark River Inlets are located at the southernmost extent and approximate center of the study area, respectively (Fig. 1).

Sampling

Daytime sampling occurred monthly from May to July, 1995 through 1999 with each sampling event occurring over a 4–6 day period (Table 1). Sampling was conducted in two zones relative to the beach, surf zone (generally within 50 m of the MLW mark at approximately 2–3 m depth) and nearshore (along the 6–7 m depth contour). Surf zone sampling consisted of 22 sampling stations spaced fairly evenly throughout the area (Fig. 1). At each site, a 0.5-m (505 µm mesh) plankton net with a three-point bridle was deployed 50 m from shore by a swimmer and then towed to shore by a team on the beach. Preliminary sampling was conducted to determine the number of tows needed to accumulate approximately 100 m^3 of water sampled. This resulted in 21 daytime tows being performed at each site on each day. The contents of all the tows were pooled and fixed with 5% formalin. Sampling was conducted simultaneously by two crews on different areas of the beach with care taken to avoid sampling near both inlets on the same day (with one exception, June 26, 1997). Nearshore sampling consisted of five replicate 5-min tows conducted at nine sites (Fig. 1) along the 6.5-m depth contour with double side-by-side 1.0 m (505 µm mesh) bongo nets. Separate surface and bottom tows were made at each site with bottom tows approximately 1–2 m off the bottom. Samples from each of the double bongo nets were pooled and fixed with 5% formalin. A General Oceanics flow meter was attached to each net. Larval abundance is expressed as number per 100 m^3. There was no opening/closing device on the bottom nets. Therefore, there was a short water-column contribution to the bottom samples. Water-quality data included salinity, dissolved oxygen (DO), temperature, and turbidity (NTU). These data were collected with a HydroLab® data logger deployed 50 m from the beach at the beginning of sampling at each surf zone station. Data were recorded at 10-min intervals and then averaged for each sampling site over the period of data logger deployment.

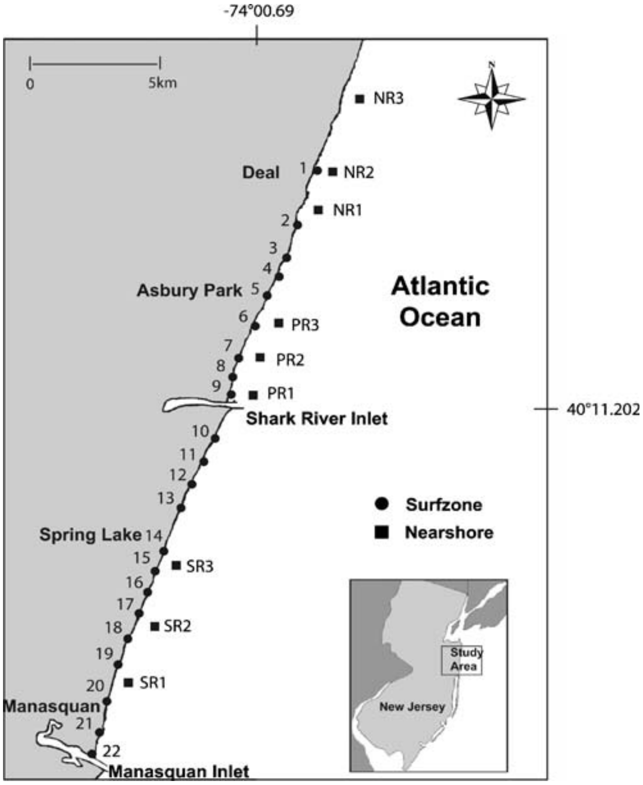

Fig. 1 Larval fish sampling locations in northern New Jersey from 1995 to 1999. Surf zone sites (*circles*) are numbered from 1–22 while nearshore sites (*squares*) have an alpha-numeric designation corresponding to North (*NR*), Project (*PR*) and South (*SR*) sampling areas

For both nearshore and surf zone samples, contents were transferred from the formalin solution and placed into 95%

Table 1 Range of environmental values observed among the 22 stations during each sampling period for water-quality parameters measured in the surf zone of northern New Jersey

Sampling period	Stations	Salinity	Temperature (°C)	Dissolved oxygen (mg/L)	Turbidity (NTU)	Correlated variables	*r*
May 1996	22	21.6–32.3	*9.5–17.0*	*7.9–14.1*	*3.2–53.6*	Sal x DO	−0.77
						Temp x Sal	−0.84
June1996	16	24.6–29.6	17.9–20.6	7.6–11.7	3.7–42.8	Temp x Sal	−0.60
July 1996	21	*27.3–33.0*	*16.5–22.9*	*6.0–9.8*	1.2–130.5	Sal x DO	−0.76
June 1997	16	*28.8–31.3*	*17.2–20.6*	*7.2–10.7*	*3.4–24.6*	Sal x DO	−0.81
						Sal x NTU	0.86
						Temp x NTU	−0.71
						Temp x Sal	−0.81
July 1997	17	*28.9–31.7*	17.5–22.4	*6.9–8.6*	4.0–17.4	Sal x DO	−0.74
May 1998	19	22.1–25.0	*14.8–19.4*	11.8–15.5	0.9–14.8	-	–
June 1998	11	23.3–29.0	*16.6–21.4*	8.5–13.9	2.9–15.9	Temp x Sal	−0.78
						NTU x DO	−0.75
July 1998	10	*27.8–30.4*	*15.3–21.1*	6.3–7.9	1.2–6.7	Temp x Sal	−0.97
May 1999	6	31.0–31.9	11.8–15.2	6.6–8.6	1.5–15.5	Few data	
June 1999	9	29.3–32.0	*14.0–19.4*	6.3–8.4	1.8–38.4	Temp x Sal	−0.89
						Temp x NTU	−0.80
July 1999	22	*29.9–31.5*	*18.2–23.1*	*7.1–10.1*	0.1–5.3	Temp x Sal	−0.84

