



Depressed resilience of bluefin tuna in the western atlantic and age truncation

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Abstract: *Following intense overfishing in the 1970s, the western stock of Atlantic bluefin tuna (Thunnus thynnus) experienced a long period of depressed abundance, which has been attributed to failure of the population to periodically produce large numbers of juveniles, the western stock mixing with the more highly exploited eastern stock (fisheries in the Northeast Atlantic Ocean and Mediterranean Sea), and regime shift in the population's ecosystem resulting in lower replacement rates. To evaluate the presence of relatively strong years of juvenile production, we analyzed age structure from a recent sample of otoliths (ear stones) collected from the western stock (2011–2013, North Carolina, U.S.A., winter fishery). Mixing levels for the recent sample were analyzed using otolith stable isotopes to test whether age structure might be biased through immigration of eastern stock bluefin tuna. Age structure from historical samples collected from United States and Canadian fisheries (1975–1981) was compared with more recent samples (1996–2007) to examine whether demographic changes had occurred to the western stock that might have disrupted juvenile production. Relatively high juvenile production occurred in 2003, 2005, and 2006. Otolith stable isotope analysis showed that these recruitments were mostly of western stock origin. However, these high recruitments were >2-fold less than historical recruitment. We found substantial age truncation in the sampled fisheries. Half the historical sample was >20 years old (mean age = 20.1 [SD 3.7]; skewness = -0.3), whereas <5% of the recent sample was >20 years old (mean age = 13.4 [SD 3.8]; skewness = 1.3). Loss of age structure is consistent with changes in fishing selectivity and trends in the stock assessment used for management. We propose that fishing, as a forcing variable, brought about a threshold shift in the western stock toward lower biomass and production, a shift that emulates the regime shift hypothesis. An abbreviated reproductive life span compromised resilience by reducing the period over which adults spawn and thereby curtailing the stock's ability to sample year-to-year variability in conditions that favor offspring survival (i.e., storage effect). Because recruitment dynamics by the western stock exhibit threshold dynamics, returning it to a higher production state will entail greater reductions in exploitation rates.*

Keywords: connectivity, fisheries, migratory populations, otolith chemistry, regime shift, storage effect

Disminución en la Resiliencia del Atún de Aleta Azul en el Atlántico Occidental y Truncamiento de Edades

Resumen: *Después de una sobrepesca intensiva en la década de 1970, la población de atún de aleta azul del Atlántico (Thunnus thynnus) pasó por un largo periodo de abundancia disminuida, la cual se ha atribuido a la falla de la población por producir periódicamente un mayor número de juveniles, a la mezcla entre la población occidental con la oriental que es más explotada por las pesqueras del Atlántico Noreste y el mar Mediterráneo, y a un cambio de régimen en el ecosistema de la población, lo que resultó en tasas de recambio más bajas. Para evaluar la presencia de años relativamente fuertes de producción juvenil, analizamos la estructura de edades de una muestra reciente de otolitos (piedras del oído) recolectada de la población occidental (2001–2013, Carolina del Norte, E.U.A., pesquera de invierno). Los niveles de mezcla para la muestra reciente fueron analizados utilizando isotopos estables de otolitos para probar si la estructura de edades puede ser tendenciosa por medio de la inmigración de atunes de la población oriental. La estructura*

