Mixed stock origin of Atlantic bluefin tuna in the U.S. rod and reel fishery (Gulf of Maine) and implications for fisheries management

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Abstract

The highly migratory Atlantic bluefin tuna (*Thunnus thynnus*) has a distribution that spans the North Atlantic and two distinct spawning populations, an eastern population originating in the Mediterranean Sea and a western population originating in the Gulf of Mexico. Atlantic bluefin tuna are managed as two separate management units (east and west) in the North Atlantic, despite observed mixing that occurs across the management boundary. Characterizing the effects of stock mixing has been identified as a priority for improving the management of Atlantic bluefin tuna. Identifying the stock composition of landings from the Gulf of Maine is of particular importance, because approximately 70% of the U.S. western Atlantic total allowable catch is removed from this region annually. The aim of our research was to apply otolith chemistry techniques to characterize the origin of bluefin tuna caught in the U.S. rod and reel fishery in the Gulf of Maine and to demonstrate how this information can be applied in fisheries management. Prior research established otolith stable isotope chemistry ($\delta^{13}C$ and $\delta^{18}O$) as an effective and reliable stock identification tool, and we applied this approach to determine the population of origin of bluefin tuna collected from fishery dependent sampling (recreational and commercial) in the Gulf of Maine. Results indicated that the majority of fish caught in the Gulf of Maine from 2010 to 2013 were eastern origin. We found the highest proportion of eastern origin fish were caught in 2012 and the proportion of eastern origin fish was greater in late summer to fall. Although the majority of fish in small and intermediate size classes were eastern origin, fish in the largest size class (>250 cm) were predominantly western origin. Using these data, we demonstrated an approach for integrating mixed stock composition information into fishery-specific harvest data (U.S. rod and reel catch, catch-at-age, and catch-per-unit-effort). This information can be used to monitor mixed stock composition of the fishery, partition catch to population of origin, and to inform management decisions aimed at controlling population of origin harvest.

Keywords: Atlantic bluefin tuna, stock composition, stock mixing, otolith chemistry, fisheries management

1. Introduction

The Atlantic bluefin tuna (*Thunnus thynnus*) is a large, highly migratory species with a distribution that spans the North Atlantic. Initially considered to be a single panmictic stock, two distinct spawning populations, an eastern population originating in the Mediterranean Sea and a western population originating in the Gulf of Mexico, were recognized and accounted for in the stock assessment process in the 1980s through the creation of separate management units. The International Commission for the Conservation of Atlantic Tunas (ICCAT) management boundary divides east and west stocks at the 45°W meridian, and the current assessment used for management purposes assumes no mixing occurs across this boundary (Anon., 2017). In recent decades, a suite of research methods has improved our understanding of Atlantic bluefin tuna movement and stock mixing. Stock identification methods, including genetics, otolith chemistry, conventional and electronic tagging, and organochlorine data, indicate that bluefin tuna populations exhibit a high rate of natal homing, as well as a high degree of stock mixing, particularly during juvenile and sub-adult life stages (Lutcavage et al., 1999, 2001; Block et al., 2005; Rooker et al., 2008a,b; Dickhut et al., 2009; Galuardi et al., 2010; Rodríguez-Ezpeleta et al., 2019). In addition, another spawning ground was recently identified in the Slope Sea of the western Atlantic, however the origin of these spawners is currently unknown (Richardson et al., 2016). Mismatch in the scale of Atlantic bluefin tuna populations' movements and stock units has important implications to the sustainable management of this species (Kerr et al., 2017).

Recent stock assessments estimate significant differences in the biomass of bluefin tuna stocks, with the eastern stock estimated to be an order of magnitude greater than the western stock (Anon., 2017). Because of these relative differences in biomass, even low movement rates of eastern origin fish into western Atlantic waters can exert significant influence on the biomass and stock composition of bluefin tuna in the western stock area (Secor et al., 2015; Kerr et al., 2017). The combined effect of asymmetric size of bluefin tuna populations and the assumption of no mixing in current stock assessments can result in an overly optimistic perception of western bluefin tuna biomass (Kerr et al., 2017). This influence can result in a decoupling of the stock and population view of the resource. In this case, the stock view provides insight on the availability of fish to the fishery within the stock area, regardless of origin, and the population view provides insight regarding the unit of production and sustainability. Both views are needed, but the current approach to assessment and management for Atlantic bluefin tuna assumes the stock and population view are equivalent and this can confound sustainable management.

Alternative approaches have been proposed to account for the impact of stock mixing on the stock assessment and management process for Atlantic bluefin tuna. Integrating the movement dynamics of bluefin tuna has been explored through fitting spatially explicit stock assessment models that incorporate tagging and stock composition data (e.g., dual zone virtual population analysis [VPA-2BOX], Porch et al., 2001; the multi-stock age structured tag integrated model [MAST], Taylor et al., 2011; the modifiable multi-stock model [M3], Anon., 2017); however, these have not been considered reliable for providing the basis of management advice to date. Modeling spatial population dynamics is statistically demanding because it requires the estimation of many additional parameters to capture both seasonal and ontogenetic spatial dynamics (Punt, 2019). Furthermore, the tagging and stock composition data (based on genetics and otolith chemistry) used to fit these statistical models is limited for certain regions, fisheries, and for historical periods (Morse et al., 2018). In addition, information from different methods can provide different perspectives on mixing that integrate across different time scales. For example, natural markers, such as otoliths, and genetic markers provide distinct ecological and evolutionary perspectives on population connectivity (Reis-Santos et al., 2018). Work is ongoing to determine the best approach for integration of this information within the context of ICCAT's management strategy evaluation of bluefin tuna (Anon., 2017). However, in the meantime, this information is not used to inform monitoring or management of bluefin tuna populations.

Analysis of otolith chemistry using stable isotopes ($\delta^{13}C$ and $\delta^{18}O$) has been established as an effective stock identification tool, providing answers to critical stock structure questions for Atlantic bluefin tuna (Rooker et al., 2008a,b; Schloesser et al., 2010; Secor et al., 2013, 2014a, 2015; Rooker et al., 2014; Siskey et al., 2016). The water chemistry in the two principal nursery regions differs significantly and leaves distinct chemical signatures in the otoliths of tuna. Fish inhabiting the cooler, more saline waters of the eastern nursery (Mediterranean Sea) exhibit elevated $\delta^{13}C$ and $\delta^{18}O$ values compared fish from the western nursery habitat (NW Atlantic shelf; Rooker et al., 2014). By analyzing the chemical composition of otoliths, we can assign fish to their respective population of origin based on this nursery signature. Otolith chemistry of archived bluefin tuna otolith samples has been used to estimate historical and recent stock mixing levels, which depend on the region sampled within the Atlantic, as well as fish size, life-stage, and year-class (see review by Rooker and Secor 2019).

Stock composition analysis of fish collected in the Gulf of Mexico and Mediterranean Sea revealed that nearly all of these fish (~ 100%) originate from their respective spawning populations, indicating natal homing and little to no mixing on the spawning grounds (Rooker et al., 2008a,b, 2014). Limited stock mixing is also evident in the eastern and central Atlantic, with fish predominantly of eastern origin (Rooker et al., 2014). However, analysis of fish caught in the U.S. western Atlantic suggests extensive mixing of eastern and western origin fish within this region (Rooker et al., 2008b; Siskey et al., 2016; Anon., 2017). Stock composition of commercial size (>185 cm CFL) bluefin tuna landed in the Gulf of Maine indicated this size class was predominately (95%) western origin fish in the 1990s (Rooker et al., 2008a). However, the sample size was relatively small (n=72), temporally short (1996 and 1998), and collected from a geographically restricted area within the Gulf of Maine (Ipswich Bay), and from one size class of fish ("giants", i.e. >140 kg, ≥ age 10; Rooker et al., 2008a). More recent work by Siskey et al. (2016) described changes in mixing of eastern and western origin bluefin tuna in the Gulf of Maine over recent decades, with fish being nearly entirely western origin in the 1970s and 2010s, but with greater representation of eastern origin fish (41%) in the 1990s. These variable results for the Gulf of Maine suggests there is a need for higher resolution sampling in this region of dynamic stock mixing to characterize stock composition and evaluate any differences across size classes, time, and location.

