PERGAMON Continental Shelf Research 19 (1999) 1171–1198

CONTINENTAL SHELF
RESEARCH

Larval fish assemblages and water mass history in a major faunal transition zone

Thomas M. Grothues*, Robert K. Cowen[1]

Marine Sciences Research Center, State University of New York at Stony Brook, Stony Brook, NY 11794-5000, USA

Received 9 June 1998; received in revised form 4 January 1999; accepted 6 January 1999

Abstract

A region of distinct oceanographic features that result from the meeting of several water masses is marked by Cape Hatteras, North Carolina, between the Middle Atlantic Bight (MAB) and South Atlantic Bight (SAB). The features are dynamic, corresponding, in part, to the degree of water exchange between the MAB and SAB. The extent of larval fish transport via these features could have implications to fish population genetics, year-class structure, zoogeography, and access to nursery habitat. As a step in the examination of larval exchange between the MAB and SAB, we studied the association of spring larval fish assemblages with environmental variables descriptive of the water mass origins. The region was clearly an oceanographic and ichthyoplankton faunal transition zone. Larval distribution corresponded to patterns of adult distributions along the entire eastern seaboard. High taxa-environment correlations described a boundary assemblage strongly influenced by oceanographic conditions. Net assemblages from mixed waters were dominated by taxa with widespread adult distributions (e. g. *Peprilus triacanthus*, synodontidae, triglidae, clupiedae, others) rather than a mix of taxa from other groups. MAB water contained *Limanda ferruginea* and *Benthosema glaciale* in deep, cold water and *Glyptocephalus cynoglossus*, *Hippoglossina oblonga*, *Scomber scombrus*, *Lophius americanus*, and others in shallow, warmer, less saline water. High densities of numerous sub-tropical species, (e.g. *Xyrichtys novacula*, *Bothus spp.*) and low densities of many others were found in SAB waters but varied greatly in distribution with depth. Taxa varied in their fidelity to environmental indicators, thereby allowing for insight into the nature of the apparent differential permeability of this boundary zone to various species and into the precision of future

---

* Corresponding author. Tel.: + 001-516-632-8701; fax: 001-516-632-8220.
E-mail address: grothues@msrc.sunysb.edu (T.M. Grothues)

[1] Present address: Marine Biology and Fisheries, Rosenteil School of Marine and Atmospheric Sciences, 4600 Rickenbacker Causeway, Miami, FL 33149-1098, USA.

PII: S0278-4343(99)00010-2

predictions regarding transport related recruitment success.

Keywords: Ichthyoplankton; Assemblage; Faunal transition; Middle Atlantic Bight; South Atlantic Bight; Cape Hatteras

1. Introduction

Marine fish distributions are limited by many factors including temperature and salinity (Fortier and Leggett, 1985), food availability (Yoder, 1983; Fortier et al., 1992), and larval supply (Bailey, 1981; Cowen, 1985; Polacheck et al., 1992). Ocean currents are among the most important regulators of these factors. Inasmuch as prominent capes figure in the topographical steering of major currents, it is not surprising that such features have been widely recognized as markers of coastal assemblage transition zones (Briggs, 1974).

The description of regions as transition zones reflects that they are not absolute barriers; instead, a gradient of species abundance across them varies in time and with species so that intermediate and dynamic boundary assemblages may be formed in their vicinity. Because the planktonic larvae of most nearshore marine fishes rely on currents for transport to nursery grounds (Leis, 1991), variability in flow impacting these zones has particular importance in affecting assemblage change over time (e.g. Govoni et al., 1989; Sabatés and Olivar, 1996; Dempster et al., 1997). Therefore, flux calculations incorporating larval concentration and flow data between nursery spawning grounds would directly impact our ability to predict recruitment variation from oceanographic conditions.

The purpose of this paper is to characterize the water mass specific distribution of larval fish for the Cape Hatteras region separating the Middle Atlantic Bight (MAB) and South Atlantic Bight (SAB) in preparation for flux calculations. Flux calculations will be made congruent with an independent study (Ocean Margins Project) of the region's flow field but requires the quantification and identification of larval fish assemblages transported in water masses as well as an examination of differences in life history traits that may modify transport. Spawning and nursery grounds at Cape Hatteras are separated by topographical or oceanographic features and basic life history traits of many resident species are known (e.g. spawning period and adult spawning location).

1.1. Background

Five major water masses meet at Cape Hatteras (Bumpus, 1973). The Slope Sea and MAB Shelf Water (with Chesapeake Bay Plume and Virginia Shelf Water components) dominate the MAB. Originating from the Gulf of Maine, MAB Shelf Water generally flows south and is of low salinity owing to riverine input (Beardsley et al., 1976). The Gulf Stream and Carolina Capes Water (CCW) dominate the northern

SAB (Pietrafesa et al., 1985). The Gulf Stream originates as the Florida Current and flows northward along the SAB shelf-break, leaving the shelf near Cape Hatteras (Brooks and Blane, 1978; Wang, 1996). Carolina Capes Water (essentially SAB shelf water in this region) has an average, but variable, flow northward driven by the Gulf Stream (Lee and Atkinson, 1983). Salinity of SAB shelf water is higher than MAB Shelf Water owing to less riverine input (Bumpus, 1973). The Slope Sea is a mixture of MAB Shelf Water and Gulf Stream water wedged between the two, but is separated from MAB Shelf Water by a dynamic shelf-slope front (Churchill and Cornillon, 1991; Aikman and Posmentier, 1985). Water is exchanged and mixed between the Gulf Stream, MAB Slope and Shelf Water by intrusions (Flagg et al., 1994) and by Gulf Stream warm core eddies (Zheng et al., 1984; Evans et al., 1985; Churchill and Cornillon, 1991).

North flowing CCW joins the Gulf Stream through mixing or occasionally enters the MAB. South flowing MAB waters turn east towards the Gulf Stream or crosses into the SAB at Cape Hatteras. This confluence of water masses is referred to as the Cape Hatteras Confluence (CHC) (Pietrafesa et al., 1994). At times, a low salinity feature is formed on the western edge of the Gulf Stream by entrainment of MAB water into the Gulf Stream. This was described first by Ford (1952) and subsequently by Fisher (1972), Churchill et al. (1993), and Lillibridge et al. (1990) and is frequently referred to as Ford Water.

While the water masses that meet at the CHC have been described, the extent of their role in larval exchange between the MAB and SAB are just beginning to be understood. Specific transport routes and larval exchange mechanisms between the SAB and MAB have been described for some species (Hare and Cowen, 1996) and transport-related recruitment success has been proposed for others (Hare and Cowen, 1991,1993,1996; Warlen, 1992). Adult spawning time and location (Nyman and Conover, 1988; Hare and Cowen, 1996; Rotunno and Cowen, 1997), and larval vertical distribution (Checkley et al., 1988; Miller et al., 1984) have been proposed as being adaptive within this region. Most studies have dealt with few species and have focused generally on the effect of tides and winds on estuarine entry. This is the first work to provide a quasi-synoptic view of larval assemblage association with environmental parameters across the MAB/SAB boundary. Inter-specific comparisons allowed by the multispecies, multivariate approach taken here can lend insight to the mechanisms of MAB/SAB exchange so that associations can be extended for predictability of larval flux to varying mixing scenarios.

2. Methods

We collected larval fishes and hydrographic data simultaneously within the CHC from May 13 to May 24, 1996. The study area extended from Chesapeake Bay to Cape Lookout (Fig. 1). Five cross-shelf transects extended from nearshore up to 120 km seaward (into the Gulf Stream) and additional stations were located between transects. Stations were 2–10 km apart along each transect. With some modifications, this was the same grid sampled concomitantly for hydrography and flow field by the

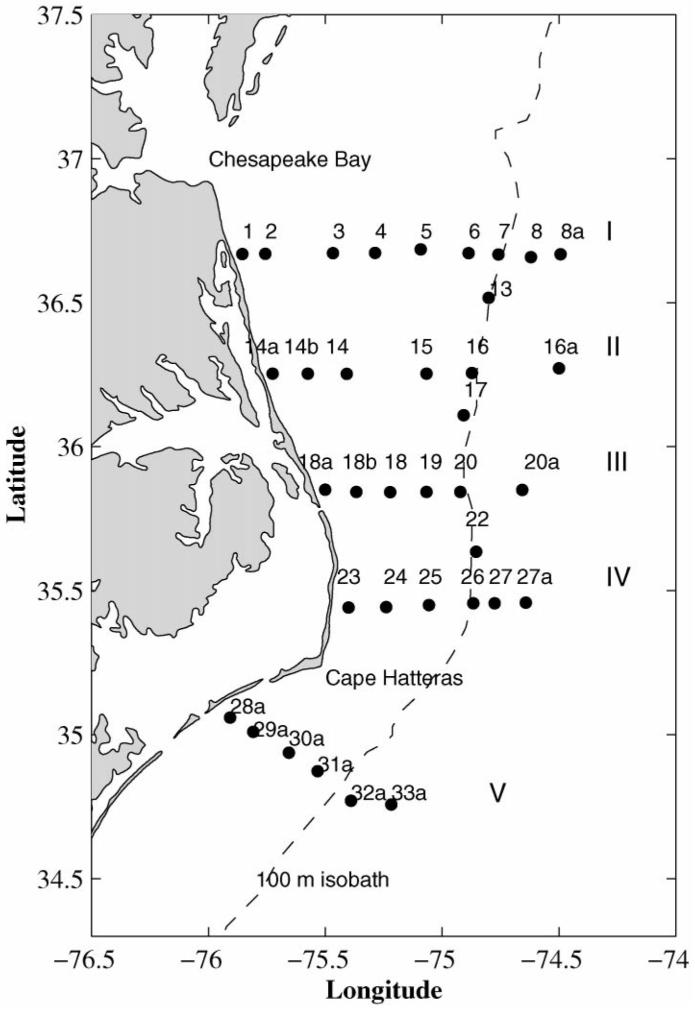


Fig. 1. The study area showing stations sampled in June of 1996. Stations 1–7 and 18a–20 were sampled twice.

Department of Energy Ocean Margins Project (OMP) so that results may be used for flux calculations in a future analysis (Grothues et al., 1999, in prep). A southern transect was added in Raleigh Bay (Transect V) to identify CCW and Gulf Stream larval assemblages before their entry into the more dynamic region off the CHC. Sampling was accomplished in two legs, with some repetition. During Leg 1, Stations 1–8 (along Transect I) and Stations 18a–20 (along Transect III) were sampled with the MOCNESS. Additionally, Station 8a, at the terminus of Transect I, was sampled with CTD only. Following a 2 day storm port call, all stations in the grid were sampled during Leg 2.