The number of stations for which data were available is given in column 2. Correlations are reported for all significant pairwise comparisons of environmental data for each sampling period. Data ranges in italics print depict significant differences between sampling dates within a sampling period ($p<0.001$, Bonferroni correction)

ethanol in the laboratory prior to removal of fishes. In instances where there was a great deal of detritus or amphipods that hindered sorting, the samples were split with a modified Folsom® plankton splitter. The sorted samples were separated by species, enumerated, and 20 individuals of each species were measured to the nearest millimeter. Individuals less than 10 mm were measured with an ocular micrometer, whereas those greater than 10 mm were measured with a dial caliper. For measured individuals, flexion stage also was recorded (Kendall et al. 1984). Standard length (SL) was recorded for post-flexion individuals and notochord length (NL) was recorded for pre-flexion and flexion individuals.

Statistical Methods

Spatial and temporal patterns in taxonomic composition were analyzed separately within the nearshore and surf zone larval fish assemblages because of differences in sampling techniques. Multivariate analyses were conducted using Primer-E statistical software (Clarke and Gorley 2001). Analysis of similarities tests (ANOSIM, Clarke and Warwick 2001) were conducted primarily at the level of species. However, data were aggregated at the genus level for those taxa in which a substantial number of individuals were identified at a lowest practical identification level such as the genus (e.g., *Anchoa* spp., *Anchoa mitchilli*, *Anchoa hepsetus*) to reduce the effects of identification-related redundancies in the data. Fourth-root transformations were conducted prior to calculation of Bray–Curtis similarity indices and non-metric multi-dimensional scaling ordinations (nMDS). ANOSIMs were used to separately test for monthly differences in the nearshore and surf zone assemblages. The potential for the inlets to influence assemblage composition was examined by comparing stations near inlets (Stations 7–12 and 20–22) with assemblage composition at the other stations. Beach location also was analyzed by comparing stations north and south of the Shark River Inlet for the surf zone samples and comparing among the North, Project, and South areas for nearshore samples (Fig. 1). ANOSIM generates a test statistic *R* that is close to 0 when no differences in assemblages exist between levels of a factor and approaches 1 as assemblage composition becomes more dissimilar. In this study, we treat *R* values>0.5 as indicating clear differences between groups with some degree of overlap (Clarke and Gorley 2001). Taxa contributing most substantially to differences between areas and time periods were identified by similarity percentages (SIMPER).

The taxonomic composition of the larval fishes captured in the surf zone was compared to nearshore samples following standardization of the data to account for the different sampling methods used in each habitat type. Thus, ANOSIM and nMDS analyses were performed using the percent composition of each taxon rather than abundance data for the analyses comparing surf zone and nearshore assemblages. Analyses were conducted separately by month. Taxa that accounted for at least 5% of the dissimilarity between surf zone and nearshore assemblages (SIMPER) are reported.

Salinity, dissolved oxygen, turbidity, and temperature data were examined for spatial and temporal patterns and correlations among variables. These water-quality parameters met normality and homogeneity of variance assumptions and were tested for differences among days within sampling periods with analysis of variance (ANOVA) tests using SYSTAT (Wilkinson 1990). A Bonferroni correction was used to control for multiple tests. The water-quality conditions were compared to nearshore and surf zone larval fish distributions through BIOENV and RELATE tests (Clarke and Warwick 2001) following normalization and Euclidean transformations of the data. Individual species with adequate abundances were tested for differences in density and size between days within sampling periods that differed in physical conditions using ANOVAs following log-transformations of the abundance data.

Results

Environmental Characteristics

Environmental conditions varied substantially within the 4–6-day-long sampling periods. For instance, environmental parameters differed significantly among dates of sampling within nine sampling periods (Table 1). Temperature was the most variable parameter, differing significantly among days of sampling in eight sampling periods (Table 1). These differences did not reflect localized spatial conditions involving sampling contiguous stations on the same day because two sampling crews worked simultaneously on most sampling dates on different sections of the study area. With one exception (June, 1997), water-quality parameters at stations near inlets did not differ from those of other stations. The exception occurred during the only sampling period in which station location (inlet vs. non-inlet) and sampling day factors were confounded. The daily variation in water quality was not due to independent fluctuations in the environmental parameters, but rather the environmental variables were correlated within sampling periods in a consistent manner (Table 1). For instance, there were negative pairwise associations between salinity and dissolved oxygen, temperature and salinity, temperature and turbidity, and dissolved oxygen and turbidity. The only positive pairwise association was between salinity and turbidity. The stations with relatively high and low values for each parameter were neither adjacent to the inlets nor consistently located elsewhere within the study area. Daily differences in environmental conditions and the consistency of correlations among the parameters indicate the temporary presence of water masses with the combined attributes of lower temperature, higher salinity, lower dissolved oxygen, and higher turbidity.

The mean values of environmental parameters for each sampling period were moderately different among months (ANOSIM $R=0.40$). The distinction in physical conditions among months was most attributable to temperature, which contributed most to distinguishing May sampling periods from June and July, whereas turbidity differed most between June and July sampling periods (SIMPER).

