

# Sensitivity of a fish time-series analysis to guild construction: a case study of the Mullica River-Great Bay ecosystem

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**ABSTRACT:** Guilds are defined as polyphyletic species groups delineated by specific attributes selected by the organizer. Functional guilds combine species on the basis of niches and ecological roles, whereas structural guilds combine species based on the use of a particular resource. Guilds can be substituted for individual species in an analysis, allowing for insight based on ecological questions with reduced variance from taxonomic differences. In this case study, we examined guilds of fishes over decades based on reproductive characteristics, and again on origin relative to the system, in an estuary in southern New Jersey, USA. These guilds were used in principal components analyses of the recruitment to an estuary of groups of fishes based on spawning origin or life history characteristics. In both cases, use of the guilds resulted in more explained variation than did use of a full species assemblage. Both 8-class and 12-class reproductive guild clusters explained more than 50% of the total variance on the first 2 eigenaxes while displaying similar trends across time in comparison with the full species assemblage. Use of an abundance-based species assemblage also resulted in more explained variation than use of the full species assemblage. Overall, reproductive guilds more accurately reflected assemblage changes within the Mullica River-Great Bay ecosystem than origin guilds. Rare species did not contribute to a long-term change in assemblage. The sensitivity of results to guild construction might differ for estuaries that are at the margins of their respective oceanographic province.

**KEY WORDS:** Guilds · Fish · Assemblage · Estuary · Long-term · Time-series

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## INTRODUCTION

Anthropogenic global change, inclusive of climate change, is one of the largest ecological concerns of this century and has the capacity to change the distribution and abundance of fishes locally and globally. Because fish are ectotherms with metabolic rates and physiological processes tied to temperature, population centers shift in phase with water conditions by changing the boundaries of their range (Perry et al. 2005, Pinsky et al. 2013). Effects on reproduction and growth can occur with little lag (Rijnsdorp et al. 2009). Responses in behavior and reproduction of each species change the number and types of fish species found in a specific system (Collie et al. 2008, Dulvy et al. 2008, Hiddink & ter Hofsted 2008). This change in fish assemblages can track

local climate velocities, with different species shifting in latitude and depth as temperatures change (Pinsky et al. 2013). Complex species interactions may also influence smaller-scale species distributions, and this may occur at different rates in comparison to global patterns (Austen et al. 1994, Pinsky et al. 2013). Examination of the full species assemblage introduces noise that may hide common trends correlated to specific mechanisms, so a more concise response variable unit is desired.

One of the ways in which ecological questions that involve whole communities can be addressed is through the use of guilds in lieu of individual species. A guild can be defined as a grouping of species into classes that exhibit certain attributes (Elliott et al. 2007). These attributes include life history, habitat use, reproductive strategy, trophic structure, and oth-

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ers relating to a species' ecological function and place within the community structure (Balon 1975, Thiel et al. 2003, Elliott et al. 2007). Guild classifications are useful as a tool for simplifying the structure of ecosystems (Simberloff & Dayan 1991, Garrison & Link 2000, Lobry et al. 2003, Franco et al. 2006) and provide a unit between the species and the ecosystem levels, especially in speciose systems (Austen et al. 1994) such as many estuaries (Franco et al. 2006). In this way, guilds may function as a 'super species' or 'surrogate species,' creating a unit that responds more predictably to environmental change, as compared to individual species (Caro & O'Doherty 1999). Additionally, the use of guilds facilitates the transfer of methodology. By providing a grouping of species based on their niches and life history characteristics, rather than those unique to the study system, the groundwork is laid for the study to be reproduced in different habitat types, at different latitudes, and over different time scales. Guilds are often designated based on function to test hypotheses relevant to those concepts. The choice of underlying guild structure is subject to what question is addressed. The species assignment to a guild may be objectively pursued through ordination methods, such as cluster analyses, principal components analyses, and correspondence analyses to standardize the assignment approach. This helps eliminate sources of author bias (Austen et al. 1994, Franco et al. 2006).

In particular, guilds are useful for understanding the functional structure of complex ecosystems. For example, Potter & Hyndes (1999) divided Australian estuarine fishes based on their life histories (Marine Straggler, Marine-estuarine Opportunist, Estuarine and Marine, Solely Estuarine, Semi-anadromous, and Catadromous), and assessed each group's contribution to the total number of estuarine fish overall. Thiel et al. (2003) used a similar approach in 2 European estuaries. Both studies also assessed the total number of individual species' contributions to the assemblage alongside the life cycle guilds. Potter & Hyndes (1999) found that the type of estuary played a role in the species making up the majority of the assemblage; systems perpetually open to marine influence showed many marine stragglers and estuarine opportunists, while estuaries that seasonally closed to marine influence had a majority of primarily estuarine species. Marine estuarine-opportunists dominated the number of individuals captured within the system, further illustrating the importance of marine species to the estuarine assemblage. Thiel et al. (2003) also found that marine species contributed the most to the composition of species in both of their study systems.

When the number of individuals captured was taken into account, however, estuarine and anadromous species dominated the catch (Thiel et al. 2003).

In this study, a long-term time series of juvenile fish distribution and abundance was examined for change in assemblage composition over time using a guild approach in a relatively undisturbed estuary. Previous analysis of changing fish assemblages in the system, based on long-term otter trawling, revealed complex changes in the assemblage, correlated primarily with summer temperature and its variance over time (Nickerson 2017, Nickerson et al. unpubl.). This change in fish assemblages was driven by a decline in 2 commonly captured and reproductively dissimilar estuarine species, Atlantic silverside *Menidia menidia* and northern pipefish *Syngnathus fuscus*. Several rarely captured species were excluded from the analysis due to a lack of confidence in their true distribution. Similar to data standardization (e.g. log transformation), the influence of these rare species and the factors driving the decline in the commonly captured estuarine species can be addressed by the use of a guild approach. Specifically, by organizing rarely captured species into more inclusive guilds, and by categorizing species based on life history traits that may have a common response to change in the system, we can ask (1) which life history traits are most closely tied to change in the system, and (2) what is the influence of rarely-captured species on change in the full assemblage?

The overall approach of the current study was to examine fish collections from a consistent sampling program for a linear temporal trend and to determine if the answer differed as a result of how the fish data were treated in guild assignment. We grouped collected fish species into guilds assigned upon reproductive characteristics, again upon origin relative to the system, and again upon their abundance or rarity as occasional strays, the occurrence of which might change as early indicators of environmental change. Each multivariate (guild or species) data set was reduced to its first major axis of variation to produce a single annual proxy score, the fluctuation of which was tested against time. Comparison of each of these results to those with an analysis using the full species set (not classified as guilds) provided insight as to which characteristics underlie any observed change. In recognition of the concern that fish might shift within the study area as a local (microhabitat) response to an underlying regional change, we amalgamated samples within each of 3 different halozones but not among them within a single study estuary.

## MATERIALS AND METHODS

### Study system

The Mullica River-Great Bay estuary, in southern New Jersey (Fig. 1), is a shallow drowned river valley with an average depth of about 2 m and a surface area of 41.6 km<sup>2</sup> (Kennish et al. 2004a,b). The freshwater-saltwater interface fluctuates tidally and seasonally on the order of kilometers, with a mean position near Lower Bank in the Mullica River, which is roughly 34 km upstream from Little Egg Inlet. Great Bay is polyhaline, with semidiurnal tidal input from Little Egg Inlet. Tidal velocities can exceed 2 m s<sup>-1</sup>. Salt marshes surround most of the shoreline. The study system has many factors in common with other Mid-Atlantic Bight (MAB) estuaries, such as a broad seasonal temperature range between -2 and 28°C and a tidal range of roughly 1.1 m near the mouth of the bay, declining to 0.9 m at the freshwater-saltwater interface upriver (Martino & Able 2003). Salinities range between 0 and 35 during periods of high fresh-

water flow, and from 10 to 35 during summer drought periods. A strong pH gradient of about 3 units corresponds to the salinity gradient. This results from naturally acidic conditions in the surrounding New Jersey Pinelands ecosystem. The Mullica River-Great Bay system is encompassed by the Jacques Cousteau National Estuarine Research Reserve (Kennish et al. 2004a).

### Biological sampling

Fish samples were collected via the Rutgers University Marine Field Station's Long-Term Otter Trawl Survey (Able & Fahay 2010). This survey was performed bi-annually, during the daytime in July and September 1997–2013, at sites throughout the estuary, Mullica River, and offshore area near Little Egg Inlet (Fig. 1). The survey used a 4.9 m wide semi-balloon otter trawl with a wing mesh of 19 mm and a cod end of 6 mm bar mesh. Three 2 min tows were performed at each site.