A $1\,m^2$ Multiple Opening-Closing Net and Environmental Sampling System (MOCNESS) was used to obtain ichthyoplankton samples from up to seven depth intervals. Nets (505 μm mesh) were opened for approximately 5 min per interval for oblique tows at speeds ca. 2 knots, collecting samples of about $280\,m^3$. Shallow water stations (<45 m water column depth) were sampled as two 5 m intervals (the first interval starting at the surface) above a maximum of three 10 m intervals. Deep water stations consisted of four 10 m intervals above a maximum of three 20 m intervals as bottom depth allowed. Salinity, temperature, depth within which the net fished, and volume sampled were recorded every four seconds by frame-mounted sensors. Pressure, salinity, and temperature data were also taken with a CTD (Seacat SBE 19-03, Seabird Electronics Inc.) prior to all MOCNESS tows. Cross-shelf sections of salinity and temperature were used to identify oceanographic features suggestive of water mass history.

Plankton samples were subsampled with a Folsom plankton splitter; halves were preserved in either 95% ethanol (for aging studies) or 5% formalin. Formalin preserved samples were sorted; individual larvae were identified to lowest possible taxon. Counts were standardized to density (larvae per $1000\,m^3$).

2.1. Analysis

The distribution of taxa was related to temperature, salinity, latitude, longitude, depth, distance offshore, and adult spawning habitat. Salinity and temperature are the best described and most accessible of the conservative water mass tracers at the CHC. The spatial variables latitude, longitude, depth and distance offshore relate these tracers to water mass history. The association of natal assemblages with water masses of particular history allows for testing of the cohesiveness of assemblages.

Taxa were classified a priori into groups based on the spawning habitat of their adult stages. Information on adult spawn location was taken from summaries in Fahay (1983) and Colton et al. (1979). Classifications were as follows: southern (SAB) reef, southern middle shelf, southern nearshore (including estuarine spawners), Gulf Stream (including Florida Current and Sargasso Sea spawners), MAB shelf, MAB slope, and outside ubiquitous and unknown (including highly variable). Temporal constraints (spawning periods) were considered in assigning classifications to species with protracted and progressive spawning migrations.

Canonical Correspondence Analysis (CCA) was chosen because of its robustness and the fact that it directly relates biological variables with abiotic gradients (Palmer, 1993; ter Braak and Verdonschot, 1995). CCA is a form of reciprocal averaging ordination in which the axes (and their associated eigenvalues) are constrained to linear combinations of the environmental variables. The underlying model assumes a unimodal taxon frequency response to environmental gradients. We used the software package CANOCO 3.15 (ter Braak, 1992) to carry out CCA with forward selection; i.e. environmental variables were considered if their sequential addition significantly ($p = 0.01$, Monte Carlo permutation test) improved the fit of species along the major CCA axis.

In MOCNESS tows that crossed fronts, sampled species could be erroneously construed as being highly variable in their association with temperature or salinity. Moreover, association of larvae with fronts does not indicate larval exchange between water masses. Therefore, we excluded from the primary analysis those samples that crossed fronts by scrutinizing the MOCNESS physical data profiles for nets with high coefficients of variation (CV) in salinity. A natural dichotomy was observed in the physical data with no nets having a salinity CV greater than 4 but less than 8. High temperature CV coincided with high salinity CV with the exception of several nets crossing out of the cold pool on the MAB shelf. Presence of a front was confirmed by inspection of transect sections from contoured CTD data. Nets that had been removed ($CV > 8$) from the first analysis were submitted to a second CCA to examine the association of species with frontal zones.

All taxa were included except larvae identified to types of which possible contributors were known to spawn in different water masses. Such taxa can cause spurious similarities between assemblages naturally divided by association with different water masses. For example, the type represented by "*Ophidion* spp." may be indistinguishable larvae from any of several different *Ophidion* species, the adults of which have distinctly different distributions along the Atlantic and Gulf Coast. In contrast, types such as "Chaetodontidae", which also represent several species, but all of which spawn in narrowly defined habitat, were retained. A taxon "No Fish" was created to prevent CANOCO from eliminating samples containing no fish. "No Fish" was assigned the minimum possible weight ($\text{density} = 0.001$) to prevent an otherwise uniform "concentration" in samples from driving the ordination. Larval concentrations were $\ln(x + 1)$ transformed. The increase in relative weight of rare species aids in the identification of natural groups characterized by a large number of uncommon species.

3. Results

3.1. Physical oceanography

All of the SAB and MAB water types described by Pietrafesa et al. (1985) were sampled during the course of the cruise (Fig. 2). Cross-shelf sections of temperature and salinity were consistent with the water masses known to be present in this region (Fig. 3). Cool, low salinity MAB shelf water was found throughout the northern part of the study area and overlay the cold pool, which declined and disappeared in cross-sectional area in more southern transects. MAB Slope Water was found below MAB Shelf Water and offshore of the cold pool (Transects I and II, both legs). Water with Slope Sea TS characteristics was also evident over the shelf in Transect IV in conjunction with frontal structures and was probably derived from both MAB and SAB nearshore waters. Chesapeake Plume Water was present as an along-shelf surface plume increasing in salinity from its origin at the Chesapeake Bay mouth towards Cape Hatteras. Gulf Stream Water was evident both on the southern section slope south of Cape Hatteras as well as in a subsurface salinity and temperature

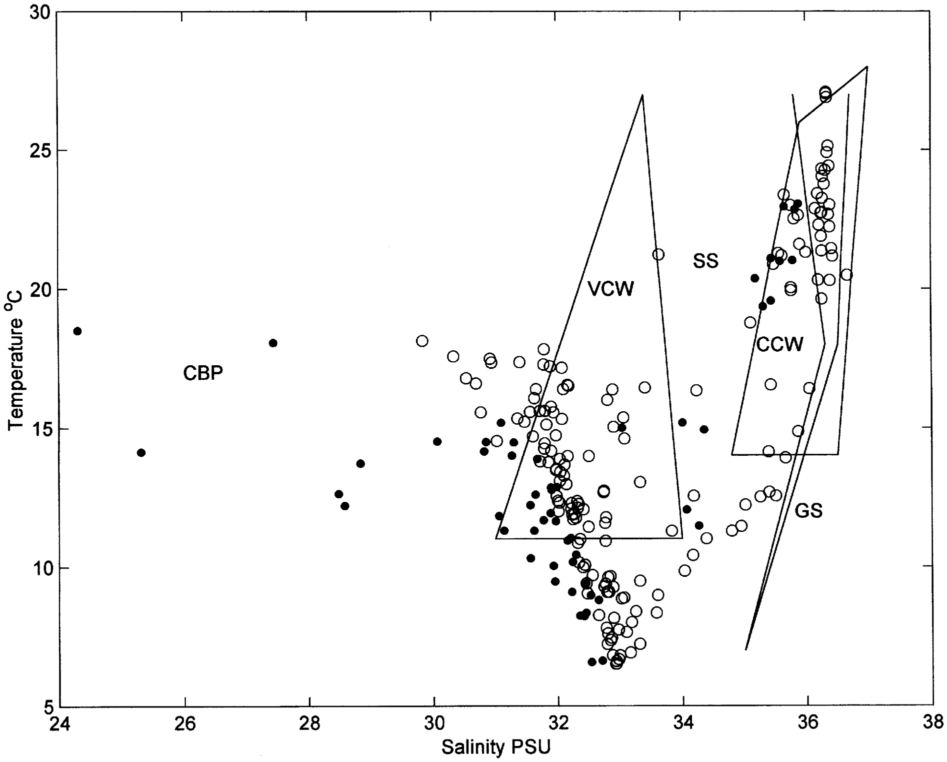


Fig. 2. *T–S* diagram of sample average by net collected by the MOCNESS sensors during each of the 222 net tows. Open circles represent nets which did not pass through fronts, solid circles mark nets that did. Superimposed are the water mass definitions in *T–S* terms as defined by Pietrafesa et al. (1985). VCW = Virginia Coastal Water, GS = Gulf Stream, SS = Slope Sea (MAB), CCW = Carolina Capes Water. Chesapeake Plume (CP) is based on our own observations and therefore unbounded. Cold water in the VCW salinity range is relict MAB winter water known as the "cold pool". The Slope Sea, a mixture of Gulf Stream and MAB shelf water from further north is not well defined by *T–S* bounds but rather by the geographical position of a strong front between it and MAB shelf water.

maximum intruding into the MAB north of Cape Hatteras. Carolina Capes Water was evident on the SAB shelf inside of the Gulf Stream in Transect V.

3.2. Larval fish collections

A total of 222 nets were collected and 4643 individuals were identified from the formalin preserved samples. Of these, 41 contained no fish larvae. Larvae represented 183 taxa belonging to 78 families (Table 1). In all, 168 samples with 181 taxa were included in the primary (no fronts) CCA analysis. The only occurrence of *Anguilla rostrata* in a sample with no other taxa was treated as an outlier; the sample was treated as containing no fish. Forty-five taxa in 54 front-associated nets were included in the secondary CCA (front crossing) data set.

3.3. Species assemblages

Larval fish assemblages were found to be highly variable among MOCNESS net-samples, but species associations with water mass were not. Species-environment correlations were very high at 0.970, 0.906, 0.814, and 0.791 for the first through fourth canonical axes (Table 2). The first four CCA axes accounted for 83 cumulative percent variance of species-environment relation (CPSE). All environmental variables contributed significantly to additional explanation of species distribution, and the effect of the combined variables on explaining distribution on the CCA axes was significant as well ($p = 0.01$, Monte Carlo permutation test, Table 2).

The most important environmental parameters in explaining larval distribution in the primary set was a linear combination of temperature, salinity and latitude. As expected from indications of water mass history, latitude varied inversely with temperature and salinity. Depth and covarying distance offshore explained distribution orthogonal to the first axis. Linear combinations of variables along the first and second axes accounted for more than 55% of the explained variance (33.6% and 21.5%); the third and fourth axis additionally explained $> 12\%$ variance each. Calculation of the *t*-values of the canonical coefficients for each environmental variable (assuming the other environmental variables are held constant) shows that a significant ($t > 2.1$, ter Braak, 1988) additional fit of the species scores fit along a particular axis was explained by at least three variables on each canonical axis (Table 3); i.e. particular combinations of the variables explained significantly more than their constituents did separately.

Two natural groups of taxa were dispersed along the first axis of the CCA plot; both varied along the second axis without natural breaks in their distribution (Fig. 4a). The two groups were associated with samples taken in either MAB or SAB environments even though samples representing transitional environments were present (Fig. 4b). Major variation within each species assemblage corresponded with depth. A relatively small group of species typified a large number of nets characterized by MAB environmental conditions (high latitudes, low temperature and salinity), while a large number of species characterized relatively few samples in SAB environments (low latitudes, high temperatures and salinity). Empty samples occurred mostly in deep, cold, northern waters, although some also occurred in shallow northern water.