Larval Temporal Characteristics

There was no obvious correspondence in monthly fluctuations between the surf zone and nearshore habitats (Fig. 2). Nearshore larval fish abundances varied greatly among sampling periods and did not differ significantly among months, averaging 767, 1,883, and 632 larvae/100 m^3 for May, June, and July, respectively. Overall abundances of surf zone fish larvae were significantly higher in May (F=4.56,

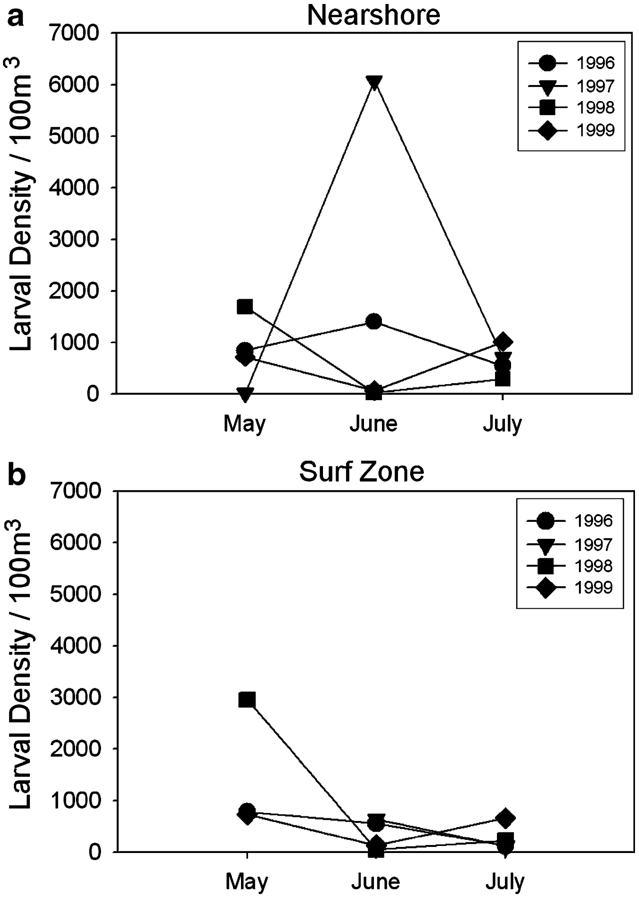

Fig. 2 Monthly larval fish densities at **a** nearshore and **b** surf zone habitats for each year of sampling

Table 2 Overall abundance and average density (number/100 m^3) of fish larvae from nearshore and surf zone habitats collected in northern New Jersey from 1995 through 1999

			Nearshore		Surf zone	
Family	Species	Origin	Abundance	Density (SE)	Abundance	Density (SE)
Achiridae	*Trinectes maculatus*	E	1	0.28	–	–
Ammodytidae	*Ammodytes* spp.	O	15	0.20(0.03)	2	2
Atherinopsidae	Atherinopsidae spp.	E	357	0.86(0.12)	616	5.81(1.07)
	Membras martinica	O	–	–	1	1
	Menidia menidia	E	9	0.60(0.37)	236	4.72(1.28)
Belonidae	*Strongylura marina*	E	2	0.45	6	2.00(0.58)
Blenniidae	*Hypsoblennius hentz*	E/O	109	5.94(3.95)	6	1.00(0)
Bothidae	*Bothus ocellatus*	O	1	0.31	2	1.00(0)
Carangidae	Carangidae spp.	O	–	–	1	1
	Caranx hippos	O	–	–	2	1.00(0)
Clupeidae	*Brevoortia tyrannus*	O	28393	23.74(4.37)	828	20.2(11.89)
	Clupeidae spp.	O	20	5	–	–
	Opisthonema oglinum	O	38	0.94(0.18)	–	–
Congridae	*Conger oceanicus*	O	1	0.21	1	1
Cottidae	*Myoxocephalus aenaeus*	E/O	2	0.15(0.04)	–	–
Cyprinodontidae	*Cyprinodon variegatus*	E	–	–	1	1
Engraulidae	*Anchoa hepsetus*	O	90	1.61(0.35)	–	–
	Anchoa mitchilli	E/O	1003	5.50(1.22)	32	2.46(0.63)
	Anchoa spp.	E/O	71304	75.25(13.37)	2110	20.89(4.10)
	Engraulis eurystole	O	32	6.64	–	–
Fundulidae	*Fundulus heteroclitus*	E	1	0.11	4	1.00(0)
Gadidae	*Enchelyopus cimbrius*	O	458	1.21(0.27)	58	3.05(0.99)
	Pollachius virens	O	2	0.15(0.01)	–	–
	Urophycis chuss	O	82	1.41(0.39)	4	1.00(0)
	Urophycis regia	O	18	0.58(0.30)	–	–
	Urophycis spp.	O	1	0.22	–	–
Gasterosteidae	*Apeltes quadracus*	E	1	0.19	1	1
	Gasterosteus aculeatus	E	10	0.70(0.39)	–	–
Gobiidae	Gobiidae spp.	E	28	0.55(0.15)	4	1.00(0)
	Gobiosoma bosc	E	6	0.42(0.14)	–	–
	Gobiosoma spp.	E	1	0.2	–	–
Labridae	*Tautoga onitis*	E/O	5942	10.21(2.87)	100	2.13(0.22)
	Tautogolabrus adspersus	O	4560	7.81(1.44)	41	2.28(0.71)
Lophiidae	*Lophius americanus*	O	1828	2.34(0.35)	195	4.06(0.99)
Moronidae	*Morone americana*	E	–	–	1	1
Mugilidae	*Mugil curema*	O	–	–	4	2.00(0)
Ophidiidae	*Ophidion* spp.	O	9	0.82(0.52)	–	–
Paralichthyidae	*Etropus microstomus*	O	701	5.06(1.25)	56	5.6(2.66)
	Hippoglossina oblonga	O	386	1.47(0.26)	29	2.07(0.40)
Pleuronectidae	*Limanda ferruginea*	O	1	0.12	–	–
	Pseudopleuronectes americanus	E	379	0.80(0.09)	24	2.67(1.30)
Pomatomidae	*Pomatomus saltatrix*	O	2431	9.57(2.03)	16	2.00(0.50)
Sciaenidae	*Bairdiella chrysoura*	E/O	1	0.36	5	1.00(0)
	Cynoscion regalis	E/O	3623	6.82(0.91)	100	2.63(0.48)
	Menticirrhus saxatilis	O	125	2.91(0.48)	3	1.00(0)
	Menticirrhus sp.	O	205	1.63(0.32)	125	4.63(1.64)

