An Examination of the Diversity and Abundance of Ichthyoplankton in the Loop Current of the Central Gulf of Mexico

Un Examen de la Diversidad y Abundancia de Ictioplancton en la Corriente del Lazo de la Región Central del Golfo de México

Un Examen de la Diversité et de l'Abondance de Ichthyoplancton dans la Boucle de Courant de la Partie Centrale du Golfe du Mexique

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ABSTRACT

The Loop Current boundary (LCB), an area characterized by the transition of environmental conditions of the water mass between the Gulf of Mexico (GOM) and Caribbean, provides increased feeding opportunities relative to the surrounding oligotrophic waters for ichthyoplankton. The goals of this study were to characterize the relative density of ichthyoplankton and to describe the community composition of the LCB. Ichthyoplankton were collected in and around the vicinity of the LCB; attempts were made to distribute samples equally across the LCB. We identified *post hoc* the origin of ichthyoplankton samples from one of three water masses: GOM, LCB, or Caribbean. We took 18 samples in four transects and caught 12,401 ichthyoplankton from 53 families. Using nonmetric multidimensional scaling, we identified three unique assemblages of ichthyoplankton at the LCB: a transition assemblage found around the LCB and two peripheral groups originating from either GOM or Caribbean water masses. We found significant dissimilarity in the pairwise comparisons of familial compositions ($p < 0.05$). The LCB ecotone displays a unique biotic assemblage of economically important fishes and may be essential to the early life history of these fishes.

KEY WORDS: Loop Current, ichthyoplankton, ecotone

INTRODUCTION

The investigation of the spatial dynamics of organismal community transitions continues to be a focus of ecological research (Geist 2012), and the dynamics of community composition at habitat margins are of special interest (Yahner 1988). Transition areas of community composition between adjacent habitats are unique because of the "edge effect" that influence taxonomic diversity and richness (Odum 1971). Habitat composition at the margin of flanking habitats generally exhibit complexity and contain multiple boundary landscape elements (Wiens et al. 1985) which can lead to increased niche diversity (Wiens et al. 1985).

The transition between organismal communities, determined by the meeting of disjoint habitat characteristics, is categorized by the spatial scale of the transition. Two community transition types are recognized: ecotones and ecoclines (Livingston 1903, Clements 1905, Whittaker 1960). Ecotones exhibit community differences at small spatial scales (Livingston 1903, Clements 1905, van der Maarel 1990). Ecotones have been reported in diverse habitat types including the disjoint boundaries that exist in forests, riverine and swamp edges, rainforests and savannah, and savannah and desert (Clark and Gilbert 1982, Gosz 1993, Welborn et al. 1996, Smith et al. 1997, Mayle et al. 2007). In contrast, ecoclines exhibit a gradual change in organismal community structure (Bolton 1983, Rietema 1995). Because ecoclines lack distinct boundaries, the community composition in the transition area is often considered a single heterogeneous community (van der Maarel 1990).

A variety of mechanisms in marine ecosystems serve to maintain the relatively greater organismal diversity that occurs in ecotones. Although they were once considered to be homogenous environments (McKelvie 1985), recent work has shown that the pelagic environment exhibits habitat differentiation; water from different origins have variable physical and chemical compositions (Bane 2001). Boundaries of water masses can exhibit pronounced habitat gradients over relatively fine scales (Herron et al. 1989). The Loop Current (LC) in the Gulf of Mexico (GOM) is a spatially and temporally dynamic mesoscale oceanographic feature in the GOM that is formed by the intrusion of warmer Caribbean water from the Yucatan Current into the central GOM (Sturges and Evans 1983, Richards et al. 1989). The LC water is typically warmer than the resident GOM water, resulting in a biologically dynamic zone of convergence at their interface (Bakun and Csirke 1998, Brown et al. 1999). The Loop Current Boundary (LCB) is a location of upwelling and downwelling caused by current flow (Bakun and Csirke 1998, Lohrenz et al. 1999). The resulting flow dynamics provides nutrient rich water to the photic zone which enhances primary production (Kingsford 1990, Biggs 1992).

Because of the physical and biological dynamics of the LCB, it has been the focus of studies examining how the boundary characteristics promote biological diversity and abundance (Richards et al. 1993, Lindo-Atichati et al. 2012). Lindo-Atichati et al. (2012) found greater densities of ichthyoplankton at the LCB than in adjacent areas. They suggested that the LC frontal feature promoted larval survivorship because of its provisioning of increased feeding opportunities (Lindo-Atichati et al. (2012). Muhling et al. (2010, 2012) reported that ichthyoplankton aggregations were associated with locations that exhibited a gradient of increased sea surface temperature (SST) and current patterns in the GOM – indicative

of LCB conditions. Similarly, the distribution of spawning adult bluefin tuna in the GOM were sensitive to the changes in SST and associated with the occurrence of fronts (Teo et al. 2007, Teo and Block 2010).

The goal of this study is to understand whether the LCB exhibits ecotone characteristics. I describe the observed changes in community composition, specifically whether the boundary area exhibits a detectable transition between ichthyoplankton communities. I characterized the spatial scale of changes in ichthyoplankton community composition and determine the abiotic components of the habitat that are responsible for contrasts in the of the community composition of the LCB and adjacent water masses.

METHODS

Ichthyoplankton were sampled in the GOM during May 2003 and June 2004 at stations placed along transects perpendicular to the LCB at the northern and western boundary regions of the LC (24.5 °N to 27.5 °N and -86.0 ° W to -89.5 °W, Figure 1). The location of transects were established *a priori* using Advanced Very High Resolution Radiometer (AVHRR) satellite imagery to detect where transitions in the SST occurred. The location of stations along transects were determined *in situ* by measuring water temperature using conductivity, temperature, and depth (CTD) and expendable bathythermograph (XBT) sensors. The objective was to sample stations within the LCB and adjacent areas. The location of the LCB was determined as the location where the temperature at 100 m was 20 °C (Lubertz 1967, Nowlin and McLellan 1967). The intent of the sampling design was to sample stations along transects in each of three areas: 1) the GOM located west or north of the LCB; 2) the LCB; and 3) the Caribbean influenced waters that are located east or south of the LCB.

Biological and physical data were collected and recorded at all stations. A discrete-depth Tucker trawl was deployed at each station for five minutes per depth bin to collect ichthyoplankton. The discrete depth Tucker trawl consisted of three separate nets with dimensions 1 m by 1.5 m with 0.333 mm mesh netting that is 5 m in length. The gear is designed to consecutively collect three separate samples at 1 m, 10 m, and 20 m depth. I restricted the analysis to only those samples collected at the 1 m depth because these samples were taken most consistently. In 2003, collections were made at 13 stations on three transects; and in 2004, collections were made at six stations along one transect. The linear distance that the trawl traveled was determined using a calibrated flow meter. All fishes collected at each station were removed from the nets and immediately preserved in 95% ethanol. Preserved samples were sorted, and individuals were identified to the family level or in some cases to the species level. Individuals in a subset of families (n = 14) were identified to the species-level including Balistidae, Caproidae, Carangidae, Coryphaenidae, Echeneidae, Exocoetidae, Gempylidae, Holocentridae, Lutjanidae, Nomeidae, Rachycentridae, Scombridae, Sphyraenidae, and Xiphiidae. These are species of economic and ecological interest and were relatively easy to identify. Individuals collected were either larvae or early juveniles, with the majority of them measuring less than 10 mm (Table 1). In this study I refer to them as ichthyoplankton.