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de edades de las muestras históricas recolectadas de las pesqueras de Estados Unidos y Canadá (1975-1981) se comparó con las muestras más recientes (1996-2007) para examinar si los cambios demográficos que le ocurrieron a la población occidental pudieron haber perturbado la producción juvenil. Una producción de juveniles relativamente alta ocurrió en 2003, 2005 y 2006. El análisis de isótopos estables de otolitos mostró que estos reclutamientos en su mayoría fueron de origen de la población occidental. Sin embargo, estos reclutamientos fueron >2 veces menos que el reclutamiento histórico. Encontramos un truncamiento sustancial de edades en las pesqueras muestreadas. La mitad de la muestra histórica fue >20 años (edad promedio=20.1 [SD 3.8]; desviación=-0.3), mientras que <5% de la muestra reciente fue >20 años (edad promedio=13.4 [SD 3.8]; desviación=1.3). La pérdida de la estructura de edad es consistente con cambios en la selectividad de pesca y tendencias en la evaluación de la población usadas para el manejo. Proponemos que la pesca, como una variable de fuerza, trago consigo un cambio de umbral en la población occidental hacia una biomasa y una producción más baja, un cambio que emula la hipótesis de cambio de régimen. Una historia de vida reproductiva abreviada puso en peligro la resiliencia al reducir el periodo en el cual los adultos desovan y acortando la habilidad de la población para muestrear la variabilidad de año con año en condiciones que favorecen la supervivencia de las crías (p. ej.: efecto de almacén). Ya que las dinámicas de reclutamiento de la población occidental exhiben dinámicas de umbrales, regresar la población a un estado de mayor producción implicará reducciones mayores en las tasas de explotación.

Palabras Clave: cambio de régimen, conectividad, efecto de almacenamiento, pesqueras, poblaciones migratorias, química de otolitos

Introduction

The near exclusive focus in traditional fisheries management on yield in stationary ecosystems has attracted increased scrutiny. Marine fish populations are influenced in nonlinear ways by fishing, climate, and other forcing variables that are mediated by demographic structuring (Beisner et al. 2003; Petitgas et al. 2010; Hidalgo et al. 2011). Depensation at low population size has been associated with increased aggregation and susceptibility to fishing and other local stresses (Hutchings 1996). Colonization of new food webs can precipitate positive feedbacks resulting in population irruptions, particularly apparent in schooling fishes such as sardines, which show periodic spikes in abundance and large increases in spatial ranges (Bakun & Cury 1999). Other demographic attributes, such as age and population structure can dissipate the influence of forcing variables (Frank & Brickman 2001; Fromentin et al. 2014).

We evaluated the role of demographic structuring in resilience of the western stock of Atlantic bluefin tuna (*Thunnus thynnus*), a population that principally originates in the Gulf of Mexico. Atlantic bluefin tuna are exceptionally large teleost fish with moderate longevity (>30 years), high fecundity (>10⁷), and relatively late maturation (western stock mean age of maturity approximately 10 years) (Rooker et al. 2007). Bluefin tuna fisheries in the Northwest Atlantic developed in the 1960s and targeted small juveniles caught in purse seines for use in canned pet food. In the 1970s, the fishery shifted to large adults captured by long-line gear for the Japanese sashimi market (Mather et al. 1995). Estimated juvenile production was high during the 1960s and early 1970s, but then the population plummeted. Three- and 5-fold declines occurred in adult and juvenile abundances (Fig. 1;

SCRS 2012). Stringent harvest controls were applied in the early 1980s through the actions of the International Commission for the Conservation of Atlantic Tunas (ICCAT). Despite these measures, the western stock has persisted at low abundances since 1981 (Fig. 1).

Following imposition of harvest reductions, there were high expectations for recovery of the western stock through the production of strong year classes (i.e., years of elevated juvenile production). Lack of subsequent recovery caused some to believe that harvest regulations were insufficiently stringent—that bluefin tuna had life history characteristics that made them vulnerable to over-exploitation (Safina & Klinger 2008; CITES 2010). Another view held that the western stock was mixing with the eastern stock, a population that originates in the Mediterranean Sea, in a manner that hindered its recovery. Higher exploitation rates in the Mediterranean and Northeast Atlantic could curtail recovery of the western stock depending on the level of connectivity between the 2 stocks (NRC 1994). After a sustained period of poor recruitment, a third proposition emerged that a shift in the late 1970s (i.e., regime shift) had occurred that curtailed recovery to historical levels. Debates on this view led ICCAT to require assessments and management reference points that relied on 2 separate premises—a high recruitment scenario (1 regime model) and a low recruitment scenario (2 regime model) (SCRS 2012). Under the 1 regime model the western stock is overfished and much more stringent harvest controls are required, but under the 2 regime model, the western stock is not overfished. Some argue that the 2 regime premise is a contrivance to maintain status quo. However, the very sharp decline of the western stock emulates a critical transition between alternative regimes (Fig. 1). On the basis of ICCAT stock assessments alone, either model is

