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Modeling the implications of stock mixing and life history uncertainty of Atlantic bluefin tuna

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Abstract

Atlantic bluefin tuna is currently managed as two separate eastern and western stocks, despite information indicating considerable stock mixing. Using a simulation model, we explored how scenarios of population-specific migration and uncertainty in aspects of bluefin tuna biology affect the magnitude, distribution, and mixed stock nature of the resource and catch of its associated fisheries. The analytical framework was a stochastic, age-structured, stock-overlap model that was seasonally and spatially-explicit with movement of eastern and western origin tuna informed by tagging and otolith chemistry data. Alternate estimates of movement and assumptions regarding maturity and recruitment regime for western origin fish were considered. Simulation of the operating model indicated considerable stock mixing in the western and central Atlantic, which resulted in differences between the stock and population view of western bluefin tuna. The relative biomass of the western population and its spatial and temporal distribution in the Atlantic was sensitive to model assumptions and configurations. Simulation modeling can provide a means to ascertain the potential consequences of stock mixing on the assessment and management of fishery resources.
**Introduction**

Migratory natural resources pose a significant management challenge that is fundamentally different from that of stationary natural resources due to their extensive and dynamic geographic distributions (Berkes 2006). This challenge is heightened for highly migratory species that experience direct exploitation and whose management can involve complex biological, economic, and political dynamics. The highly migratory Atlantic bluefin tuna (*Thunnus thynnus*) exemplifies this complex challenge, because of the broad and dynamic spatial distribution of the resource and its associated fisheries and the fact that this species crosses international boundaries requiring international cooperation in its assessment and management.

Atlantic bluefin tuna is distributed and exploited across the entire North Atlantic Ocean and Mediterranean Sea. A combination of genetics, conventional and electronic tagging, organochlorine tracers, and otolith chemistry data has identified two distinct spawning populations of bluefin tuna in the Atlantic, originating in the Gulf of Mexico in the west and the Mediterranean Sea in the east (Boustany et al. 2008, Rooker et al. 2008a,b, Dickhut et al. 2009). Bluefin tuna is managed by the International Commission for the Conservation of Atlantic Tunas (ICCAT) as two stocks, east and west divided at the 45° west meridian (Figure 1). The stocks are assessed separately, and the current stock assessment approach assumes no mixing across the management boundary (ICCAT 2014). Evidence indicates that adult bluefin tuna exhibit a high degree of natal homing (near 100%) to their respective spawning grounds (Mediterranean Sea and Gulf of Mexico, Rooker et al. 2008a,b, 2014). However, there is also evidence of extensive trans-Atlantic migrations by juveniles and adults that have been related to feeding (Block et al. 2001, 2005, Galuardi et al. 2010, Quílez-Badi et al. 2014, Secor et al. 2015). Increased focus on
understanding the movement of this species has revealed complex spatial dynamics that differ
between populations and over the lifetime of individuals. For example, otolith chemistry data has
revealed mixed stock composition of bluefin tuna that varies by region, size/life-stage, and year-
class of fish (Rooker et al. 2008a,b, 2014). Stock mixing rates suggest the potential for large
contributions (as high as 73% for school size [50-100 cm curved fork length] juveniles) of
eastern-origin fish in mid-Atlantic US fisheries (Siskey et al. 2016).

The definition of a fish stock and the spatial delineation of the management unit boundaries
establish the spatial framework through which we assess the status of fishery resources and
implement management strategies. Mismatch in the geographic scale of a fish’s life cycle and its
management units (i.e., ‘stocks’) can have profound implications for the accuracy of stock
assessment and the effectiveness of fishery management (Kell et al. 2009, Ying et al. 2011, Kerr
et al. 2014b). This problem has been recognized for many migratory species for which unit stock
areas do not match the scale of fish movement (e.g., Atlantic herring, Secor et al. 2009, Kell et
stock’ assumption that underlies many stock assessment approaches. However, these issues often
remain unresolved due to the difficulty of characterizing the extent of mixing (Secor 2015). As a
result, the data collected to inform separate assessments of stocks for which mixing is a concern
are likely composed of fish of mixed stock origin, and this mixed-stock data can confound
indices of abundance, catch estimates, characterization of life history parameters (e.g., growth,
maturity-at-age), and stock-recruit relationships. Therefore, ignoring stock mixing can
potentially result in inaccurate estimates of stock abundance and sustainable yield as well as
misinterpretation of apparent trends and stock status (Kerr et al. 2014a). Stock mixing can
disproportionately impact stocks at relatively low abundance that exhibit a high degree of spatial
overlap with stocks at much greater abundance (i.e., asymmetric production between stock units,
Secor 2015). Achieving conservative exploitation rates in mixed stock fisheries is difficult, and
harvest of mixed stock aggregations can lead to overfishing of less productive populations and
under-fishing more productive populations (Ricker 1958, Hilborn and Walters 1992, Cadrin and
Secor 2009). Understanding the spatio-temporal scale of fish movement in relation to
management units is important for well-informed assessment and effective management.

Stock mixing scenarios have been explored for several species in the context of the stock
assessment, including bluefin tuna (e.g., Porch et al. 2001, Taylor et al. 2011), yellowtail
flounder (Goethel et al. 2015), and Bering Sea pollock (Hulson et al. 2011), but there are few
examples of this approach being used to provide advice for management (Kerr et al. In Press).