In addition to collecting ichthyoplankton, a suite of environmental variables was collected from each station using *in situ*, modeled, and remotely-sensed sources. *In situ* data consisted of SST (ºC), salinity (ppt), dissolved oxygen concentration (mg/L), wind speed (m/s), and time of day of the collection. Modeled estimates of temperature (°C) at 100 m depth, surface current velocity (cm/s) and direction, and sea surface height (m) were obtained from the Hybrid Coordinate Ocean Model (HYCOM, Chassignet et al. 2007). Remotely-sensed chlorophyll *a* measurements were made using eight-day composite images of ocean-color from the Moderate Resolution Imaging Spectroradiometer (MODIS) sensor.

All family-specific abundance data for each station were converted to a density estimate based on the volume of water sampled for each tow using $\log_{10}(1 + \text{density}_{family,station})$. A community resemblance matrix (Bray-Curtis similarity) was created from the transformed density data for ordination. Nonmetric multidimensional scaling (MDS) was used to describe the dissimilarity among family-specific ichthyoplankton densities of each station. I used a similarity profile (SIMPROF) test, a form of hierarchical clustering, to arrange station-specific familial assemblages in ordination space. The "BEST" procedure (BIO-ENV/BVSTEP) was used to determine which environmental data had power to describe the observed similarities and dissimilarities in the family-specific density composition (Clarke and Ainsworth 1993).

Two different *post hoc* analyses were used to understand the observed differences among qualitatively-

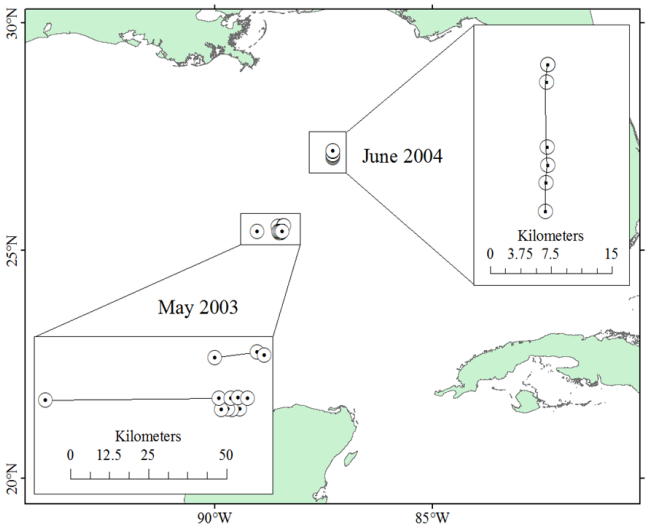

Figure 1. The study design surveyed in and around the Loop Current Boundary of the Gulf of Mexico. Circles represent stations sampled in a transect which were enlarged to show the transects in the bottom left and top right corners. Illustrated are lines that connect the stations in a sampled transect. The bottom magnification box shows transects that were sampled in May of 2003, and the top right transect was sampled in June 2004. Three to seven stations on each of the transect were sampled.

identified group compositions. The first analysis, "analysis of similarity" (ANOSIM), ranks similarities between pairs of identified groups. The second *post hoc* analysis performed was "similarity percentages" (SIMPER) which was conducted at two taxonomic levels of family and species. A SIMPER analysis was performed to determine which families composed the majority of the dissimilarity percentage for each MDS assemblage and then for 25 identified species of those families (Clarke and Warwick 2001). Shannon-Wiener diversity, richness, and evenness indices were used to describe ecological community composition in each assemblage (Shannon 1948, Legendre et al. 2005, Molles 2012).

RESULTS

A total of 4,927 individual fish from 37 families were collected and analyzed for community analysis. A total of 4,119 (83.6%) were identified to the taxonomic level of family and 2,423 of these fish (49.2%) were identified to the taxonomic level of species. Scombridae (tunas) had the greatest relative abundance among the selected 14 families collected followed by Myctophidae (lanternfish), Carangidae (jacks), Gonostomatidae (bristlemouths), and Exocoetidae (flyingfish) (Table 2).

The MDS analysis indicated the existence of three distinct assemblages: an assemblage in between two assemblages termed the "Transition" and "peripheral" assemblages. These assemblages were clustered at 40 percent similarity (Figure 2). Surface chlorophyll *a* (mg/m^3), surface current velocity (m/s), and SST (°C) had explanatory power to describe the contrast in community patterns (Global R = 0.481). Peripheral Group One was associated with greater concentrations of surface chlorophyll *a* and surface current velocity, and Peripheral Group Two is associated with greater values of SST (Figure 3, Table 3).

Each of the recognized community assemblages was significantly dissimilar in their family composition (One-way ANOSIM $R = 0.588$, $p < 0.01$). The greatest R value resulted from the pairwise comparison of the peripheral assemblages, indicating that Peripheral Group One and Peripheral Group Two were the most significantly dissimilar ($R = 0.684$, Table 4). The lowest R value resulted from the pairwise comparison of Peripheral Group Two and the Transition Assemblage ($R = 0.396$, Table 4). Family Myctophidae (lanternfish) and Exocoetidae (flyingfish) were characteristic of Peripheral Group One (Figure 4). Scombridae and Carangidae were dominant taxa of the Transition assemblage but were present in all three assemblages (Figure 4). Ichthyoplankton families Sphyraenidae (barracudas), Istiophoridae (billfishes), Hemiramphidae (halfbeaks), Scorpanidae (scorpionfishes), Gonostomatidae, Tetraodontidae (puffers), and Echeneidae (remoras) were characteristic of Peripheral Group Two (Figure 4).

The SIMPER analysis indicated that a relatively small subset of taxa contributed to the significant differences between the three assemblages. The relative density of the families Scombridae, Myctophidae, Exocoetidae, and Carangidae contributed the most to the differences in pairwise dissimilarity of each assemblage (Table 5). Overall Peripheral Group One exhibited the lowest densities of ichthyoplankton among samples (Table 6, Figure 4). The family Scombridae exhibited the greatest mean density (Table 2) in all assemblages, particularly in the Transition assemblage (Figure 4), and contributed to the largest portion of pairwise dissimilarity between each of the assemblages (Table 5). Scombridae member *Auxis rochei* contributed to over 20% of the dissimilarity between assemblages (Table 7) and was present in all assemblages (Table 8). Scombridae members *Thunnus albacares* and *T. atlanticus* also contributed to over 10% of the dissimilarity between assemblages (Table 7) and were present in all assemblages (Table 8). Carangidae exhibited the third greatest mean density (Table 2) of which the greatest densities were found in the Transition assemblage. Carangidae was present in all assemblages (Table 2, Figure 4) and contributed over six percent of the dissimilarity between each of the assemblages. Myctophidae exhibited a similar pattern of relatively high densities and occurred within Peripheral Group One and the Transition assemblage. Myctophidae had the greatest mean density in Peripheral Group One (Table 6). Two of 18 samples were collected at night did not influence the density of family Myctophidae which is generally considered nocturnal. Exocoetidae exhibited greatest densities in Peripheral Group Two and contributed over 30% of the dissimilarity between the other two assemblages. Sphyraenidae exhibited the greatest densities for Peripheral Group Two and contributed more than 17% in dissimilarity between Peripheral Group Two and Peripheral Group One.