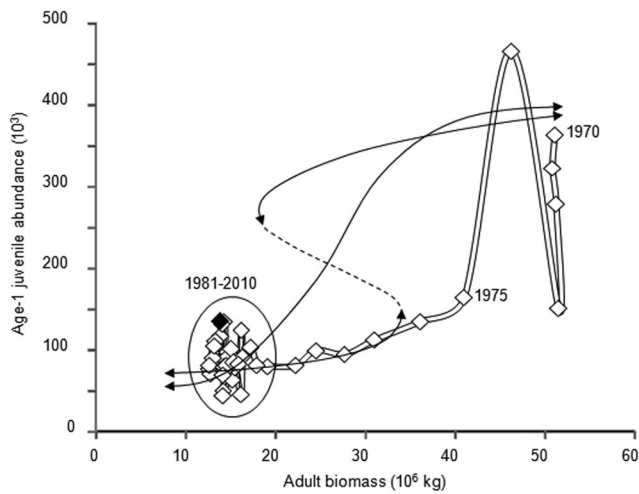


Figure 1. Juvenile production and adult biomass for western stock Atlantic bluefin tuna, 1970–2010. Two hypothetical curves showing smooth and discontinuous transitions between population states are shown (SCRS 2012) (solid diamond, 2003 year-class).

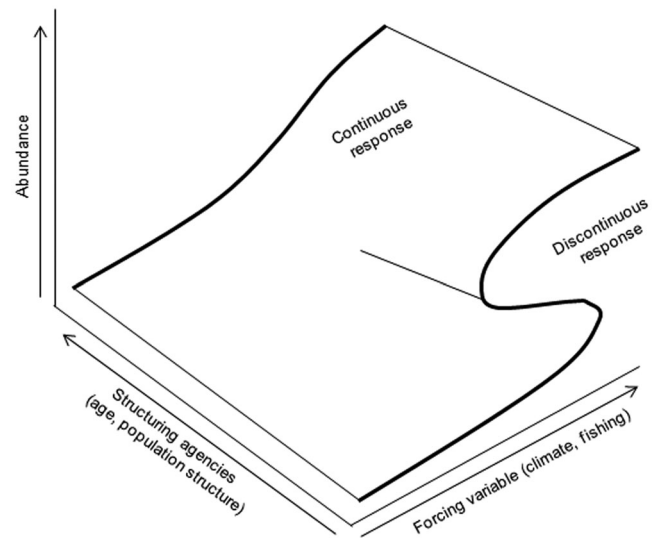


Figure 2. Convergence from a discontinuous population state to a continuous one through the action of structuring variables (Collie et al. 2004; Secor 2015).

feasible. In the broader context, the decline of Atlantic bluefin tuna mirrors that of other large pelagic fishes (Myers & Worm 2003), which directs caution against shifting baseline expectations (Pauly 1995) for how such populations should perform.

Fishing influences stability and resilience of populations by truncating age structure either by selecting larger fish because they are more valuable or accessible or by increasing overall mortality in the population (Law 2000; Planque et al. 2010). Age structure builds response diversity and cross-scale resilience in populations, which contributes to stability and persistence (Elmqvist et al. 2003) (Fig. 2). The storage effect (Warner & Chesson 1985)—defined by repeated spawning and placement of young into varying conditions over a long reproductive life span—is an example of response diversity. Offspring survival and recruitment vary each year, but by spawning across many years a population buffers against this variability on a generational basis (Longhurst 2002; Secor 2007). Cross-scale stability occurs when reproductive behaviors or attributes change over a fish's life, such as when older females spawn earlier or produce larger offspring than smaller females (e.g., Hutchings & Myers 1993; Rijnsdorp 1994; Berkeley et al. 2004). Age-specific spawning times, egg attributes, or other maternal effects need not confer consistent survival advantages to offspring (e.g., Marshall et al. 2010); rather, they lead to a range of outcomes over a generation (Warner & Chesson 1985).