The goal of our research was to characterize the stock composition of bluefin tuna landed in the U.S. rod and reel fishery in the Gulf of Maine (2010-2013) using otolith chemistry techniques and to demonstrate how results could be used to inform fisheries management. The concentration of landings in the Gulf of Maine, approximately 70% of the entire U.S. bluefin tuna quota allocation, highlights the importance of understanding mixing dynamics of bluefin tuna in this region on a finer spatial and temporal scale.

2. Material and Methods

2.1. Sample Selection

Atlantic bluefin tuna otoliths were sampled from an archived otolith collection held at the Gulf of Maine Research Institute and collected by the University of Maine. The otoliths were dissected from tuna heads that were donated by commercial and recreational fishermen who typically discard the heads when landing fish. This collection is the most comprehensive archive to date for Atlantic tuna landed in the Gulf of Maine with samples that are representative of the recreational and commercial components of the U.S. rod and reel fishery. Samples that had the most associated data (e.g., length, sex, location of capture) were preferentially selected for otolith chemistry analysis. Samples were selected across the duration of the fishing season (June – October), as well as across a spectrum of size classes to represent the fishery and account for isotopic differences by time of year or age of fish. A total of 782 otoliths were analyzed for stable isotope chemistry in this study.

2.2. Otolith Preparation and Analysis

Sagittal otoliths were removed from sampled fish, cleaned of adhering tissue, and dried. One randomly selected otolith from each pair was embedded in a fast curing high visibility epoxy (EpoHeat, Buehler Inc.). A transverse section (1.5 mm) which included the nucleus and distal knob (protuberance) of the otolith was prepared using a Buehler IsoMet 1000 Precision Saw and attached to a sample plate using SPI Crystalbond 509 thermoplastic glue with the nucleus side up. The region corresponding to the first year of growth, which was identified from measurements of transverse sections of otoliths from yearling bluefin tuna (Rooker et al., 2014), was isolated and powdered using a New Wave Research MicroMill (Fig. 1). A series of 14 drill passes at 55 µm/sec and 55 µm depth per pass were run over a pre-programmed drill path by a 500 µm diameter carbide drill bit until a depth of approximately 770 µm was reached. Powder was collected with a microspatula, folded into wax paper, and sealed into plastic sample vials. Processing tools were cleaned with 95% EtOH to prevent cross contamination among specimens.

Otolith powder was analyzed for $\delta^{13}C$ and $\delta^{18}O$ using an automated carbonate preparation coupled to a gas chromatograph – isotope ratio mass spectrometer (Finnigan MAT 252; Thermo Fisher Scientific, Inc.) at the University of Arizona Environmental Isotope Laboratory. Powdered samples were reacted with dehydrated phosphoric acid under vacuum at 70°C. Analytical precision of the mass spectrometer has been measured at ±0.1% for $\delta^{18}O$ and ±0.06% for $\delta^{13}C$ (1 standard deviation; Schloesser et al., 2010). Isotope ratios were calibrated based on repeated measurements of NBS-19 and NBS-18 and reported relative to the Pee Dee Belemnite (PDB) standard. $\delta^{13}C$ values were corrected for the Suess effect:

$$Suess\ Effect_{13C} = \beta_{13C} * (Year\ of\ Baseline - (Year\ of\ Capture - Age)) \quad (1)$$

where year of baseline (2006) was chosen as the modal year over which the baseline sample was collected (1998-2011; Siskey et al., 2016) and β_{13C} was calculated as the slope of $\delta^{13}C$ data in this study plotted against year class β_{13C}= -0.0299.

The corresponding otolith of each pair was sectioned (0.8 mm thickness) along a transverse plane on the distal side of the nucleus and using a series of gritted papers polished for ageing purposes. Otolith preparation conventions and age interpretation procedures followed the standardized procedures adopted by past international efforts (Secor et al., 2014b; Busawon et al., 2014). Blind counts of annuli were conducted twice from the images using Adobe Photoshop CS2 Version 9.0. When counts differed by <2 years, the second count was accepted. When counts differed by >2 years, the image was inspected a third time along with the two previous annulus assignments.

2.3. Mixed Stock Analysis

Population assignment methods use stock identification information to ascertain population membership of individuals (individual assignment) or groups of individuals (mixture analysis; Manel et al., 2005). Alternative methods can support different inferences because of different assumptions. Mixture analysis estimates the proportion of individuals that each source population contributes to a mixed sample, whereas individual assignment classifies each individual to the population with the highest likelihood and estimated mixture proportions are the sum of the individual assignments (Manel et al., 2005). We applied both mixture and individual assignment methods to understand the influence on conclusions regarding mixed stock composition of bluefin tuna in the Gulf of Maine.

Mixture analysis, specifically a maximum likelihood mixture model, has been applied in the majority of previous studies on Atlantic bluefin tuna stock composition (Rooker et al., 2008a,b; Schloesser et al., 2010; Secor et al., 2013, 2014a, 2015; Rooker et al., 2014; Fraile et al., 2015; Siskey et al., 2016). We applied a conditional maximum likelihood mixture model (CMLE) fit using the program HISEA (PC executable of FORTRAN program) as described by Millar (1990a,b), as this is the most frequently applied mixture assignment approach for continuous characters. This procedure fits the mixture distribution based on the source population distributions of the characters and possible mixing proportions in the unknown sample. Mixture analysis (CMLE) provided mixed stock composition for all samples in terms of the mean and standard deviation of the proportion of eastern and western origin fish based on bootstrapping with 10,000 simulations. Individual assignment is increasingly being applied in otolith chemistry studies, and ICCAT has adopted this approach in compiling a database of stock of origin information on bluefin tuna across the Atlantic (Anon., 2017). The application of individual assignment requires a decision on both the statistical approach (e.g., discriminant analysis, random forest, or other machine learning methods) and the appropriate threshold probability level for assignment. Results can vary based on both of these choices. Individual probabilities of belonging to the eastern or western population were assigned using the random forest technique (RF). RF is based on classification trees that are built from a random bootstrap resampling (with replacement) of the data. One of the benefits of this approach is that there are no *a priori* distributional assumptions (Mercier et al., 2011). In comparative analyses with other common statistical approaches, such as linear discriminant analysis and neural network analysis, RF was shown to be a powerful tool for classification based on otolith chemistry (Mercier et al., 2011). The RF approach provided assignment of individuals based on an associated probability. In assigning individual probabilities, we adopted a threshold probability level of 0.7 based on ICCAT's thresholds for assignment wherein the probability level for assignment to eastern or western origin was $\geq$0.7 and some individuals were not able to be assigned to origin (Anon., 2017). Individual assignment analysis was conducted in the R programming environment (R Development Core Team, 2018).