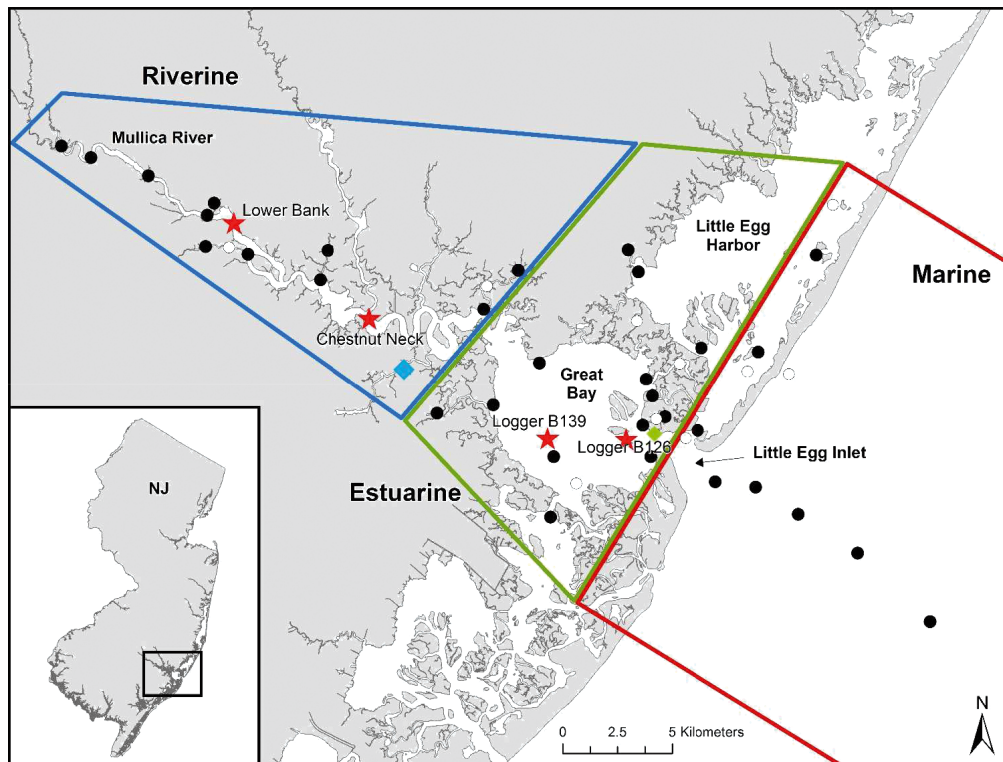


Fig. 1. Sampling sites in the Mullica River-Great Bay estuary in southern New Jersey, USA. Trawl sites are marked by filled circles. Each grouping of stations is enclosed in a polygon, and labeled according to its halozone classification (riverine, estuarine, and marine). All stations enclosed in polygons and represented by filled circles were used in the analysis. Open circles are infrequently sampled sites, stars denote SWMP (System Wide Monitoring Protocol) logger locations, and the blue square represents the location of the weather monitoring station. The green diamond denotes the location of the Rutgers University Marine Field Station. This system is relatively undisturbed, and is included in the Jacques Cousteau National Estuarine Research Reserve

Trawling sites were classified into 3 broad area categories or halozones: riverine, estuarine, and marine (Fig. 1). Halozone divisions were delineated based on physiochemical and geographic parameters throughout the estuary following Martino & Able (2003). This makes the spatial scale of the analysis relevant to the spatial scale of variation in the influence of climatic drivers of conditions among halozones (e.g. upwelling at the coast, rainfall in the watershed) but not patches or dynamic microhabitats (e.g. ephemeral mussel beds) within a halozone. The sampling protocol was consistent since 1997 across all 3 halozones (Martino & Able 2003, Able & Fahay 2010, Fig. 1). Catch data from 3 trawls at each site were combined into 1 sample of site, year, and month and then combined as the sum of stations within a halozone as a measure of catch per unit effort (CPUE). Samples from July and September were kept distinct as they reflect different seasonal recruitment processes (Nickerson 2017, Nickerson et al. unpubl.). This division accounts for 3 spatial and 2 temporal sample strata  $\text{yr}^{-1}$ , resulting in 6 samples  $\text{yr}^{-1}$  for 16 yr. For this study, each halozone-month combination was condensed into a single variable in order to examine change over time more succinctly, and to focus on the response of guilds across the entirety of the system, as change across specific habitat types have been accounted for in previous studies (see Nickerson 2017, Nickerson et al. unpubl.)

### Guild and assemblage classifications

For the first 2 analyses, fish species were assigned to guilds based on reproductive characteristics following Able & Fahay (2010). Characters for consideration included spawning season, place of spawning, and egg type. Species were assigned all characters of a variable (trait) that fit with their life history, sometimes with multiple characters assigned to the same category. Species were arranged into a matrix with true–false (1,0 values) pertaining to having that trait (Table 1), and a cluster analysis invoked this matrix. Two different cluster values were then established using a dendrogram produced in MATLAB (dendrogram.m), with distance calculated as Hamming distance, using complete linkage. The dendrogram was arbitrarily pruned at the 8- or 12-cluster level under the constraint that the resulting clusters were recognizable on a known nominal ecological basis and were named accordingly. This tested sensitivity to guild classification level. For the 8-cluster reproductive guilds, we identified Unknown Location/Egg

Type Spawners, Summer Spawners with Unknown Eggs, Estuarine Live Spawners, Pelagic Summer Spawners, MAB Spawners, Demersal Estuarine Spawners, Freshwater Spawners, and Pelagic Shelf Spawners. The 12 clusters had several identical categories, including Freshwater Spawners, Unknown Spawners, Demersal Estuarine Spawners, Estuarine Live Spawners, and Summer Spawners with Unknown Eggs. The addition of lower cluster branches also allowed for the inclusion of Summer Shelf Spawners, Fall Shelf Spawners, Winter Shelf Spawners, and Spring Shelf Spawners. MAB Spring Spawners and South Atlantic Bight (SAB) Pelagic Spawners were also identified.

A third analysis applied guild assignment based on characters of origin relative to the estuary using the breakdown of the estuarine usage functional group of Potter et al. (2015) (Table 1). Four guilds were thus defined: Resident Species, Transient Species, Shelf Stray Species, and Southern Stray Species. Information on life history characters used for these species assignments were drawn from Able & Fahay (2010) and from the literature.

The 3 analyses based on guild classifications were compared with 3 analyses performed at the species level, one with the full species (hereafter 'full assemblage analysis') set and another excluding rare species. Species within the tail of an abundance distribution curve are often abundant elsewhere, and can influence the overall shift in an assemblage by virtue of their rarity within the system (Murray et al. 1999). Species represented by fewer than 20 individuals over the entirety of the dataset were classified as 'rare species,' and dropped from the assemblage. The remaining species were classified as 'abundant species' (hereafter 'abundant species assemblage') in another analysis (Table 1). The excluded 'rare' species were also analyzed separately as a group ('rare species assemblage') in order to determine their influence on change in the assemblage. This resulted in a total of 6 trend lines (see Nickerson 2017 for additional details).

### DATA ANALYSIS

The change in fish assemblages over the time period, as ordered by guilds, was analyzed for sensitivity to guild organization using ordinary least squares regression. To account for the fact that assemblages are multivariate, the response variables were amplitudes from principal components analysis (PCA), which replaces the abundance of guild mem-

Table 1. Species and their classifications in each guild. Origin classifications were taken from Able & Fahay (2010), and reproductive guilds were assigned based on cluster analysis of 3 reproductive factors: egg type, spawning location, and spawning season. Cutoffs at 8 and 12 clusters were chosen based on graphic representation of the results. Rare species were classified as those for which fewer than 20 individuals were captured over the course of the study period. All species with  $\geq 20$  or more captures were classified as Abundant. MAB: Mid-Atlantic Bight, SAB: South Atlantic Bight