Statistical, spatially-explicit stock assessment models that rely on time series data cannot always
be successfully fit to the available data. The reliability of parameter estimation in single area,
single stock assessments can be tenuous (Ludwig and Walters 1984, NRC 1998, Deroba 2014),
and the problem is even greater for mixed stock applications, because there are many more
parameters to estimate. The Atlantic bluefin tuna stock assessment is an archetypical example of
this problem. One challenge is that modeling spatial population dynamics is statistically
demanding, because it requires the estimation of many additional parameters to capture seasonal
and spatial dynamics. A second major difficulty is that most historical data used to condition or
fit the statistical models (catch, indices of abundance, size/age composition information,
conventional or electronic mark-recapture observations) cannot be assigned to stock of origin,
because the majority of stock composition data is only available for recent periods. The result is
that analysts and decision makers can be faced with just enough movement and stock composition data to know that mixed stock spatial population dynamics are occurring, but without enough data to reliably estimate the parameters describing the system with statistical models.

An alternative to the statistical modeling approach is to develop operating models to simulate stock mixing and to explore a range of hypotheses about population structure and connectivity and its impact on conservation and management goals (Kerr and Goethel 2014). An advantage of simulation models is the flexibility in accommodating multiple types of information and structural organization to address a wide variety of questions (Kerr and Goethel 2014). In general, simulation models have fewer limitations and a less confining framework than estimation models, and therefore have the potential to more readily incorporate a broader range of hypotheses about the state of nature with fewer simplifying assumptions (Goethel et al. 2015). However, simulation models must be carefully constructed to accurately represent the best available science, as well as associated uncertainties, on the species and populations they aim to represent to assure that simulation testing is meaningful (Kerr and Goethel 2014).

Stock mixing is recognized as a major source of uncertainty in informing Atlantic bluefin tuna fisheries management strategies and annual catch advice (Porch 2005, ICCAT 2014). Additionally, there is uncertainty with respect to assumed differences in age at maturation and recruitment for the western stock of bluefin tuna (ICCAT 2014), and assessment model results are highly sensitive to these assumptions. Recruitment and maturity are important corollaries of movement as they influence our understanding of the relative productivity of stocks and life stage-related movements. The goal of this study was to develop a biologically realistic
simulation model for Atlantic bluefin tuna that incorporates the most plausible hypotheses of bluefin tuna population structure and was informed by the best available science on movement. We used this model as a platform to examine the consequences of incorporating complex movement dynamics of Atlantic bluefin tuna as well as uncertainty in aspects of western bluefin tuna biology (i.e., assumptions regarding recruitment regime and maturity at age). We evaluated the impact of these factors on our perception of the magnitude, distribution, and the mixed stock composition of the resource and the catch of its associated fisheries throughout the Atlantic Ocean and adjacent seas. We compared the outcomes of simulated scenarios when the resource was viewed from a population and a stock unit perspective (assuming no mixing).

Methods

The operating model includes two spawning populations, originating in (1) the Mediterranean Sea and (2) the Gulf of Mexico, based on known spawning locations and the distribution of early life stages. A recent discovery of larval bluefin tuna in the Slope Sea suggests that western bluefin tuna may have another spawning ground there (Richardson et al. 2016), although how this spawning group relates to Gulf of Mexico spawners or western stock recruits remains highly uncertain. Therefore, this new pattern of spawning was not incorporated in the model. The model was a stochastic age-structured (ages 1 to 29), temporally-explicit (quarterly seasons) and spatially-explicit (seven geographic zones) overlap model. An overlap model allows for spatial overlap of populations, but constrains them to exhibit spawning site fidelity, which is biologically realistic for bluefin tuna (Block et al. 2005, Rooker et al. 2008). Quarterly time steps were considered to be sufficient to represent changes in bluefin tuna movement patterns and the associated fisheries (ICCAT 2001). The principal fisheries for bluefin tuna operating in each
region were represented in the model including rod and reel, harpoon, longline, and purse
seine in the western stock area and purse seine, bait boat, longline and trap in the eastern stock area.

The spatial strata of the model were a composite of previous stratifications based on information
on the distribution, movement, life history, fisheries, and management of bluefin tuna and
represent the consensus of experts on bluefin tuna mixing (Table 1, Figure 1; ICCAT 2001,
Rooker et al. 2007, Taylor et al. 2011). The strata included the known spawning areas for
western (Gulf of Mexico) and eastern (Mediterranean Sea) bluefin tuna populations and five
regions where various degrees of spatial overlap occur between populations (Table 1, Figure 1).

Simulation Scenarios

Alternative operating model settings (i.e., scenarios) were explored to examine the consequences
of complex movement dynamics of bluefin tuna as well as uncertainty in aspects of bluefin tuna
biology that are important corollaries to movement. Eight scenarios were simulated to evaluate
the sensitivity of model results to different methods of estimating movement, and to examine the
implications of different assumptions of the productivity regime and maturity schedule for
western bluefin tuna. A series of 500 stochastic model runs, each conducted over a 200-year time
period, were performed for each model scenario (only the last 100 years were used in analyses to
allow simulations to approach a dynamic equilibrium). Across model runs, mean spawning stock
biomass (SSB) and yield were calculated for each spawning population in each geographic zone
and quarter (with quarter one representing spring) and for each unit stock across quarters. The
long-term expectations produced from model simulations were conditional on the assumed
parameter values under the scenario of status quo fishing mortality, the specific method used to
estimate movement (gravity or bulk transfer), and the assumptions of recruitment regime (low, high) and maturity (older, younger) for the western population.