To evaluate the set of stock status premises for the western stock of bluefin tuna—recruitment failure, stock mixing, and regime shift—we conducted an assessment

of age structure and mixing for a moderately strong year of juvenile production: 2003 (Fig. 1). This year class appeared initially in U.S. recreational fisheries targeting juveniles (curved fork length [CFL] < 183 cm; approximately <9 years old) and was detected in the ICCAT assessment (SCRS 2012), suggesting that strong recruitments might still occur. Still, these U.S. fisheries catch fish from both western and eastern stocks (Block et al. 2005; Rooker et al. 2008; Dickhut et al. 2009), so mixing might have biased detection of a strong year class.

We analyzed otoliths (ear stones) of bluefin tuna to document the presence of strong year classes (2003 and others) in recent U.S. fisheries, determine whether mixing biased the detection of strong year classes, and contrast recent and historical age structure with those predicted by the ICCAT stock assessment in U.S. and Canadian samples of adults. For Atlantic bluefin tuna, interpretation of age through direct counts of otolith annuli (rings) has been verified through bomb radiocarbon dating analysis (Neilson & Campana 2008). Additionally, stable isotope tracers $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ within the otoliths of Atlantic bluefin tuna predict natal source with 85% confidence and are currently being used to evaluate population mixing levels throughout the species range (Rooker et al. 2008; Schloesser et al. 2010).

Methods

Year-Class Detection and Mixing

Otoliths (sagittae) were sampled during January–April 2011–2013 from over 30% of all fish landed in North

Carolina (U.S.A.) ($N = 321$). Twelve fish were also sampled at Virginia Beach in 2012. To compare stock mixing levels for this sample with those observed approximately 10 years ago, a subset of the data reported by Rooker et al. (2008) was included. This subset was collected as part of the Large Pelagic Biological Survey for the National Marine Fisheries Service (1996–2002) from U.S. mid-Atlantic (including North Carolina) and New England fisheries. Two size ranges, 100–200 cm and 140–200 CFL, were selected to allow comparison of the Rooker et al. sample with the entire North Carolina sample and with larger members of the North Carolina sample that corresponded to the 2003 year class.

For the analysis of stock mixing levels, classification to source populations was performed by a maximum likelihood estimation method (HISEA; Millar 1990). This procedure fits the mixture distribution; it maximizes the likelihood function to the source population distributions and possible mixing proportions in the unknown sample. Source population data were derived from samples of 265 age-1 juveniles collected in the U.S. Mid-Atlantic and Mediterranean in 1998–2011 (Rooker et al. 2014). The Mediterranean is a more evaporative basin than U.S. shelf waters, which causes otolith $\delta^{18}\text{O}$ to be higher in juveniles from the Mediterranean than those from U.S. shelf waters (Rooker et al. 2008).

For the unknown sample, otolith material containing the natal chemistry (i.e., that deposited during the first year of life) was isolated. A single otolith was embedded in plastic resin and a 2.0-mm-thick section was cut from its center, which contained the juvenile and surrounding portions of the otolith (see Schloesser et al. [2010] for details on otolith processing). The juvenile portion of the otolith was then milled into a powder with a New Wave Micromill. Powdered carbonate samples were analyzed for $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ at the University of Arizona Environmental Isotope Laboratory.

Ages for the same unknown sample described above were estimated through interpretation of annuli. Following micromilling, otolith section thickness was reduced to permit visualization of annuli for age determination. To account for timing of annulus formation, 1 year was added to estimated year of birth (collection year minus adjusted age). Precision of age determination with this method was 6%, or <1 year for most individuals (Secor et al. 2014).