Population assignment for Atlantic bluefin tuna relied on a baseline of yearling (age 1) samples. These were collected in both principal nursery systems during the past 15 years (Rooker et al., 2014). One assumption of the mixture analysis is that the predictor variables (i.e., stable isotope ratios) are independent. Oxygen and carbon stable isotopic ratios are driven by different processes, with $\delta^{18}O$ influenced by water temperature and salinity at the time of otolith precipitation, and $\delta^{13}C$ ratios reflecting metabolic sources and ontogenetic changes in rates (Trueman et al., 2012). Previous investigations of this baseline have demonstrated temporal stability of $\delta^{18}O$, the primary marker for bluefin tuna classification (Rooker at al., 2008b; Rooker et al., 2014). Classification success based on linear discriminant function analysis of the most up-to-date baseline is 90% east and 75% west (overall 83% classification accuracy; Rooker et al., 2014). Specimens of unknown origin were compared with yearling baseline samples and classified to eastern or western nurseries using both mixture classification and individual assignment approaches.

We characterized the stock composition of Atlantic bluefin tuna in the Gulf of Maine by year (2010-2013), month of capture (June-October), general size classes (<150, 150-199, 200-249, >250 cm curved fork length [CFL]), age classes (ages <4, 4-6, 7-9, 10-12, 13-15, 16-18, ≥19), and by sex. In addition, we characterized stock composition by U.S. rod and reel size categories 66-114 cm (small school), 115-144 cm (large school), and >177 cm (combined large medium-large school).

2.4 Integration of Mixed Stock Information in Fisheries Data

We developed a data parsing approach for integrating stock of origin information into fishery-specific harvest data for the purpose of monitoring and informing management decisions. The data parsing approach involves revising the fishery-dependent data, including catch, catch-at-age, and catch-per-unit-effort (CPUE) collected for each size category of the fishery to reflect mixed stock composition information. Thus, instead of assigning a fishery's catch series to either the eastern or western stock, as currently assumed by ICCAT assessments, total catch biomass from each fishery is proportionally assigned to eastern and western populations based on stock composition information (Kerr et al., 2017; Morse et al., 2018). This approach requires identification of samples analyzed for mixed stock composition that are representative of the timing and location of fishery operation, as well as the size classes targeted by the fishery.

We illustrate the application of this approach to U.S. rod and reel recreational fishery data and commercial fishery data which is categorized by size classes: 66-114 cm (small school),115-144 cm (large school), and >177 cm (combined large medium-large school) from the 2017 ICCAT stock assessment (Anon., 2017). We utilized mixed stock composition from this study, as well as a previous study (Siskey et al., 2016; note results were re-estimated using the RF approach for consistency), to inform parsing of U.S. rod and reel fishery data. Size category-specific (*i*) catch, catch-at-age (*a*), and CPUE data representing the mixed western stock (*ws*) were revised by removing the proportion of eastern origin fish caught in western fisheries to derive western origin (*wo*) data series. The revised size category-specific catch ($C_{wo,i,y}$), catch-at-age ($C_{wo,i,y,a}$), and U.S. rod and reel combined catch-at-age ($C_{wo,y,a}$) of western origin fish were calculated as:

$$C_{wo,i,y,a} = C_{ws,i,y,a}\left(P_{i,y,a}\right) \quad (2)$$

$$C_{wo,i,y} = \sum_{a}^{a_{max}} C_{wo,i,y,a} \quad (3)$$

$$C_{wo,y,a} = \sum_{i} C_{wo,i,y,a} \quad (4)$$

where $C_{ws,i,y,a}$ is the annual size category-specific catch-at-age of fish by western stock fisheries, and $P_{i,y,a}$ is the annual age-specific proportion of western origin fish in mixed stock catches by the fishery. Size category-specific CPUE of western mixed stocks ($U_{ws,i,y}$) were adjusted downward to derive CPUE of western origin fish ($U_{wo,i,y}$), using the proportion of western origin fish for catch at age and weight at age ($w_{y,a}$):

$$U_{wo,i,y} = U_{ws,i,y} \frac{\sum_{a}^{a_{max}} P_{i,y} C_{ws,i,y,a} w_{y,a}}{\sum_{a}^{a_{max}} C_{ws,i,y,a} w_{y,a}} \quad (5)$$

3. Results

3.1. *Sample Characteristics*

In total, 782 otoliths were analyzed from Atlantic bluefin tuna caught in the Gulf of Maine from 2010 to 2013 (2010 = 221, 2011 = 255, 2012 = 149, 2013 = 157, Table 1). Fish were landed from June to November and descriptive location information was provided. Specific location information from a subsample of fish indicated that catches ranged from Nantucket, Massachusetts (~41ºN) to Mid Coast Maine (~44ºN; Fig. 2). Fish ranged in size from 84 to 305 cm CFL with the majority of samples within the 150 to 199 and 200 to 249 cm CFL length bin categories (Table 2). Fish ranged in age from 1 to 26 years, with 47% between the ages of 8 and 10, and birth years ranging from 1986 to 2012. Sex was determined for 479 individuals (female = 175, male = 304, Table 2). Across U.S. rod and reel size categories, the majority of samples were within the largest size category (US RR 66-114 cm = 24, US RR 115-144 cm = 41, US RR >177 cm = 412, Table 3).

3.2. Alternative Approaches to Mixed Stock Analysis

The classification accuracy of the mixture analysis and individual assignment methods were similar based on the baseline classification accuracy. Baseline classification accuracy of yearlings to eastern and western nurseries using mixture analysis (quadratic discriminant function analysis) was 90 and 73%, respectively (overall 83%; Rooker et al., 2014). Classification accuracy of yearlings to their respective eastern and western nurseries using the RF approach was also 83%. Between the two methods, the RF approach consistently provided lower estimates of eastern contribution compared to the mixture analysis. The choice of cutoff value of 0.7 for probability of assignment using the RF method meant that fish with eastern and western origin probabilities less than 0.7 were not classified. This resulted in differences in sample size difference between the two methods. However, when all samples were assigned through the RF approach the results varied as well.

3.3. Mixed Stock Analysis

Results for all samples combined indicated that the majority of individuals caught in the Gulf of Maine during 2010-2013 were of eastern origin (CMLE: 85% ± 12% and RF: 67% eastern origin; Table 1). Across the years, the mixed stock composition of bluefin tuna was dominated by eastern origin fish, with the highest percentage of eastern origin fish caught in 2010 (CMLE: 89% ± 9% and RF: 73% eastern origin) and 2012 (CMLE: 93% ± 9% and RF: 73% eastern origin) with slightly lower eastern origin catches in 2013 (CMLE: 82% ± 13 and RF: 63% eastern origin) and 2011 (CMLE: 76% ± 19% and RF: 61% eastern origin; Table 1, Fig. 3). Estimated mixed stock composition by month of capture indicated that the majority of bluefin tuna caught from June to October in the Gulf of Maine were consistently eastern origin (Table 1, Fig. 3). However, the greatest proportion of eastern origin fish were caught in August to October (Table 2, Fig. 3) with slightly lower proportions caught in June to July (Table 1, Fig. 3). Estimated mixed stock composition by size class indicated that the majority of the small and intermediate size classes of bluefin tuna caught in the Gulf of Maine were estimated to be of eastern origin (<150 cm, 150-199 cm, and 200-249 cm; Table 2, Fig. 3). However, the largest size class (>250 cm) of bluefin tuna was estimated to be predominantly western origin fish or nearly equal proportions of east and west, depending on classification method (CMLE: 48% ± 21%; RF: 63% western origin, Table 2, Fig. 3). Likewise, mixed stock analysis by age class indicated that younger fish were more likely to be of eastern origin (≤ age 12) compared to the oldest group of fish sampled (≥ age 13, Table 2, Fig. 3). For samples with sex information, mixed stock analysis indicated that both male and female fish were predominantly eastern origin fish, with a slightly higher proportion of female fish being eastern origin (Table 2, Fig. 3).