Mean diversity, richness and evenness were not significantly different among the three identified assemblages, though the Transition assemblage exhibited the greatest variation about the mean relative to the other assemblage groups for diversity, richness, and evenness (Figure 5). Peripheral Group One exhibited narrow range dispersion for each index of diversity, richness, and evenness and the lowest mean richness of the three assemblages.

The conceptual model of the relative densities, significantly dissimilar distribution of families, and associated environmental factors in the area of the LCB is illustrated using a Venn diagram (Figure 6). The families Scombridae (particularly *A. rochei,* Table 8) and Carangidae (Table 6) were considered to be cosmopolitan families present in all assemblages with varying densities. In contrast, Coryphaenidae was only present in the Transition assemblage at low relative abundance (Table 6, Figure 4). Families Istiophoridae, Tetraodontidae, Sphyraenidae, Hemiramphidae, Scorpaenidae, Gonostomatidae, Echeneidae, and Exocoetidae had elevated densities in the Transition assemblage and Peripheral Group Two (Table 6, Figure 4). Exocoetidae were present but were relatively less dense in Peripheral Group One than the Transition assemblage. Myctophidae exhibited greater densities in Peripheral Group One. Peripheral Group One was associated with elevated concentrations of chlorophyll *a* and increased current velocity. The Transition assemblage and Peripheral Group Two were associated with increased SST.

Table 1. Mean, standard deviation, minimum, and maximum length (mm) of ichthyoplankton organized by family for each specimen (*n*) measured. The first 50 of each species identified at a station were measured but lengths were not measured at each station collected.

Family	*n*	Mean	SD	Minimum	Maximum
Carangidae	339	3.06	1.43	1.3	14
Coryphaenidae	29	3.11	1.60	1.7	10
Echeneidae	7	4.20	1.00	3	5.6
Exocoetidae	15	4.27	1.38	2.6	7.3
Gempylidae	56	4.11	1.56	1.7	8.8
Gonostomidae	166	4.53	1.81	1.8	11.3
Hemiramphidae	15	5.31	1.19	4	8.1
Istiophoridae	56	3.18	0.86	1.6	5.6
Myctophidae	301	3.57	1.10	1.6	9.6
Scombridae	655	3.38	1.25	1.5	10.7
Scorpaenidae	64	2.48	1.04	1.1	7.1
Sphyraenidae	27	3.74	1.41	1.8	6.6

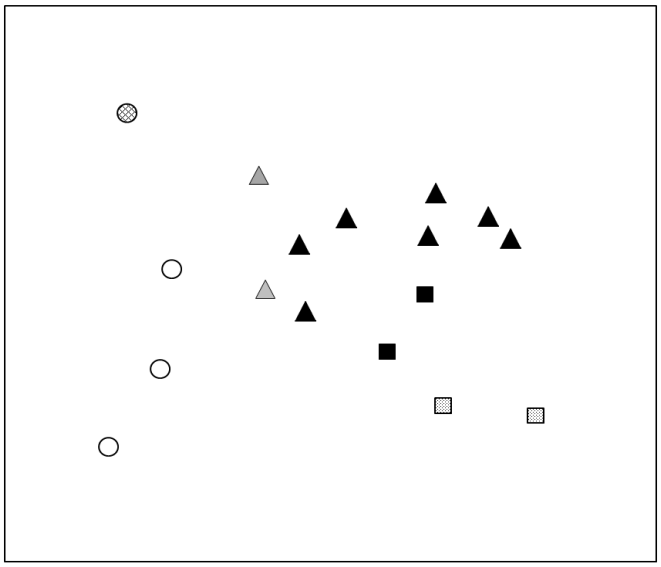

Figure 2. Nonmetric multidimensional scaling biplot (stress = 0.14). Groups were clustered using 40 percent similarity using SIMPROF. Open circles, checkered circles, grey triangles, black triangles, black squares, and dotted squares each illustrates a significantly branched cluster using SIMPROF. MDS groups were illustrated using shapes and were chosen based on SIMPROF cluster and MDS. The Transition assemblage is represented by black and grey triangles. Peripheral Group One is represented by the checkered and open circles, and Peripheral Group Two is represented by black and dotted squares.

Table 2. Total, minimum, maximum, mean, and standard deviation of density (fish/100 m^3) for each family from discrete depth Tucker Trawl stations (*n* = 20) from one meter. 37 families were caught in the one meter from 20 discrete depth Tucker trawls and are listed in order of abundance. A total of 4,927 individuals were caught from one meter depth Tucker trawl; 808 individuals were unidentified (16.3 %).

Family	Total	Minimum	Maximum	Average	SD
Scombridae	774.7	0.00	448.3	38.74	105.0
Exocoetidae	161.9	0.00	146.9	8.09	32.72
Carangidae	81.7	0.00	29.3	4.08	6.90
Myctophidae	58.7	0.00	15.1	2.93	4.40
Istiophoridae	46.4	0.00	24.4	2.32	6.04
Sphyraenidae	36.0	0.00	10.8	1.80	2.65
Coryphaenidae	24.7	0.00	9.3	1.23	2.61
Gonostomatidae	22.7	0.00	4.7	1.14	1.55
Hemiramphidae	22.4	0.00	13.6	1.12	3.30
Holocentridae	18.8	0.00	9.01	0.94	2.45
Scorpaenidae	13.4	0.00	5.51	0.67	1.33
Paralichidae	11.7	0.00	3.79	0.59	1.09
Tetraodontidae	11.8	0.00	7.28	0.58	1.65
Priacanthidae	10.8	0.00	4.69	0.54	1.15
Gempylidae	5.78	0.00	1.66	0.29	0.50
Gerreidae	5.01	0.00	1.96	0.25	0.56
Echeinidae	2.59	0.00	1.22	0.13	0.29
Synodontidae	2.54	0.00	1.93	0.13	0.44
Caproidae	2.38	0.00	0.83	0.12	0.26
Triglidae	2.19	0.00	2.19	0.11	0.49
Muraenidae	1.32	0.00	0.97	0.07	0.23
Balistidae	1.17	0.00	0.92	0.06	0.21
Xiphidae	1.03	0.00	0.61	0.05	0.16
Ophichthidae	0.86	0.00	0.34	0.04	0.11
Chlorophthalmidae	0.83	0.00	0.83	0.04	0.19
Lutjanidae	0.69	0.00	0.41	0.03	0.11
Rachycentridae	0.61	0.00	0.61	0.03	0.14
Nomeidae	0.59	0.00	0.59	0.03	0.13
Mugilidae	0.49	0.00	0.49	0.02	0.11
Monocanthidae	0.34	0.00	0.34	0.02	0.08
Syngnathidae	0.33	0.00	0.33	0.02	0.07
Serranidae	0.32	0.00	0.32	0.02	0.07
Chaetodontidae	0.28	0.00	0.28	0.01	0.06
Ophididae	0.28	0.00	0.28	0.01	0.06

Table 3. Mean, standard deviation, minimum, and maximum of the environmental parameters used in BEST procedure, an optimal matching procedure for environmental data linking community data. Temperature, salinity, dissolved oxygen, and wind were compiled from observed; chlorophyll *a* were compiled using satellite data from Moderate Resolution Imaging Spectroradiometer (MODIS) sensors; and temperature at 100 m, current velocity and direction, and sea surface height were compiled from Hybrid Ocean Coordinate Model (HYCOM) for each nonmetric multidimensional scaling (MDS) assemblage.