Historical Age Structure Comparisons

Demographic comparisons were made for adult bluefin tuna (age >8 years) obtained from U.S. and Canadian government-sponsored sampling programs conducted from 1975 to 1981 ($n = 156$) and 1996 to 2007 ($n = 135$). Otoliths from commercially harvested adults (180–319 cm CFL) were collected from summer-fall feeding aggregations in the Gulf of St. Lawrence, Sco-

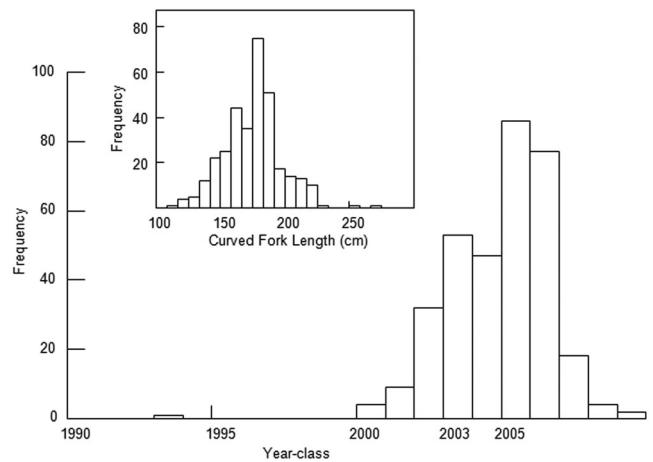


Figure 3. Year-class frequency distribution estimated from direct age estimates in the North Carolina bluefin tuna recreational fishery. Inset shows the related size frequency.

tian Shelf, and Gulf of Maine. Spawners from the Gulf of Mexico were obtained from Tag a Giant Program ($N = 13$) (Rooker et al. 2008) or from the U.S. National Marine Fisheries Service ($N = 27$) (Secor et al. 2013). Previous analysis of these sets of otoliths indicated that >95% of these adult samples were drawn from the western stock (Rooker et al. 2008; Schloesser et al. 2010; Secor et al. 2013). Historical demographic and fishing selectivity estimates were compiled from the 2012 Virtual Population Assessment (VPA) on the western stock conducted for ICCAT (SCRS 2012).

Results

The North Carolina sample ranged from 4 to 18 years old, and its frequency distribution exhibited modes attributable to 2003, 2005, and 2006 year-classes (Fig. 3). According to age estimates, the 2003 year-class was well represented in the sample ($N = 53$, 16% of total sample) and was estimated to be almost exclusively of western origin (95.9% [SD 4.1]; Table 1). The western contribution for the entire NC sample was 76.0% (SD 4.1). For strong year-classes produced in 2005 and 2006 the western contribution was 65.9% (SD 6.2). The 2003 year-class had lower $\delta^{18}\text{O}$ values (MANOVA, $P = 0.01$, $N = 333$), suggesting a stronger western contribution relative to other cohorts (Supporting Information). The historical sample collected for the size range 100–200 cm CFL had a fairly even split between eastern and western stock individuals, but when the subset of larger fish was examined (140–200 cm CFL), the large majority of these were estimated to originate from the western stock (Table 1).

Adult age structure significantly differed between the 1975–1981 and 1996–2007 periods (Fig. 4). Mean age

Table 1. Population mixing levels in Atlantic bluefin tuna sampled in North Carolina and Virginia Beach January–April 2011–2013 and in a historical sample (1996–2002) (Rooker et al. 2008).

Year class	Years sampled (CFL ^a) (cm [SD])	Location	n	Population ^b	MLE% ^c	MLE SD ^d
2003	2011–2013 (189.6 [19.4])	Virginia and North Carolina	53	west east	95.9 4.1	4.1
2005 and 2006	2011–2013 (167.3 [16.2])	Virginia and North Carolina	163	west east	65.9 34.1	6.2
1993–2009	2011–2013 (174.7 [22.0])	Virginia and North Carolina	333	west east	76.0 24.0	4.1
1988–1997	1996–2002 (143.8 [31.2])	Mid-Atlantic, New England	110	west east	56.2 44.8	6.5
1988–1994	1996–2002 (175.1 [15.9])	Mid-Atlantic, New England	60	west east	98.6 1.4	3.1

^aCurved fork length (CFL).

^bPopulation references west (Gulf of Mexico or U.S. Atlantic Ocean nursery system) or east (Mediterranean Sea nursery system).

^cMaximum likelihood estimate of mixing level.

^dStandard deviation of mixing level.