3.4. Integration of Mixed Stock Information in Fisheries Data

Integration of mixed stock information in U.S. rod and reel data required characterization of mixed stock composition by U.S. fleet size categories, rather than generic size bins (as described previously). Also, in this characterization we adopted the RF classification as this is now the prescribed approach used by ICCAT. This revealed that fish in the U.S. rod and reel size category 66-114 cm and 115-144 cm had a higher proportion of eastern origin fish (RF: 78% and 79% eastern origin, respectively) compared to fish in the >177 cm size category (RF: 65% eastern origin, Table 3). The application of mixed stock information to inform fishery-specific catch, catch-at-age, and CPUE demonstrates an approach to separate mixed stock fishery-dependent data into population-of-origin data. We applied stock composition estimates from this study and Siskey et al. (2016) that aligned with the size class, timing (years of collection), and geographic location of the U.S. rod and reel fishery data. Although we do not have stock composition information that spans the full time series of the data, this exercise can provide insight into the utility of collecting data at this scale in the future. The estimated CPUE, catch, and catch-at-age of western origin fish in the U.S. rod and reel fishery (size categories: 66-114 cm, 115-144 cm, and >177 cm) were considerably less than that of the western mixed stock, reflecting the dominance of eastern origin fish in the stock composition (Table 3, Figs. 4, 5, 6). Across the U.S. rod and reel size categories, the catch of >177 cm fish had the greatest contribution of western origin fish to western Atlantic fisheries (Fig. 6).

4. Discussion

4.1. Mixed Stock Analysis of U.S. Fishery Landings

Identification of the origin of Atlantic bluefin tuna landed in the Gulf of Maine provides critical information on stock mixing in the primary U.S. commercial fishing grounds. The number of otolith samples we analyzed from recently collected fish allows for robust estimates of stock composition for the U.S. rod and reel fishery and permits estimation of stock composition over time of capture (year and month), sex, size and age classes, and by fishery size categories. Population assignment based on otolith chemistry provides origin information that enables us to track the population origin of landings, in addition to the stock view of Atlantic bluefin tuna landings which is routinely tracked by fishery managers. This information is critical to understanding both how many fish are available to the fishery (stock view) and the status of bluefin tuna populations, or units of production (population view).

Otolith chemistry indicated a high degree of mixing of the eastern and western origin bluefin tuna in the Gulf of Maine, with eastern fish typically dominating the composition of the catch. The prevalence of eastern origin fish caught by western fisheries represents a revised perception of the composition of fish in the U.S. rod and reel fishery relative to the current assumption underlying ICCAT's assessment and management of the bluefin tuna (i.e., no stock mixing). The representation of eastern fish in the U.S. rod and reel fishery catches relates to both the movement rate of eastern origin fish into the Gulf of Maine and relative differences in the biomass of eastern and western origin fish. The most recent ICCAT stock assessment (Anon., 2017) supports a significant increase in eastern stock biomass. There is also evidence of a moderate increase in western stock biomass (Anon., 2017). However, it is unclear if this increase reflects increased western origin biomass or increased mixed stock biomass augmented by migrating eastern origin fish. In addition, substantial shifts in the spatial distribution of Atlantic bluefin tuna have been documented in response to changing ocean conditions and prey distributions (e.g., Golet et al., 2013; Fromentin et al., 2014; MacKenzie et al., 2014; Druon et al., 2016; Faillettaz et al., 2019). Increased productivity of eastern bluefin tuna and changing movement rates in relation to changing ocean conditions are likely drivers of the current high prevalence of eastern origin fish in western fisheries. Recent evidence supports an alternative spawning ground for Atlantic bluefin tuna in the Slope Sea region of the western Atlantic with spawning occurring at different times of year (June-August) than in the Gulf of Mexico (Richardson et al., 2016). The effect of this potential third group of spawning fish on assumptions for baseline information for otolith chemistry is unknown, but the collection of samples from this area is a high priority among bluefin tuna researchers.

It is important to note that stock mixing is a dynamic process and trends across years support this interpretation, with a change on the order of 10-20% in the mixed stock composition between 2010 and 2013. Furthermore, we find patterns across months with an increased proportion of eastern origin fish present in the fall months (September to October) as compared to early in the summer. This temporal trend could be indicative of spatial and temporal differences in habitat use in the Gulf of Maine by eastern and western origin fish. There were also apparent ontogenetic trends in stock composition, with the smallest size and age classes dominated by eastern origin fish and the largest composed predominantly of western origin fish. This pattern supports previous studies that have shown high rates of transoceanic migration of eastern origin fish at younger sizes (Rooker et al., 2008b; Dickhut et al., 2009). Changes in stock composition do not appear to be sex-specific, as there was no trend between sexes with near equal representation of eastern and western origin fish for males and females. Differences across grouping factors highlight the need to understand the details of where and when fish were collected and the demographic characteristic of the fish (e.g., length and age) to more accurately interpret and understand mixed stock composition information as these factors can influence the mixed stock composition in both subtle (e.g., month of capture) or significant ways (e.g., size based differences).

Another important finding of this study is the differences in stock composition results based on assignment method (individual and mixture analysis). We observed that while the overall trend between approaches was similar across grouping factors (i.e., time of capture, sex, size, and age classes), the absolute values differed (Fig. 3). In general, mixture analysis is expected to offer more accurate estimates of stock composition than summing individual assignments to determine the mixture proportions as uncertainty in the classification of individuals may lead to estimation bias (Manel et al., 2005). Furthermore, the approach of summing individual assignments ignores the uncertainty associated with each individual assignment. ICCAT has adopted an individual assignment approach in compiling a database of stock of origin information on bluefin tuna across the Atlantic as this offers an advantage when sharing assignment data and allows for individuals to be easily regrouped to address new questions (Anon., 2017). However, when integrating data in this manner, it is important to standardize the assignment methodology and model decisions, such as threshold values for assignment. Recognizing the influence of assignment method is critical to resolving similarities across studies and synthesizing data for a broader picture of mixed stock composition that can be applied in fisheries management.

Comparison of our results with previous results from U.S. and Canadian fisheries revealed some alignment and differences with other studies. Previous work by Siskey et al. (2016) indicated that ~95% of bluefin tuna in the Gulf of Maine in 2011 were of western origin. In contrast, our analysis using the same baseline and assignment method (mixture analysis based on CMLE) indicate that 24% ±19 % of fish were of eastern origin during the same year. These large differences may relate to subtleties in the spatial, temporal, or demographic scale of sampling between these two projects. Our results align with stock composition results from U.S. harvested Atlantic bluefin tuna sampled in 2015 and landed in Maryland and New York (Barnett et al., 2017). Stock contribution estimates for all 2015 samples combined indicated that the majority were eastern origin fish (72%). Similarly, Barnett et al. (2017) found decreased mixing with increasing size with an eastern contribution of 79%, 64%, 50%, and 37% respectively for school (69-117 cm CFL), large school (119-147 cm CFL), medium (150-203 cm CFL), and giant (≥206 cm CFL) size bluefin tuna. An increased presence of eastern origin fish has also been observed recently in Canadian fisheries, where the fishery had traditionally been composed of western origin fish nearly exclusively (Busawon et al., 2015) and has now shifted to be predominantly eastern origin fish (Hanke et al., 2017; Busawon *personal communication*).