MDS Assemblage	Source	Environmental Parameter	Mean	SD	Minimum	Maximum
Peripheral Group 1	MODIS	Chlorophyll *a* (mg/m^3)	0.12	0.02	0.09	0.15
	HYCOM	Temperature (℃), 100 m	20.91	0.91	19.58	21.76
	observed	Salinity (ppt)	36.10	0.22	36.00	36.50
	observed	Temperature (℃)	27.62	0.58	27.10	28.60
	observed	Dissolved Oxygen (mg/L)	8.36	1.15	6.30	9.00
	HYCOM	current velocity (cm/s)	-0.61	0.29	-0.98	-0.21
	HYCOM	current direction	2.29	1.42	-0.05	3.50
	HYCOM	sea surface height (m)	0.18	0.19	-0.07	0.36
	observed	wind (m/s)	7.40	4.04	1.00	12.00
Transition	MODIS	Chlorophyll *a* (mg/m^3)	0.09	0.02	0.06	0.11
	HYCOM	Temperature (℃), 100 m	20.57	0.71	19.58	21.62
	observed	Salinity (ppt)	36.18	0.24	36.00	36.50
	observed	Temperature (℃)	28.58	0.51	27.80	29.50
	observed	Dissolved Oxygen (mg/L)	7.83	1.34	6.20	9.00
	HYCOM	current velocity (cm/s)	-0.71	0.13	-0.89	-0.52
	HYCOM	current direction	1.71	1.55	-0.10	3.10
	HYCOM	sea surface height (m)	0.19	0.23	-0.09	0.41
	observed	wind (m/s)	5.80	2.90	1.00	9.00
Peripheral Group 2	MODIS	Chlorophyll *a* (mg/m^3)	0.10	0.04	0.06	0.15
	HYCOM	Temperature (℃), 100 m	21.02	0.51	20.48	21.62
	observed	Salinity (ppt)	36.14	0.21	36.00	36.40
	observed	Temperature (℃)	28.98	0.43	28.60	29.60
	observed	Dissolved Oxygen (mg/L)	7.50	1.39	6.30	8.80
	HYCOM	current velocity (cm/s)	-0.49	0.24	-0.71	-0.28
	HYCOM	current direction	1.56	1.95	-0.13	3.30
	HYCOM	sea surface height (m)	0.13	0.27	-0.10	0.37
	observed	wind (m/s)	5.50	3.42	2.00	10.00

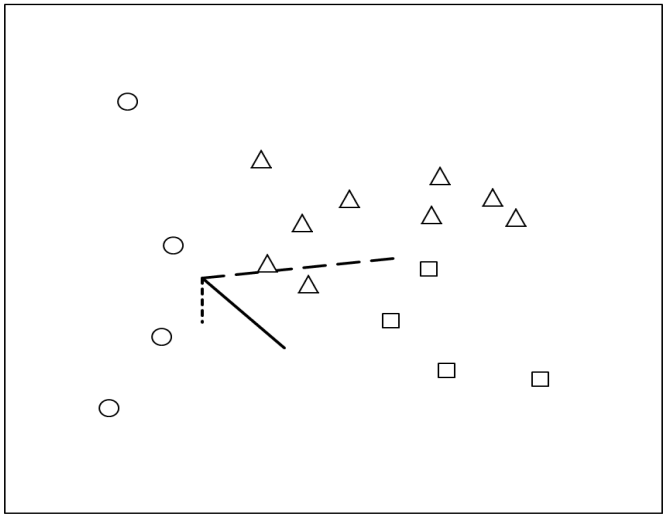

Figure 3. Nonmetric multidimensional scaling biplot (stress = 0.14). Groups were clustered using 40 percent similarity. Groups designated with open triangles represent the Transition assemblage. The other two groups represented by open circles and open squares are the Peripheral Group One and Two respectively. Vectors are imposed on the MDS using the BEST procedure representing the environmental variables that best explain the variation in the community patterns. The BEST procedure resulted in a Global R value of 0.481. Surface chlorophyll *a* (mg/m^3, represented by a short-dashed line), and surface current velocity (m/s, represented by a solid line) are associated with Peripheral Group One. Peripheral Group Two and the Transition assemblage are associated with sea surface temperature (°C, represented by a long-dashed line).

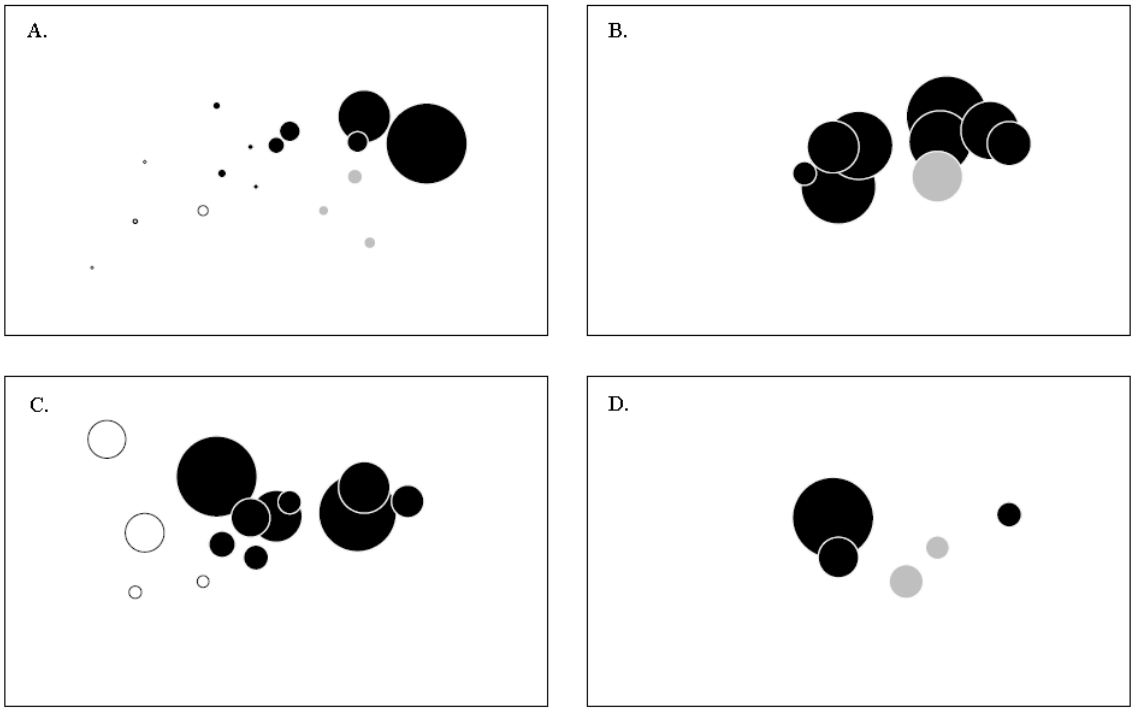

Figure 4. Relative densities for each family represented as a bubble plot of the following: A.) Scombridae, B.) Gonostomatidae, C.) Myctophidae, D.) Tetraodontidae. Groups designated with black circles represent the Transition assemblage, open circles and gray circles are the Peripheral Group One and Two, respec-