Table 2 (continued)

			Nearshore		Surf zone	
Family	Species	Origin	Abundance	Density (SE)	Abundance	Density (SE)
	Micropogonias undulatus	O	2	0.94	–	–
	Sciaenidae	O	3	0.47	6	3.00(1.00)
Scombridae	*Auxis sp.*	O	1	0.21	–	–
	Scomber scombrus	O	8726	28.84(5.96)	1140	26.51(9.62)
	Scomberomorus maculatus	O	4	0.40(0.11)	2	2
	Scomberomorus sp.	O	2	0.3	3	1.50(0.50)
	Scombridae sp.	O	13	1.86	–	–
Scophthalmidae	*Scophthalmus aquosus*	E/O	5507	7.90(1.51)	1183	21.51(7.43)
Serranidae	*Centropristis striata*	O	82	3.73(1.80)	23	2.09(0.44)
Stichaeidae	Stichaeidae sp.	O	2	0.32	–	–
	Ulvaria subbifurcata	O	8	0.16(0.02)	1	1
Stromateidae	*Peprilus triacanthus*	O	148	1.87(0.37)	364	16.55(4.89)
Syngnathidae	*Syngnathus fuscus*	E	600	1.30(0.20)	116	1.84(0.19)
Tetraodontidae	*Sphoeroides maculatus*	E	74	0.70(0.14)	10	1.00(0)
Triglidae	*Prionotus carolinus*	O	316	2.80(0.41)	6	1.50(0.29)
	Prionotus evolans	O	688	2.89(0.38)	55	2.12(0.32)
	Prionotus spp.	O	18	0.59(0.15)	8	1.33(0.21)
Uranoscopidae	*Astroscopus guttatus*	E/O	31	1.85(0.71)	2	2
	Unidentified fish		2861	5.67(1.60)	256	5.95(1.45)
Grand totals			141263		7789	

Origin is designated as either Estuarine (E), Oceanic (O), or Estuarine/Oceanic (E/O). See Fig. 1 for sampling locations

$p<0.05$) than June or July, averaging 1,870, 353 and 220 larvae/100 m^3, respectively.

Taxonomic richness, based on combined nearshore and surf zone collections, was relatively high with 51 species identified over the 5 years from 1995–1999 (Table 2). Taxonomic richness varied among years ranging from 28 taxa represented in 1996 to 38 taxa collected in 1997 and 1999. The composite nearshore and surf zone larval collection was dominated by a diverse assemblage of fishes from 33 families in which the engraulids, gadids, sciaenids, and scombrids were the most speciose (Table 2). In the nearshore habitat, taxonomic richness was also highest in July ($F=7.4$, $p<0.05$), averaging 20 taxa per sampling period compared to 15 and 16 taxa for May and June, respectively. Taxonomic richness in the surf zone also was highest in July ($F=6.9$, $p=0.01$), averaging 18 taxa compared to an average of 10 and 9 taxa collected in May and June samples, respectively.

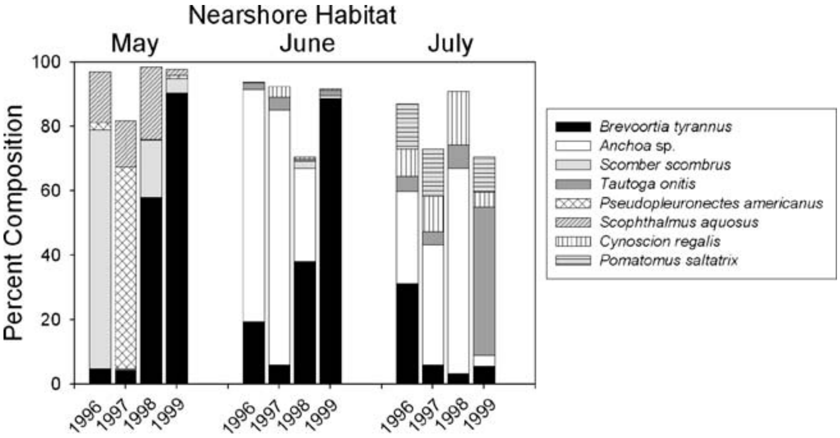

Fig. 3 Taxonomic composition of larval fish assemblages by month for all years combined for taxa contributing at least 5% on average to the overall composition of each month