Species	Origin guild	Assemblage abundance	Reproductive guild	
			8 clusters	12 clusters
<i>Alosa aestivalis</i>	Transient	Abundant	Freshwater	Freshwater
<i>Alosa mediocris</i>	Transient	Rare	Freshwater	Freshwater
<i>Alosa pseudoharengus</i>	Transient	Abundant	Freshwater	Freshwater
<i>Aluterus heudelotii</i>	Southern Stray	Rare	Unknown	Unknown
<i>Aluterus schopfii</i>	Southern Stray	Rare	Unknown	Unknown
<i>Aluterus scriptus</i>	Southern Stray	Abundant	Unknown	Unknown
<i>Ameiurus catus</i>	Resident	Abundant	Freshwater	Freshwater
<i>Ameiurus nebulosus</i>	Resident	Rare	Freshwater	Freshwater
<i>Ammodytes americanus</i>	Resident	Abundant	Demersal Estuarine	Demersal Estuarine
<i>Anchoa hepsetus</i>	Transient	Abundant	Pelagic Summer	Summer MAB/SAB
<i>Anchoa mitchilli</i>	Transient	Abundant	Pelagic Summer	Summer MAB/SAB
<i>Anguilla rostrata</i>	Transient	Abundant	Unknown	Unknown
<i>Apeltes quadracus</i>	Resident	Rare	Demersal Estuarine	Demersal Estuarine
<i>Astroscopus guttatus</i>	Shelf Stray	Abundant	Pelagic Summer	Summer MAB/SAB
<i>Bairdiella chrysoura</i>	Transient	Abundant	Pelagic Summer	Unknown Pelagic
<i>Brevoortia tyrannus</i>	Transient	Rare	Pelagic Shelf	MAB Pelagic Fall
<i>Caranx crysos</i>	Transient	Abundant	Unknown	Unknown
<i>Caranx hippos</i>	Transient	Abundant	Pelagic Shelf	SAB Pelagic
<i>Catastomus commersoni</i>	Resident	Abundant	Unknown	Unknown
<i>Centropristis striata</i>	Transient	Rare	Pelagic Summer	Summer MAB/SAB
<i>Chaetodon ocellatus</i>	Southern Stray	Rare	Demersal Estuarine	Demersal Estuarine
<i>Chasmodes bosquianus</i>	Resident	Abundant	Pelagic Shelf	SAB Pelagic
<i>Chilomycterus schoepfi</i>	Transient	Rare	Summer Unknown Eggs	Unknown Summer
<i>Citharichthys arcifrons</i>	Southern Stray	Rare	Unknown	Unknown
<i>Clupea harengus</i>	Transient	Rare	Spring MAB	Spring MAB
<i>Conger oceanicus</i>	Transient	Abundant	Summer Unknown Eggs	Unknown Summer
<i>Ctenogobia boleosoma</i>	Southern Stray	Rare	Pelagic Summer	Summer MAB/SAB
<i>Cynoscion regalis</i>	Transient	Rare	Unknown	Unknown
<i>Dactylopterus volitans</i>	Southern Stray	Abundant	Unknown	Unknown
<i>Decapterus punctatus</i>	Shelf Stray	Rare	Pelagic Shelf	SAB/MAB Pelagic Spring
<i>Engraulis eurystole</i>	Shelf Stray	Abundant	Unknown	Unknown
<i>Erimyzon oblongus</i>	Resident	Abundant	Unknown	Unknown
<i>Esox niger</i>	Resident	Abundant	Unknown	Unknown
<i>Etheostoma olmstedii</i>	Resident	Rare	Pelagic Summer	Summer MAB/SAB
<i>Etropus microstomus</i>	Transient	Rare	Unknown	Unknown
<i>Fistularia tubacaria</i>	Southern Stray	Abundant	Demersal Estuarine	Demersal Estuarine
<i>Fundulus diaphanus</i>	Resident	Abundant	Demersal Estuarine	Demersal Estuarine
<i>Fundulus heteroclitus</i>	Resident	Rare	Unknown	Unknown
<i>Gasterosteus aculeatus</i>	Transient	Rare	Unknown	Unknown
<i>Gobiosoma bosc</i>	Resident	Abundant	Demersal Estuarine	Demersal Estuarine
<i>Hippocampus erectus</i>	Transient	Rare	Estuarine Live Bearers	Live Estuarine
<i>Hippoglossina oblonga</i>	Shelf Stray	Abundant	Unknown	Unknown
<i>Lagodon rhomboides</i>	Transient	Rare	Pelagic Shelf	SAB/MAB Pelagic Spring Winter
<i>Leiostomus xanthurus</i>	Transient	Abundant	Unknown	Unknown
<i>Lepomis gibbosus</i>	Resident	Abundant	Unknown	Unknown
<i>Lepomis macrochirus</i>	Resident	Abundant	Unknown	Unknown
<i>Leucoraja erinacea</i>	Shelf Stray	Abundant	Unknown	Unknown
<i>Lophius americanus</i>	Shelf Stray	Rare	Unknown	Demersal Estuarine
<i>Lucania parva</i>	Resident	Rare	Demersal Estuarine	SAB Pelagic
<i>Lutjanus griseus</i>	Southern Stray	Rare	Pelagic Shelf	Demersal Estuarine
<i>Menidia beryllina</i>	Resident	Rare	Demersal Estuarine	Demersal Estuarine
<i>Menidia menidia</i>	Transient	Abundant	Demersal Estuarine	Summer MAB/SAB
<i>Merluccius bilinearis</i>	Shelf Stray	Abundant	Pelagic Summer	Unknown

(Table continued on next page)

Table 1 (continued))

Species	Origin guild	Assemblage abundance	Reproductive guild	
			8 clusters	12 clusters
<i>Menticirrhus saxatilis</i>	Transient	Abundant	Unknown	Unknown Summer
<i>Microgobius thalassinus</i>	Southern Stray	Rare	Summer Unknown Eggs	Summer MAB/SAB
<i>Micropogonias undulatus</i>	Transient	Rare	Pelagic Summer	Freshwater
<i>Morone americana</i>	Resident	Abundant	Freshwater	Freshwater
<i>Morone saxatilis</i>	Transient	Abundant	Freshwater	SAB/MAB Pelagic Spring Winter
<i>Mugil cephalus</i>	Transient	Abundant	Pelagic Shelf	SAB Pelagic
<i>Mugil curema</i>	Transient	Rare	Pelagic Shelf	Unknown
<i>Mullus auratus</i>	Southern Stray	Rare	Unknown	Spring MAB
<i>Mustelus canis</i>	Transient	Rare	Spring MAB	SAB/MAB Pelagic Spring Winter
<i>Mycteroperca microlepis</i>	Transient	Abundant	Pelagic Shelf	Demersal Estuarine
<i>Myoxocephalus aeneus</i>	Resident	Rare	Demersal Estuarine	Unknown
<i>Notemigonus crysoleucas</i>	Resident	Rare	Unknown	Unknown
<i>Ophidion marginatum</i>	Transient	Abundant	Unknown	SAB/MAB Pelagic Spring
<i>Opisthonema oglinum</i>	Transient	Abundant	Pelagic Shelf	Demersal Estuarine
<i>Opsanus tau</i>	Resident	Rare	Demersal Estuarine	Unknown
<i>Orthopristis chrysoptera</i>	Southern Stray	Abundant	Unknown	MAB Pelagic Fall
<i>Paralichthys dentatus</i>	Transient	Rare	Pelagic Shelf	Unknown
<i>Paralichthys oblongus</i>	Shelf Stray	Abundant	Unknown	Summer MAB/SAB
<i>Peprilus triacanthus</i>	Shelf Stray	Rare	Pelagic Summer	Summer MAB/SAB
<i>Pogonias cromis</i>	Transient	Abundant	Pelagic Summer	Unknown
<i>Pollachius virens</i>	Transient	Abundant	Unknown	SAB/MAB Pelagic Spring
<i>Pomatomus saltatrix</i>	Transient	Rare	Pelagic Shelf	Summer MAB/SAB
<i>Prionotus evolans</i>	Transient	Rare	Pelagic Summer	Summer MAB/SAB
<i>Prionotus carolinus</i>	Transient	Abundant	Pelagic Summer	Demersal Estuarine
<i>Pseudopleuronectes americanus</i>	Resident	Abundant	Demersal Estuarine	Unknown
<i>Pseudupeneus maculatus</i>	Southern Stray	Abundant	Unknown	Unknown
<i>Raja eglantaria</i>	Shelf Stray	Abundant	Unknown	Unknown
<i>Rhinoptera bonasus</i>	Transient	Rare	Estuarine Live Bearers	Live Estuarine
<i>Scomber scombrus</i>	Shelf Stray	Abundant	Unknown	Unknown
<i>Scomberomorus maculatus</i>	Southern Stray	Abundant	Unknown	Unknown
<i>Scophthalmus aquosus</i>	Transient	Rare	Unknown	Unknown
<i>Selar crumenophthalmus</i>	Southern Stray	Abundant	Unknown	Unknown
<i>Selene setapinnis</i>	Southern Stray	Rare	Unknown	Unknown
<i>Selene vomer</i>	Southern Stray	Rare	Unknown	Unknown
<i>Seriola zonata</i>	Shelf Stray	Rare	Unknown	Unknown
<i>Spheroides maculatus</i>	Transient	Rare	Demersal Estuarine	Unknown
<i>Sphyrna borealis</i>	Transient	Rare	Unknown	Demersal Estuarine
<i>Stenotomus chrysops</i>	Transient	Rare	Pelagic Summer	Summer MAB/SAB
<i>Strongylura marina</i>	Transient	Rare	Demersal Estuarine	Demersal Estuarine
<i>Syngnathus fuscus</i>	Transient	Abundant	Estuarine Live Bearers	Unknown
<i>Synodus foetens</i>	Transient	Abundant	Unknown	Live Estuarine
<i>Tautoga onitis</i>	Transient	Rare	Pelagic Summer	MAB Pelagic Fall
<i>Tautoglabrus adspersus</i>	Resident	Rare	Pelagic Shelf	Summer MAB/SAB
<i>Trachurus lathami</i>	Southern Stray	Abundant	Unknown	Unknown
<i>Trichiurus lepturus</i>	Shelf Stray	Abundant	Unknown	Unknown
<i>Trinectes maculatus</i>	Resident	Abundant	Pelagic Summer	Summer MAB/SAB
<i>Urophycis chuss</i>	Shelf Stray	Abundant	Pelagic Summer	Summer MAB/SAB
<i>Urophycis regia</i>	Transient	Abundant	Pelagic Summer	Summer MAB/SAB

bers with a single proxy 'assemblage' score that accounts for the best fit through their co-varying fluctuations. PCA was performed using CANOCO software (v 4.5, ter Braak & Smilauer 2012), for each set of guilds (8-cluster reproductive, 12-cluster reproductive, origin, abundant, and rare species) and for

the full assemblage. CPUE data were  $\log_{10}(y+1)$ -transformed before analysis. Inter-species (inter-guild) correlations were not post-transformed. Samples were centered by guilds, with biplot scaling, and standardized. This protocol was kept consistent for each individual guild and assemblage analysis in the

study. Analysis was guided by several null hypotheses:  $H_0-1$ , there is no change over time related to the reproductive guilds;  $H_0-2$ , there is no change over time related to the origin of fishes; and  $H_0-3$ , there is no change over time related to the abundance of rarely captured species.