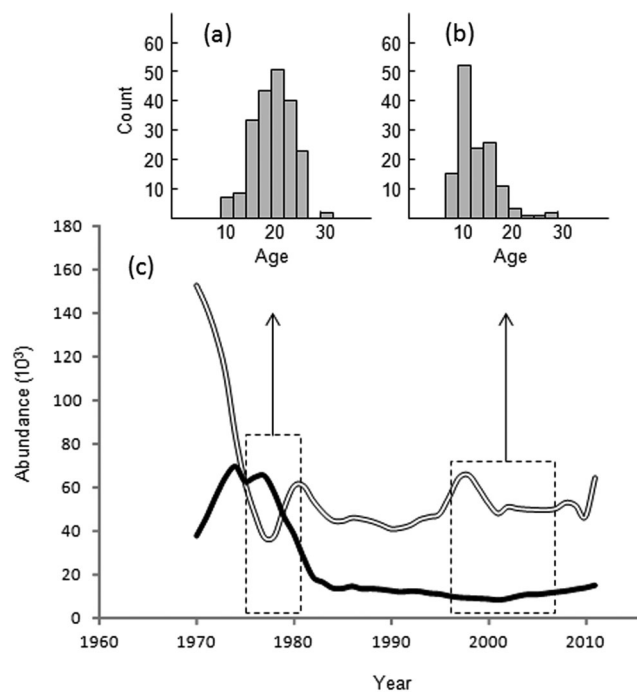


Figure 4. Direct age estimates of western stock adult Atlantic bluefin tuna for (a) 1975–1981 and (b) 1996–2007. (c) Age-class information (recruit and older spawners) over the entire series from the official international assessment (SCRS 2012) (open line, recruit spawners [9–12 years]; solid line, older spawners [>15 years]; dashed boxes, sampling periods for direct ages). Ages are from Secor et al. (2008).

declined by 33% from 20.1 years (SD 3.7) to 13.4 years (SD 3.8). Mean CFL declined less during this interval (14%), from 271.9 cm (SD 14.4) to 232.8 cm (SD 25.1). Adjusting for the influence of CFL on age, the decline in mean age was significant (analysis of covariance on log-transformed ages: $df = 251$; $P = 0.001$). Arithmetic

means were not fully representative of age structure; the more recent distribution was highly skewed to the right and toward younger age classes (skewness = 1.3, SD 0.2) relative to the more normally distributed historical sample (skewness = -0.3 , SD 0.2). Thus, about half of the historical sample was over 20 years, while $<5\%$ was over 20 years in the more recent period (Supporting Information).

The VPA employed to assess the western stock relies on ages derived from length data and an accepted growth model (Restrepo et al. 2010), meaning that historical changes in age structure for the oldest stock component cannot be followed accurately. Still, large changes were apparent for the oldest estimated cohort, those >15 years old (Fig. 4). During 1975–1985, this cohort diminished 4.5-fold, while the cohort of young adults (9–12 years) remained fairly stable. Very high abundances of young adults in the early 1970s detected by the VPA (SCRS 2012) did not translate into strong cohorts of older adults in the 1980s. Fishing selectivity showed patterns similar to age structure (Supporting Information); fishing rates for juveniles were extremely high (represented by age 2) early in the 1970s ($>45\%$ removal/year; $F_2 > 0.6$) but low during the past 2 assessed decades (mean removal = 5%/year; $F_2 = 0.05$, SD 0.05). Fishing removal rates increased for the older age classes (represented by age 14) from 3%/year in 1970 to a maximum of 24%/year in 1981. After 1981, mean removal rate for this group was 13%/year ($F_{14} = 0.14$, SD 0.04).

Discussion

Our retrospective analysis supports the view that fishing brought about a threshold shift in the western stock of Atlantic bluefin tuna toward lower biomass and production. Whether the shift was continuous or discontinuous remains unknown (Fig. 1), but nonlinear dynamics seem likely given the long-term persistence of a low abundance

state and likely compromised resilience in this population associated with age truncation and a reduced storage effect. Although a moderately strong 2003 year-class was detected through direct age estimates and supported by stock composition analysis, the VPA indicated that this year-class was similar in abundance to others during the recent 1981–2010 period of depressed recruitment (Fig. 1) (SCRS 2012). Thus, it seems unlikely that the 2003 year-class or similarly strong year-classes such as those detected for 2005 and 2006 are sufficient in size to restore the stock to historical (pre-1975) levels.