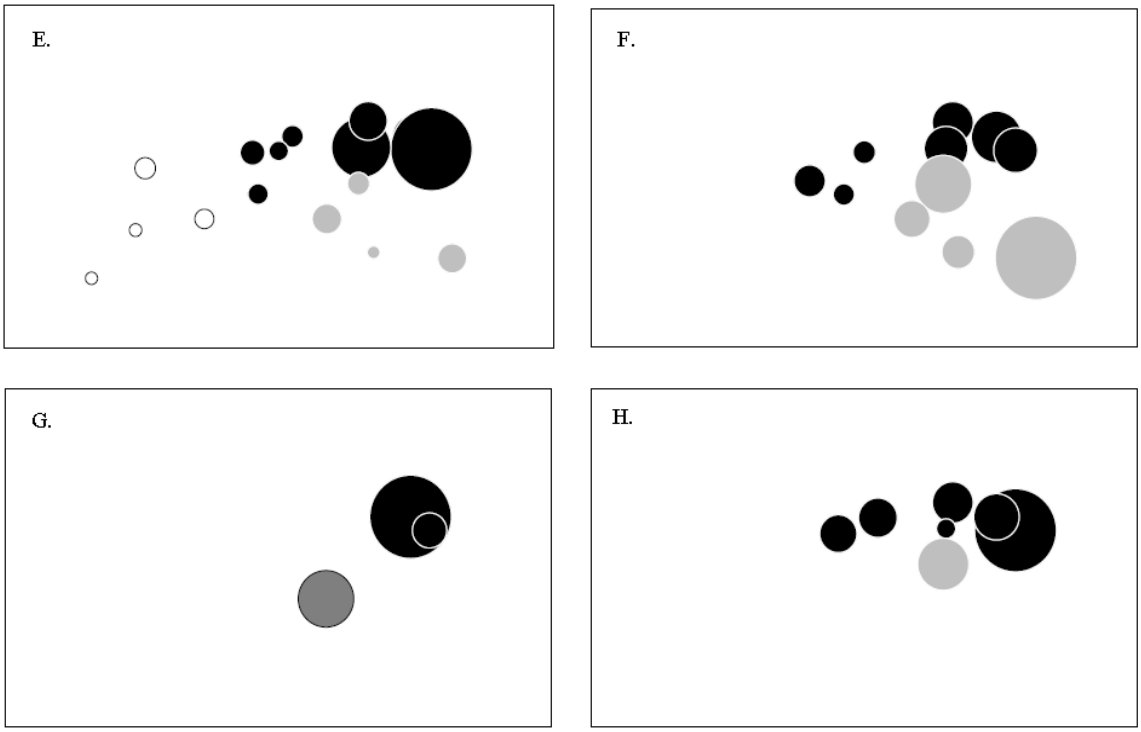

Figure 4 continued. Relative densities for each family represented as a bubble plot of the following: E.) Carangidae, F.) Sphyraenidae, G.) Hemiramphidae, H.) Scorpaenidae. Groups designated with black circles represent the Transition assemblage, open circles and gray circles are the Peripheral Group One and Two, respectively.

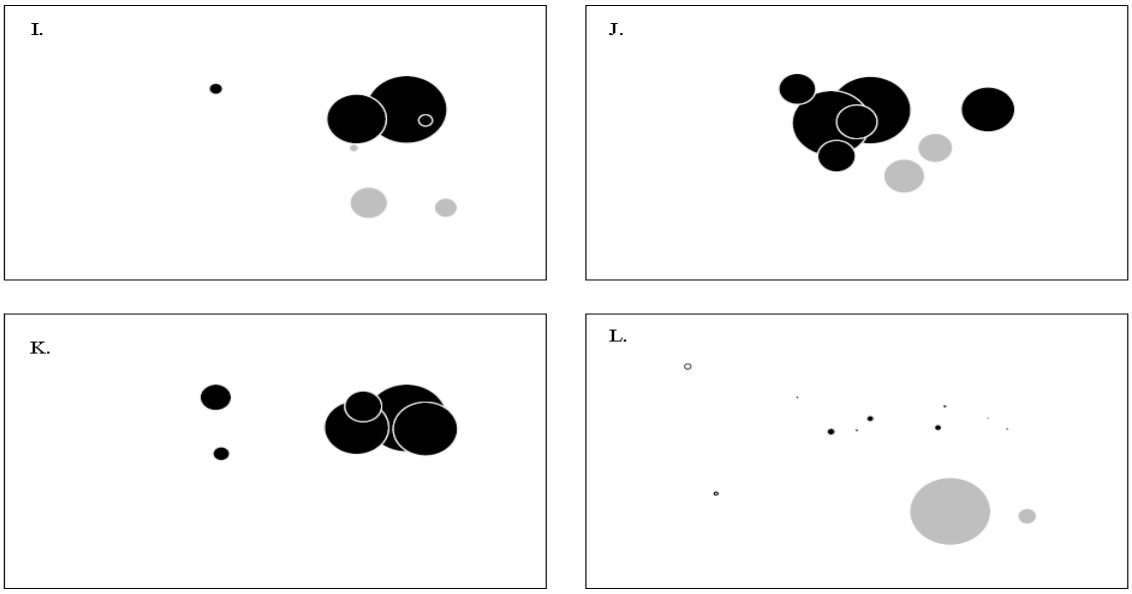

Figure 4 continued. Relative densities for each family represented as a bubble plot of the following: I.) Istiophoridae, J.) Gempylidae, K.) Coryphaenidae, L.) Exocoetidae. Groups designated with black circles represent the Transition assemblage, open circles and gray circles are the Peripheral Group One and Two

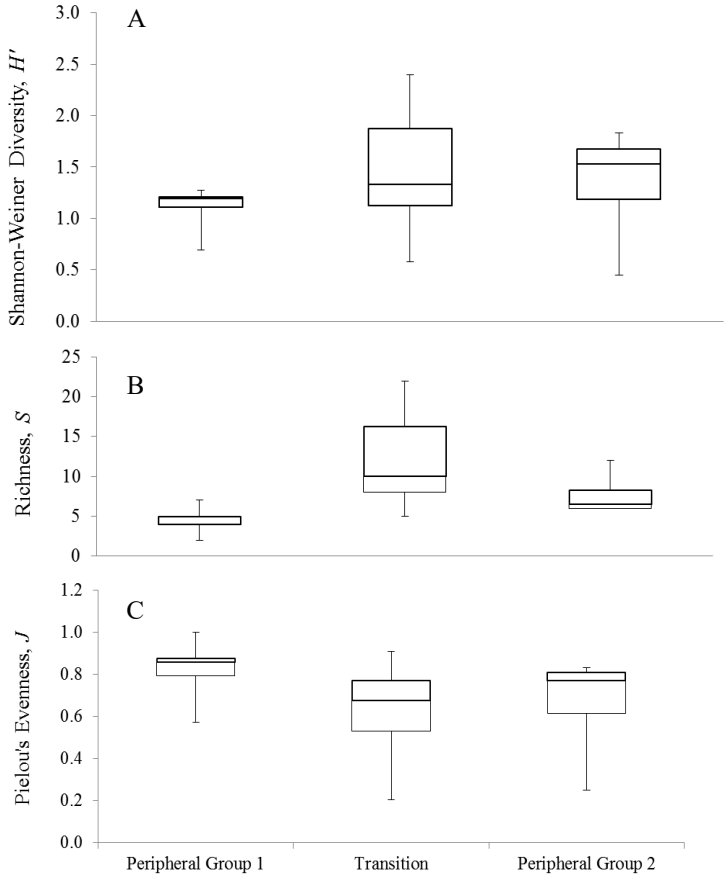

Figure 5. Box plots of A.) the Shannon-Wiener diversity index, B.) richness, C.) and Pielou's evenness at each qualitative MDS assemblage: peripheral group 1 (n = 5) , Transition (n = 10), peripheral group 2 (n = 5). Rectangles contain 50 percent of all the values and the plot extends to the smallest and largest value of the range.