Three factors were considered when assessing the 'sensitivity' of guilds and assemblages to change: trends over time, the spread and pattern of their residuals, and the accumulated explained variation. These measures were assessed for each guild classification and assemblage type. The explained variation accumulated was calculated simply as the cumulative sum of the first 4 consecutive principal factor eigenvalues for each analysis. Notably, for the origin guild classifications, the use of only 4 guilds in the analysis would naturally result in 100% explained variation over the first 4 axes. This was taken into account when assessing variance explained by each guild and assemblage type. A linear regression of sample score vs. year in each guild or species assemblage treatment tested for the presence and direction of a significant temporal trend with ANOVA in Microsoft Excel's Data Analysis package, with  $\alpha = 0.05$ . Residual plots were examined for each treatment. Those guild classifications and assemblages that displayed a high amount of accumulated variation at the first 2 axes, significant change over time when considering all halozones, and largely linear residual plots, were considered to be the most sensitive to change.

## RESULTS

### Guild and assemblage trends over time

The response of the analyses varied between guilds and assemblages over time (Table 2). Reproductive guild scores changed significantly over time for both the 8-cluster and 12-cluster guild constructions. The 8-guild analysis yielded a slightly steeper slope ( $m = 0.046$  vs.  $0.045$ ) and greater explained variance ( $r^2 = 0.051$  vs.  $0.049$ ). The scores of the origin guilds did not change significantly over the study period. The analyses of assemblages containing all species ('full') and also that which excluded rare species ('abundant') did change significantly over the study period, with identical slope and explained variance parameters ( $m = 0.049$ ,  $r^2 = 0.058$ , Table 2). The rare species assemblage did not change significantly over time. When proportions of each origin guild were calculated for species in the rare assemblage, the majority

Table 2. Linear regression statistics for each guild and assemblage. **Boldface** indicates significance at  $\alpha = 0.05$ . Classifications of guilds and assemblages as in Table 1

	<i>m</i>	<i>r</i> <sup>2</sup>	<i>F</i>	<i>p</i>	Error variance
<b>8-cluster reproductive</b>	<b>0.046</b>	<b>0.051</b>	<b>5.30</b>	<b>0.023</b>	<b>0.97</b>
<b>12-cluster reproductive</b>	<b>0.045</b>	<b>0.049</b>	<b>5.13</b>	<b>0.0257</b>	<b>0.97</b>
Origin	0.006	<0.001	0.088	0.77	1.02
Rare species	-0.005	<0.001	0.054	0.82	1.03
<b>Abundant species</b>	<b>0.049</b>	<b>0.058</b>	<b>6.14</b>	<b>0.015</b>	<b>0.96</b>
<b>Full</b>	<b>0.049</b>	<b>0.058</b>	<b>6.14</b>	<b>0.015</b>	<b>0.96</b>

were Southern Strays (34%) with Transients (28%), Residents (20%), and Shelf Strays (18%) making up the remaining classifications of rare species. This shows that species considered rare in the system are generally not native to the study area.

For reproductive guilds, Freshwater Spawners had a high first axis amplitude (explained much of the variance of sample distribution along the first principal component), while Estuarine Spawners, both Demersal and Live, had the lowest first axis amplitudes in both the 8- and 12-cluster guilds (Table 3, Fig. 2). (Note that the axis direction is arbitrary in coenospace, but covariation among species or guild variables is expressed as inverse by a negative amplitude). Shelf and MAB spawners did not vary in amplitude to the same degree as the Freshwater and Estuarine spawners (Fig. 2). Among these, guilds that included summer spawners declined more relative to the abundance of fish in

Table 3. Comparison of first eigenvalues and total percentage variance of the full assemblage and guild PCA scores. Classifications of guilds and assemblages as in Table 1. Higher first axis eigenvalues indicate a higher amount of explained variance, and fewer axes needed to project change into the future. Guilds and assemblages that show higher values are therefore more useful for examining long-term change

	Eigenvalues	Total percentage variance of species data
Origin guild	0.45	100.0
Abundant species	0.23	43.7
8-guild analysis	0.43	80.3
12-guild analysis	0.30	64.5
Full assemblage	0.13	27.3
Rare species	0.064	23.4

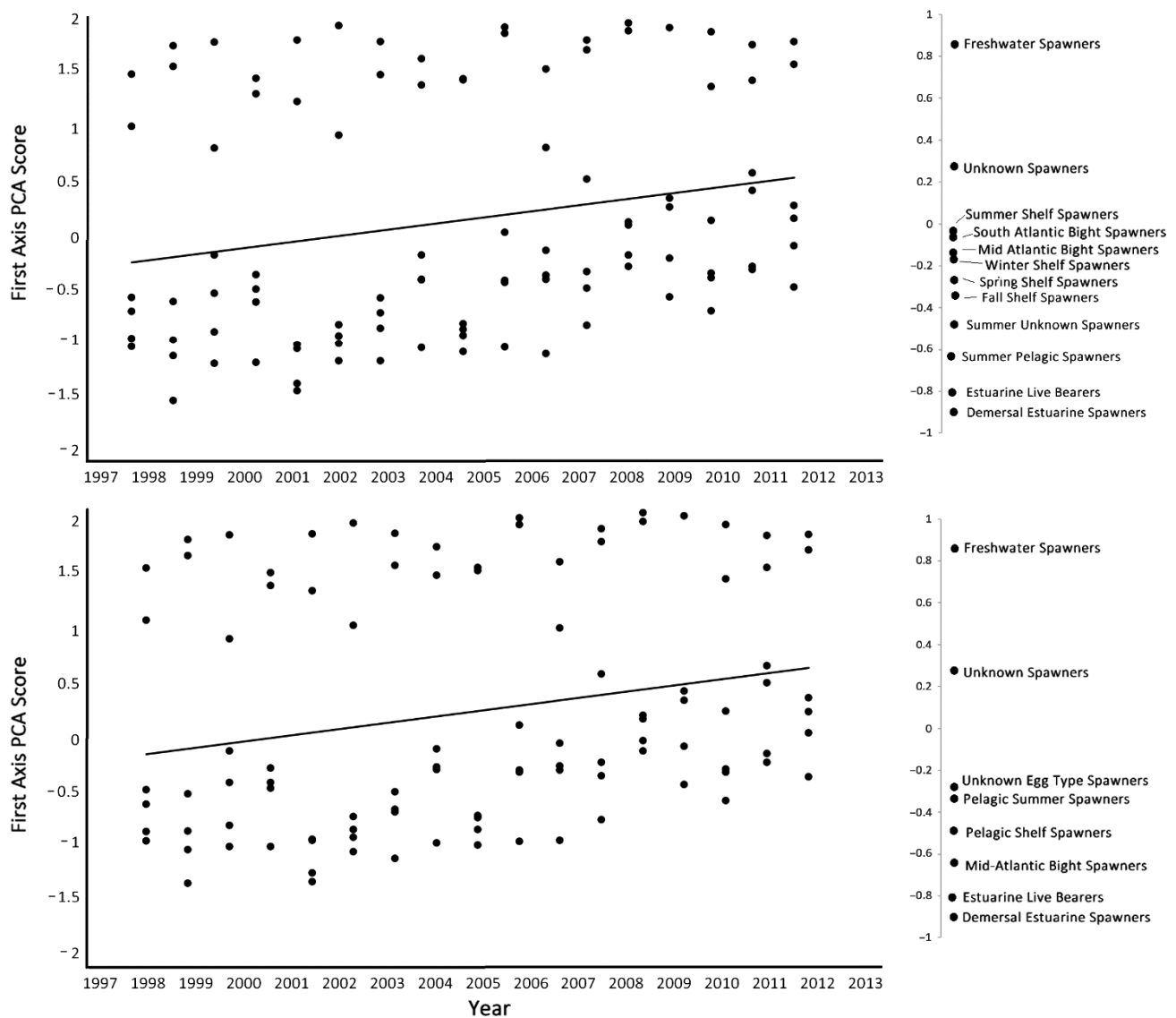


Fig. 2. Amplitude (left y-axis) of otter trawl samples on the first principal component by sample year for the 8-cluster (top) and 12-cluster (bottom) analyses. The first eigenaxes explain over half the variation in each dataset. The amplitudes of the guilds that drive the sample variation are shown on the second y-axis. Guilds with greater amplitude magnitude (absolute value) explain more of the variation in the sample data on that axis. Note that the sign of the amplitude in PCA is arbitrary. Samples with lower amplitude have more fish in guilds with lower amplitude. In this depiction (positive trend line), guild members with positive scores have increased over time

guilds that spawned in other seasons. A positive trend over time in the relative abundance of Unknown Spawners drove both the 8- and 12-cluster guild ordinations, although not to the same degree that Freshwater Spawners did (Fig. 2). In the origin guilds, Resident and Transient species displayed the strongest trends on either end of the axes. Shelf Strays and Southern Strays had negative values of lesser amplitude than Resident and Transient guilds, with Shelf Strays representing a greater amplitude than Southern Strays (Tables 3 & 4, Fig. 3).