Integration of mixed stock data into fisheries management

Understanding patterns in mixed stock composition can provide a means of monitoring and potentially managing fishing pressure at the population level, in addition to the stock level. The application of stock composition results to revise catch, catch-at-age, and CPUE time series can enable us to more closely track fishing pressure on western origin fish, as well as the age/size structure and relative abundance of this population. One of the most relevant findings to fisheries conservation and management from our study was the size-based differences in mixed stock composition. Increased representation and dominance of western origin fish in the largest size class provides an opportunity for more precise regulation of harvest of western origin fish based on size restrictions (e.g., slot limits) or size-based quotas for this component of the fishery.

Our stock composition information for the U.S. rod and reel fishery complements ongoing population assignment work for other fisheries in the eastern and western stock areas and contributes to ICCAT's aim of synthesizing this information to get a more comprehensive view of stock mixing across fisheries and areas (Anon., 2017). There is ongoing work to fit models to mixed stock composition based on otolith chemistry and genetics (Carruthers and Butterworth, 2019). A key challenge of this effort is the lack of historical data and that all bluefin tuna fisheries (e.g., longline, purse seine, bait boat) are not well sampled and characterized. If this type of population-level information were available across fisheries, it could be integrated into a stock assessment model to estimate population status (Kerr et al., 2017; Cadrin et al., 2018; Morse et al., 2018). Operational use of otolith chemistry to inform an assessment of bluefin tuna that includes stock mixing could transform the accuracy of bluefin tuna stock assessment and effectiveness of management (Kerr et al., 2017; Cadrin et al., 2018; Morse et al., 2018). More immediately, this information can be used outside of the stock assessment to monitor mixed stock composition of the fishery in near real time and to inform management decisions aimed at controlling population of origin harvest.

5. Conclusions

Application of otolith chemistry techniques to characterize the origin of bluefin tuna caught in the U.S. rod and reel fishery in the Gulf of Maine revealed the majority of fish caught from 2010 to 2013 originated from the Mediterranean Sea (eastern origin), not the Gulf of Mexico (western origin). While fish in small and intermediate size classes were primarily eastern origin, fish in the largest size class (>250 cm) were predominantly western origin. It is important to recognize the influence that alternative approaches to assignment (individual and mixture) can have on results. Such uncertainties should be taken into consideration in ongoing stock assessment and management strategy evaluation analysis. Integrating mixed stock composition information into fishery-specific harvest data (catch, catch-at-age, and catch-per-unit-effort) could be used to inform monitoring and management objectives for the fishery.

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Figure Captions

Fig 1. *Left panel:* Transverse section of bluefin tuna otolith. Solid lines represent the micromill drill path to be powered. Small dashed lines depict the targeted region of the otolith representing year one growth. *Right panel:* Stable isotope values ($\delta^{13}C$ and $\delta^{18}O$) of Atlantic bluefin tuna from the Gulf of Maine (gray circles) compared to eastern (n=150) and western (n=115) baseline samples based on yearling bluefin tuna (Rooker et al., 2014).

Fig. 2. Illustration of known spawning habitat (dark grey) of western and eastern origin Atlantic bluefin tuna and recently discovered slope sea spawning area (light gray). Note the region of capture of fish from the U.S. Rod and Reel fishery (hatched area) and the ICCAT management boundary (dashed horizontal line).

Fig. 3. Mixed stock composition of all Atlantic bluefin tuna sampled and stock composition by (a) year of capture (2010-2013), (b) month of capture, (c) size class (cm CFL), (d) sex, and (E) age class. Values shown are the proportion of eastern origin fish in the sample as estimated by two methods: conditional maximum likelihood (light gray; error bars indicate standard deviation) and by individual population assignment using a random forest approach (dark gray).

Fig. 4. Catch-per-unit-effort of Atlantic bluefin tuna from mixed stock (solid line) U.S. Rod and Reel fishery (size categories 66-114 cm [a], 115-144 cm [b], and >177 cm [c]) in the western Atlantic. Stock of origin is determined for two time periods (1996-2002 and 2010-2015) for which stock composition data exist for these fishery size categories (dashed lines).

Fig.5: Catch-at-age of bluefin tuna from mixed-stock U.S. rod and reel fishery in the Gulf of Maine (white circles) and of western origin Atlantic bluefin tuna (black circles). Stock of origin

is determined for two time periods (1996-2002 and 2010-2015) for which stock composition data exist for this fishery.

Fig. 6: Catch-at-age of bluefin tuna from mixed-stock U.S. rod and reel fishery size categories (size categories 66-114 cm [a], 115-144 cm [b], and >177 cm [c]) in the Gulf of Maine (white circles) and of western origin Atlantic bluefin tuna (black circles). Stock of origin is determined for two time periods (1996-2002 and 2010-2015) for which stock composition data exist for this fishery.

Tables

Table 1. Mixed stock composition of all Atlantic bluefin tuna sampled and stock composition by year of capture (2010-2013) and by month (June- Oct.) as estimated by two assignment methods (conditional maximum likelihood estimator [CMLE] and random forest). Values for CMLE shown are the mean and standard deviation (in parentheses) of the proportion of eastern and western origin fish in the sample.

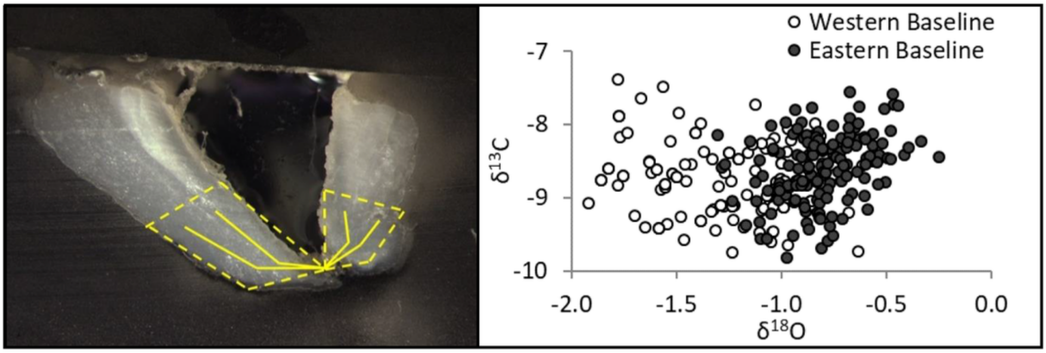
Time	Population	n	Conditional Maximum Likelihood	n	Random Forest (Prob. > 0.7)
All samples	East	782	0.85 (0.12)	491	0.67
	West		0.15 (0.12)		0.33
2010	East	221	0.89 (0.09)	146	0.73
	West		0.11 (0.09)		0.27
2011	East	255	0.76 (0.19)	134	0.61
	West		0.24 (0.19)		0.39
2012	East	149	0.93 (0.09)	101	0.73
	West		0.07 (0.09)		0.27
2013	East	157	0.82 (0.13)	110	0.63
	West		0.18 (0.13)		0.37
June	East	107	0.84 (0.14)	65	0.66
	West		0.16 (0.14)		0.34
July	East	166	0.73 (0.18)	101	0.57
	West		0.27 (0.18)		0.43
August	East	229	0.87 (0.11)	148	0.72
	West		0.13 (0.11)		0.28
September	East	205	0.90 (0.10)	135	0.71
	West		0.10 (0.10)		0.29
October	East	67	0.87 (0.14)	37	0.70
	West		0.13 (0.14)		0.30

Table 2. Mixed stock composition of all Atlantic bluefin tuna sampled and stock composition by size class (curve fork length, cm), age-class, and sex as estimated by two assignment methods (conditional maximum likelihood estimator [CMLE] and random forest). Values for CMLE shown are the mean and standard deviation (in parentheses) of the proportion of eastern and western origin fish in the sample.