A priori classification of taxa by adult spawning habitat revealed that variation was dissimilar between natal groups (Fig. 5). Centroids of taxa from groups “outside ubiquitous” and “southern offshore” were narrowly distributed with temperature, salinity and latitude but widely distributed with depth and distance offshore. “MAB shelf” spawning species centroids were narrowly clustered at high latitude and low temperature and salinity. “Southern reef” and “southern nearshore” species centroids were distributed at low latitude, warm temperature, and high salinity. Centroids of taxa from the three latter groups varied little along Axis 1, but within-group distribution along the second CCA axis differed. “Southern reef” taxa centroids varied with depth and distance offshore, while “southern nearshore” and “MAB shelf” taxa did not. With the exception of a taxa centroid representing the single occurrence of a trichiurid, “Gulf Stream” taxa were dispersed offshore in the SAB. “MAB slope”

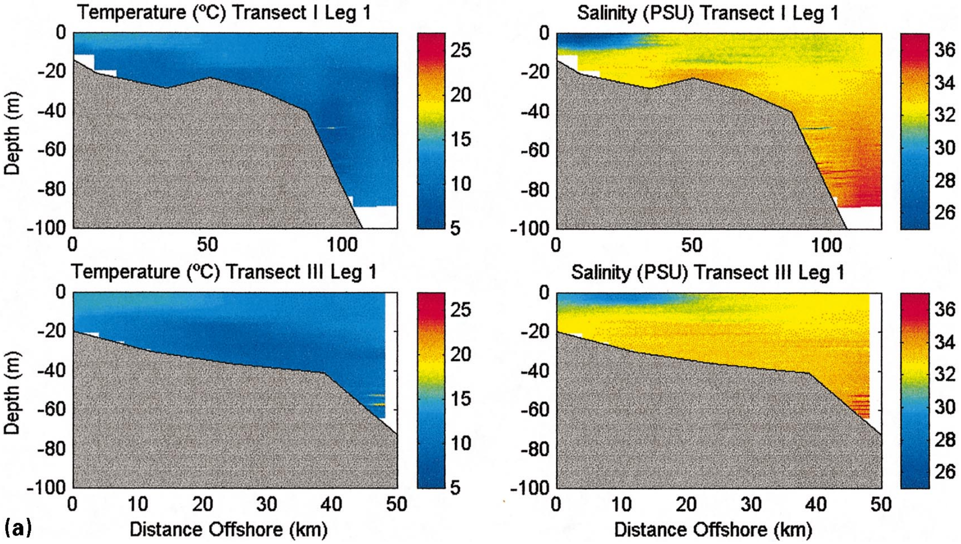


Fig. 3. Salinity and temperature contours of the five cross shelf transects. Stations along Transects 1 and 3 were sampled twice. The Chesapeake Bay plume is relatively warm, low salinity water nearshore on Transects I, II, and III. A salinity maximum corresponding with warm water at a depth of 20–40 m offshore along transect III is a Gulf Stream intrusion; along Transect IV the Gulf Stream front is visible top to bottom with the intrusion impinging on the shelf. Only SAB water is visible along Transect V.

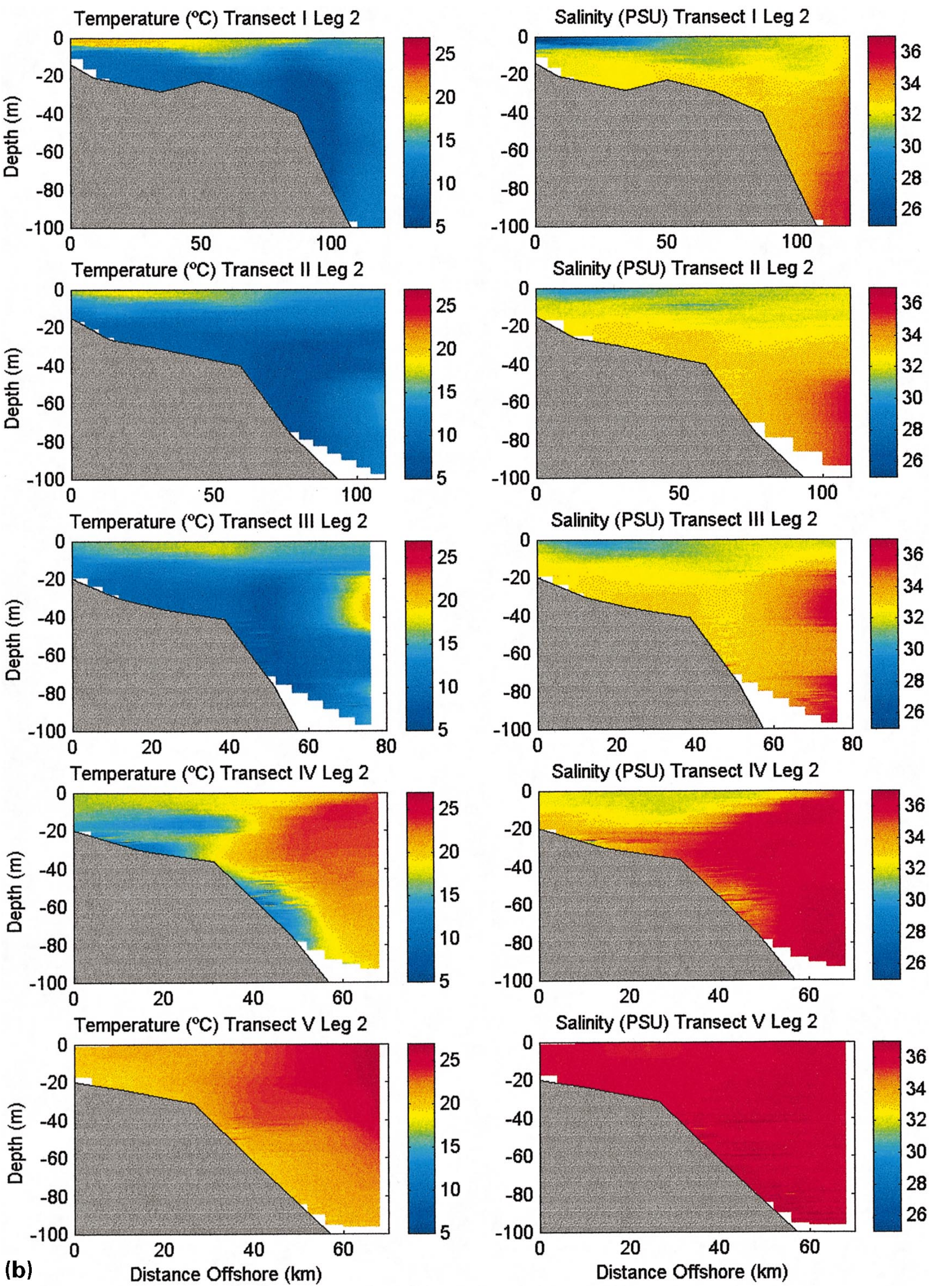


Fig. 3. (*Continued*.)

Table 1
Collected taxa and standardized density (larvae/1000 m^3)

Family	Taxon	CCA code	Class	Density
Clupeidae	Clupeidae	Clu	Un	27.7
Engraulidae	Engraulidae	En	Un	81.2
Megalopidae	*Megalops atlanticus*	Ma	Sn	7.6
Unknown	Leptocephalus Type 1*	Lepto	Un	7.5
Anguillidae	*Anguilla rostrata*	Al	GS	7.4
Congridae	Congridae	Co	GS	9.8
Muraenidae	Muraenidae	Mur	Sr	10.0
Ophichthidae	Ophichthidae*	Oc	Un	12.1
Serrivomeridae	Serrivomeridae	Sv	GS	7.0
Chauliodontidae	*Chauliodus sloani*	Cl	Ou	9.3
Sternoptychidae	*Sternoptyx* spp.	St	Ou	7.0
Chlorophthalmidae	*Chlorophthalmus agazzisi*	Cz	Ou	7.6
Gonostomatidae	*Cyclothone braueri*	Cyb	Ou	13.8
	Gonostoma atlanticum	Ga	Ou	20.5
	Gonostoma elongatum	Ge	Ou	15.9
	Gonostomatidae Type 1	G	Ou	6.5
	Maurolicus muelleri	Mm	Ou	24.0
	Vinciguerria attenuata	Va	Ou	5.3
	Vinciguerria nimbaria	Vn	Ou	9.6
	Vinciguerria poweri	Vp	Ou	19.5
Myctophidae	*Centrobranchus nigroocellatus*	Cn	Ou	9.6
	Protomyctophum arcticum	Pa	MABsl	20.1
	Benthosema glaciale	Bg	MABsl	79.4
	Benthosema suborbitale	Bs	Ou	9.3
	Ceratoscopelus maderensis	Cm	MABsl	9.4
	Ceratoscopelus warmingi	Cw	Ou	9.0
	*Diaphus**	Di	Ou	40.5
	Diaphus Type2*	Dia	Ou	10.1
	Diogenichthys atlanticus	Dy	Ou	16.0
	Gonichthys cocco	Go	Ou	7.1
	Hygophum reinhardti	Hr	Ou	10.7
	Hygophum spp.*	Hy	Ou	16.0
Myctophidae	*Lampadena* spp.	Lp	Ou	7.3
	Lampanyctus crocodilus	Lc	Ou	8.8
	Lampanyctus spp.	Ls	Ou	11.3
	Myctophum affine	Mf	Ou	14.5
	Myctophum nitidulum	Mn	Ou	14.0
	Myctophum obtusirostra	Mob	Ou	6.5
	Myctophum punctatum	Mpu	Ou	9.5
	Myctophum selenops	Mse	Ou	8.4
	Notolynchus valdive	Nv	Ou	9.0
	Myctophidae UID*	My	Un	18.2
Paralepididae	*Sudis hyalina*	Sh	Ou	8.4
	Lestidiops affinis	La	Ou	7.3
	Lestidium atlanticus	Lat	Ou	7.1
	Lestrolepis intermedia	Li	Ou	12.1
Synodontidae	Synodontidae	Syd	Un	46.2

(*Continued in next page*)

Table 1 (*Continued*)