## Residuals

Residual plots were generally linear in their scatter pattern for the 8-cluster reproductive guild analysis, but with nearly symmetrical oscillation in the spread (Fig. 4). 12-cluster reproductive guild residuals also varied in a largely linear pattern, with similar oscillation in the spread. Residuals of the origin guild analysis were more random but still reflected the oscillation. The residuals for the rare species analysis were linear over time, and tightly clustered in comparison

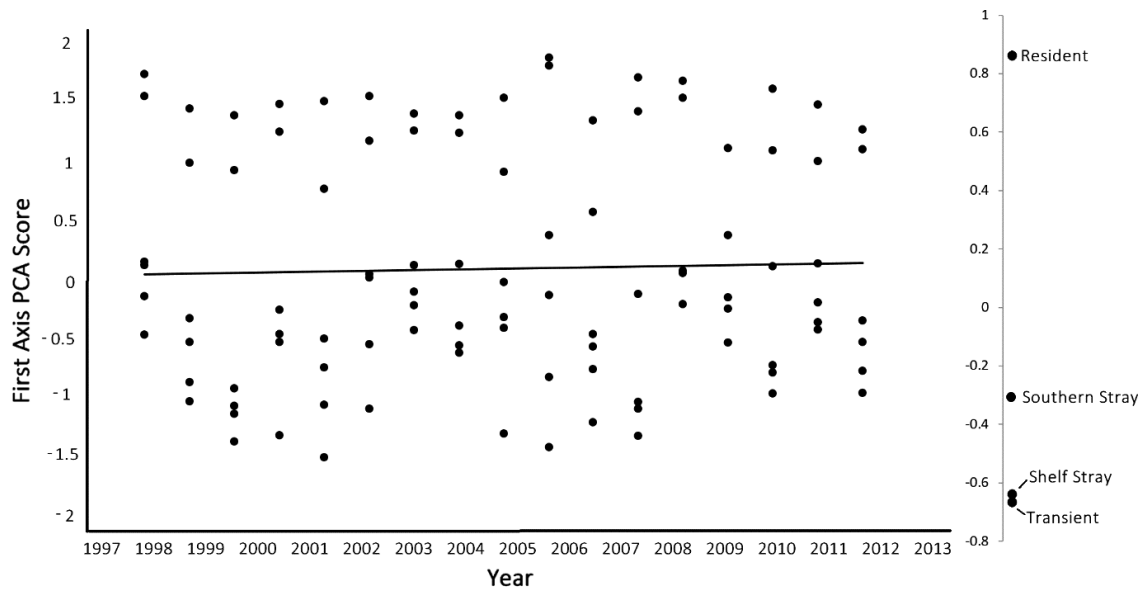


Fig. 3. Amplitude (left y-axis) of otter trawl samples on the first principal component by sample year for the origin guild analyses. The amplitudes of the guilds that drive the sample variation are shown on the second y-axis. Guilds with greater amplitude magnitude (absolute value) explain more of the variation in the sample data on that axis. Samples with lower amplitude have more fish in guilds with lower amplitude and vice versa. The flat trend line indicates that guild membership distribution has not changed over time

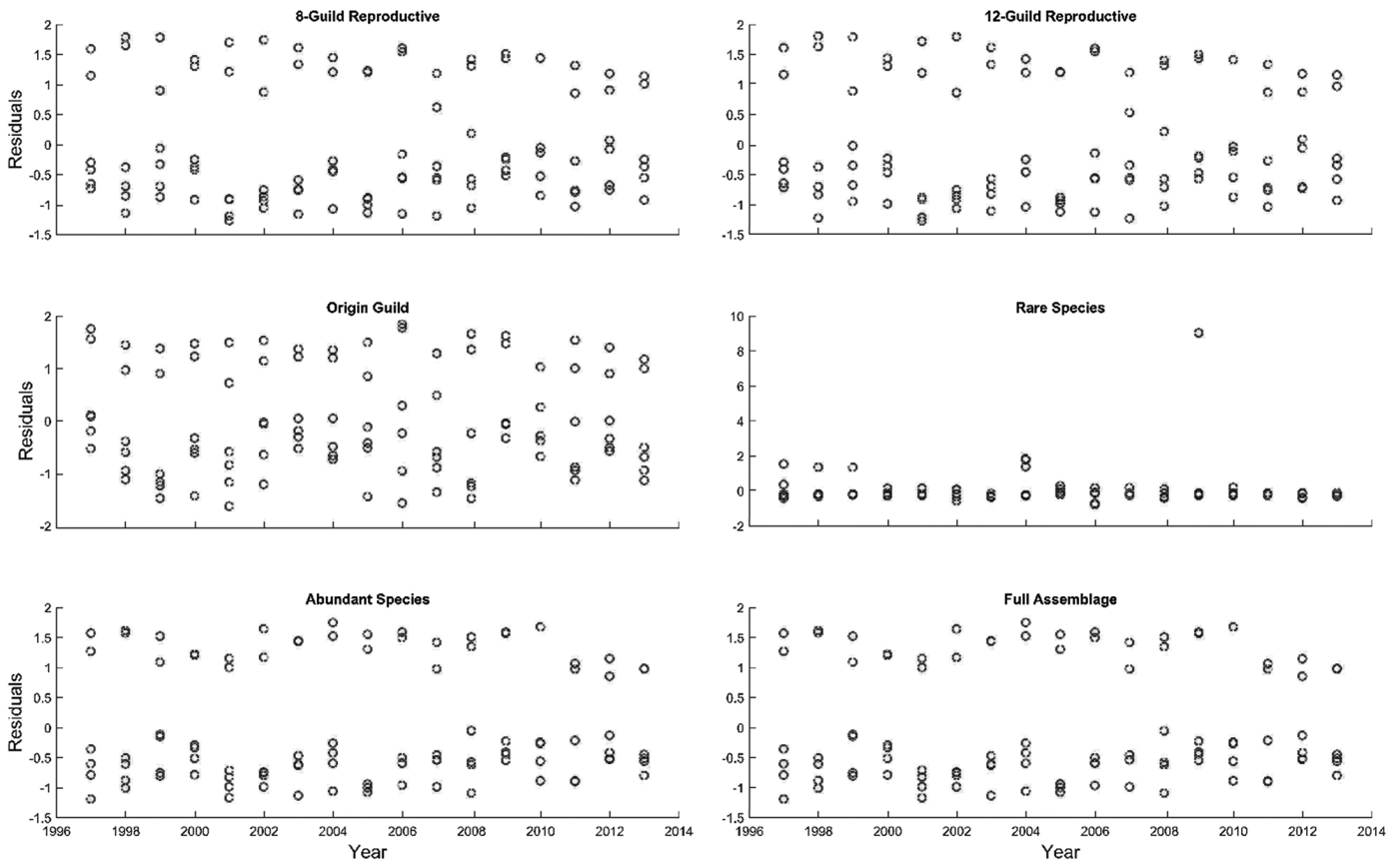


Fig. 4. Residual plots for each guild treatment and assemblage analyzed. The shape of each residual plot indicates how well the data fit the model used in analysis. A more randomly dispersed plot indicates that a linear model is a good fit for the data. More structured plots point to different models being a better choice

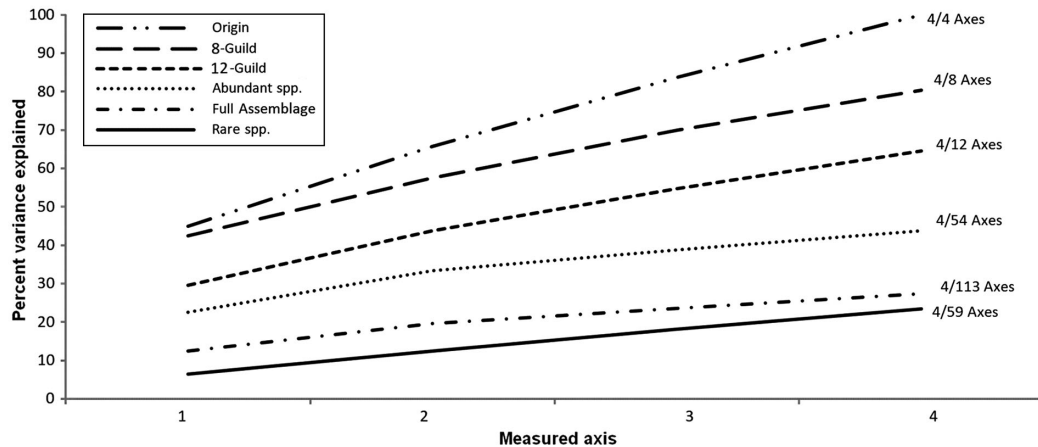


Fig. 5. Accumulation of variance at each axis for all 5 guild types and the full assemblage. The 8- and 12-cluster reproductive guilds accumulate the fastest at the first axis. The origin guilds accumulate to 100%, but because only 4 guilds were used in the analysis, this accumulation is inevitable. The number of axes to full accumulation of 100% variance is shown with respect to the number of axes measured for each guild

to other analyses. The residuals for the abundant and full assemblage analyses had virtually identical residual plots, both of which displayed a spatially, but not temporally, bimodal distribution. Overall, the spread of residuals across all of the guild and assemblage treatments supports the fit of the linear model to the dataset overlying a shorter period modality, the highs and lows of which are increasing over time.