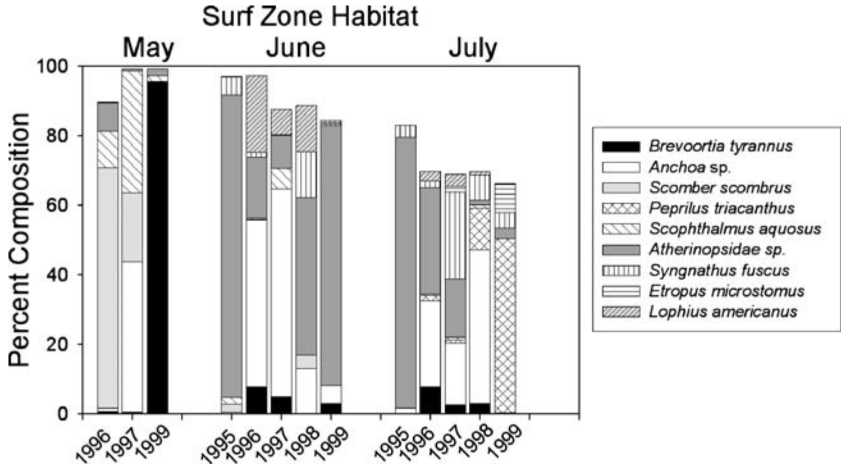

Fig. 4 Taxonomic composition of larval fish assemblages by month for all years combined for taxa contributing at least 5% on average to the overall composition of each month

Temporal differences in the taxonomic composition of larval fish assemblages were very evident. In the nearshore habitat, larval fish assemblages differed among months across all years (Fig. 3; R=0.79, p<0.001). Anchovies (*Anchoa* spp.), which contributed the most (8×14%) to overall dissimilarities between months (SIMPER), were not captured in May samples, but were a dominant taxon in June and July samples (Fig. 3). Three species, Atlantic mackerel (*Scomber scombrus*), Atlantic menhaden (*Brevoortia tyrannus*), and windowpane flounder (*Scophthalmus aquosus*) made up 97% of the ichythyoplankton captured in all May samples (Fig. 3). These species were either minor components or not present in the larval assemblages during June and July. The July larval samples were more speciose, with eight species comprising 90% of the catch (Fig. 3).

Monthly distinctions in taxonomic composition of the surf zone assemblages of larval fish were not as strong (Fig. 4; R=0.45, p=0.002). Anchovy larvae were present in the surf zone in all months sampled, whereas *S. scombrus* and *S. aquosus* were a substantial component of the assemblage only in May (Fig. 4). The differences in surf zone assemblages between June and July are primarily attributable to declining percent composition of anchovies and *B. tyrannus* and increasing contribution of kingfish, *Menticirrhus* sp., and butterfish, *Peprilus triacanthus* (Fig. 4). These three taxa accounted for approximately 30% of the dissimilarity in larval fish composition between June and July (SIMPER).

Larval Spatial Characteristics

The distribution of larvae along the 15 km shoreline of the study area was relatively homogeneous, with no areas with consistently high or low densities. Larval densities and assemblage structure also were not associated with proximity to inlets. Stations nearest the inlets did not differ in taxonomic composition from those in other parts of the study area. Silversides (*Menidia menidia* and Atherinopsidae) were the only taxa that exhibited a distributional trend within the study area. Silversides were significantly more abundant at stations south of Shark River Inlet than north of that point (F=8.0, p<0.01) averaging 20.7 and 8.2 larvae/100 m^3, respectively.

Taxonomic richness for nearshore samples was fairly even between bottom (45 taxa) and surface (42 taxa) tows. Larval fish abundance in bottom samples (n=92,945) was nearly twice that of surface samples (n=48,318). Most of this difference is accounted for by higher abundances of small anchovies (*Anchoa* spp.) in bottom (n=59,189) compared to surface (12,115) samples. Most anchovy larvae were identified only to the genus because they were too small (mean=3.36 mm SL) to be identified by species.

The taxonomic composition of nearshore larval fish assemblages was relatively homogeneous across stations within the study area. Comparisons (ANOSIM) between the three nearshore areas (North—NR, Project—PR, and South—SR) did not reveal any significant differences in taxonomic composition either overall or when analyzed by month.

Surf zone and nearshore assemblages did not differ strongly in taxonomic composition in either May (ANOSIM R=0.11), June (R=0.33), or July (R=0.16) samples. Some species were restricted in the habitats in which they occurred (Table 2). Those only collected in the nearshore samples included striped anchovy (*A. hepsetus*), Atlantic thread herring (*Opisthonema oglinum*), silver anchovy (*Engraulis eurystole*), spotted hake (*Urophycis regia*), and threespine stickleback (*Gasterosteus aculeatus*). Species that appeared disproportionately abundant in the nearshore were *Anchoa* spp., tautog (*Tautoga onitis*), and bluefish (*Pomatomus saltatrix*). There were no abundant species that were found only in the surf zone. However, several species were relatively more abundant there, including Atlantic silverside (*Menidia menidia*), silversides (Atherinopsidae), and butterfish (*Peprilus triacanthus*).