Family	Taxon	CCA code	Class	Density
Gadidae	*Gadus morhua*	Gm	MABsh	7.3
	Melanogrammus aeglefinus	Ma	MABsh	8.7
Moridae	Moridae	Mr	MABsh	9.5
Phycidae	*Enchelyopus cimbrius*	Ec	MABsh	9.0
	Urophycis chuss	Up	MABsh	9.1
	Urophycis regia	Ur	MABsh	5.3
Bregmacerotidae	*Bregmaceros atlanticus*	Ba	So	18.6
	Bregmaceros cantori	Bc	So	9.8
	Bregmaceros houdei	Bh	So	13.0
Ophidiidae	*Lepophidium profundurum*	Lp	MABsl	12.7
	Lepophidium spp.*	Le	Un	11.2
	Lepophidium Type 2*	Le2	Un	13.3
	Ophidiidae UID*	Op	Un	10.2
	Ophidion marginatum	Om	MABsl	13.9
	Ophidion selenops	Os	So	13.4
	Ophidion Type 1*	O1	Un	12.8
	Ophidion Type 2*	O2	Un	8.3
	Otophidium omostigmum	Oo	So	38.2
Carapidae	*Echiodon dawsoni*	Ed	Un	8.2
Lophiidae	*Lophius americanus*	Lam	MABsh	31.3
Chaunacidae	Chaunacidae	Cj	Ou	10.4
Ogcocephalidae	Ogcocephalidae	Og	Un	8.5
Oneirodidae	Oneirodidae	On	Ou	8.3
Holocentridae	Holocentridae	Hl	Sr	7.5
Melamphaeidae	*Melamphaes simus*	Ms	Un	7.5
Aulostomidae	Aulostomidae	Au	Sr	8.7
Syngnathidae	*Hippocampus erectus*	Hi	Sr	14.5
	Syngnathus spp.	Syn	Un	8.2
Dactylopteridae	Dactylopteridae	Dp	Un	14.9
Scorpaenidae	*Helicolenus dactylopterus*	Hd	MABsl	6.4
	Scorpaenidae	Scr	Un	16.9
Cottidae	Cottid Type1	Cd	Un	18.8
Triglidae	Triglidae	Tr1	Un	33.3
Peristeidae	*Peristedion* Type 1	P1	So	6.8
Malacanthidae	*Lopholatilus chaemeleonticeps*	Lch	MABsl	9.4
	Malacanthus plumeri	Mp	Sr	12.9
Percichthyidae	*Synagrops* spp.	Syg	Un	15.7
Serranidae	Anthiinae	An	Sr	15.6
	Centropristis spp.*	Ct	Un	6.9
	Epinephelinae	Epi	Sr	10.7
	Pseudogramma gregoryi	Pg	Un	6.4
	Rypticus spp.	Ry	Sr	7.5
	Serraninae	Ser	Sr	10.7
	Symphysanodon spp.	Sms	Un	7.0
Priacanthidae	Priacanthidae	Pr	Un	11.9
Apogonidae	Apogonidae	Ap	Sr	11.3
Epigonidae	*Epigonus* spp.	Ep	So	8.0
Pomatomidae	*Pomatomus saltatrix*	Ps	So	26.8
Carangidae	*Caranx* spp.	Cx	Un	9.1

(*Continued in next page*)

Table 1 (*Continued*)

Family	Taxon	CCA code	Class	Density
	Decapturus punctatus	Dpu	Un	10.5
	Elagatis bipinnulatus	Eb	Un	16.9
	Selar crumenophthalamus	Sel	Un	13.2
Echineidae	Echineidae	E	So	38.4
Lutjanidae	*Lutjanus campechanus*	Lcm	Sr	13.1
	Lutjanus spp.	Lu	Sr	33.4
	Rhomboplites aurorubens	Ra	Sr	19.9
Gerriidae	*Eucinostomus* spp.	Eu	Sn	17.1
	Gerriidae Type 1	G1	Un	15.9
	Gerriidae Type 2	G2	Un	19.7
Haemulidae	Haemulidae*	H	Un	16.4
Sparidae	*Archosargus probatocephalus*	Apb	Sn	51.3
	Lagodon rhomboides	Lr	Sn	552.6
Sciaenidae	*Cynoscion nebulosus*	Cyn	Sn	15.4
	Cynoscion regalis	Cyr	Sn	104.1
	Larimus fasciatus	Lf	Sn	17.5
	Menticirrhus spp.	Me	Sn	10.0
Chaetodontidae	Chaetodontidae	Ch	Sr	6.8
Pomacanthidae	*Centropygi argi*	Ca	Sr	13.0
Pomacentridae	Pomacentridae	Po	Sr	15.0
Cirrhitidae	*Amblycirrhus pinos*	Am	Sr	15.2
Mugilidae	*Mugil cephalus*	Mu	Un	16.0
Sphyraenidae	*Sphyraena barracuda*	Sba	Un	7.4
	Sphyraena borealis	Sbo	Un	7.3
Labridae	*Clepticus parri*	Cpr	Sr	7.4
	Halichoeres spp.	Ha	Sr	13.5
	Tautoga onitis	To	MABsh	18.1
	Thalassoma bifasciatum	Tb	Sr	17.1
	Xyrichtys novacula	Xno	Sr	24.0
	Xyrichtys spp.	Xs	Sr	7.3
Scaridae	*Scarus* spp.	Sc	Sr	9.1
	Sparisoma spp.	Sp	Sr	11.8
Dactyloscopidae	Dactyloscopidae	Ds	Un	14.6
Uranoscopidae	*Astroscopus guttatus*	Ag	Un	9.4
Percophidae	*Bembrops* spp.	Be	So	7.5
Blenniidae	Blenniidae Type 1	Bl	Un	13.9
Callionymidae	*Callionymus pauciradiatus*	Cp	Sr	10.9
	Callionymus spp.	Cs	Sr	8.7
Gobiidae	*Gobionellus* spp.	Gbl	Un	21.7
	Gobiosoma bosci	Gbs	Un	14.0
	Goby B10	B10	Un	8.0
	Goby CH1	CH1	Un	8.5
	Goby CH2	CH2	Un	10.7
	Goby CH3	CH3	Un	8.5
	Goby CH4	CH4	Un	6.9
	Goby CH5	CH5	Un	7.1
	Goby CH6	CH6	Un	7.3
	Ioglossus spp.	Io	Un	12.8

(*Continued in next page*)

Table 1 (*Continued*)

Family	Taxon	CCA code	Class	Density
Acanthuridae	Acanthuridae	Ac	Sr	9.7
Gempylidae	*Diplospinus multistriatus*	Dm	GS	9.8
	Gempylus serpens	Gs	GS	5.3
Trichiuridae	Trichiuridae Type 2	Tc1	GS	7.3
	Trichiurus lepturus	Tl	GS	7.2
Scombridae	*Auxis* spp.	Ax	GS	26.1
	Acanthocybium solanderi	As	GS	7.5
	Euthynnus alletteratus	Ea	GS	6.4
	Sarda sarda	Ss	So	9.5
	Scomber japonicus	Sj	Un	22.5
	Scomber scombrus	Ssc	Un	11.2
	Scomberomorus cavalla	Sc	GS	6.5
Ariommidae	*Ariomma melanum*	Ar	GS	19.1
Centrolophidae	Centrolophidae	Ce	GS	8.5
Nomeidae	*Cubiceps pauciradiatus*	Cb	GS	7.7
	Psenes cyanophrys	Psc	GS	6.5
	Psenes pellucidus	Psp	GS	10.8
Stromatidae	*Peprilus triacanthus*	Pt	So	37.2
Paralichthyidae	*Citharichthys arctifrons*	Ci	Un	17.9
	Citharichthys cornutus	Cc	Sm	19.8
	Citharichthys gymnorhinus	Cg	Sm	18.6
	Citharichthys spp.	C	Sm	13.2
	Cyclopsetta spp.	Cyc	Sm	12.9
	Etropus crossotus	Ecr	Sm	12.1
	Etropus microstomus	Emr	MABsh	56.7
	Hippoglossina oblonga	Ho	MABsh	13.1
	Paralichthys dentatus	Pd	MABsh	7.8
	Syacium spp.	Sy	Sm	83.2
Bothidae	*Bothus* spp.	Bo	Sm	63.8
Scophthalmidae	*Scophthalmus aquosus*	Sa	MABsh	14.2
Pleuronectidae	*Glyptocephalus cynoglossus*	Gc	MABsh	14.0
	Limanda ferruginea	Lm	MABsh	47.8
Cynoglossidae	*Symphurus* spp.	Sm	Un	31.0
Soleidae	*Trinectes maculatus*	Tm	Un	9.0
Monacanthidae	*Monacanthus hispidus*	Mo	GS	19.8
Diodontidae	Diodontidae	Dio	Sr	7.8
Ostraciidae	*Lactophrys* spp.	L	Sr	7.7
Sphoeroides spp.	*Sphoeroides* spp.	Sph	Un	19.6
Tetraodontidae	Tetraodontidae	Te	Sr	15.6
Unknown	Unknown*	U	Un	9.9
No Fish	No Fish	No	Un	0.0

Density values are mean for nets in which a taxa occurred. CCA taxa abbreviations are given as well as their a priori classification based on spawn site. Class abbreviations are: GS = Gulf Stream, Sr = Southern reef, Sn = Southern nearshore, Sm = Southern mid shelf, So = Southern offshore (includes slope water under Gulf Stream), MABsh = MAB shelf, MABsl = MAB slope, Ou = Outside ubiquitous, Un = Unclassified. Asterisk denotes taxa that were not included in the no fronts CCA.