**Alternative Approaches to Movement Estimation**

Estimation of fish movement rates is a challenge and results can be sensitive to model assumptions and configurations (Taylor et al. 2011). We explored the impact of two alternative methods of estimating movement matrices: 1) gravity, and 2) bulk transfer (Taylor et al. 2011). The gravity method estimates an ‘attraction’ coefficient for each area to derive residence, and movement is derived from the relative attraction of other areas in that season. The bulk transfer method is more statistically demanding, because it estimates probabilities of all movements among areas (i.e., transfer coefficients from one area to another).

**Life history Uncertainty**

Two alternative productivity regimes (termed ‘low’ and ‘high’ recruitment regimes, ICCAT 2014) were examined for western origin fish. ICCAT has derived maximum sustainable yield (MSY) reference points for the western Atlantic bluefin stock using two scenarios of recruitment since 1993 (Punt and Butterworth 1995). Because of the consistent low biomass of the western stock in recent decades and similar shape of these stock recruitment relationships at low biomass, ICCAT concluded that no strong evidence exists to favor either scenario and they represent reasonable upper and lower bounds on rebuilding potential.

The age at maturity of western origin bluefin tuna is also uncertain. In the most recent stock assessment (ICCAT 2014), the western stock is assumed to mature at age-9, but both older (12–
16 years, Diaz and Turner 2007, Diaz 2011) and younger ages at maturity have been proposed (4-7 years, Knapp et al. 2014, Heinisch et al. 2014, Richardson et al. 2016). The eastern bluefin tuna stock assessment assumes a maturity at age schedule of 50% maturity at age-4 and 100% maturity at age-5 (Mather et al. 1995, ICCAT 2010). If currently-held assumptions of differences in age at maturity between eastern and western bluefin tuna are accurate, they could represent evolved stock-specific differences in biological rates (Schirripa et al. 2011, ICCAT 2014).

Alternatively, shifts in gene frequencies could have occurred through differential size-specific fishing mortality between stocks that resulted in a shift in age at maturity (Schirripa et al. 2011, ICCAT 2014). However, there is also a strong possibility that the current assumptions regarding age at maturity are inaccurate and bias has been introduced based on the difficulty in obtaining a random sample of a population of a wide-ranging schooling fish and the possibility that younger fish may spawn outside of Gulf of Mexico (Schirripa et al. 2011, Richardson et al. 2016).

Model Structure

The recruitment of western bluefin tuna (abundance of age-1 fish) was calculated using a Beverton Holt stock-recruit curve under the high recruitment scenario (Eqn. 1, Table 2, 3) and a hockey stick stock-recruit model under the low recruitment scenario (Eqn. 2, Table 2, 3). Recruitment of eastern bluefin tuna was calculated using a hockey stick stock-recruit model (Eqn. 2, Table 2, 3). For stock-recruit calculations, the spawning biomass of bluefin tuna upon their arrival on the spawning ground in quarter one was used. Stochasticity in recruitment was incorporated as an error term in these models and modeled as a random lognormal variate scaled to approximate recruitment variability observed for each stock.

Abundance of fish at age in each population was calculated over time and space and was

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calculated for fish ages 2 to 29 in quarter 1 by Eqn. 3 (Table 2, 3) and in quarters 2 to 4 by Eqn. 4 (Table 2, 3). Spawning stock biomass of eastern and western bluefin tuna in each geographic zone over time was calculated as a function of the number-at-age, weight-at-age, and maturity-at-age of fish from each population (Eqn. 5, Table 2, 3). Yield of eastern and western bluefin tuna populations across geographic zones was calculated as a function of the Baranov catch equation (Eqn. 6, Table 2, 3). Biomass and yield were also characterized for eastern and western stocks using modifications of Eqn. 5 and 6. The biomass and yield of eastern and western stock units was calculated based on the abundance of all bluefin tuna within a stock area regardless of origin. Note that our characterization of the mature biomass within stocks areas was based on the maturity assumptions of the respective population associated with the stock (e.g., the assumed maturity of western-origin fish was applied to all fish within the western stock area).

Model Parameters

The values of several model parameters were informed by the Multi-stock Age-Structured Tag-integrated stock assessment model (MAST model, described below) and recent ICCAT stock assessments. Other model parameters were drawn from peer-reviewed research on movement, mixing, reproductive schedules, and geographic variation in life history traits.

The MAST model (see Taylor et al. 2011 for full description) was used to generate movement matrices, fishing mortality rates, and gear selectivity that informed the operating model. MAST is a statistical catch-at-age model that integrates stock structure and stock mixing information into a single assessment model (Taylor et al. 2011). The model incorporated electronic and conventional tagging, catch, and otolith chemistry data to model seasonal matrices of regional
population movements by Atlantic bluefin tuna using two methods: 1) gravity and 2) bulk transfer. Bayesian methods were used for parameter estimation, which permitted simultaneous use of diverse types of data to estimate past abundance trends, movement, and fishing mortality rates. Taylor et al (2011) showed that $F_{MSY}$ estimates and rebuilding expectations for the western stock were sensitive to the choice of method. In the context of the MAST model, the gravity method required estimation of 178 parameters, whereas the bulk transfer method required 244 parameters.