Size and Stage Composition

While the sampling nets in the nearshore and surf zone collections differed in size and mode of deployment, the size ranges of larvae were similar between habitats across years (Fig. 5). Most individuals were less than 5 mm, but individuals up to 15 mm were fairly equally represented in both surf zone and nearshore samples. The smallest larval fish (<2 mm SL) were relatively more abundant in the smaller mesh net (505 μ) used in the surf zone. These smaller larvae comprised 17% of the overall surf zone subsample that was measured compared to only 10% of nearshore larvae. As examples, this pattern was highly pronounced for Atlantic menhaden, *B. tyrannus*, and windowpane flounder, *S. aquosus*, for which the smallest larvae were a larger percentage (11% and 21%, respectively) of the catch in the surf zone than nearshore habitat (3% and 5%, respectively).

Larval stage composition was also similar between habitats, but stage composition changed over time as reflected by a significant interaction between larval stage and month in both the surf zone ($F=10.0$, $p<0.001$) and nearshore ($F=3.3$, $p<0.05$; Fig. 6) environments. In May, the majority of larvae captured were in the pre-flexion stage of development (Fig. 6a) regardless of their presumed origin (estuarine, estuarine/oceanic, or oceanic) or habitat where captured (surf zone vs. nearshore). By June, post-flexion larvae were more common, especially among larvae of estuarine origin (Fig. 6b). In July, post-flexion larvae of all origins were common in both habitat types (Fig. 6c). The pre-flexion stage was the most common stage sampled for most species in both the nearshore and surf zone habitats (Table 3). Only one species, the smallmouth flounder *Etropus microstomus*, was collected almost exclusively in the post-flexion stage.

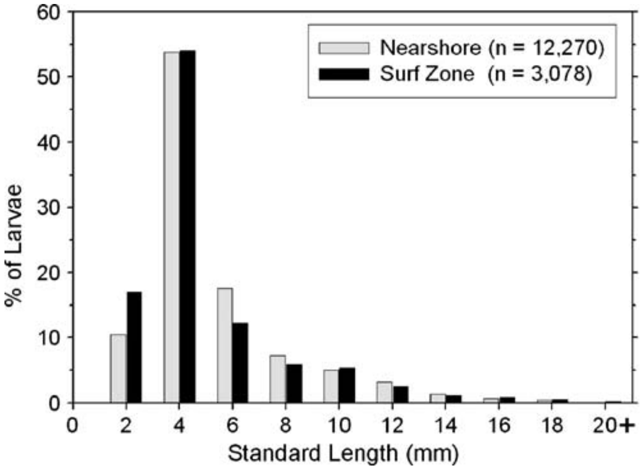

Fig. 5 Length-frequency distributions of total larvae captured in the nearshore (mean=4.85 mm, range=1.0 to 106.5 mm) and surf zone (mean=5.68 mm, range=1.0 to 98.1 mm) habitats

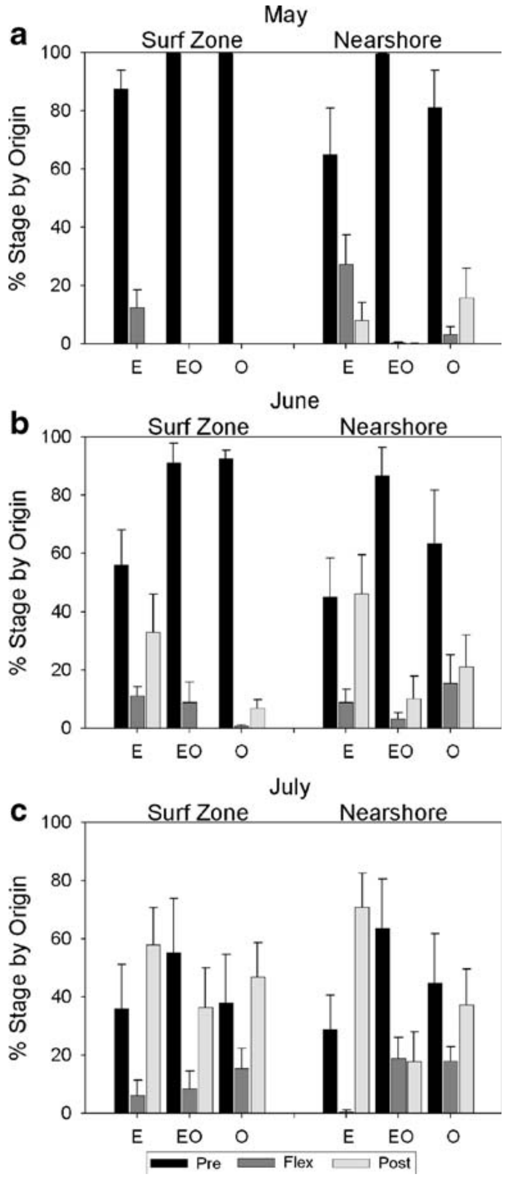

Fig. 6 Percent (+ standard error) of fish larvae in each developmental stage (pre-flexion, flexion, post-flexion) by estuarine (*E*), estuarine/ocean (*EO*), and oceanic (*O*) origin for **a** May, **b** June, and **c** July samples in both the surf zone and nearshore habitats

Relationship Between Assemblages and Environmental Variables

The taxonomic composition of the surf zone larval fish assemblages was not associated with the daily changes in the environmental conditions observed in the surf zone habitat. Assemblages were not segregated by day of sampling (MDS, ANOSIM) and were not related to the environmental variables within sampling periods (BIOENV). However, for some species, larval densities and size differed at times that corresponded to short-term fluctuations in physical conditions. For example, larval Atlantic mackerel (*S. scombrus*) were significantly less abundant ($F=9.6$, $p=0.006$) and smaller