Table 2

Results of CCA based on the density-standardized, log transformed occurrence of 181 taxa in 168 cases (nets which did not pass through fronts)

Axes	1	2	3	4
Eigenvalues	0.839	0.536	0.382	0.313
Species-environment correlations	0.970	0.906	0.814	0.791
Cumulative percentage variance				
Of species data	4.4	7.2	9.2	10.8
Of species-environment relation	33.6	55.1	70.4	83.0
Sum of all unconstrained eigenvalues (Total inertia)				19.117
Sum of all canonical eigenvalues				2.494

Summary of Monte Carlo test on significance of first canonical axis for the CCA above. (This tests the first eigenvalue of the above CCA against the distribution of eigenvalues generated from CCA on 100 random permutations of sample number in the same environmental space. If species distribution in the tested data set is related to the environmental parameters, the tested eigenvalue will be significantly higher than those of the random permutations)

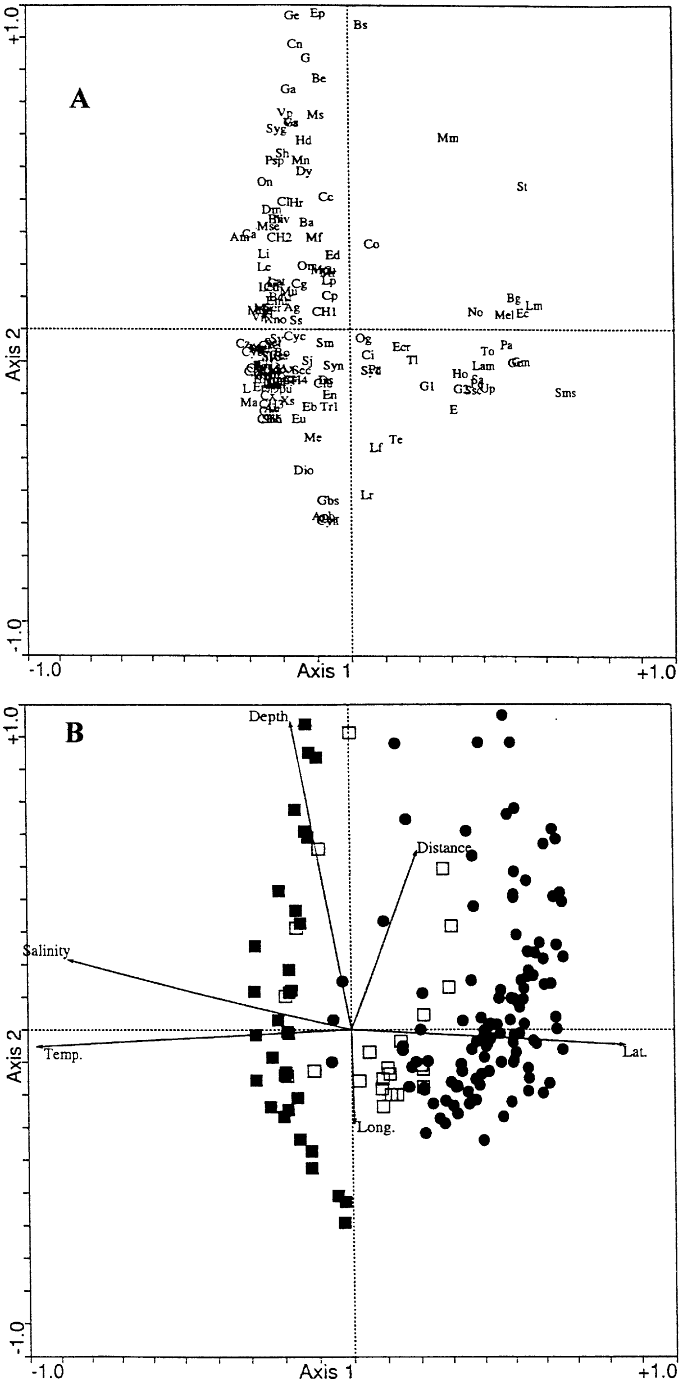
Test of significance of first canonical axis:	Eigenvalue	0.84
	F-ratio	7.29
	P-value	0.01

Table 3

Canonical coefficients for standardized variables of CCA from nets that did not pass through fronts and their *t*-values

Name	AX1	AX2	AX3	AX4
Latitude	0.42	– 0.15	– 0.33	– 0.32
Longitude	0.32	0.08	– 0.03	– 0.23
Distance	0.21	0.29	1.07	0.22
Depth	– 0.02	1.03	– 0.71	0.36
Salinity	– 0.07	– 0.61	0.26	– 2.14
Temperature	– 0.57	0.29	– 0.18	1.61
t-values of canonical coefficients				
Latitude	**8.6**	– 1.6	**−2.4**	– 2.1
Longitude	**9.9**	– 1.3	– 0.3	**−2.3**
Distance	**8.0**	**5.9**	**14.4**	**2.8**
Depth	– 0.7	**20.9**	**−9.4**	**4.4**
Salinity	– 1.5	**−6.8**	1.9	**−14.5**
Temperature	**−13.3**	**3.6**	– 1.5	**12.1**

Note: Canonical coefficients are partial regression coefficients and are calculated assuming other environmental variables are held constant. Unlike the intra-set correlations indicated for environmental variables by the angle between environmental vectors on an ordination plot (see Fig. 4), canonical coefficients of closely correlated environmental variables are not an indication of their relative importance. A value of $|t| > 2.1$ is considered significant for canonical coefficients. Significant t values are in Bold.


A
Ge
Ep
Bs
Cn
G
Be
Ga
Vp
Ms
Syg
Hd
Mm
Sh
Psp
Mn
Dy
On
St
Cc
ClHr
Dm
Ba
Msc
Am
CH2
Mf
Co
Li
Ed
Lc
Cg
Lp
Cp
Bg
Lm
Ag
CH1
No
Mel
Ec
Vi
Ss
Cyc
Sm
Og
Ecr
Ci
Tl
To
Pa
Sj
Syn
SPd
Lam
Ho
Gl
Sms
L
En
Ma
Xs
Eb
Trl
E
Eu
Me
Te
Lf
Dio
Gbs
Lr
Axis 1
Axis 2
-1.0
+1.0
B
Depth
Distance
Salinity
Temp.
Lat.
Long.
Axis 1
Axis 2
-1.0
+1.0

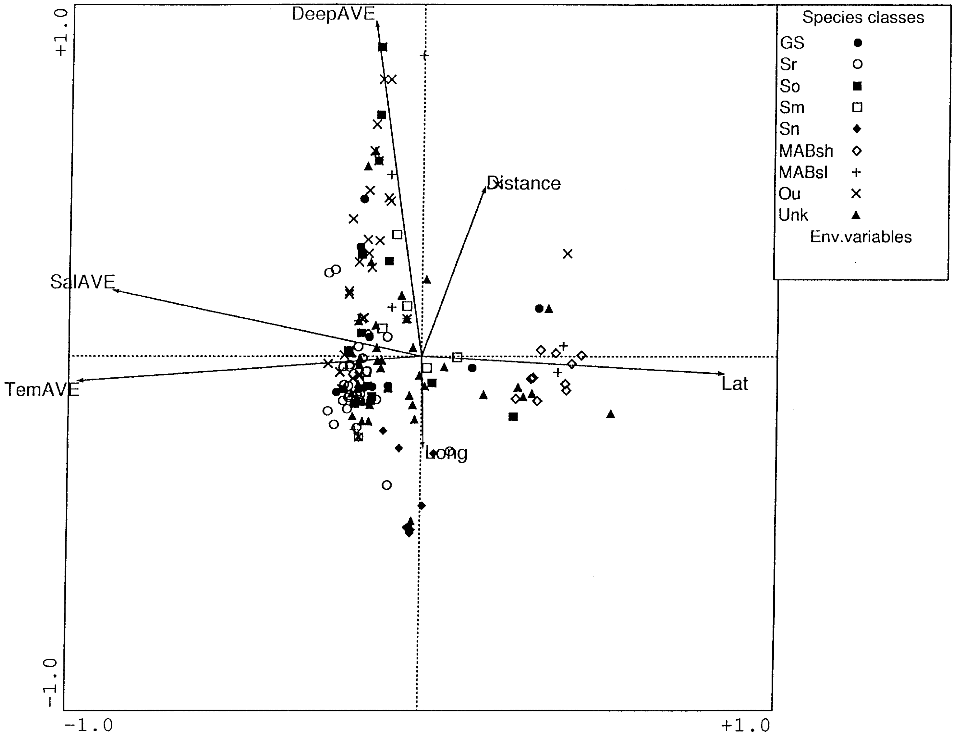


Fig. 5. Distribution of nominally classified taxa and environmental variables showing results from nets that did not cross fronts. Sample locations have been removed for clearer viewing. Species have been classified a priori based on adult spawning habitat when known. Class abbreviations are: GS = Gulf Stream, Sr = Southern reef, Sn = Southern nearshore, Sm = Southern mid shelf, So = Southern offshore (includes slope water under Gulf Stream), MABsh = MAB shelf, MABsl = MAB slope, Ou = Outside ubiquitous, Un = Unclassified. Species classifications are given in Table 1.

◄

Fig. 4. Distribution of taxa along scales of temperature, salinity, depth, distance offshore, latitude and longitude, and the distribution of nets along the same gradients. The first axis describes an environmental gradient co-varying in temperature, salinity, and latitude, and is of greater importance (Eigenvalue = 0.8) than the second (Eigenvalue = 0.5), which describes the effect of depth and distance offshore. Many species (A) were collected in relatively few nets (B) that came from south of Cape Hatteras (Transect V, solid squares). Despite a higher sampling effort in MAB type water, few species were collected in this cold, low temperature, low salinity environment, which was found only north of Cape Hatteras (Transects I–III and Stations 13 and 17, solid circles). Few species with broad distributions characterize the transition environment encountered at Transect IV and Station 22 (open squares). The SAB species group varied more with depth than did the MAB species group.

The figure represents results from a simultaneous ordination of environment, taxa, and nets but has been separated into two layers for easier reading. Taxa names have been abbreviated but can be looked up in Table 1. This ordination is calculated only from nets which did not pass through fronts. Environmental parameters have been unit-variance-standardized in this and all following CCA ordination plots.

spawners were distributed along the temperature/salinity/latitude gradient; however, MAB slope spawners were limited to shallower water in the MAB than in the SAB.

To test whether the distribution of larvae within natal groups were significantly related to the environmental variables that describe water mass history, we substituted the spawning group designation for the names of all included taxa, and repeated the CCA. All class centroids were ordered in agreement with environmental variables indicative of origin (Fig. 6). The MAB Slope class was centered in a MAB slope environment despite that individual members had been centered in different locations; therefore, numbers of MAB slope taxa centered outside of the MAB were scarce. Comparison of the environmental vectors between plots of the original and combined grouping (Fig. 4a, Fig. 4b and Fig. 6) indicates that temperature, salinity, and latitude again explained most of the variation. Explanatory power of depth,

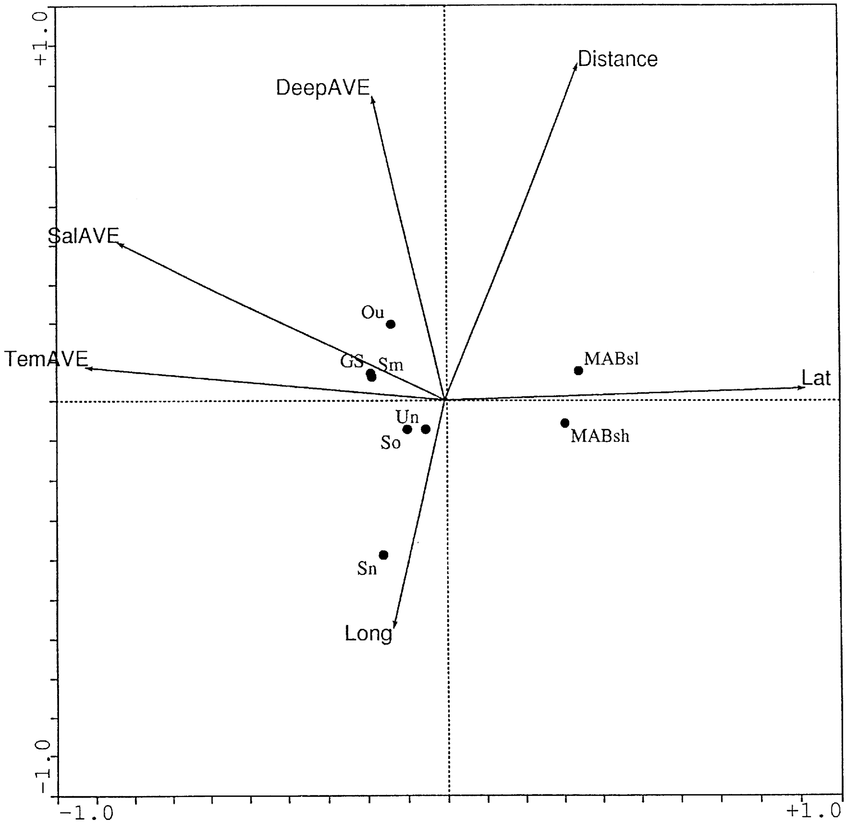


Fig. 6. Distribution of larval groups classified by spawn location. Nets have again been removed for easier viewing. A Monte Carlo simulation test of the first axis showed it to be significant in the ordination, as was the overall order by the trace statistic. Location of class Un reflects that most MAB species encountered are identifiable.