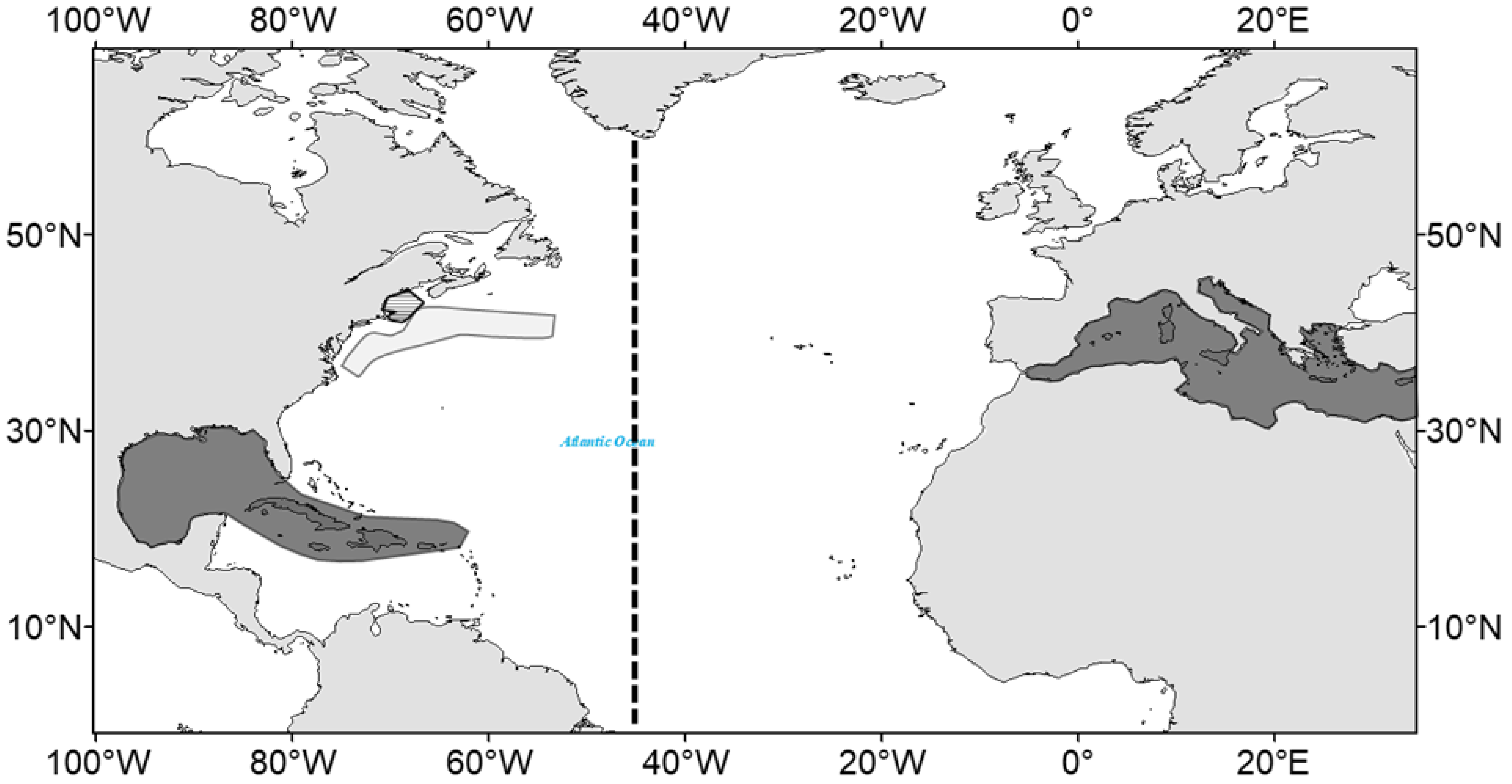
Size/Age/Sex	Origin	n	Conditional Maximum Likelihood	n	Random Forest (Prob. > 0.7)
< 150 cm	East	81	0.96 (0.06)	69	0.80
	West		0.04 (0.06)		0.20
150-199	East	233	0.86 (0.13)	143	0.66
	West		0.14 (0.13)		0.34
200-249	East	325	0.92 (0.10)	201	0.76
	West		0.08 (0.10)		0.24
>250 cm	East	143	0.52 (0.21)	78	0.37
	West		0.48 (0.21)		0.63
Age <4	East	27	0.94 (0.08)	23	0.83
	West		0.06 (0.08)		0.17
Age 4-6	East	85	0.97 (0.05)	74	0.82
	West		0.03 (0.05)		0.18
Age 7-9	East	321	0.85 (0.13)	191	0.65
	West		0.15 (0.13)		0.35
Age 10-12	East	207	0.94 (0.09)	125	0.78
	West		0.06 (0.09)		0.22
Age 13-15	East	51	0.58 (0.21)	32	0.44
	West		0.42 (0.21)		0.56
Age 16-18	East	46	0.29 (0.23)	22	0.27
	West		0.71 (0.23)		0.73
Age ≥19	East	45	0.51 (0.22)	24	0.38
	West		0.49 (0.22)		0.63
Female	East	175	0.90 (0.12)	115	0.69
	West		0.10 (0.12)		0.31
Male	East	304	0.84 (0.13)	191	0.65
	West		0.16 (0.13)		0.35

Table 3. Estimates of stock composition for the U.S. Rod and Reel fishery across size categories applied to revise fishery dependent data (US rod and reel: 66-114 cm, 115-144 cm, and >177 cm, ICCAT 2018), including catch per unit effort, catch at age, and partial catch at age. Note, representative size class information was not available from the 1990s for US Rod and Reel 115-144 cm category .