Table 3 Percentage of larvae by flexion stage for the dominant species (≥5% of the overall composition of each month)

	Nearshore			Surf Zone		
	Pre-flexion	Flexion	Post-flexion	Pre-flexion	Flexion	Post-flexion
Anchoa spp.	89.0	7.2	3.8	97.2	0.3	2.5
Atherinopsidae spp.	92.9	6.6	0.5	94.6	5.2	0.2
Brevoortia tyrannus	77.8	8.2	14.0	86.9	1.5	11.5
Cynoscion regalis	83.6	12.0	4.4	99.0	1.0	0.0
Etropus microstomus	1.4	0.0	98.6	0.0	0.0	100.0
Lophius americanus	99.4	0.6	0.0	99.3	0.7	0.0
Peprilus triacanthus	13.4	20.6	66.0	8.5	30.3	61.2
Pomatomus saltatrix	39.3	37.2	23.5	6.7	40.0	53.3
Pseudopleuronectes americanus	64.5	27.7	7.8	60.0	40.0	0.0
Scomber scombrus	99.1	0.7	0.3	99.1	0.6	0.3
Scophthalmus aquosus	96.6	1.4	1.9	98.7	0.3	1.0
Tautoga onitis	68.0	11.8	20.2	73.3	12.8	14.0

(F=9.1, p=0.015) on May 20 and 21, 1996 when the water was colder and higher in salinity compared to other days in the sampling period (Fig. 7a). Anchovies (*Anchoa* spp.) were significantly more abundant (F=4.3, p=0.029) on the sampling date with colder more saline water in June 1997 (Fig. 7b) and butterfish (*P. triacanthus*) collected on the coldest, highest salinity day of sampling in July 1999 were significantly smaller (Fig. 7c) than those captured on other days during that sampling period (F=7.9, p=0.013).

Mean environmental conditions for each sampling period were related to the overall surf zone larval fish assemblages of each sampling period (RELATE, Rho=0.58, p=0.001). Salinity, turbidity, and temperature were most highly associated with the taxonomic composition of the surf zone fish assemblages (BIOENV, r=0.61). The relationship between nearshore larval fish assemblages and the environmental parameters measured in the surf zone was not as strong (RELATE, Rho=0.46, p=0.002) and this relationship was most highly associated with salinity and temperature (BIOENV, r=0.58).

Discussion

Although the surf zone is increasingly recognized as habitat for larval fish, its role is poorly understood. Results of this study present, for the first time, an extensive analysis of fish larvae in the surf zone on the northeast coast of the United States and in slightly deeper, nearshore waters, which had not been examined previously in the New York Bight. Larval fish assemblages were sampled during the peak summer reproductive period in the Middle Atlantic Bight (Able and Fahay 1998) and generally resembled the taxonomic composition of the continental shelf (Cowen et al. 1993) and estuarine (Croker 1965; Witting et al. 1999) larval fish assemblages reported for the New York Bight area. Many of the species collected in the surf zone and nearshore habitats commonly occur as larvae in the central part of the Middle Atlantic Bight based on an 11-year data set from NMFS-MARMAP surveys (Morse et al. 1987; Berrien and Sibunka 1999). The overlap between continental shelf, surf zone, nearshore, and adjacent estuarine larval fauna is due, in large part, to the common pattern of spawning in the ocean and subsequent transport to estuaries exhibited by many species in the region (Able and Fahay 1998; Able et al. 2006). Further, the broad seasonal spawning migrations of many species ensure that the eggs and early larvae are broadly distributed and mixed across habitats (Grosslein and Azarovitz 1982; Able and Fahay 1998). Anchovies were numerically dominant in the surf zone and nearshore habitats, which were similar in larval diversity to offshore assemblages although differences in sampling gear preclude formal comparisons. In South Africa, larval fish species diversity and evenness was intermediate in the surf zone habitat compared to the adjacent estuarine and nearshore coastal waters, which had the highest diversity (Harris et al. 2001).

Pre-flexion larval fish were common in the surf zone and nearshore habitat (Table 3) indicating these areas provide important habitat for recently hatched individuals. The possibility that many species spawn in relatively shallow waters of the continental shelf is supported by prior studies (see Able and Fahay 1998 for a review; Morse et al. 1987; Berrien and Sibunka 1999). The prevalence of post-flexion individuals as well as all three developmental stages (pre-flexion, flexion, and post-flexion) in the South African surf zone may indicate that the pelagic phase of these larval fishes is completed in the surf zone habitat (Pattrick and