Table 4. One-way ANOSIM (Analysis of Similarity) test of differences between each of the three community assemblages. If *R* is zero then there is no difference between the groups. Global R for ANOSIM is 0.558 with a corresponding p value of 0.001, indicating significant dissimilarity for the Loop Current Boundary community.

Assemblage	R	P value
Peripheral Group 1 v. Transition	0.629	0.003
Peripheral Group 2 v. Transition	0.396	0.016
Peripheral Group 1 v. 2	0.684	0.008

Table 5. Percent contribution and percent cumulative contribution of each family from similarity percentages (SIMPER) analysis. Families listed comprised 85% or greater of the cumulative dissimilarity percentage. Families in bold contributed more than ten percent of dissimilarity.

Assemblage Comparison	Family	% Contribution	% Cumulative
Peripheral Group 1 v. Transition			
	Scombridae	**44.3**	**44.3**
	Myctophidae	**13.1**	**57.4**
	Carangidae	6.8	64.3
	Gonostomatidae	5.9	70.2
	Istiophoridae	4.9	75.1
	Tetraodontidae	4.5	79.7
	Sphyraenidae	3.2	83.0
	Coryphaenidae	3.0	86.0
	Gempylidae	1.7	87.7
	Hemiramphidae	1.6	89.4
	Exocoetidae	1.6	91.1
Peripheral Group 2 v. Transition			
	Scombridae	**31.1**	**31.1**
	Exocoetidae	**24.0**	**55.1**
	Myctophidae	7.9	63.1
	Sphyraenidae	7.3	70.4
	Carangidae	4.8	75.2
	Istiophoridae	4.6	79.9
	Hemiramphidae	4.3	84.2
	Gonostomatidae	2.7	87.0
	Tetraodontidae	2.4	89.4
	Coryphaenidae	2.0	91.4
Peripheral Group 1 v. 2			
	Exocoetidae	**32.1**	**32.1**
	Sphyraenidae	**16.9**	**49.0**
	Scombridae	**15.9**	**65.0**
	Hemiramphidae	7.3	72.3
	Carangidae	6.8	79.2
	Myctophidae	4.3	83.6
	Istiophoridae	2.9	86.5
	Gerreidae	2.0	88.5
	Tetraodontidae	2.0	90.5

Table 6. Mean density (fish/100 $m^{3)}$ for the most abundant families at each qualitative assemblage determined by using nonmetric multidimensional scaling.

Assemblage	Family	Total	Mean	SD
Peripheral Group 1	Myctophidae	199.3	39.9	31.9
	Scombridae	167.6	33.5	61.1
	Gonostomatidae	47.0	9.4	8.7
	Carangidae	31.7	6.3	6.1
	Paralichidae	15.8	3.2	2.7
	Muraenidae	11.8	2.4	5.3
	Paralepidae	9.4	1.9	3.3
	Gobiidae	5.9	1.2	1.7
	Serranidae	5.6	1.1	0.4
	Scorpaenidae	5.0	1.0	1.0
Transition	Scombridae	1136.7	103.3	163.5
	Myctophidae	421.3	38.3	75.4
	Carangidae	183.4	16.7	17.3
	Gonostomatidae	138.5	12.6	11.4
	Paralichidae	51.4	4.7	6.3
	Istiophoridae	40.9	3.7	8.2
	Coryphaenidae	30.5	2.8	3.7
	Scorpaenidae	27.8	2.5	3.4
	Holocentridae	21.7	2.0	3.8
	Sphyraenidae	21.0	1.9	2.3
Peripheral Group 2	Scombridae	206.7	51.7	15.0
	Exocoetidae	164.6	41.1	76.7
	Carangidae	97.8	24.5	22.3
	Sphyraenidae	29.7	7.4	6.3
	Gonostomatidae	17.0	4.3	5.0
	Myctophidae	16.7	4.2	3.5
	Paralichidae	11.2	2.8	2.1
	Scorpaenidae	11.0	2.7	2.1
	Istiophoridae	9.6	2.4	3.4
	Gempylidae	7.7	1.9	2.4

Table 7. Percent contribution and percent cumulative contribution of each species from similarity percentages (SIMPER) analysis. Species listed comprised 85% or greater of the cumulative dissimilarity percentage. Species in bold contribute more than ten percent of dissimilarity.

Assemblage Comparison	Species	% Contribution	% Cumulative
Peripheral Group 1 v. Transition			
	Auxis rochei	**30.5**	**30.5**
	Thunnus albacores	**15.9**	**46.6**
	Thunnus atlanticus	**12.4**	**58.8**
	Coryphaena hippurus	9.3	68.2
	Auxis thazard	4.5	72.8
	Thunnus thynnus	4.6	77.1
	Selar crumenophtalamus	3.8	80.9
	Coryphaena equisetis	3.1	84.6
	Decapterus punctatus	2.0	86.6
Peripheral Group 2 v. Transition			
	Auxis rochei	**28.5**	**28.5**
	Thunnus albacores	**11.5**	**40.1**
	Thunnus atlanticus	**10.6**	**50.7**
	Coryphaena hippurus	8.7	59.5
	Thunnus thynnus	6.4	66.0
	Decapterus punctatus	6.0	72.0
	Selar crumenophtalamus	3.6	75.6
	Coryphaena equisetis	3.5	79.1
	Euthynnus alletteratus	2.9	82.1
	Cubiceps pauciradiatus	2.7	84.4
	Auxis thazard	2.5	87.4
Peripheral Group 1 v. Peripheral Group 2			
	Auxis rochei	**20.9**	**20.9**
	Thunnus albacores	**14.0**	**35.0**
	Thunnus thynnus	**13.8**	**48.8**
	Euthynnus Alletteratus	**12.3**	**61.1**
	Cubiceps pauciradiatus	**12.2**	**73.3**
	Decapterus punctatus	**10.6**	**83.9**
	Thunnus atlanticus	**10.2**	**94.1**

Table 8. Mean density (fish/100 $m^{3)}$ for the species at each qualitative assemblage determined by using nonmetric multidimensional scaling.