Table 4
Results of CCA on taxa pooled into 10 spawning classes. Data is only from nets which did not pass through fronts.

Axes	1	2	3	4
Eigenvalues	0.559	0.158	0.061	0.033
Species-environment correlations	0.901	0.710	0.469	0.488
Cumulative percentage variance				
Of species data	20.2	25.9	28.1	29.4
Of species-environment relation	68.2	87.4	94.9	98.9
Sum of all unconstrained eigenvalues (total inertia)				2.763
Sum of all canonical eigenvalues				0.820

Summary of Monte Carlo test on significance of first canonical axis for above CCA (See Table 2 caption for explanation of Monte Carlo test)

Test of significance of first canonical axis:		
	Eigenvalue	0.56
	F-ratio	40.84
	P-value	0.01

however, was decreased in the pooled ordination, probably because species from similar natal habitats were distributed differently in the water column within a water mass. The effect of the first axis on explaining variability was significant at $p = 0.01$ (Monte Carlo simulation, Table 4).

We found similarly high species-environment correlations in analyzing samples from nets that did pass through fronts (Table 5). Variance explained by environmental parameters was similar to that from the "no fronts" samples (sum of canonical eigenvalues = 2.482). Axes, however, were constrained by different linear combinations of the environmental variables (Fig. 7). In front crossing samples, the correlation between temperature and salinity was weaker as was the inverse relationship between temperature and latitude. Distance offshore was more important than depth in explaining variation along the second, orthogonal, axis. More front crossings were located in MAB latitudes and low salinity and temperature water; these were distributed along the distance offshore gradient more so than were those in SAB environments. MAB shelf, MAB slope, and "outside ubiquitous" spawning taxa were collected in northern front crossing samples, which represented mostly crossings between Chesapeake Plume and Virginia Shelf waters; taxa with southern spawning locations were collected in samples from the south. Several southern mid-shelf and middle outside taxa were centered midway along the environmental gradients despite the absence of samples collected there, indicating that these taxa occurred similarly in samples from both MAB and SAB latitudes. MAB slope and southern outside spawning taxa occurred in samples which crossed fronts in southern latitudes.

We summarized the distribution of taxa along CCA axes by interpreting them with respect to the more applicable terms of distribution with water mass (Table 6). Only the more common species are listed because of their utility as potential water mass tracers. Position along all four CCA axes was considered in assigning membership to a group. Position along the first axis was used to define distribution as MAB or SAB.

Table 5
Results of CCA based on the density-standardized, log transformed occurrence of taxa in 54 cases (nets which did pass through fronts)

Axes	1	2	3	4
Eigenvalues	0.793	0.519	0.342	0.327
Species-environment correlation	0.966	0.876	0.871	0.884
Cumulative percentage variance				
Of species data	8.2	13.6	17.1	20.5
Of species-environment relation	32.0	52.9	66.6	79.8
Sum of all unconstrained eigenvalues				9.645
Sum of all canonical eigenvalues (total inertia)				2.482

Summary of Monte Carlo test of significance of first canonical axis for above CCA (See Table 2 caption for explanation of Monte Carlo test)

Test of significance of first canonical axis:
Eigenvalue = 0.56
F-ratio = 40.84
P-value = 0.01

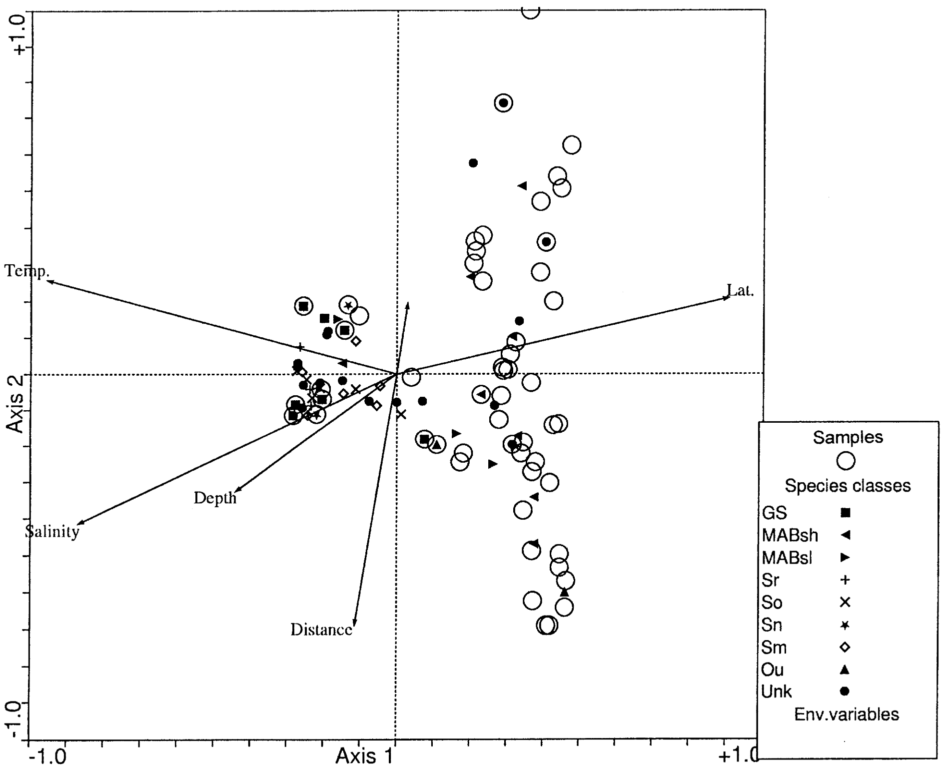


Fig. 7. Relationship of taxa, nets, and environment from analysis of nets that did cross frontal features. Taxa abbreviations have been replaced in favor of their a priori classification symbols.

Table 6
Summary of affiliation with water mass for larvae of commonly encountered taxa during May 1996

Middle Atlantic Bight Shelf Water

Limanda ferruginea[a] (0.25)
Scomber scombrus (0.29)
Glyptocephalus cynoglossus (0.41)
Benthosema glaciale[a] (0.43)
Lophius americanus (0.52)
Hippoglossina oblonga (0.53)

Chesapeake Plume Water
Absence of fish (0.07)
Engraulids (0.65)

Middle Atlantic Bight Slope Water
Absence of fish (0.07)
Maurolicus muelleri (0.67)

Transition group
Triglidae (0.53)
Etropus crossotus (0.57)
Clupeidae (0.59)
Engraulidae (0.65)
Peprilus triacanthus (0.75)
Citharichthys arctifrons (0.79)
Synodontidae (0.80)

Carolina Capes Water (nearshore)
Cynoscion regalis (0.00)
Cynoscion nebulosus (0.00)
Archosargus probatocephalus (0.16)
Larimus fasciatus (0.24)
Lagodon rhomboides (0.30)

Carolina Capes Water (mid-shelf) and Gulf Stream
Chaunacidae (0.06)
Halichoeres spp. (0.09)
Rhomboplites aurorubens (0.12)
Otophidium omostigmum (0.12)
Etropus microstomus (0.13)
Scorpaenidae (0.13)
Thalassoma bifasciatum (0.13)
Cyclothone braueri (0.15)
Monacanthus hispidus (0.16)
Sparisoma spp. (0.16)
Pomacentridae (0.18)
Anthiinae (0.18)
Vinciguerria nimbaria (0.19)
Syacium spp. (0.19)
Sphoeroides spp. (0.21)
Muraenidae (0.21)
Bregmaceros houdei (0.23)
Mugil cephalus (0.24)
Citharichthys gymnorhinus (0.25)
Serraninae (0.26)
Ariomma melanum (0.30)
Xyrichtys novacula (0.033)
Bothus spp. (0.33)
Citharichthys cornutus (0.034)
Ophidion selenops (0.35)
Auxis spp. (0.37)
Pomatomus saltatrix (0.38)
Diogenichthys atlanticus (0.38)
Bregmaceros atlanticus (0.40)
Symphurus spp. (0.50)
Scomber japonicus (0.77)
Congridae (0.80)

Assignment is based on position along all four CCA axis from samples not taken in frontal features. Within each group, taxa are listed in order of increasing tolerance (root mean square deviation, shown in parentheses) along the first canonical axis. The transition group was defined by us as those taxa whose distribution was centered both between the recognizable SAB and MAB assemblages as well as being centered mid-way along the encountered temperature, salinity, and latitude regimes. Species with narrow tolerance to deep SAB waters were diverse but all were relatively uncommon.

[a] Deeper distributed larvae are centered in the cold pool.

Position along the second and third axis helped resolve depth and distance offshore to determine membership with specific water masses in these two environments as seen in the physical oceanography sections shown in Fig. 4. Relationship with temperature/salinity combinations expressed by position along the fourth axis was used in confirmation.

In reviewing the summary, it should be remembered that despite distinct differences in assemblage membership between groups from the MAB and SAB, variation in water mass assemblage within these two groups was a continuum. Therefore, we used the root mean square deviation (Tolerance) of their dispersion along the first CCA axes as an indication of taxa affinity to water mass. Taxa are therefore listed in order of increasing tolerance (decreasing affinity); species listed first would be expected to be the best tracers of their constituent water masses.