Movement matrices were estimated for two age-groups (ages 1-7 and ages 8+) in non-spawning quarters and each age class (1 to 29) during the spawning quarter. The MAST model estimated movement matrices for five geographic regions. These movement matrices were modified to accommodate the seven zone model structure used in this study by dividing the eastern Atlantic, previously one region in Taylor et al. (2011), into three zones (central Atlantic, eastern Atlantic, and northeastern Atlantic, Figure 1). Residence within and movement out of the entire region remained the same. However, the distribution of juvenile and adult fish within the region was informed by movement constraints among the three zones (see constraints listed below), based on knowledge of the life history and movement of Atlantic bluefin tuna. This represented a shift from the previous assumption of homogeneous distribution of life stages in this region to a more biologically realistic distribution (Rooker et al. 2007). Movement constraints imposed on the model also served the purpose of simplifying estimation of movement matrices. These constraints were based on the following assumptions and supporting literature: 1) mature fish return to their respective spawning grounds during the spawning quarter (Block et al. 2005, Rooker et al. 2008; the maturity ogives used to constrain movement varied by scenario and are
described in more detail below), 2) no stock mixing occurs on spawning grounds (Rooker et al. 2014; Secor et al. 2015), 3) only western-origin fish move into the Gulf of St. Lawrence (Schloesser et al. 2008), 4) only juvenile and adolescent fish of western origin move into the eastern Atlantic, but all life stages of eastern origin fish move into this region (Rooker et al. 2007), and 5) only eastern origin fish move into the northeast Atlantic (Rooker et al. 2007).

Because movement rates were conditioned on maturity (Taylor et al. 2011), consideration of alternative maturity at age required revised estimates of movement. MAST is parameterized in such a way that the goodness of fit to the mark-recapture data depends on maturity assumptions, and a maturity at age younger than the current assumption in the stock assessment (i.e., 100% maturity at age 9) was incompatible with the data. Two plausible alternative estimates of maturity at age were examined for western origin fish. One model scenario (termed the younger maturity at age scenario) assumed 50% maturity at age-8 and 100% maturity at age-10. This is similar to the maturity assumption in the most recent stock assessment (ICCAT 2014), although slightly older due to issues with model convergence when estimating movement of mature fish to the Gulf of Mexico at younger ages (i.e. the tagging and otolith chemistry data did not support a younger age at maturity). The other scenario (termed the older maturity at age scenario) assumed 50% maturity at age-12 and 100% maturity at 16 (Diaz and Turner 2007, Taylor et al. 2011).

Recent mean annual fishing mortality rates (2008-2009) by gear type (longline, purse seine, bait boat, and other), quarter, and zone estimated in the MAST model informed simulations of the operating model (Figure 2; Taylor et al. 2011). The fishing mortality value estimated for the eastern Atlantic region in the MAST model was applied to the central, eastern, and northeast Atlantic zones of the current model (Figure 2). Gear selectivity at age was estimated in the
MAST model as a global selectivity across gear types (Taylor et al. 2011). While gear selectivity undoubtedly differed between fleet and country, the modeling involved to consider these effects in the MAST model was too parameter intensive. Thus, fleet-specific selectivity was not considered in the MAST model in favor of model parsimony and computational efficiency to capture movement dynamics (Taylor et al. 2011). We chose to maintain a constant $F$ and selectivity in simulations in order emphasize the impact of stock mixing, rather than changes in management.

Life history parameters specified in the operating model were based on recent ICCAT stock assessments and the peer-reviewed literature. Weight-at-age was estimated based on von Bertalanffy growth models and length-weight relationships from recent stock assessments (western origin: Parrack and Phares, 1979, ICCAT 2010, Nielson and Campana 2008; eastern origin: Cort 1991, ICCAT 2012). Natural mortality of eastern and western origin bluefin tuna was assumed to be age-independent ($M = 0.14 \text{ yr}^{-1}$, Anon 1997, ICCAT 2014) and was based on the current assumption in the western stock assessment. Fonteneau and Maguire (2014) recommended that identical natural mortality rates be used for eastern and western bluefin tuna, as there is no biological reason to assume different natural mortality, however, age-independent mortality is not entirely realistic.

To parameterize the operating model’s recruitment dynamics, values from existing stock assessments were used. The parameters of the Beverton-Holt stock recruit curve representing the high recruitment scenario for the western population were estimated from SSB and recruitment data from 1971 to 2008 ($\alpha = 432,982$, $\beta = 61,344$, $\epsilon = 0.37$, ICCAT 2010). Parameters of the hockey-stick model characterizing the low recruitment scenario were based on maximum
recruitment \((R_{max})\) estimated as the geometric mean number of recruits from 1976-2006, and the spawning biomass threshold estimated as the average SSB from 1990-1995 \((R_{max} = 84,363; SSB^*_p = 12,236, \epsilon = 0.37, \text{ICCAT 2010})\). The parameters of the hockey stick model used to describe the stock-recruit relationship for eastern origin fish was based on recruitment and spawning biomass data from 1955-2007 \((R_{max} = 1,889,896, SSB^*_p = 215,584, \epsilon = 0.43; \text{ICCAT 2010})\). Asymptotic recruitment \((R_{max} \text{ for eastern and } \alpha \text{ for western populations})\) and equilibrium age structure were used to initialize simulations of the operating model, because our objectives were long-term projections. The model was initialized in each populations’ respective spawning area (Gulf of Mexico for western origin fish and Mediterranean Sea for eastern origin fish) and spawning time (quarter 1) with the initial abundance of bluefin tuna populations in non-spawning zones during year 1, quarter 1 set equal to zero.