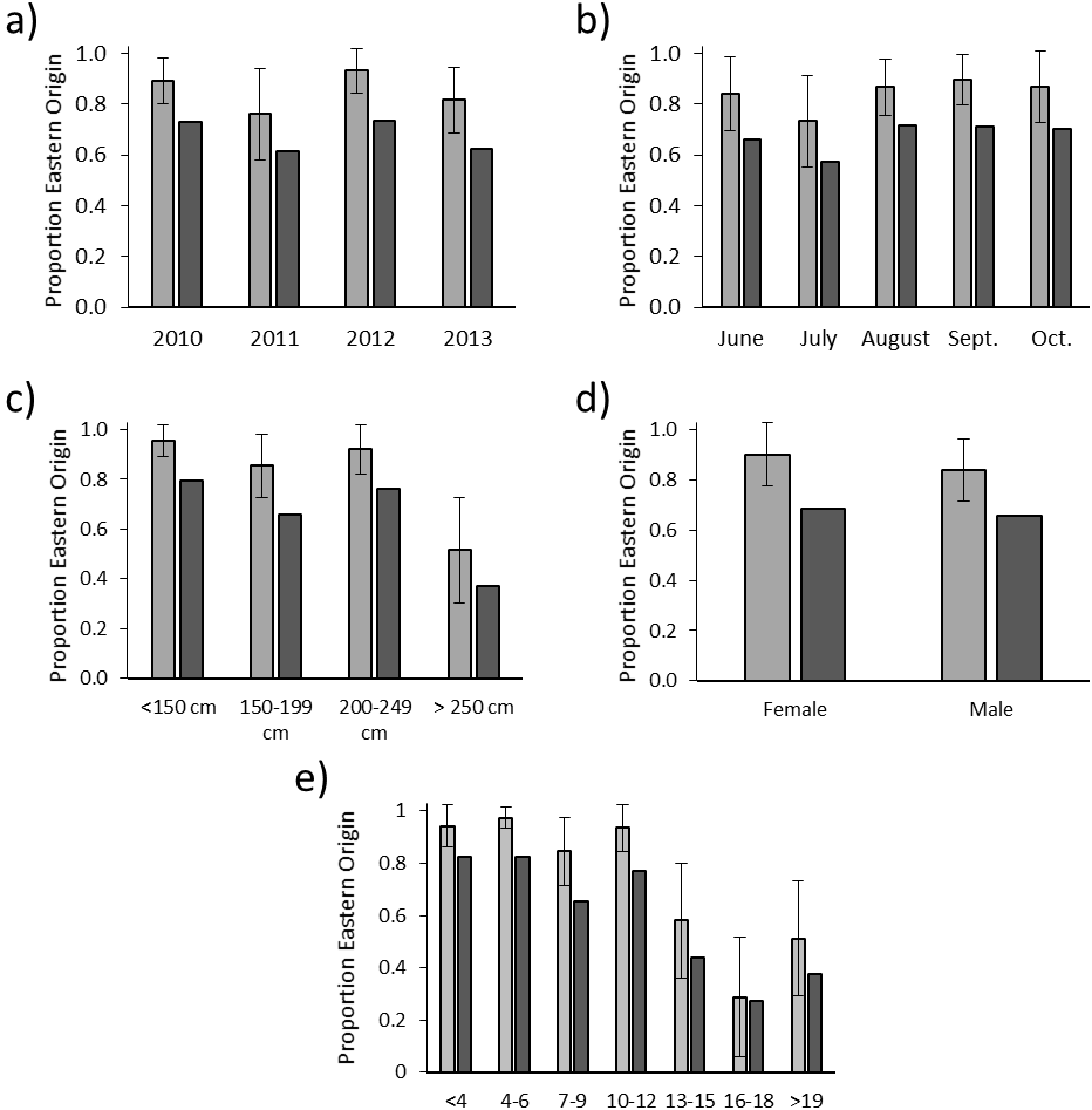
Size Category	Time Frame	N	Proportion Western	Proportion Eastern	Source
US RR 66-114 cm	2010-2013	24	0.21	0.79	This study
	1996-2002	24	0.21	0.79	Siskey et al., 2016
US RR 115-144 cm	2010-2013	41	0.22	0.78	This study
	1996-2002	NA	NA	NA	NA
US RR >177 cm	2010-2013	412	0.35	0.65	This study
	1996-2002	52	0.54	0.46	Siskey et al., 2016