4. Discussion

The Cape Hatteras transition zone was readily characterized during May 1996 both on the basis of larval fish assemblages and on the basis of environmental parameters. The distribution of ecological assemblages could be explained by these gradients. Taxa collected included representatives of adult assemblages with known affinities to diverse habitats along the entire eastern seaboard, onshore and offshore. Larval fish distributions in temperature/salinity and in three-dimensional space (latitude, longitude and depth) reflected, within the narrow confines of the sample area, the distributions of adults of their species.

The sharpest gradient was in the distribution between MAB and SAB affiliated species. Few larvae of adults with high fidelity to either the MAB or SAB were found together in net assemblages. Mixing of MAB/SAB water was evident from temperature and salinity in collections from nets near the center of the study area, but larval collections in this area were characterized by a few species widely distributed as adults, rather than by the relative abundance of MAB and SAB endpoint species together in a net. The commonly occurring *Peprilus triacanthus*, as well as numbers of *Etropus crossotus*, *Citharichthys arctifrons*, clupeids and engraulids were important in this respect. Synodontids and triglids also held a central position and are therefore important, but not definitive, descriptors of the transition assemblage. These widespread and common taxa smear the boundary between MAB and SAB populations and have an effect counter to that of rare taxa collected here; the latter would describe a centrally located assemblage unique to the mixing area. However, only two taxa unique to the area (Ogcocephalid Type 1 and *Trichiurus lepturus*) were collected, and because these were each represented by only a single occurrence we draw no meaning from their position.

MAB and SAB larval assemblages both grade with depth. Distribution covaried with distance offshore and culminated in shallow water shelf assemblages on one end and deeper dwelling slope/outside assemblages on the other. Southern offshore and southern reef spawning species overlap in a continuous distribution that makes it impossible to separate assemblages on a depth basis. Southern reef and nearshore fishes (particularly sciaenids and sparids) represent one endpoint for this large group and a mix of southern offshore and outside ubiquitous species, (myctophids, paralepidids, and gonostomatids) define the other endpoint. This grade is consistent with mixing and variability in the position of fronts between SAB coastal waters and Gulf Stream water south of Cape Hatteras (Lee and Atkinson, 1983).

While we found evidence for larval translocation between the SAB and the MAB via MAB intrusions of Gulf Stream water, we did not find evidence of significant exchange of larvae between northern and southern water types. Gulf Stream spawned fish did occur in very low numbers both within the MAB shelf water T–S domain, but in association with the intrusion. Southern and Gulf Stream species in the subsurface intrusion of Gulf Stream water (e.g. *Auxis* spp., *Bothus* spp., *Cyclopsetta fimbriata*), were above it in MAB water as well. No distinctly MAB species were found in the intrusion, but MAB species were also scarcely represented in MAB water above or below it.

With such limited larval exchange, the potential for an exchange of transporting water to effect recruitment under similar temperature conditions depends on the residence time and nature of SAB water in the MAB and vice versa. For example, Gulf Stream water flooding and residing on the MAB shelf as a detached, low inertia filament could allow southern spawned species to recruit in the MAB without undergoing mixing.

Differences in statistical tolerance (i.e. niche breadth, ter Braak and Verdonschot, 1995) indicate a selective permeability to larval exchange of common species between the SAB and MAB and warrant further investigation. Such differences are potentially caused by specific behavioral mechanisms (Cowen et al. 1993; Forward et al., 1996) or developmental stage-specific deterministic movement (Suthers and Frank, 1991). Larvae exhibiting narrow or water mass-specific depth preferences may differentially affect their flux at fronts through vertical migration between stratified water masses or preferential accumulation and advection at horizontal convergences (Kingsford, 1990; Govoni, 1993; Miller and McCleave, 1994). This could explain the high tolerance along Axis 1 for taxa such as *Bothus* and *Auxis* that appear above the Gulf Stream intrusion in MAB shelf water. The importance of *P. triacanthus* as a member of the transition assemblage owes to its spawning migration and spawning location (Horn, 1970; Rotunno and Cowen, 1997).

Mechanisms allowing for the dispersion of the other transition group taxa are less well known. Regardless of the behavior of larvae or adults, larvae must be physiologically tolerant of the range in temperature and salinity associated with their dispersion. This alone may be sufficient to separate the transition group taxa from the more narrowly distributed temperate or subtropical taxa. Physiological constraint may set statistical tolerance under mixing and exposure to inimical temperature or salinity. This is equivalent to tolerance in the classical sense (Neill et al., 1994). The distribution of some tropical taxa around salinity or latitude centroids should increase in years when springtime MAB waters are warmer or as the season progresses. Many southern reef species, (e.g. epinephalines, chaetodontids, aulostomids, and syngnathids), recruit to nearshore waters of the MAB and persist until October/November when waters cool and these species disappear (Hoff and Ibara, 1977; Able and Fahay, 1998).

A third explanation for differences in tolerance is that the water masses in which larvae hatch are themselves variable. For example, the Gulf Stream front varies zonaly and meridianly, but is narrowly defined by salinity. The cold pool is constrained to high latitudes and mid-longitudes. Larvae spawned in different water masses should reflect the ranges of these parameters in their statistical tolerance unless or until water mixing occurs. Parent waters that do not mix substantially with other masses cannot exchange larvae that are acting as tracers and the larval realized niche will stay narrow. This action is evident for some species that were present in cross-front samples. Some forty nets crossed fronts in northern latitudes (potentially combining MAB slope, MAB shelf, and Chesapeake Plume Water), and these samples contained only nine species of the recognized spawning habitat classes (six MAB shelf, two MAB slope and one outside ubiquitous). Chesapeake Plume Water was nearly devoid of larvae. Eight nets crossed fronts in southern latitudes and samples contained sixteen species of known spawn habitat (one each species of Gulf Stream, MAB shelf, MAB slope, and outside ubiquitous, as well as six southern outside, five southern middle-shelf, and three southern reef species). Only five MAB/SAB transition samples crossed fronts, potentially combining larvae of one Gulf Stream and one southern mid-shelf species. This does not indicate that larvae between parent water masses, particularly those from MAB shelf, MAB slope and southern affinity, are not often exchanged, but only that water mixing was not an important exchange mechanism during our cruise. In contrast, exchange of southern originating waters and their larvae with those of northern origin by way of Gulf Stream rings and streamers well to the north is documented (Cox and Weibe, 1979; Wroblewski and Cheny, 1984; Flierl and Wroblewski, 1985; Hare and Cowen, 1991,1996).

Interpretation of assemblage structure and association with environmental parameters can clearly be made because of the structured nature of oceanographic conditions seen during this cruise. Hydrography was highly ordered with regard to the likely origins of water masses encountered: southern water types were found at low latitudes, MAB water types at high latitudes, fresher water inshore of the Gulf Stream in the southeast. Temperature and salinity covaried inversely with latitude because Gulf Stream water arrived into the sample area mostly from the southeast while MAB water types of lower salinity and temperature were in the north. The ordered hydrography provides a well-structured baseline from which to measure the effect of dynamic interactions between water masses in following years.

Our findings suggest a potential for high spatial and temporal variability in the structure of the transition zone assemblage. Virginia Coastal Water penetration of Diamond Shoals (Pietrafesa et al., 1985), Gulf Stream front migration (Miller, 1994; Wang, 1996), Gulf Stream flooding of the MAB shelf (Gawarkiewicz et al., 1996), high salinity mid-water intrusions of the MAB shelf and slope and migration of the shelf-break front (Churchill and Cornillon, 1991; Flagg et al., 1994), and offshore entrainment of shelf water as Ford Water (Fisher, 1972) are all mesoscale features that could change the relationships of larvae to each other and to the environmental parameters that we observed here. Long-term changes associated with global climate trends, such as changes in the mean flow or position of the Gulf Stream front, water temperature, or salinity, could result in significant alterations of faunal distribution and regional biodiversity as well.

With such distinct assemblage boundaries as those seen here, mesoscale advective events should dominate processes of larval exchange between the MAB and SAB; the effects of such events would then be mediated by biology during or after transport (Cowen and Bodkin, 1993). It is necessary still to examine the effect of temporal dynamics in the reshaping of this transition group. Even under similar physical conditions, the supply of larvae being transported is probably affected by adult spawning time and biomass. Time series studies will allow us to test the predictions made for distribution under different circulation scenarios. If variability is predictable, flux calculations between the MAB and SAB will be more accurate. Predictable variability would also allow us to test predictions as to the dynamics of permeability in this zone as a function of larval life history, physiology, and behavior.

Acknowledgements

We thank the officers and crew of the NOAA Ship *Ferrel*, field assistants Elizabeth Braga, Nancy Craig, Kim Roberts and Maria Udarbe, and especially Jon A. Hare, whose effort and experience greatly improved our sampling capabilities. Heidi Neglia, Jos Selig, and Mark Sullivan helped sort samples. Drafts were greatly improved by reviews from Bob Cerrato, Michael Fahay, Charlie Flagg, Jeff Govoni, Jon Hare and two anonymous reviewers. We benefited from the technical advice of Bob Cerrato and Brian Steves. This paper is a result of research funded by the National Oceanic and Atmospheric Administration award #NA46RG0090 to the Research Foundation of State University of New York for New York Sea Grant. The US government is authorized to produce and distribute reprints for governmental purposes notwithstanding any copyright notation that may appear hereon. The views expressed herein are those of the authors and do not necessarily reflect the views of NOAA or any of its subagencies. Additional funding was provided by the North Carolina Department of Coastal Management. This is contribution number 1137 from the Marine Sciences Research Center.

References

Able, K.P., Fahay, M.P., 1998. The first year in the life of estuarine fishes in the Middle Atlantic Bight. Rutgers University Press, New Brunswick, New Jersey, 342 pp.

Aikman III, F., Posmentier, E.S., 1985. Stratification and shelf slope interaction in the Middle Atlantic Bight. Journal of Geophysical Research 90 (C3), 4895–4905.

Bailey, K.M., 1981. Larval transport and recruitment of Pacific hake *Merluccius productus*. Marine Ecology Progressive Series 6, 1–9.

Beardsley, R.C., Boicourt, W.C., Hansen, D.V., 1976. Physical oceanography of the Middle Atlantic Bight. American Society of Limnology and Oceanography, Special Symposia 2, 20–33.

Briggs, J.C., 1974. Marine Zoogeography. McGraw-Hill, New York.

Brooks, D.A., Blane Jr., J.M., 1978. Gulf Stream deflection by a bottom feature off Charleston. South Carolina. Science 201, 1225–1226.

Bumpus, D.F., 1973. A description of the circulation on the continental shelf of the east coast of the United States. Progress in Oceanography 6, 111–157.