**Results**

**Gravity Movement Rates**

**Magnitude and Distribution of Atlantic Bluefin Tuna Spawning Biomass and Yield**

The magnitude of long-term SSB and yield differed between eastern and western bluefin tuna spawning populations, with values one to two orders of magnitude greater for the eastern compared to the western population (Table 4, Figure 3a,b). The distribution of eastern and western population biomass varied greatly across geographic zones and seasonal quarters (Figure 3a,b). In spring (quarter 1), the long-term expectation of SSB of the western population was greatest in the Gulf of Mexico based on the model constraint that mature fish return to spawn in their respective spawning habitat in quarter one (Figure 3a). In summer (quarter 2), SSB of
western origin fish was consistently greatest in the Gulf of Mexico, followed by the western and central Atlantic zones, and then the Gulf of St. Lawrence (Figure 3a). Scenarios that assumed a younger age at maturity exhibited considerably greater western origin biomass in the western Atlantic in summer compared to scenarios that assumed an older age at maturity (Figure 3a). In fall (quarter 3), SSB was greatest in the western Atlantic when a younger age at maturity was assumed and in the Gulf of Mexico when an older age at maturity was assumed. Spawning stock biomass was consistently greatest in the western Atlantic in winter (quarter 4) across all scenarios. Western origin fish were present outside of the western management unit (i.e., in the central and eastern Atlantic) across all quarters (Figure 3a). Western origin fish were absent from the northeast Atlantic and Mediterranean Sea because of constraints in the model that restricted their movement into these areas. The majority of the long-term yield of western origin bluefin tuna came from the central Atlantic and the Gulf of Mexico (particularly in quarter 1), with moderate contributions from the western and eastern Atlantic, and minor contributions from the Gulf of St. Lawrence (Figure 3c). Long-term yield of the western population was greatest in the summer, followed by the fall (quarter 2 and 3 respectively; Figure 3c).

Across seasons, the long-term SSB of eastern origin fish was consistently greatest in the Mediterranean Sea (Figure 3b). This region comprised an average of 91% of the total SSB of the eastern population across scenarios. Eastern origin fish were present in the central, eastern, and northeastern Atlantic at biomass levels two orders of magnitude lower than in the Mediterranean (Figure 3b). Eastern origin fish were present within the western stock area with the highest biomass of eastern origin tuna outside of the Mediterranean Sea in the western Atlantic (Figure 3b). Eastern origin fish were absent from the Gulf of Mexico and Gulf of St. Lawrence based on
the movement constraints in the model. Across quarters, the long-term yield of eastern origin fish was greatest in the Mediterranean Sea, with the greatest yields occurring during summer (quarter 2, Figure 3d). The combined yield of eastern origin fish from the western, central, eastern, and northeastern Atlantic comprised 6 to 10% of the total yield of the eastern population across scenarios (Figure 3d).

Scenarios with alternative western population recruitment and maturity assumptions exhibited substantial differences in SSB and yield for western bluefin tuna, with little impact on the magnitude of the SSB and yield of the eastern resource (Figure 3a,b). Across alternative scenarios, long-term average SSB of the western population in quarter one ranged from 31,767 to 107,867 mT and SSB of the eastern population ranged between 1,165,943 and 1,169,926 mT (Table 4). Long-term average annual yield of the western population ranged from 1,290 to 5,028 mT and yield of the eastern population ranged from 40,615 to 40,769 mT (Table 4). The highest SSB and yield values for the western population occurred in the scenario assuming high western recruitment and a younger age at maturity, and the lowest values occurred when low western recruitment and older age at maturity was assumed (Table 4).

Mixed Stock Composition

Due to model constraints, the composition of SSB and catch in the Gulf of Mexico and Gulf of St. Lawrence was composed exclusively of western origin fish and the composition of tuna in the northeastern Atlantic and Mediterranean Sea was exclusively of eastern origin. Spawning stock biomass and catch in the western, central and eastern Atlantic was of mixed origin (Figure 4). The SSB in the western Atlantic was dominated by eastern origin fish with 62 to 98% of mature
fish expected to be of eastern origin outside of the spawning quarter (Figure 4a-d). However, there was a more substantial contribution of western origin fish to long-term yield of bluefin tuna within the western Atlantic (ranging from 19 to 62% outside of the spawning quarter and 78 to 99% in the spawning quarter), because immature fish were susceptible to the fisheries in the region (Figure 4e-h). The SSB in the central Atlantic was generally dominated by eastern origin fish across alternative scenarios, with the exception of the high recruit, younger maturity scenario in which SSB in the central Atlantic was composed of 60 to 86% western origin fish across quarters (Figure 4a). Outside of the spawning quarter, the composition of yield in the central Atlantic varied from being dominated by the western population (high recruit, younger maturity scenario), to dominated by the eastern population (low recruit, older maturity scenario), to near equal proportions of eastern and western origin fish (high recruit, older maturity and low recruit, younger maturity scenarios; Figure 4e-h). The SSB and yield in the eastern Atlantic was dominated by the eastern population, with the exception of the spawning quarter due to the model constraint that mature eastern fish return to the Mediterranean Sea to spawn.

*Population and Stock View of the Atlantic Bluefin Tuna Resource*

The population view of the bluefin tuna resource, which accounts for fish originating from two spawning areas and mixing in the Atlantic Ocean, was compared to the stock view of the resource which assumes the two populations remain within the two Atlantic stock areas with no mixing. Because of the constraint for mature individuals to return to their spawning region in the spawning quarter, quarter one does not reflect differences between the population and stock unit view of the resource (i.e., stock is approximately equal to population in this quarter; Figure 5). The SSB of the western stock unit was equal or greater than that of the western population across
quarters and scenarios (Figure 5). The difference between the stock and population view of the resource was greatest in scenarios assuming a lower age at maturity and low western recruitment (Figure 5). Total yield of western origin fish was greater (up to 2.8 times) than the mixed stock catch in the western stock area across most scenarios (Figure 5). This indicates a significant amount of unaccounted for mortality of western origin fish in the eastern stock area.