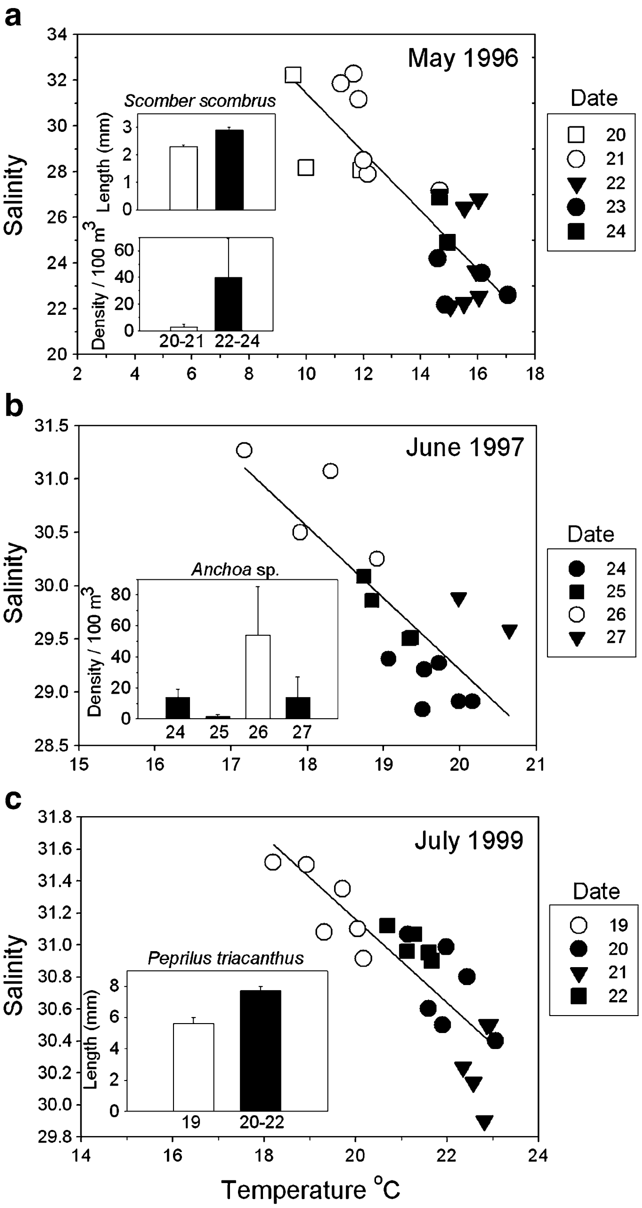

Fig. 7 Significant correlations between surf zone water temperature and salinity for **a** May 1996, **b** June 1997, and **c** July 1999 (Table 1). Sampling dates within sampling periods are depicted with different symbols. *Open and black symbols* distinguish between time periods with significant differences in temperature. *Insets* depict species that differed in either density and/or size coincident with the daily change in physical factors. *Bar shading* corresponds to time periods depicted by shading of symbols

Strydom 2008). Additional studies that control for gear type are needed to reliably demonstrate the relative roles of estuarine, surf zone, and nearshore habitats in the New York Bight area for the different stages of larval fish development.

Although linkages between water masses (typically defined by temperature and salinity relationships) and larval fish assemblages have been described in estuarine (e.g., Fortier and Leggett 1985; Tzeng and Wang 1993) and continental shelf (e.g., Dempster et al. 1997; Grothues and Cowen 1999) environments in conjunction with well-defined hydrographic boundaries, this relationship is not previously reported for the surf zone habitat. In this study, however, distinct water masses occurred in the surf zone over a short (days) temporal scale. Differences in environmental conditions suggest that colder, higher salinity water masses move onshore into the surf zone for a period of 1 to 2 days (Neuman et al. 2002; Chant et al. 2004). These events were common during the May to July sampling periods (Neuman et al. 2002). The range in water temperatures commonly spanned 4 to 7°C (Table 1) over the course of the 4–5-day sampling periods. Higher salinities, lower dissolved oxygen, and higher turbidity frequently accompanied the colder water within each sampling period (Table 1). Wind data were not recorded during sampling; however, the intrusion of deeper oceanic water with the aforementioned characteristics is consistent with westerly winds that push surface waters (Chant et al. 2004) and the Hudson River plume offshore under summertime conditions in this area (Bowman 1978; Cowen 1996; Glenn et al. 2007; Zhang et al. 2009).

Although the taxonomic composition of surf zone larval fish assemblages did not change in accordance with these upwelling events, there were several species that changed in abundance and/or size concurrent with the short-term changes in surf zone water conditions (Fig. 7). The larvae of ocean-spawning Atlantic mackerel (*Scomber scombrus*) were less abundant and smaller during an upwelling event in May 1996 (Fig. 7a). Because physical and biological processes affect the distribution and temporal variability of larval fish communities (Cowen et al. 1993; Dempster et al. 1997; Azeiteiro et al. 2006), more focused studies are needed to discern the potential causative mechanisms that may underlie observed patterns in larval abundance and size in the surf zone.

Temporal changes in assemblage composition during the transition from late spring to summer months were evident in both the nearshore (Fig. 3) and surf zone (Fig. 4) habitats. The larval assemblages became more speciose with the progression of spawning and warming temperatures from May to July. Even though environmental cues that affect larval distributions and densities, such as seasonal changes in temperature, most likely differed for each of the months in different years, the similarity in assemblage composition by month suggests a pattern of occurrence in these habitats that is repeated annually. A similar, predictable, repeated progression of seasonal larval fish assemblages also was observed in a southern New Jersey estuary (Witting et al. 1999).

The short-term upwelling events observed in this study were only evident when the data within sampling periods were examined for daily patterns, thus confirming a cautionary observation made by Cowen et al. (1993) that over-averaging data can obscure small and meso-scale variability and patterns. The problem of confounding small-scale temporal variability in larval fish assemblages with large-scale spatial differences (e.g., from sampling cruises that sample different locations on different days) was recognized by Gray (1996) who suggested that descriptions of daily variability in assemblage structure at each location are essential. Ecological and environmental studies of larval fish assemblages in the surf zone must also acknowledge the potential importance of daily variability that, in the New York Bight area, may be related to short-term upwelling events and/or buoyancy-driven flows from the Hudson River plume. If multiple days are needed to sample a study area, sampling date can be confounded with areas of interest (e.g., topographical features, reference, and impact sites) unless temporal factors are part of the sampling design.

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