Checkley Jr., D.M., Raman, S., Maillet, G.L., Mason, K.M., 1988. Winter storm effects on the spawning and larval drift of a pelagic fish. Nature 355, 346–1988.

Churchill, J.H., Cornillon, P.C., 1991. Gulf Stream water on the shelf and upper slope north of Cape Hatteras. Continental Shelf Research 11 (5), 409–431.

Churchill, J.H., Levine, E.R., Connors, D.N., Cornillon, P.C., 1993. Mixing of shelf, slope and Gulf Stream water over the continental slope of the Middle Atlantic Bight. Deep Sea Research 40, 1063–1085.

Colton, J.B., Smith, W.G., Kendall, A.W., Berrian, P.L., Fahay, M.P., 1979. Principle spawning areas and times of marine fishes. Cape Sable to Cape Haterras. Fisheries Bulletin 76, 911–915.

Cowen, R.K., 1985. Large scale pattern of recruitment by the temperate labrid, *Semicossyphus pulcher*: causes and implications. Journal of Marine Science 43, 719–742.

Cowen, R.K., Bodkin, J.L., 1993. Annual and spatial variation of the kelp forest fish assemblage at San Nicolas Island, California. In: Hochberg, F.G. (Ed.), Third California Islands Symposium. Santa Barbara Museum of Natural History, Santa Barbara, pp. 463–474.

Cowen, R.K., Hare, J.K., Fahay, M.P., 1993. Beyond hydrography: can physical processes explain larval fish assemblages within the Middle Atlantic Bight. Bulletin of Marine Science 53 (2), 567–587.

Cox, J., Weibe, P.H., 1979. Origins of Oceanic plankton in the Middle Atlantic Bight. Estuarine and Coastal Marine Science 9, 509–527.

Dempster, T., Gibbs, M.T., Rissik, D., Suthers, I.M., 1997. Beyond hydrography: daily ichthyoplankton variability and short term oceanographic events on the Sydney continental shelf. Continental Shelf Research 17 (12), 1461–1481.

Evans, R.H., Baker, K.S., Brown, O.B., Smith, R.C., 1985. Chronology of warm-core ring 82B. Journal of Geophysical Research 90, 8803–8811.

Fahay, M.P., 1983. Guide to the early stages of marine fishes occurring in the western North Atlantic Ocean, Cape Hatteras to the southern Scotian Shelf. Journal of the Northwest Atlantic Fisheries Science 4, 1–423.

Fisher, A., 1972. Entrainment of shelf water by the Gulf Stream northeast of Cape Hatteras. Journal of Geophysical Research 77, 3248–3255.

Flagg, C.N., Houghton, R.W., Pietrafesa, L.J. 1994. Summertime thermocline and sub-thermocline cross-frontal intrusions in the Mid-Atlantic Bight. Deep Sea Research II, 409–431.

Flierl, G.R., Wroblewski, J.S., 1985. The possible influence of warm core Gulf Stream rings upon shelf water larval fish distributions. Fisheries Bulletin 83, 313–330.

Ford, W.L., Longard, J.R., Evans, R.E., 1952. On the nature, occurrence and origin of cold low salinity water along the edge of the Gulf Stream. Journal of Marine Research 11, 282–293.

Fortier, L., Leggett, W.C., 1985. A drift study of larval fish survival. Marine Ecology Progressive Series 25, 245–257.

Fortier, L., Levasseur, M.E., Drolet, R., Therriault, J.C., 1992. Export production and the distribution of fish larvae and their prey in a coastal jet frontal region. Marine Ecology Progressive Series 85, 203–218.

Forward, R.B., Burke, J.S., Rittschof, D., Welch, J.M., 1996. Photoresponse of larval Atlantic menhaden (*Brevoortia tyrannus* Latrobe) in offshore and estuarine waters: implications for transport. Journal of Experimental Marine Biology, 199, 123–135.

Gawarkiewicz, G., Ferdelman, T.G., Church, T.M., Luther, G.W., 1996. Shelfbreak frontal structure on the continental slope north of Cape Hatteras. Continental Shelf Research 16 (14), 1751–1773.

Govoni, J.J., Hoss, D.E., Colby, D.R., 1989. The spatial distribution of larval fishes about the Mississippi River plume. Limnology and Oceanography 34, 178–187.

Govoni, J.J., 1993. Flux of larval fishes across frontal boundaries examples from the Mississippi River plume front and the western Gulf Stream front in winter. Bulletin of Marine Science 53 (2), 538,566.

Grothues, T.M., Cowen, R.K., Pietrafesa, L.J., Weatherly, G., Flagg, C.N. Flux of larval fishes around Cape Hatteras, in preparation.

Hare, J.A., Cowen, R.K., 1991. Expatriation of *Xyrichtys novacula* (Pisces: Labridae) larvae: evidence of rapid cross-slope exchange. Journal of Marine Research 49, 801–823.

Hare, J.A., Cowen, R.K., 1993. Ecological and evolutionary implications of the larval transport and reproductive strategy of bluefish (*Pomatomus saltatrix*). Marine Ecology Progressive Series.

Hare, J.A., Cowen, R.K., 1996. Transport mechanisms of larval and pelagic juvenile bluefish (*Pomatomus saltatrix*) from South Atlantic Bight spawning grounds to Middle Atlantic Bight nursery habitats. Limnology and Oceanography 41 (6), 1264–1280.

Hoff, J.G., Ibara, R.M., 1977. Factors affecting the seasonal abundance, composition and diversity of fishes in a New England estuary. Estuarine and Coastal Marine Science 5, 665–678.

Horn, M., 1970. Systematics and biology of the Stromateoid fishes of the genus *Peprilus*. Bulletin of the Museum of Comparative Zoology 140 (5), 165–262.

Kingsford, M.J., 1990. Linear oceanographic features: a focus for research on recruitment processes. Australian Journal of Ecology 15, 391–401.

Lee, T.N., Aitkinson, L.P., 1983. Low frequency current and temperature variability from Gulf Stream frontal eddies and atmospheric forcing along the southeast U.S. outer continental shelf. Journal of Geophysical Research 88, 4541–4567.

Leis, J., 1991. The pelagic stage of reef fishes: the larval biology of coral reef fishes. In: Sale, P.F. (Ed.) The Ecology of Fishes on Coral Reefs. Academic Press, San Diego, pp. 183–230.

Lillibridge, J.L., Hitchcock, G., Rossby, T., Lessard, E., Monk, M., Golmen, L., 1990. Entrainment and mixing of shelf/slope waters in the near surface Gulf Stream. Journal of Geophysical Research 95, 13065–13087.

Miller, J., 1994. Fluctuations of Gulf Stream frontal position between Cape Hatteras and the Straits of Florida. Journal of Geophysical Research 99 (C3), 5057–5064.

Miller, M.J., McCleave, J.D., 1994. Species assemblages of leptocephali in the subtropical convergence zone of the Sargasso Sea. Journal of Marine Research 52, 743–772.

Miller, J.M., Reed, J.P., Pietrafesa, L.J., 1984. Patterns, mechanisms and approaches to the study of estuarine dependent fish larvae and juveniles. In: McCleave, J.D., Arnold, G.P., Dodson, J.J., Niell, W.H. (Eds.) Mechanisms of migration in fishes. Plenum Press, New York, pp. 209–225.

Neill, W.H., Miller, J.M., van der Veer, H.W., Winemiller, K.O., 1994. Ecophysiology of marine fish recruitment: A conceptual framework for understanding interannual variability. Netherlands Journal of Sea Research 32 (2), 135–152.

Nyman, R.M., Conover, D.O., 1988. The relation between spawning season and the recruitment of young-of-the-year bluefish, *Pomatomus saltatrix*, to New York. Fisheries Bulletin 86 (2), 237–250.

Palmer, M.W., 1993. Putting things in an even better order: the advantages of Canonical correspondence analysis. Ecology 74 (8), 2215–2230.

Pietrafesa, L.J., Janowitz, G.S., Wittman, P.A., 1985. Physical oceanography in the Carolina Capes. In: Atkinson, L.P., Menzel, D.W., Bush, K.A. (Eds.), Oceanography of the Southeastern U.S. Continental Shelf. Coastal and Estuarine Shelf Sciences 2, pp. 23–32.

Pietrafesa, L.J., Morrison, J.M., McCann, M.P., Churchill, J., Houghton, R.W., 1994. Water Mass exchange between the Middle and South Atlantic Bights. Deep Sea Research 41, 365–389.

Polacheck, T., Mountain, D., McMillan, D., Smith, W., Berrien, P., 1992. Recruitment of the , 1987 year class stock of Georges Bank Haddock (*Melanogrammus aeglefinus*). Canadian Journal of Fisheries and Aquatic Science 49, 484–496.

Rotunno, K.T., Cowen, R.K., 1997. Temporal and spatial spawning patterns of the Atlantic butterfish (*Peprillus triacanthus*) in the South and Middle Atlantic Bights. Fisheries Bulletin 95, 785–789.

Sabatés, A., Olivar, M.P., 1996. Variation of larval fish distributions associated with variability in the location of the shelf-slope front. Marine Ecology Progressive Series 135, 11–20.

Suthers, I.M., Frank, K.T., 1991. Comparitive persistence of marine fish larvae from pelagic versus demersal eggs off southwestern Nova Scotia. Canada Marine Biology 108, 175–184.

ter Braak, C.J.F., 1992. CANOCO – A FORTRAN program for Canonical Community Ordination. Microcomputer Power, Ithaca, New York, USA.

ter Braak, C.J.F., Verdonschot, P.F.M., 1995. Canonical correspondence analysis and related multivariate methods in aquatic ecology. Aquatic Science 57 (3), 255–289.

Wang, W., 1996. The Gulf Stream near 73°W: veiws from observations and a primitive equation model. Deep Sea Research 44 (7), 1147–1166.

Warlen, S.M., 1992. Age, growth, and size distribution of larval Atlantic menhaden off North Carolina. Transactions of the American Fisheries Society 121, 588–598.

Wroblewski, J.S., Cheny, J., 1984. Ichthyoplankton associated with a warm core ring off the Scotian Shelf. Canadian Journal of Fisheries and Aquatic Science 41, 294–303.

Yoder, J., 1983. Statistical analysis of the distribution of fish eggs and larvae on the southeastern U.S. continental shelf with comments on oceanographic processes that may effect survival. Continental Shelf Science 17, 637–650.

Zheng, Q., Klemas, V., Huang, N.E., 1984. Dynamics of the slope water off New England and its influences on the Gulf Stream as inferred from satellite IR data. Remote Sensing of Environment 15, 135–153.