The SSB of the eastern stock unit was nearly equal or slightly less (~1%) than that of the eastern population across quarters (Figure 5). The expected yield of the eastern stock unit was slightly more (~1-2%) than that of the eastern population due to western origin fish harvested within the eastern stock area (Figure 5). Yield of the eastern stock unit was highest in the scenario with the highest expected western biomass (high recruitment, younger maturity scenario). However, differences between the eastern stock and population were well within one standard deviation and are essentially negligible.

**Bulk Transfer Movement Rates**

**Magnitude and Distribution of Atlantic Bluefin Tuna Spawning Biomass and Yield**

Similar to scenarios based on gravity method movement estimates, the magnitude of long-term SSB and yield based on bulk transfer rates was one to two orders of magnitude greater for eastern compared to western bluefin tuna populations (Figure 6a,b). Patterns in the distribution of eastern and western populations across geographic zones were similar across scenarios.

Outside of the spawning season (quarter 1), the SSB of western origin fish was consistently greatest in the western Atlantic (Figure 6a). This concentration of fish in the western Atlantic
differs from results using gravity movement and is attributable to higher rates of residency in the
western Atlantic estimated using the bulk transfer method for western origin fish and lower rates
of movement to other zones. Western origin fish were present at low levels in the central
Atlantic, eastern Atlantic, and Gulf of St. Lawrence (Figure 6a). The majority of the expected
yield of western bluefin tuna came from the western and central Atlantic, with moderate
contributions from the Gulf of Mexico (during quarter 1) and eastern Atlantic, and minor
ccontributions from the Gulf of St. Lawrence. Total long-term yield of western origin fish was
greatest in the summer and fall (Figure 6c).

The long-term average SSB of eastern origin fish was consistently greatest in the Mediterranean
Sea (Figure 6b); SSB in this zone comprised 88 to 93% of the total SSB outside of the spawning
quarter. Relative to biomass in the Mediterranean Sea, eastern bluefin tuna biomass in the
central, eastern, and northeastern Atlantic was considerably less (Figure 6b). The long-term yield
of eastern origin fish was greatest in the Mediterranean Sea, with the highest long-term yields
occurring during the summer and followed by the fall (Figure 6d). The combined yield of eastern
origin fish from the western, central, eastern, and northeastern Atlantic regions comprised 2 to
6% of the total eastern origin tuna yield across scenarios.

Similar to scenarios informed by gravity movement estimates, alternative recruitment and
maturity assumptions influenced the magnitude of SSB and yield of the western population with
little impact on the eastern population. Long-term SSB of the western population in quarter one
ranged from 26,168 to 122,877 mT and the SSB of the eastern population ranged from 1,187,171
to 1,177,510 mT (Table 4). Long-term annual yield of the western population ranged from 1,589
to 5,423 mT and the yield of the eastern population ranged from 40,019 to 39,811 mT. The
highest western origin SSB and yield values occurred in the scenario assuming high western
recruitment and a younger age at maturity, and the lowest values occurred when low western
recruitment and older age at maturity was assumed.

*Mixed Stock Composition*

Similar to scenarios informed by gravity movement estimates, the long-term SSB and yield of
bluefin tuna in the Gulf of Mexico and Gulf of St. Lawrence was constrained to be composed
exclusively of western origin fish, and SSB in the northeastern Atlantic and Mediterranean Sea
was composed exclusively of eastern origin fish. The western, central, and eastern Atlantic
regions were composed of a mixture of eastern and western origin fish. The percentage of
western origin fish that composed SSB in the western Atlantic ranged from 23 to 57% outside of
the spawning quarter under the younger maturity scenarios, and 56 to 96% under the older
maturity scenarios with the highest percentage of western fish under high recruitment scenarios
(Figure 7). SSB in the central and eastern Atlantic was dominated by eastern origin fish, but
yield from these regions was either in near equal proportions or dominated by western origin fish
(Figure 7).

*Population and Stock View of the Atlantic Bluefin Tuna Resource*

Under scenarios informed by bulk transfer movement estimates, the stock unit view of western
SSB was greater than the population view of the resource when a younger age at maturity was
assumed and equal or less than the population view when an older age at maturity was assumed
(Figure 8). Total yield of the western population was greater than the expected yield for the
western stock under most scenarios with the exception of the low recruit, younger maturity
scenario (Figure 8). Across scenarios, there was little difference between the eastern stock and eastern population view of bluefin tuna SSB and yield (Figure 8). Spawning biomass and yield of the eastern stock differed slightly across scenarios, however these differences were within one standard deviation (Figure 8).

Discussion

The goal of this study was to develop a simulation model for Atlantic bluefin tuna that incorporated the current state of knowledge of bluefin tuna population structure and movement patterns. Additionally, we aimed to evaluate how key uncertainties in bluefin tuna life history interacted with movement in the model and altered our perception of the resource. Given the expense and uncertainty in understanding the movements and population dynamics of highly migratory fishes, we will never have a perfect understanding of fish movement and life history for species like bluefin tuna. However, harvest decisions must still be made in spite of this uncertainty. The integration of existing information into simulation models can allow us to consider best available or novel empirical information as alternative hypotheses against which proposed stock assessment approaches and harvest control rules can be evaluated through management strategy evaluation.