Assemblage	Species	Total	Mean	SD
Peripheral Group 1	*Auxis rochei*	2.7	1.3	0.8
	Thunnus atlanticus	2.5	2.5	-
	Decapterus punctatus	2.2	1.1	1.1
	Thunnus thynnus	1.0	1.0	-
	Thunnus albacores	0.9	0.9	-
	Euthynnus alletteratus	0.6	0.6	-
	Cubiceps pauciradiatus	0.6	0.6	-
	Antigonia capros	0.3	0.3	-
Transition	*Auxis rochei*	655.0	65.5	141.9
	Thunnus albacores	24.2	6.1	6.9
	Coryphaena hippurus	18.9	3.1	2.7
	Thunnus thynnus	11.6	5.8	0.9
	Thunnus atlanticus	11.1	2.8	2.6
	Auxis thazard	8.5	2.8	3.8
	Selar crumenophtalamus	5.8	1.4	0.8
	Coryphaena equisetis	5.8	1.4	1.2
	Decapterus punctatus	3.7	1.8	0.9
	Sphyraena borealis	3.1	3.1	-
	Prognichthys Occidentalis	1.7	0.6	0.3
	Antigonia capros	1.4	0.7	0.2
	Katsuwanus pelamis	1.2	0.6	0.3
	Naucrates ductor	0.8	0.8	-
	Gempylus serpens	0.7	0.7	-
	Rachycentron Canadum	0.6	0.6	-
	Xiphias gladias	0.6	0.6	-
	Exocoetus obtusirostris	0.4	0.4	-
	Oxyporamphus micropterus	0.3	0.3	-
	Balistes capriscus	0.2	0.2	-
	Euthynnus alletteratus	0.2	0.2	-
Peripheral Group 2	*Auxis rochei*	6.9	3.5	0.7
	Thunnus albacores	4.2	2.1	0.0
	Thunnus atlanticus	3.7	3.7	-
	Auxis thazard	1.5	1.5	-
	Thunnus thynnus	0.6	0.6	-
	Katsuwanus pelamis	0.3	0.3	-

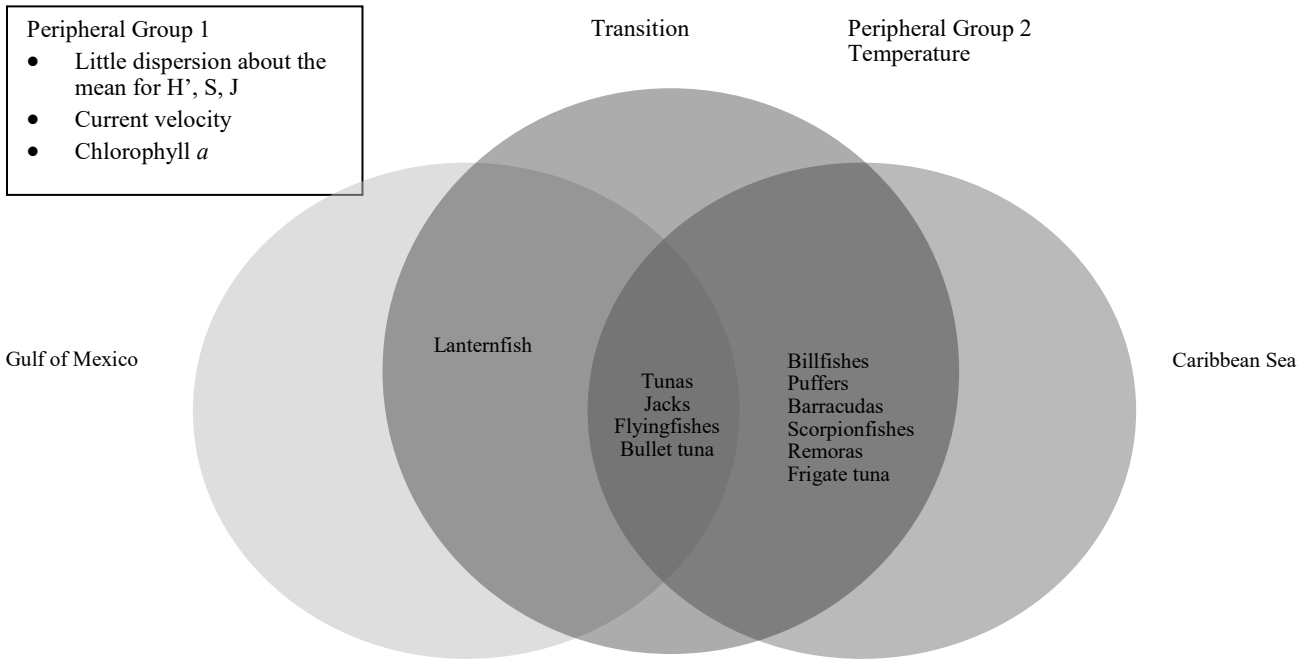

Figure 6. Conceptual model of the Loop Current Boundary ecotone. Each assemblage is represented by a circle of the Venn-diagram. The left circle represents Peripheral Group One, the middle circle the Transition assemblage, and the right circle represents Peripheral Group 2. The shared space in the middle of assemblages represents the LCB ecotone and color represents each assemblage and its interaction except the upper portion of the Transition assemblage which does not share the other assemblage space. Families highlighted in the similarity percentages (SIMPER) analysis.

DISCUSSION

In this study, I identified and characterized three pelagic assemblages of ichthyoplankton that were associated with different geographic regions of the LCB in the GOM using multivariate methods to detect and analyze assemblage structure. The ichthyoplankton analysis presented here indicates that the LCB is an area of change between adjacent ichthyoplankton communities. The LCB is an ecotone that is a combination of the two peripheral assemblages. This study identified a suite of fish taxa that contributed to the significant dissimilarity between each assemblage as well as the identification of some taxa that exhibited relatively cosmopolitan distributions. I found that the environmental conditions consistent with the LCB are a combination of two contributing water masses, GOM and Caribbean Sea.

Because of the dynamic nature of the LCB, it was expected that the current boundary area would be characterized by increased organismal diversity and richness (Clark and Gilbert 1982). Rathmell (2007) and Richards et al. (1993) reported that the transition habitat in the LCB was characterized by slight changes in temperature and salinity. Although the magnitude of difference in sea surface temperature observed in this study were relatively small (26 °C to 30 °C SST), they likely influence the presence of ichthyoplankton by determining, in part, individual growth and survival (Levin 1991, Baltz et al. 1998). Growth and survival are also partially determined by the availability of feeding opportunities (Kingsford 1990, Bakun 2006). One of the characteristics of the LCB is the increase in primary and secondary production that occurs in the region, which could lead to increased feeding opportunities (Biggs and Ressler 2001, Belkin et al. 2009). I observed that the Transition assemblage was unique in terms of its familial composition – the relative density of Scombridae, Carangidae, Coryphaenidae, Istiophoridae, and Tetraodontidae were an intermediate combination of those family densities in the peripheral assemblages.

The community composition of the LCB and peripheral regions are associated with differences in abiotic conditions. Peripheral Group One was characterized by taxa Myctophidae and increased chlorophyll *a* concentration and current velocity. Increased concentration of chlorophyll *a* and current velocity suggested the presence of a frontal boundary and water influenced by the GOM (Kingsford 1990, Richards et al. 1993). Myctophidae have been characterized as a member of the 'oceanic' assemblage by Richards et al. (1993) because Myctophidae is generally associated with deep water but family Myctophidae may also be influenced by productivity of the LCB. The productivity of the LCB is able to support higher densities of Myctophidae and the presence of this family may demonstrate the relative increase in productivity of the LCB compared to that of the open ocean (Nelson 1994a, Muhling et al. 2012).

Peripheral Group Two was characterized by the unique composition of several taxa and was associated with increased temperature. Increased temperature and reduced chlorophyll *a* concentration levels are consistent with water originating from the Caribbean Sea (Sturges 1965, Alvera-Azcárate et al. 2009). The dominant taxa in Peripheral Group Two are Exocoetidae, Gemylidae, Hemiramphidae, Scorpaenidae, Sphyraenidae, and Tetraodontidae. Adults and larvae of these families reside in Caribbean waters and have a tropical distributions and affinities (Nakamura and Parin 1993, Nelson 1994c, b).