### Variance

Explained variance accumulated most rapidly in the 8- and 12-cluster reproductive guilds (Fig. 5). The rare species assemblage displayed minimal increase, while the full and abundant species assemblages were separated by roughly 20 percentage points. The origin guilds accumulated explained variance at a steadier rate across all 4 axes (explained less of the total variance on the first axis) as sharply as the 2 reproductive guild analyses did. Overall, the 8-cluster reproductive guilds captured the strongest variation with the greatest data reduction, with 12-cluster reproductive guilds capturing the second-strongest, when the origin guilds are discounted due to the small number of classifications used.

### DISCUSSION

The juvenile fish assemblage in the Mullica River-Great Bay estuary has changed in the last 25 yr (Nickerson 2017), but the mechanisms behind this change are not clear. The current work, using a 16 yr

time series, shows that condensing the assemblage into reproductive guilds or as a subset of abundant species tracks the 25 yr and 16 yr change of the full assemblage, while ordinations of the origin guilds and rare species do not. This provides some understanding of the ecology behind the change and provides direction for further research. Importantly, it is counter to the supposition that southern species at the northern fringe of their range should accumulate. With global temperatures rising, a research focus on the increase of southern-origin species, often considered rare in the assemblage, is logical and has been supported on a large scale (Perry et al. 2005, Pinsky et al. 2013), but that is not apparent in this work. Below, we discuss some of the implications and caveats to these new findings.

The potential causes of the observed trend towards increased relative abundance of Freshwater Spawners and decreased relative abundance of several estuarine and marine spawning types in the abundance of reproductively classified guilds include that (1) the reproductive habits of species that use the system are changing, (2) species of some of the guilds are spawning elsewhere, or (3) the relative survival rate of their progeny is changing. Examples of all of these mechanisms appear for individual species in the literature, and specifically along the US eastern seaboard. Examples of both reproductive timing and location change, along with change in nursery use, occur for Atlantic menhaden *Brevoortia tyrannus*. Most spawning for this species in the latter part of the 1990s occurred during southern migrations and in the southeastern US continental shelf system, resulting in larvae using various estuarine nursery habitats

Table 4. Cumulative frequency fitted for each variable (guild or species) over the first 4 principal components as a fraction of the total explained variance (Variance (y)) of that guild/species

Analysis	Name	Principal component				Variance(y)
		1	2	3	4	
8-guild	Frequency fitted	0.5974	0.146	0.077	0.0665	
	Unknown Spawners	0.0772	0.2625	0.4961	0.585	0.55
	Pelagic Shelf Spawners	0.2939	0.6453	0.7296	0.9784	0.97
	Estuarine Live Bearers	0.6556	0.6655	0.7896	0.7897	0.95
	Mid-Atlantic Bight Spawners	0.4451	0.7114	0.7713	0.9549	1.12
	Pelagic Summer Spawners	0.1148	0.12	0.1341	0.1342	0.06
	Demersal Estuarine Spawners	0.8323	0.8491	0.9255	0.9269	1.93
	Freshwater Spawners	0.7636	0.9307	0.9622	0.9717	2.23
	Unknown Egg Type Spawners	0.1001	0.1694	0.1764	0.243	0.19
12-guild	Frequency fitted	0.5187	0.1393	0.1008	0.0684	
	South Atlantic Bight Spawners	0.0032	0.1542	0.1548	0.173	0.12
	Winter Shelf Spawners	0.0376	0.0535	0.0547	0.0773	0.1
	Summer Shelf Spawners	0.001	0.0769	0.0791	0.1398	0.2
	Fall Shelf Spawners	0.1519	0.1831	0.2325	0.2355	0.26
	Mid-Atlantic Bight Spawners	0.0286	0.4493	0.928	0.9312	1.19
	Summer Pelagic Spawners	0.4499	0.6778	0.705	0.8015	1.51
	Unknown Spawners	0.0807	0.0996	0.5234	0.6896	0.71
	Summer Unknown Spawners	0.2908	0.4736	0.6815	0.7261	1.25
	Estuarine Live Bearers	0.6506	0.6639	0.6647	0.784	1.22
	Spring Shelf Spawners	0.1125	0.1208	0.1209	0.1363	0.08
	Demersal Estuarine Spawners	0.8332	0.8463	0.8471	0.9354	2.48
	Freshwater Spawners	0.7567	0.9288	0.9364	0.976	2.87
Origin	Frequency fitted	0.5284	0.2539	0.1891	0.0286	
	Residents	0.7184	0.996	0.9999	1	1.62
	Shelf Strays	0.3904	0.5308	0.9999	1	1.06
	Southern Strays	0.1012	0.1214	0.1242	1	0.13
	Transients	0.4401	0.7878	0.9993	1	1.2
Abundant	Frequency fitted	0.3424	0.156	0.0698	0.0598	
	<i>Alosa aestivalis</i>	0.0273	0.0337	0.0449	0.0453	0.15
	<i>Alosa pseudoharengus</i>	0.4575	0.4948	0.6513	0.6518	1.79
	<i>Ameiurus catus</i>	0.691	0.7064	0.8142	0.8225	1.75
	<i>Ameiurus nebulosus</i>	0.5683	0.5797	0.6917	0.6963	0.86
	<i>Anchoa hepsetus</i>	0.1138	0.1656	0.1666	0.2331	0.88
	<i>Anchoa mitchilli</i>	0.1826	0.8304	0.8528	0.91	5.31
	<i>Anguilla rostrata</i>	0.0918	0.1341	0.1572	0.1912	0.38
	<i>Apeltes quadracus</i>	0.103	0.204	0.3815	0.3941	1.9
	<i>Bairdiella chrysoura</i>	0.0782	0.1984	0.5174	0.6002	2.11
	<i>Brevoortia tyrannus</i>	0.004	0.339	0.3625	0.6603	2.22
	<i>Caranx hippos</i>	0.0065	0.0413	0.0453	0.0653	0.09
	<i>Catostomus commersoni</i>	0.2883	0.3022	0.3772	0.3781	0.11
	<i>Centropristis striata</i>	0.1756	0.265	0.3355	0.3366	0.57
	<i>Chilomycterus schoepfi</i>	0.1771	0.2543	0.2562	0.2606	0.17
	<i>Cynoscion regalis</i>	0.2527	0.3297	0.4015	0.6111	2.4
	<i>Engraulis eurystole</i>	0.0179	0.0346	0.0348	0.0384	0.09
	<i>Esox niger</i>	0.2376	0.2394	0.3056	0.3074	0.05
	<i>Etheostoma olmstedi</i>	0.3742	0.3799	0.4425	0.4429	0.37
	<i>Etropus microstomus</i>	0.1268	0.599	0.5998	0.5999	0.93
	<i>Fundulus diaphanus</i>	0.1392	0.1409	0.1837	0.1849	0.37
	<i>Fundulus heteroclitus</i>	0.0189	0.0297	0.0459	0.0463	0.49
	<i>Gobiosoma bosc</i>	0.1047	0.274	0.3419	0.3419	0.5
	<i>Hippocampus erectus</i>	0.1637	0.2037	0.2117	0.2215	0.11
	<i>Ictalurus punctatus</i>	0.107	0.1095	0.1447	0.1452	0.41
	<i>Lagodon rhomboides</i>	0.0251	0.0471	0.0472	0.0639	0.17
	<i>Leiostomus xanthurus</i>	0	0.0318	0.1998	0.2222	1.26
	<i>Lepomis gibbosus</i>	0.2437	0.2465	0.2593	0.2669	0.17

(Table continued on next page)

Table 4 (continued)