The results of our simulation modeling demonstrated that explicitly modeling stock mixing altered our perception of both the magnitude and distribution of the bluefin tuna resource in space and time. Across scenarios, the perception of eastern-origin bluefin tuna SSB was similar whether viewed as a population or as a unit stock due to the general balance in losses of eastern origin and gains of western origin fish within the stock area. However, there were large
differences between the stock and population view of the western bluefin tuna resource with the
tendency for the stock view of SSB to be higher than the population view. This is attributable to
migrants from the more abundant eastern population supplementing biomass within the western
stock area. Attribution of these eastern origin fish to the western resource can result in an overly
optimistic view of the potential production and yield of western origin fish. Additionally, a
substantial biomass of western origin fish was caught by fisheries operating in the eastern
management unit in model simulations. This represents unaccounted fishing mortality on the
western population when only the stock-view of the resource is considered. The only instances in
which the western population and stock views of SSB converged were when an older maturity at
age was assumed in scenarios informed by bulk transfer movement. In these instances, a large
portion of eastern-origin fish present within the western stock area was not accounted for as they
were assumed immature based on the western maturity ogive. Additionally, there was a tendency
for less movement of western-origin biomass out of the western stock area in scenarios informed
by bulk transfer movement. The western population and stock views of yield converged when
low recruitment was assumed for western origin fish. In these scenarios, there was less western
biomass caught within the eastern stock area (i.e., less unaccounted for mortality). Recognizing
the extent of mixing between eastern and western populations, and how it varies in space and
time, is critical to an accurate understanding of the status of these populations and the potential
to predict their response to alternative management actions.
Alternative Movement Estimates and Life History Scenarios

The magnitude and distribution of productivity and yield of western bluefin tuna populations was sensitive to the method of estimating movement (gravity and bulk transfer) and this had an appreciable impact on stock composition. Differences in the estimated movement of fish, led to differences in the concentration of eastern and western origin fish across geographic zones and exposure to different fishing mortalities. There was little difference in SSB and yield (1-2%) for eastern bluefin tuna based on the method of estimating movement as both methods located the majority of biomass within the Mediterranean Sea. The expected magnitude of western population and stock SSB was greater (18-36%) in scenarios informed by gravity movement estimates when an older age at maturity was assumed (Table 4). However, when a younger age at maturity was assumed the western population and stock SSB was greater (7-12%) in scenarios informed by bulk transfer movement estimates (Table 4). Higher western SSB under certain scenarios was due to more mature western origin fish remaining within the western management area in these scenarios, a region of lower fishing mortality, compared to the central and eastern Atlantic.

Simulation of alternative maturity schedules for western bluefin tuna both directly, based on the age classes considered to be mature, and indirectly, through the linkage of the maturity schedule to fish movement, impacted the expected SSB and yield of bluefin tuna. Scenarios which assumed a younger age at maturity for western origin fish resulted in a higher expected western SSB due to the fact that more age classes were included in the calculation of mature biomass. A tendency for higher yields when a younger age at maturity was assumed related to more western-origin biomass distributed in the central Atlantic, a region of higher relative fishing mortality.
Because movement rates estimated using the MAST model (Taylor et al. 2011) during the spawning quarter were linked to the maturity schedule for each population, changing maturity schedules altered the movement of western origin biomass within the model. Of the two maturity scenarios, the MAST model indicated a superior goodness of fit of the mark-recapture data to the older age at maturity scenario (100% maturity at age-16) which is older than the current assumption of maturity for the western stock in the current stock assessment (100% maturity at age-9; ICCAT 2014), and three times the age of 100% maturity used for eastern stocks. Resolving the maturity schedule of bluefin tuna is challenging because sexually mature individuals tend to geographically segregate from immature individuals, thus comprehensive sampling to determine the percentage of mature fish at a given age/length class is difficult. Resolution of the question of western bluefin tuna maturity schedule should be a research priority due to its considerable impact on expected mature biomass, the spatial distribution of the stock, reference points, and potential yield for the bluefin tuna resource. Uncertainty in the implied stationarity of the stock-recruit relationship is an increasingly common concern in fisheries assessment. Bluefin tuna are likely subject to non-stationarity either as a result of a shift in environmental regime or internal dynamics (Secor et al. 2015). The low recruitment scenario implies a regime shift in bluefin tuna productivity in the mid-1970s (ICCAT 2014). However, Secor et al. (2015) proposed that this shift may be attributable to truncation of age structure of spawners, with younger spawners now dominating the population and exhibiting a reduced spawning period resulting in decreased recruitment success. Simulation of scenarios which assumed a high recruitment regime for the western population exhibited higher SSB and yield than corresponding scenarios which assumed a low recruitment regime. There was no
appreciable impact on eastern-origin biomass of these alternative assumptions of recruitment for
the western resource. The most recent stock assessment of bluefin tuna stocks suggests an
upward trend in western SSB (ICCAT 2014), which may enable resolution of the recruitment
regime question in coming years as we move away from observations at low biomass.

Simulation of the operating model indicated a general trend of considerable mixed stock
composition of the mature tuna biomass and yield in the western and central Atlantic, with little
mixing in the eastern Atlantic. The modeled stock composition in the western and central
Atlantic varied greatly across quarters, suggesting that these are regions of dynamic stock mixing
within the Atlantic Ocean. Recent otolith chemistry studies have demonstrated mixed stock
composition in the western, central, and eastern Atlantic within our modeled range (Rooker et al.
2014; Siskey et al. 2016). These direct measures of stock composition were not included in the
otolith chemistry results that informed movement estimates in the MAST model (Rooker et al.
2008) and, therefore, provided an independent means of model validation. In general, scenarios
informed by bulk transfer movement estimates appear to align more closely with direct
observations of stock composition based on otolith chemistry. However, until we have further
resolution of stock composition within the western Atlantic it is difficult to suggest a single
model that best characterizes mixing in this region. Further investments in resolving stock
composition by season and life history stage in this region are needed.