An alternate explanation for depressed abundances of the western stock is source–sink dynamics associated with juvenile emigration to Northeast Atlantic and Mediterranean fisheries. Moderate mixing levels of eastern stock juveniles in Northwest Atlantic fisheries (Table 1) suggest that the converse is likely—that juvenile western stock bluefin tuna migrate into Northeast Atlantic and Mediterranean fisheries where they encounter higher exploitation rates. For 1982–2008, juveniles aged 2–5 were estimated to experience about 2-fold higher exploitation rates in these fisheries than in U.S. fisheries (SCRS 2012). However, otolith stock composition indicates that very few western stock individuals (<3%) contribute to Northeast Atlantic and Mediterranean fisheries (Rooker et al. 2014). This low recapture is largely the outcome of differential production between the stocks: the eastern stock is approximately 10-fold more productive than the western stock (SCRS 2012). Conventional tags and electronic tags demonstrate transoceanic migrations occur at moderate frequency (>10%) (Block et al. 2005; Rooker et al. 2007). At these frequencies, harvests in the Northeast Atlantic and Mediterranean are likely depressing recovery of the western stock (NRC 1994). Resolving how mixing compromises western stock resilience is complex and will require assessment frameworks that integrate movement and mortality estimates with stock status for the 2 principal stocks (Taylor et al. 2011; Kerr & Goethel 2013).

Age truncation and increased skewness associated with depressed abundance in the western stock are consistent with shifts in selectivity patterns by the fishery. Intense purse-seine fisheries for small juveniles (1–3 years old) developed in the late 1960s and later targeted strong year classes produced in the 1970s (Mather et al. 1995). Subsequently, the emergence of long-line fisheries for sashimi-grade tuna (large adults) in the late 1970s led to further exploitation of these year-classes along with the accumulated biomass of very old individuals (>20 years). Without this new fishery on large bluefin tuna, strong year-classes from the 1970s would have likely recruited into the adult population. The VPA detected a sharp rise in fishing mortality for fish >12 years after 1975; mortality peaked in 1981 when removal rates were 27%/year for the oldest age classes (>14 years old; SCRS 2012). Thus, the combination of the purse-seine and long-line fisheries

brought about a demographic shift in the population's age structure and productivity. Although the average reproductive life time of the western stock historically spanned over a decade, the current population is largely composed of first-time spawners. More recently (2010–2012), otolith-based ageing has detected very few adult bluefin tuna >20 years old, consistent with results from the 1996 to 2007 period (Secor et al. 2014).

Age truncation in Atlantic bluefin tuna compromises resilience owing to a diminished storage effect. Large size and experience are expected to improve survival prospects for old bluefin tuna, resulting in a resilient cohort of iteroparous spawners. Accumulation of spawning stock biomass in older age-classes would increase the capacity to produce strong year-classes when environmental conditions favor them. Northern cod (*Gadus morhua*) off Labrador and Chesapeake Bay striped bass (*Morone saxatilis*) provide important case studies on the role of age structure on changed population states (Secor 2015). Atlantic cod and striped bass live >20 years, are highly fecund, mature relatively late (in approximately 6–8 years for females), and spawn frequently throughout their reproductive life-span (Hutchings & Myers 1993; Secor 2000). Both stocks experienced a period of intense overfishing that led to fishing moratoria to promote their recovery. Northern cod populations have not recovered, but in less than a decade striped bass recovered to an abundance that exceeded pre-collapse levels. Historical fishery preferences for striped bass and their age-specific migration behaviors caused older age classes to be lightly exploited relative to younger ones. For the Northern cod stock, age structure was severely truncated through overfishing, resulting in aggregations that were nearly exclusively composed of first-time spawners (Myers et al. 1996). Wholesale loss of age structure may have also contributed to lost spawning and migration behaviors (Hutchings & Myers 1993; Rose 1993). Truncated generational age structure thus preconditioned the cod stock for collapse and arguably shifted the stock to a different production state, where it persists today despite efforts to rebuild biomass, age structure, and spatial structure. In contrast, conserved age structure in striped bass led to its high resilience when fishing was relaxed (Fig. 2).