Two peripheral assemblages surrounded the Transition assemblage and was comprised of families from both assemblages. The dominant taxa in the Transition assemblage were Scombridae, Myctophidae, and Carangidae. Individuals in the family Coryphaenidae were only found in the Transition assemblage. Carangidae and Scombridae in the Transition assemblage are members of the 'frontal' assemblage Richards et al. (1993). The composition of the Transition assemblage is intermediate to the Peripheral assemblages because it shares families Myctophidae with Peripheral Group One and the families Echenidae, Exocoetidae, Istiophoridae, Scorpanidae, Sphyraenidae with Peripheral Group Two. Grothues and Cowen (1999) reported a widely varied Transition assemblage in the Gulf Stream which included families Clupeidae, Triglidae, and Synodontidae. The work of Richardson et al. (2010) and Grothues and Cowen (1999) reinforce the premise that the Transition assemblage is a region of intermediate community composition between two peripheral communities. In this study, the Transition assemblage shares some of the same environmental qualities of both peripheral assemblages, and serves to extend the range of distribution for families in those assemblages.

The familial compositions of the LCB assemblages were affected by the different environmental conditions between GOM and Caribbean waters. The LC meanders and exhibits large variability in its spatial and temporal extent. Despite the variability of the LCB, the environment within the LCB is relatively homogenous over a small scale, environmental variations are small for parameters of chlorophyll *a*, current velocity, and temperature (Richards et al. 1989, Bakun and Csirke 1998). The relatively homogenous environment could maintain the assemblage structure over the geographic space of each transect sampled. The observed diversity and richness of families of the Transition assemblage and the variation in chlorophyll *a*, current velocity, and temperature indicated that those organisms demonstrate a wide tolerance and use the available microhabitats (Richards et al. 1993, Baltz et al. 1998, Bakun 2006, Lopez et al. 2010, Lindo-Atichati et al. 2012).

Families that composed the assemblages of the LCB were similar to both peripheral assemblages. Istiophoridae are reported to spawn within a narrow range of temperatures and salinities from May to September (Brown-Peterson et al. 2008, Simms et al. 2010, Kraus et al. 2011). Relative changes in density of Istiophoridae, present in the Transition assemblage and Peripheral Group Two, contributed to the small portion of dissimilarity between each assemblage. Similar to family Istiophordae, Coryphaenidae are distributed tropically and spawn in the early spring and summer (Palko et al. 1982) but were only present in the Transition assemblage and are recognized as a unique Transition assemblage family in this study. Lindo-Atichati et al. (2012) recognized that Coryphaenidae were found primarily near a frontal boundary which suggests that Coryphaenidae prefer the unique environment at the boundary (Curtis 1959, Odum 1971, Lindo-Atichati et al. 2012). Conversely, Scombridae and Carangidae were tolerant of changes in SST and were distributed across all assemblages and are considered cosmopolitan assemblage members, although their relative densities varied. The families Scombridae and Carangidae were the largest contributors to differences in similarity. Within the family Scombridae, the species, *A. rochei*, *T. albacares*, and *T. atlanticus* accounted for the largest differences in assemblage contribution (Richardson et al. 2010).

Abiotic conditions are important in the early life-history phases of larval fishes and serve to influence their spatial distribution (Lasker 1975, Kingsford 1990, Bakun and Csirke 1998). Understanding the influence of abiotic covariates, such as SST and chlorophyll *a* concentration, on relative abundance has implications for understanding recruitment success and inter-annual population dynamics (Roughgarden et al. 1988, Blanchette et al. 2006). Espinosa-Fuentes and Flores-Coto (2004) noted that wind, temperature, and currents affect assemblage composition at fronts and speculated that combined biotic and abiotic conditions influence larval survival and recruitment. Teo et al. (2007) reported that slight increases in temperature is a key factor in determining assemblage composition of Scombridae and Carangidae. The large variation in the Transition assemblage indicates that families Scombridae and Carangidae are tolerant of a range of abiotic conditions.

Traditionally, the term ecotone has been applied to terrestrial environments. The LCB provides a transition from the GOM water mass to the Caribbean water mass (Sturges and Evans 1983). Because the LCB does not exhibit a distinct boundary over a small distance, the transition area between water masses of the GOM, LC, and Caribbean Sea is difficult to determine (McKelvie 1985, Muhling et al. 2012). Because of the meandering quality of the LCB, the term ecotone needs to be modified to account for its variable nature. The LC varies in location spatially and seasonally in the GOM; two assemblages from either water mass mixing at a transition area, the LCB, are present despite the spatial flux. To term the LCB as a "transient ecotone" implies the LCB has the qualities of an ecotone and is an area of constant flux.

Future efforts to refine the identified assemblages and designated LCB zones in the ecotone should focus on taking collections along longer transects across the boundary with adequate replication and consistent gear type collections. The environmental changes across the LCB were slight, which made the assignment of *a priori* zones difficult. I made use of *post hoc* remote sensing data to determine which water mass was associated with the station of a transect in reference to the LC, and then XBT/CTD was used to determine the LCB *in situ*. I found poor correlation with the HYCOM modeled data and satellite data for temperature at 100 m. Using sea surface height, similar to methods used by Lindo-Atichati et al. (2013) would be

useful to identify the LCB instead of temperature alone.

MDS is used regularly to describe community assemblages and detect environmental gradients. Cluster analysis is often used in addition to MDS to identify natural groups; however, cluster analysis uses a different method to identify groups from the same dataset. Using the cluster analysis and MDS together can help support the findings of each (McKelvie 1985, McCune and Grace 2002). Since there could be discrepancies between the results of the natural groups from the two analysis, assessing the similarities will likely result in a conclusion that is more representative of the data and provide further insight as to which samples are unique (McKelvie 1985). Analysis of similarity was used to determine if those groups identified by the cluster and MDS analysis were significantly dissimilar; however, ANOSIM results could be misleading if there is a low R value and significant *p* value (Anderson and Walsh. 2013). The results of the ANOSIM from this study was a high *R* value, significant *p* value, and lower than expected chance of a high *R* value; so these results were considered appropriate for interpretation (Clarke and Ainsworth 1993, Anderson and Walsh 2013). Using traditional indices such as diversity and evenness are limited, relative to the multivariate analytical tools. The calculation of indices of diversity, richness, and evenness serve to condense information, conversely MDS expands upon existing patterns (Clarke and Warwick 2001, Legendre et al. 2005).

The blending of two water bodies of the GOM and Caribbean Sea form a Transition area. The small variation in abiotic conditions of chlorophyll *a*, current velocity, and temperature of the LCB could allow for an increased chance of survival for many species of ichthyoplankton (Lasker 1975, Kingsford 1990, Teo et al. 2007). This study examined the LCB on a fine-scale and found a highly complex community composition and structure. The scale used to examine an ecosystem determines if an ecosystem is an ecotone or an ecocline (Daly and Smith 1993, Gosz 1993, Smith et al. 1997). Lindo-Atichati et al. (2012) described the LC as a boundary community that is well-defined on a coarse scale. If using a coarse-scale, the LCB can be well-defined using sea surface height (Lindo-Atichati et al. 2012, Lindo-Atichati et al. 2013). However, this study examined the LCB and adjacent waters, and ichthyoplankton based on collections taken along a transect using a fine-scale (less than 2 km), and found a widely varied or heterogeneous Transition assemblage surrounded by two assemblages. The LCB is a geographically dynamic region that supports a widely varied Transition assemblage (van der Maarel 1990, Baltz et al. 1998) because it is comprised of two assemblages influenced by two different water masses which describes a transient marine ecotone.

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