Analysis	Name	Principal component				Variance(y)
		1	2	3	4	
	<i>Menidia beryllina</i>	0.0168	0.0327	0.0433	0.0436	0.06
	<i>Menidia menidia</i>	0.6897	0.6978	0.7996	0.8535	5.61
	<i>Menticirrhus saxatilis</i>	0.119	0.1192	0.147	0.2291	0.27
	<i>Micropogonias undulatus</i>	0.0588	0.0748	0.0765	0.4015	1.28
	<i>Morone americana</i>	0.8441	0.8549	0.9284	0.9332	5.19
	<i>Morone saxatilis</i>	0.2126	0.2322	0.2712	0.2713	0.15
	<i>Mustelus canis</i>	0.1314	0.1362	0.1362	0.146	0.13
	<i>Notemigonus crysoleucas</i>	0.4544	0.4618	0.5134	0.5231	0.57
	<i>Ophidion marginatum</i>	0.0908	0.1183	0.1485	0.45	0.17
	<i>Opsanus tau</i>	0.2851	0.3752	0.3802	0.3838	0.71
	<i>Paralichthys dentatus</i>	0.0752	0.1293	0.1293	0.1802	0.45
	<i>Peprilus triacanthus</i>	0.2156	0.5339	0.6265	0.7309	2.34
	<i>Perca flavescens</i>	0.333	0.3461	0.3981	0.3994	0.14
	<i>Pomatomus saltatrix</i>	0.0007	0.1389	0.1393	0.1753	0.36
	<i>Prionotus carolinus</i>	0.1829	0.5395	0.6245	0.6947	1.2
	<i>Prionotus evolans</i>	0.1718	0.1946	0.1979	0.2495	0.39
	<i>Pseudopleuronectes americanus</i>	0.1539	0.1623	0.179	0.2081	0.62
	<i>Raja eglantaria</i>	0.1072	0.3576	0.3708	0.3916	0.34
	<i>Leucoraja erinacea</i>	0.0453	0.2561	0.2742	0.2839	0.23
	<i>Scophthalmus aquosus</i>	0.1234	0.5694	0.572	0.6156	0.66
	<i>Sphoeroides maculatus</i>	0.298	0.3146	0.3322	0.3446	0.77
	<i>Stenetomus chrysops</i>	0.3395	0.3852	0.4003	0.4455	0.94
	<i>Syngnathus fuscus</i>	0.6544	0.6615	0.6831	0.7091	2.28
	<i>Tautoglabrus adspersus</i>	0.0583	0.1102	0.1125	0.225	0.17
	<i>Tautoga onitis</i>	0.2731	0.4399	0.4416	0.4433	0.55
	<i>Trinectes maculatus</i>	0.5653	0.6298	0.6522	0.6604	1.69
	<i>Urophycis regia</i>	0.0913	0.6486	0.6534	0.6718	1.12
Rare	Frequency fitted	0.1177	0.0748	0.0683	0.065	
	<i>Alosa aestivalis</i>	0.9682	0.9769	0.9811	0.9811	6.15
	<i>Alosa mediocris</i>	0.0264	0.0342	0.0604	0.1449	2.28
	<i>Aluterus heudelotii</i>	0.0003	0.0005	0.0006	0.0006	0.16
	<i>Aluterus schoepfii</i>	0.0005	0.0009	0.0009	0.001	0.16
	<i>Ammodytes americanus</i>	0.0069	0.479	0.4991	0.5118	0.79
	<i>Astroscoptes guttatus</i>	0.0003	0.0148	0.0169	0.0247	1.92
	<i>Caranx crysos</i>	0.0112	0.1725	0.3242	0.4062	0.77
	<i>Chasmodes bosquianus</i>	0.0013	0.0021	0.0035	0.0041	1.03
	<i>Chaetodon ocellatus</i>	0.0005	0.0009	0.0009	0.001	0.4
	<i>Chrysemys picta</i>	0.0001	0.0016	0.002	0.0103	0.64
	<i>Citharichthys arcifrons</i>	0.0004	0.0181	0.061	0.1547	0.79
	<i>Clupea harengus</i>	0.0008	0.002	0.0022	0.0031	0.4
	<i>Conger oceanicus</i>	0.0005	0.0011	0.0012	0.0012	1.07
	<i>Dactylopterus volitans</i>	0.0019	0.0037	0.0074	0.0261	0.16
	<i>Decapterus punctatus</i>	0.0013	0.0031	0.0034	0.0101	0.79
	<i>Engraulis eurystole</i>	0.0147	0.9042	0.9499	0.9606	3.5
	<i>Erimyzon oblongus</i>	0.0075	0.0077	0.0077	0.0083	0.56
	<i>Esox niger</i>	0.1278	0.1315	0.1338	0.1703	1.93
	<i>Eucinostomus argenteus</i>	0.0021	0.0024	0.0067	0.1212	0.64
	<i>Fistularia tabacaria</i>	0.0031	0.224	0.2414	0.2444	0.16
	<i>Gasterosteus aculeatus</i>	0.0028	0.0039	0.004	0.0057	1.7
	<i>Gobionellus boleosoma</i>	0.0009	0.0058	0.0133	0.0169	0.64
	<i>Gobiosoma ginsburgi</i>	0.0137	0.0137	0.1387	0.1519	1.42
	<i>Hippoglossina oblonga</i>	0.0028	0.0057	0.0101	0.0111	0.56
	<i>Lepomis macrochirus</i>	0.0003	0.0008	0.0009	0.0021	0.16
	<i>Libinia dubia</i>	0.0073	0.0076	0.0096	0.0114	1.51
	<i>Lophius americanus</i>	0.0003	0.0005	0.0006	0.0006	0.4
	<i>Lucania parva</i>	0.0152	0.0193	0.0203	0.0228	0.79
	<i>Lutjanus griseus</i>	0.0036	0.0674	0.082	0.0823	0.47
	<i>Menidia beryllina</i>	0.003	0.072	0.2541	0.6649	2.25

(Table continued on next page)

Table 4 (continued)

Analysis	Name	Principal component				Variance(y)
		1	2	3	4	
	<i>Merluccius bilinearis</i>	0.0051	0.0051	0.1988	0.24	0.71
	<i>Microgobius thalassinus</i>	0.0055	0.0107	0.0201	0.1135	0.86
	<i>Mugil cephalus</i>	0.0005	0.0024	0.0063	0.0067	0.16
	<i>Mugil curema</i>	0.0007	0.0014	0.003	0.1271	0.32
	<i>Mullus auratus</i>	0.0001	0.0487	0.1827	0.494	0.4
	<i>Mycteroperca microlepis</i>	0.0011	0.0022	0.0024	0.0024	0.47
	<i>Myoxocephalus aeneus</i>	0.0018	0.009	0.0111	0.0132	0.71
	<i>Opisthonema oglinum</i>	0.0007	0.0016	0.0016	0.0052	0.16
	<i>Orthopristis chrysoptera</i>	0.0012	0.0027	0.0027	0.0027	1.59
	<i>Paralichthys oblongus</i>	0.0013	0.0029	0.003	0.003	0.71
	<i>Pogonias cromis</i>	0.0033	0.0036	0.0037	0.2928	2.85
	<i>Pomoxis nigromaculatus</i>	0.031	0.031	0.0311	0.0324	0.16
	<i>Pseudupeneus maculatus</i>	0.0004	0.0006	0.0018	0.0022	0.16
	<i>Rhinoptera bonasus</i>	0.0026	0.0053	0.0077	0.0297	0.56
	<i>Scomberomorus maculatus</i>	0.0006	0.0014	0.0015	0.004	0.4
	<i>Scomber scombrus</i>	0.0013	0.0028	0.0115	0.0137	0.16
	<i>Selar crumenophthalmus</i>	0.0005	0.0009	0.0009	0.001	0.16
	<i>Selene setapinnis</i>	0.008	0.0132	0.744	0.9017	3.21
	<i>Selene vomer</i>	0.0073	0.0142	0.0145	0.0831	2.03
	<i>Seriola zonata</i>	0.0008	0.002	0.0022	0.0031	0.16
	<i>Sphyræna borealis</i>	0.0011	0.0442	0.1469	0.3162	0.95
	<i>Strongylura marina</i>	0.0009	0.0418	0.1234	0.33	0.71
	<i>Trachurus lathami</i>	0.0003	0.0018	0.004	0.0079	0.16
	<i>Trichiurus lepturus</i>	0.0004	0.0009	0.0011	0.0011	1.26
	<i>Urophycis chuss</i>	0.0038	0.008	0.0143	0.0159	1.78

along the coast depending on their spawning location and time (Berrien & Sibunka 1999, Warlen et al. 2002). This is changing, with potentially more MAB-spawned or even estuarine-spawned contributions (Able & Fahay 2010). The recruitment of another species with a similar range, bluefish *Pomatomus saltatrix*, often manifests as 2 annual cohorts (spring and summer) using different coastal habitats depending on their spawn date (Callihan et al. 2008), with adults spawning in both the MAB and SAB habitats as they migrate (Chiarella & Conover 1990, Berrien & Sibunka 1999). The dynamics of cohort formation are tied to changes in adult movement (extending farther north in the fall, Walsh et al. 2015) and geophysical circulation (Hare et al. 2001, 2002), which also appears to be changing (Shearman & Lentz 2010, Chen et al. 2014, 2015). In another example, recruitment of a southern shelf spawning species, Atlantic croaker *Micropogonias undulatus*, is increasing in the MAB, including the study system, in response to climate. During warmer winters, more larvae survive, and the effects of the larger year class can be seen throughout the duration of the cohort's life cycle as increasingly common 'outbursts' (Hare & Able 2007). In yet another example, American eels *Anguilla rostrata* have been arriving into the study system later be-

cause recruiting leptocephali cue on the discharge of estuarine plumes, which have changed over time (Sullivan et al. 2006). Further, American conger eels *Conger oceanicus* are arriving earlier, resulting in increased potential interaction with *A. rostrata* (Musumeci et al. 2014).