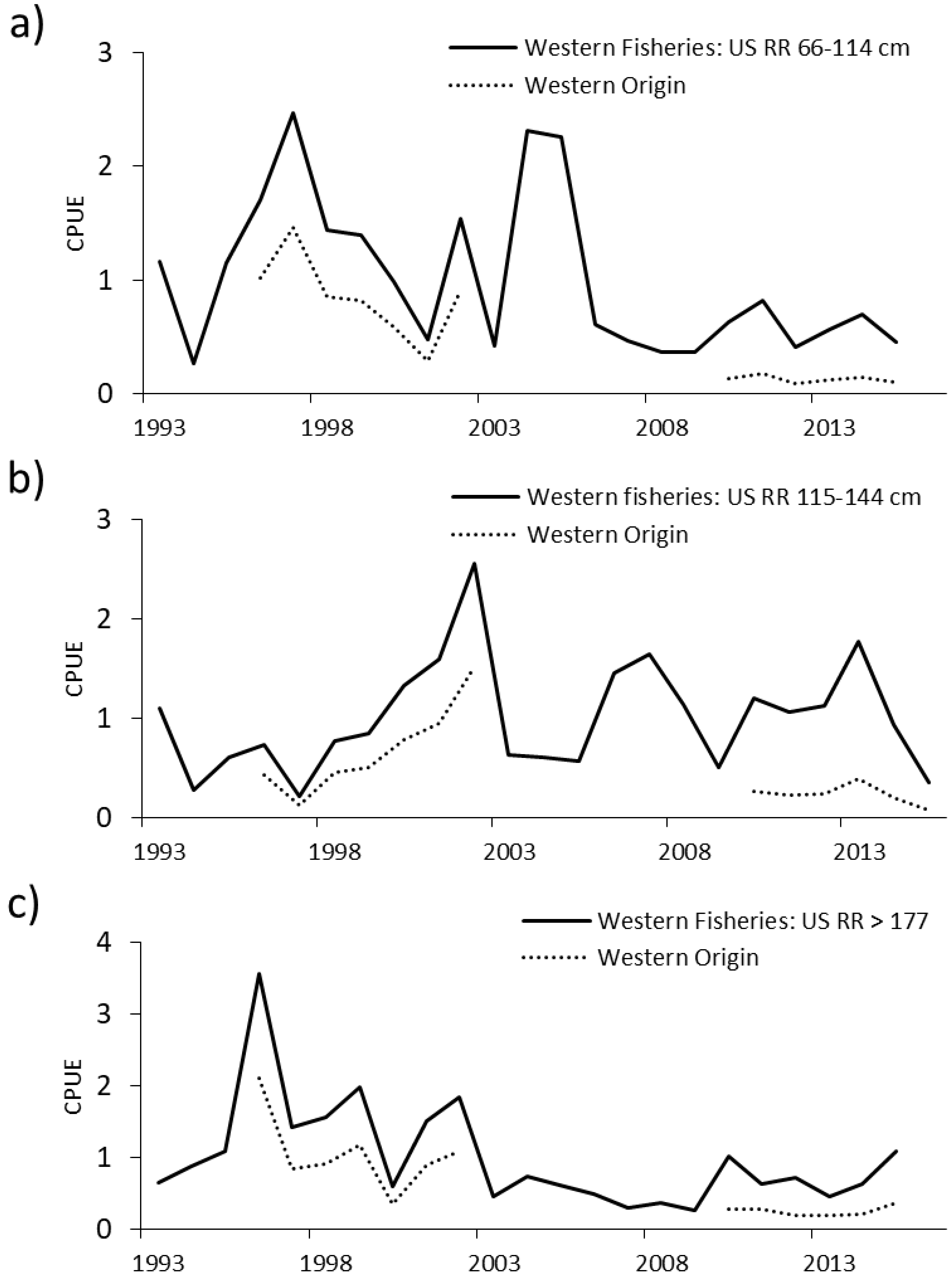


Western Baseline
Eastern Baseline
-7
-8
-9
-10
δ13C
-2.0
-1.5
-1.0
-0.5
0.0
δ18O

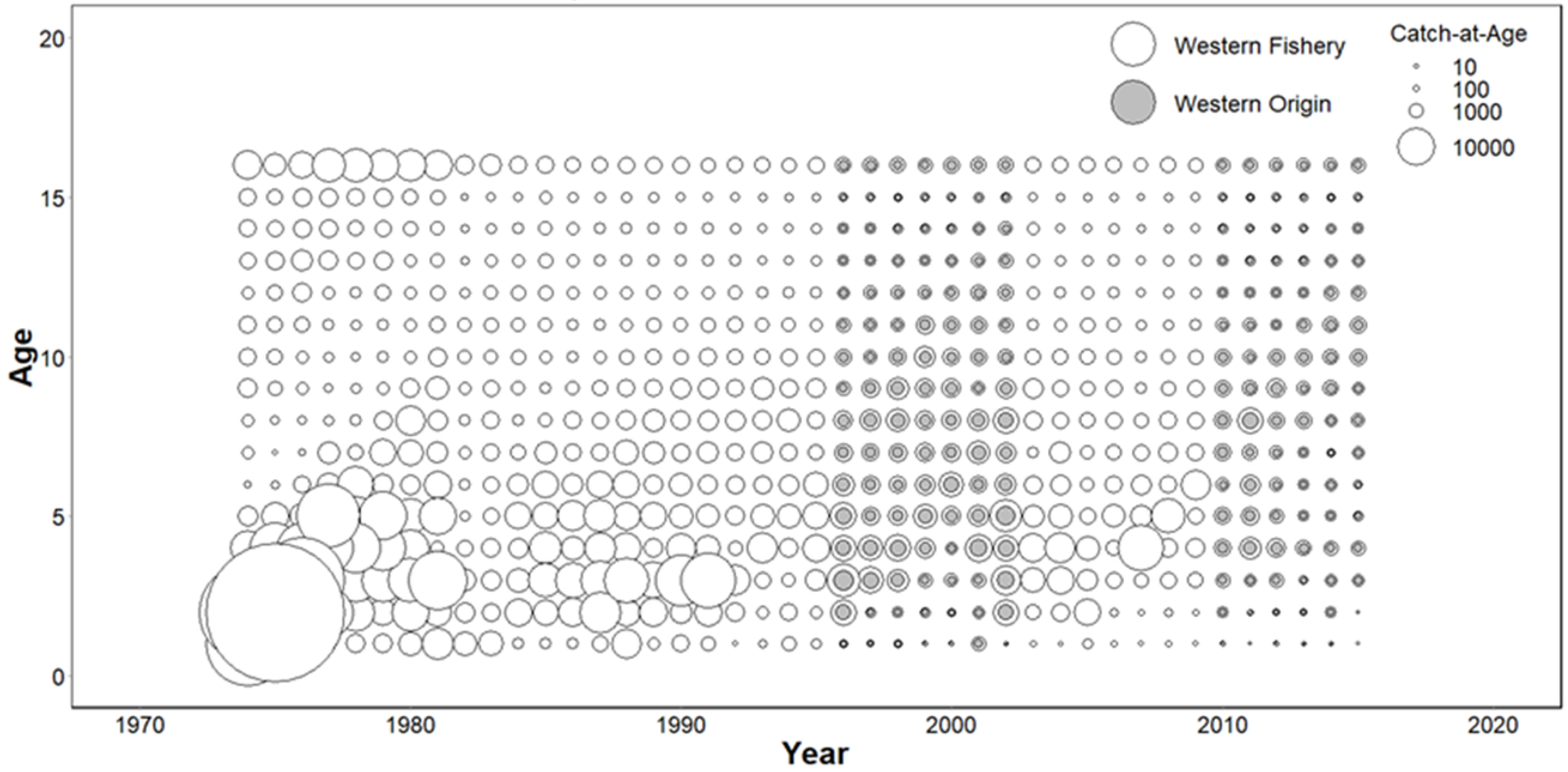


100°W
80°W
60°W
40°W
20°W
0°
20°E
50°N
30°N
10°N
Atlantic Ocean

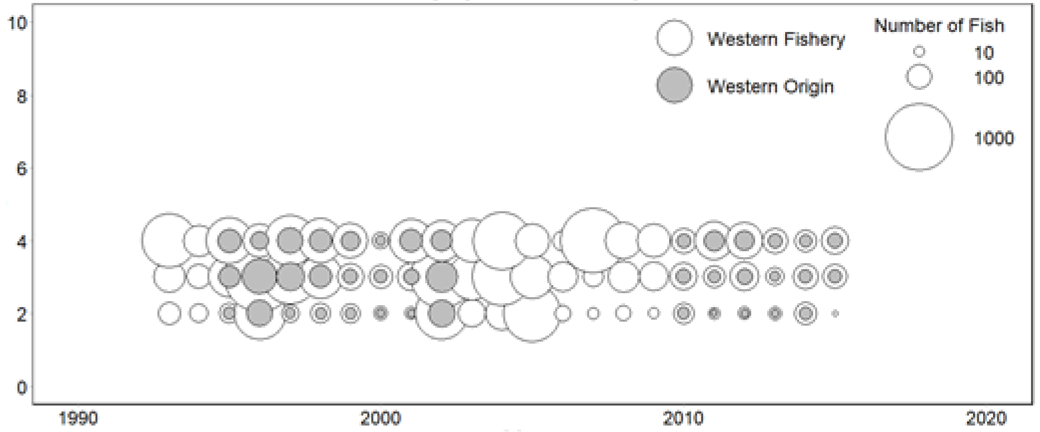

a)
Proportion Eastern Origin
1.0
0.8
0.6
0.4
0.2
0.0
2010
2011
2012
2013
b)
Proportion Eastern Origin
1.0
0.8
0.6
0.4
0.2
0.0
June
July
August
Sept.
Oct.
c)
Proportion Eastern Origin
1.0
0.8
0.6
0.4
0.2
0.0
<150 cm
150-199 cm
200-249 cm
> 250 cm
d)
Proportion Eastern Origin
1.0
0.8
0.6
0.4
0.2
0.0
Female
Male
e)
Proportion Eastern Origin
1
0.8
0.6
0.4
0.2
0
<4
4-6
7-9
10-12
13-15
16-18
>19


a)
Western Fisheries: US RR 66-114 cm
Western Origin
CPUE
b)
Western fisheries: US RR 115-144 cm
Western Origin
CPUE
c)
Western Fisheries: US RR > 177
Western Origin
CPUE
1993
1998
2003
2008
2013

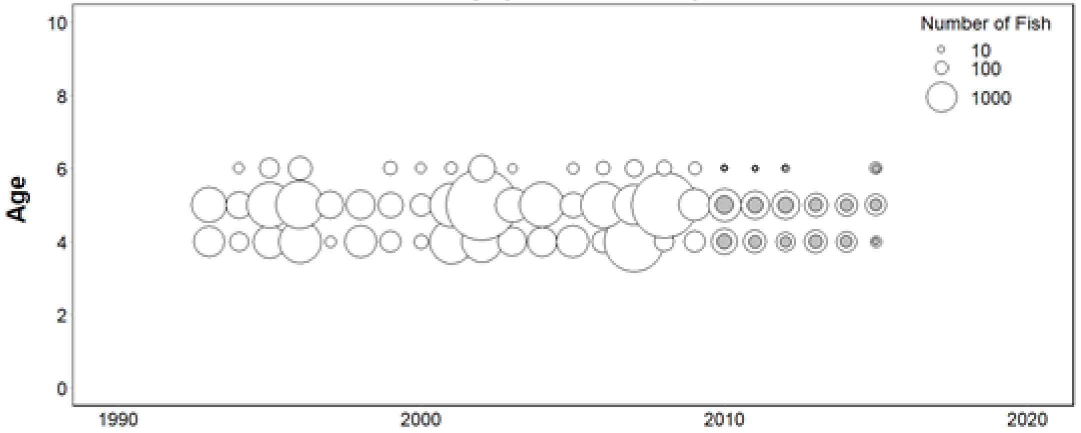
U.S. Rod and Reel Fishery



U.S. Rod and Reel Fishery (66-114 cm)



U.S. Rod and Reel Fishery (115-144 cm)



U.S. Rod and Reel Fishery (>177 cm)