In our study, changes in fishing selectivity patterns likely biased the samples available for age structure representations. However, since about 1984, large adults in U.S. and Canadian fisheries have experienced the highest levels of fishing selection (SCRS 2012), which supports the view that the oldest age classes were similarly targeted over both sampling periods. Continued effort should be devoted to making adjustments to age structure that account for fishing selectivity, but here we argue that the inference of age truncation would be robust regardless of selectivity patterns.

Over longer periods, the western stock likely experiences cyclic changes in its abundance. For the

eastern stock of Atlantic bluefin tuna, there is strong evidence for 20-year cycles from historical (AD 1600–1960) Mediterranean harvest data (Ravier & Fromentin 2001). These oscillations suggest climate effects, yet a careful examination showed that age structure acted to regulate these rhythms in population states. Termed age resonance (Bjørnstad et al. 2004), strong and weak year-classes (stochastic recruitments) are reflected onto the population over generations and cause oscillations that emulate regime shifts but do not directly correspond to changes in climate, exploitation, or other forcing variables. Density-dependent regulation (e.g., cannibalism) at high abundance states was a suggested mechanism that entrains the cycle (Bjørnstad et al. 2004).

Fishery management reference points relevant to age structure have been proposed that relate to resilience functions. Functional redundancy is captured in indices that consider equivalent contributions between age-classes such as the number of age-classes (Lambert 1987) or the uniformity of their distribution (Marteinsdóttir & Thorarinnsson 1998; Marshall et al. 2003). By weighting age-classes according to their expected contributions to fecundity, Secor (2000) developed a reference point that relates to functional diversity. Mean age of adults and relative abundance of older age-classes have also been proposed (Hutchings & Baum 2005; Brunel & Piet 2013). All of the aforementioned indices represent aspects of cross-scale resilience, but the key is conservation of longevity. Brunel and Piet (2013) evaluated the response of simulated populations of cod, herring (*Clupea harengus*), and plaice (*Pleuronectes platessa*) to management measures designed to conserve age structure. Their exercise shows that age structure indices can be effectively implemented through length-based harvest controls.

Despite the success of length-based controls to protect larger adults of other marine species, their implementation for Atlantic bluefin tuna will be confounded by individual growth dynamics and the high commercial value attached to giant bluefin tuna (>205 cm CFL). For older bluefin tuna (>12 years old), growth in length is highly variable and diminishes substantially with age. Still, a maximum size limit (e.g., 230 cm CFL) would protect the oldest spawners, but careful studies would be needed to evaluate the survival of landed and released bluefin tuna of this size (Block et al. 2005; Skomal 2007). A recent study showed low (<5%) post-release mortality for large bluefin tuna caught by recreational fisheries in Canada (Stokesbury et al. 2011). Recovering adult age structure will likely require implementation of increased harvest controls across all size classes and fishing sectors. Because the western stock may exhibit alternate state characteristics (hysteresis), the path to recovery from its current depressed albeit stable state will likely require substantial accumulation of biomass in older age-classes, more so than what would have been required 30 years ago. Embarking on this path will entail considerable so-

cioeconomic burdens on existing bluefin tuna fisheries and will depend on whether stakeholders accept recovery of western Atlantic bluefin tuna to a more abundant, resilient state.

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Supporting Information

Figures related to stock mixing (Appendix S1) and age distributions (Appendix S2) available online. The authors are solely responsible for the content and functionality of these materials. Queries should be directed to the corresponding author.

Figure S1. Otolith $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ for (a) North Carolina Atlantic bluefin tuna (2011–2013) and (b) similar age-class U.S. Atlantic bluefin tuna (1996–1998).

Figure S2. Cumulative frequency plots for age distributions for adult Atlantic bluefin tuna sampled during 1975–1981 and 1996–2007.

Figure S3. Fishing selectivity estimates from the 2012 ICCAT assessment (SCRS 2012).

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