These studies, however, consider species spawned in the ocean that recruit into the estuary as larvae, and thus share class memberships in the origin guild (which has not changed as a group) as well as the reproductive mode guild. In fact, the rare species assemblage in the present study is comprised primarily of Transients and Southern Strays. However, the current work points to the greatest response being a relative change in the abundance of Resident Spawners, particularly a decrease in those that use the lower estuary compared to those that spawn in the river (see also Nickerson 2017). The system thus appears to be relatively insensitive to the dynamics of the ocean/shelf-reproducers over the study period, despite the earlier examples. Perhaps this is because they are too dynamic as a group over the period examined, in that they respond more strongly to a number of orthogonal pressures rather than slowly changing local averages. The location of their early life history stages has them many steps removed from

ultimate arrival in the study system, any one of which might affect other members of the guild independently despite similar local pressures. The Mullica River-Great Bay estuary is located at the zonal center of the MAB, which sees settlement of the larvae of both northern and southern ocean spawning species throughout its 855 km shoreline from Cape Hatteras, North Carolina, to Cape Cod, Massachusetts (Able & Fahay 2010). These recruits are 'winners' as survivors of a large annual 'portfolio' of young spawned at different locations along the coast (Cowen et al. 1993, Grothues & Cowen 2002, Secor 2007, Schindler et al. 2010). Inclusion of the MAB estuaries as nursery habitat is part of an evolved bet-hedging trait (Juanes & Conover 1994, Able et al. 2013), which further includes intra-cohort compensatory mechanisms such as lipid storage vs. growth (e.g. Slater et al. 2007) and facultative habitat choice (Kraus & Secor 2004, Taylor et al. 2007). The position of the study area in the middle of the recruitment range means that it may more often have temperatures within the suitable range for those species than do estuaries at the range margins, or that its average may be near the modal temperature of the range to which these species' young have evolved. This could stabilize the assemblage. A synthesis of fine-scale temperature variation from estuaries across this range would help address this. In all cases, the explained variance ( $r^2$ ) was very low, indicating that a change would be barely recognizable except to the long-term observer due to the high inherent variability.

In the current study, the 12-cluster classification of reproductive guilds did not elucidate more change than did the 8-cluster classification and may even have confounded the pattern. The addition of more cluster branches in this case broke the reproductive strategies of examined species into subcategories of the MAB and SAB spawning habitats. The full assemblage analysis supports this conclusion (see also Nickerson 2017), with the Estuarine Spawners *Menidia menidia* and *Syngnathus fuscus* and Freshwater Spawners white perch *Morone americana* and white catfish *Ameiurus catus* explaining the most variation in the ordinations in the prior study. However, increase of the guild represented by the latter 2 was relative, as some constituents of the other guilds decreased (Nickerson 2017). In particular, *M. menidia* and *S. fuscus* represent the Estuarine Spawners that decreased significantly (Nickerson 2017). These species and others in the guild complete most of their life cycle in the estuary, and some are perennial species. Thus, they may be locally adapted. A series of careful common garden experiments documented

important trends in physiology and morphology for *M. menidia* along the east coast. For instance, the capacity for growth in *M. menidia* increases with latitude (Conover et al. 2005), and fishes from northern populations consume more, grow faster, and produce more eggs than those from southern populations (Billerbeck et al. 2001). However, these faster-growing northern fish have a higher mortality rate and decreased swimming ability, and are more susceptible to predation (Munch & Conover 2003). These northern *M. menidia*, then, are adapted to take advantage of optimal growth conditions during the shorter period of the year during which they occur (Conover & Present 1990). They do, however, experience trade-offs in order to offset winter mortality, which increases with latitude and decreases with larger body sizes (Conover & Present 1990). Both the response of sex ratio to temperature (Lagomarsino & Conover 1993) and size-related winter mortality (Schultz et al. 1998) also differ for populations at different latitudes. Clearly, local conditions matter for these species, enough to influence populations at a genetic level (Conover et al. 2005).

How do the patterns elucidated here, particularly a lack of sensitivity to rare southern species, relate to conflicting evidence for change, especially in an expected climate signal in the recruitment and settlement of southern species to the study system (e.g. Able & Fahay 2010)? First, such studies are surprisingly rare for the MAB. Daniels et al. (2005) documented the decline of northern-affiliated rainbow smelt *Osmerus mordax* and Atlantic tomcod *Microgadus tomcod* in the Hudson River. Both are fresh/estuarine substrate spawners that would have been included in the same guild with *M. menidia* and *S. fuscus*. Taylor & Palance (2012) found the replacement of northern-affiliated winter flounder *Pseudopleuronectes americanus* (another benthic estuarine spawner) by southern affiliated summer flounder *Paralichthys dentatus* in Narraganset Bay. This could have been due to anthropogenic redistribution of habitat characteristics along which these species segregate (Taylor et al. 2016). Further, both are the subjects of intense fisheries, neither is rare, and neither is southern. The abundance of *P. americanus* juveniles, corrected for spawning stock biomass, did decline in long-term trap and larval samples in the study system (Able et al. 2014). In fact, most of the documented changes for northern advancement of southern species come from plankton sampling of larval stages (Able & Fahay 2010). The breakdown of the pattern with life history stage may be a result of processes beyond settlement (i.e. winter mortality,

McBride & Able 1998, Able & Fahay 2010). This could, however, be dampened in the current study, where trawling selected heavily for spring- and summer-settled young of the year rather than overwinter survivors, with the exception of the aforementioned *Micropogonias undulatus*.

This point does lead to another consideration. The current study considers those species and sizes that are vulnerable to daytime trawling, in trawlable habitat only. Other potential harbingers of change related to climate, such as the diverse subtropical but cryptic gobies, may be better sampled by different gears. The adults of these species are becoming more speciose in the study system, despite rarely being captured in the trawl (Able & Fahay 2010). Sampling during the day could also underestimate the abundance of nocturnally active species such as eels (*A. rostrata* and *C. oceanicus*). In the current study, samples also include some large and mobile individuals caught only as adults (e.g. cownose ray *Rhinopterus bonasus*), the nature of which makes them statistically rare, in a purely stochastic way, and different from that of colonizing recruits, yet they are conflated. This highlights some challenges of guild use.

A guild classification intentionally rejects finer-scale community dynamics (Fountain-Jones et al. 2015). Guilds can thereby skew distribution curves, as a single species can statistically weight the data for the entire guild. For instance, if a single species within a guild thrives, while the other members of the guild decline, such an 'outlier' may be enough to maintain high abundance of a specific guild on a statistical level, while in the field, the other members of the guild are declining and experiencing negative effects (Caro & O'Doherty 1999). It is important, therefore, to consider both the use of guilds and the species assemblage analysis as we have done here (and see Nickerson 2017). The use of guilds can statistically explain variance associated with certain mechanisms driving change in a system (although whether they are the cause still needs to be determined by manipulative experimentation), but these associations can only be elucidated when the full system change is also taken into account.

While guilds are useful as a tool for understanding the structure of extensive ecosystems and for the spatial and temporal understanding of estuarine resources, there is still little information available regarding quantitative changes in guilds and the species composing them (Eick & Thiel 2014). In comparing the change in guild classifications over time to the change in the full fish assemblage, we can both assess the factors driving change in the system,

and gain insight into the factors that might therefore drive change in the system in the future. Our findings indicate that change in representation of fishes classified by reproductive guilds most closely matches the change in the full assemblage, and that, as a guild, their relative abundance oscillates on a 5–7 yr period and has changed over time. This provides guidance for future studies. For example, the observation of this oscillation with a directional bias is reminiscent of observations for the El Niño Southern Oscillation Index (L'Heureux et al. 2013). Why (if this is the case) this would affect reproductive-sorting more than origin-sorting guilds would be interesting. Changes in spawning time, in phenology, or in survival of larvae and juveniles, would be logical next steps for analysis.

The possibility that other guild (such as trophic) structures reflect long-term change is also interesting, although not easily analyzed for lack of a thorough understanding of where juveniles of different species fit in such a classification. Additionally, the origin guilds' lack of significance can be used to plan future steps. Breaking the origin characteristics down into more detailed factors may help to clarify the role that the origin of species relative to the system plays in determining how the assemblage is changing. The importance of stragglers and pioneers to assemblage composition has been noted in the literature (Murray et al. 1999). For example, moonfish *Selene setapinnis* and lookdown *S. vomer*, both of which are uncommon in the system, have been captured with increasing frequency over the more recent years of the time series, even though their presence in the catch has remained small overall. These species are not resident within the system, primarily residing in southern waters, yet their increasing abundance may have an effect on the overall structure of the assemblage, as has been suggested (Able & Fahay 2010). This pattern is reflected by the more abundant but similarly southern-affiliated silver perch *Bairdiella chrysoura*. Silver hake *Merluccius bilinearis*, on the other hand, a species associated with cold conditions, was not captured in this trawl survey between 2006 and 2013. As the time series progresses, the origin of species relative to the system may become more important, and may begin to show significant change over time. Continuing to monitor these guilds and assess how their role in driving change is shifting over time is important in order to both understand change, and to predict future changes.

Overall, the use of guilds to determine the factors driving change in the Mullica River-Great Bay eco-

system is exploratory in nature. By using guilds as a 'super species,' the ecological factors that are driving the observed change in the full assemblage can be assessed. The exact mechanisms by which these changes are happening, however, are not made clear by a broad guild analysis. Further investigation into the change in the characteristics themselves will be required to paint a more thorough picture of change in the ecosystem.

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