Model Uncertainties

The operating model is subject to several sources of uncertainty. There is uncertainty in the
characterization of fish movement and how movement rates may vary with time: several
alternative parameterizations of movement are possible other than the ones explored here, and
each of these could result in different perceived population dynamics. Changes in movement of
the eastern population across the stock boundary would have considerable impact on the western
resource because of the asymmetry in biomass between eastern and western populations.
Additionally, changes in the productivity of the eastern population would likely impact the
biomass of eastern origin fish moving into the western stock area. Because of the sensitivity of
the perceived status of the western stock to movement of bluefin populations, further
development and application of the operating model approach is warranted along with
determining the relative plausibility rankings of alternative operating models. Furthermore,
fishing mortality and selectivity are included as constant parameters in the model. Because of
these simplifying assumptions of the model and the fact that time-varying properties were not
used, uncertainty associated with estimates of SSB and yield is underestimated. A key area of
operating model development needed to capture realistic dynamics will be incorporation of time
and fleet varying selectivity. This aspect has not been explored to date and the impact on
simulations is currently unknown.

The operating model is also subject to some of the same uncertainties in life history parameters
found in the current stock assessment framework. In addition to uncertainty in maturity
schedules and recruitment regime, there is uncertainty in estimates of natural mortality for
bluefin tuna stocks. Natural mortality is considered one of the least well estimated parameters in
the current stock assessment model (ICCAT 2013). Furthermore, parameters such as natural
mortality may fluctuate in response to predators whose population sizes also exhibit non-
stationarity (Esteban et al. 2016). Thus, improved information on life history and how these
quantities might be changing for each bluefin tuna stock will increase the realism of this
simulation model. Another dimension of complexity, not captured in the current model, are
indications of sub-population structure within the Mediterranean spawning population (e.g.,
Riccioni et al., 2010; ICCAT 2013) and evidence of bluefin tuna spawning outside of the Gulf of
Mexico (Richardson et al. 2016). Both of these scenarios could be explored further through
expanding the current operating model structure.

The operating model was conditioned on the stock-recruitment relationships derived from stock
assessment results. The simulations also assume several of the same vital rates as the stock
assessments (e.g., assumed natural mortality of the western stock and maturity of the eastern
stock), so the long-term productivity derived from stock assessments and our simulations are
generally similar. However, asymptotic recruitment and equilibrium age structure were used to
initialize simulations of the operating model, rather than the age structures estimated from stock
assessments, and constant fishing mortality was simulated rather than annually varying fishing
mortality. Therefore, the stock assessment estimates for the time series of stock size are not
directly comparable to our long-term simulations because of differences in starting stock size and
the time series of fishing mortality. Although we used the model framework for long-term
projections under status quo management, the modeling framework could also be used to project
current abundance at age, derived from stock assessment, for short-term catch projections or
medium-term rebuilding scenarios that account for movement and stock mixing.

To inform realistic models of fish movement and stock mixing, parameter values used in an
operating model (e.g., maturity, natural mortality, form of stock-recruitment relationships)
should be consistently estimated and ideally not come from various sources. However, internal
consistency of parameter values is a challenge for complex operating models. We used an integrated estimation model (MAST, Taylor et al. 2011) to simultaneously estimate key parameters, including fishing mortality, selectivity and movement rates, and supplemented the model with parameter values from ICCAT assessments where necessary (i.e. stock-recruitment relationships). Given the substantial amount of mixing suggested from simulation scenarios, estimates of stock-recruitment relationships are likely to be influenced by stock mixing. Therefore, further developments in simulations should be coordinated with advancements in spatially-explicit estimation models so that the operating model has stock-recruitment relationships, maturity, movement, fishing mortality and selectivity parameters that are mutually consistent.

*Lessons Learned from Simulation Modeling*

Simulation modeling demonstrated that the existing mismatch in the scale of bluefin tuna movement and management units (i.e., stocks) can have profound implications for the accuracy of stock assessment and the effectiveness of fishery management. Currently, the abundance of the eastern bluefin tuna stock is estimated to be an order of magnitude greater than the western Atlantic stock (ICCAT 2014). This asymmetry in production is reflected in the model and simulations illustrate that, because of the much greater abundance of the eastern stock compared to the west, even low movement rates of eastern origin fish into the western Atlantic will considerably influence the abundance and stock composition of bluefin tuna in the western stock unit. Likewise, western-origin bluefin tuna that move into the central and eastern Atlantic impact the stock composition in these regions and experience considerably greater fishing mortality that is unaccounted for in the current assessment framework. Simulations indicate that the eastern
stock is minimally impacted by explicit consideration of fish movement. However, the stock
view of the western resource can differ considerably from the population view.

This study exposed several key uncertainties for stock assessment and management of Atlantic
bluefin tuna. One of the primary lessons from this simulation study is that alternative approaches
to estimating movement (i.e., gravity and bulk transfer methods) produced alternative estimates
of movement that have important implications for long-term expectations. These differences in
modelled outcomes could have large consequences to management, and there is a need to resolve
this uncertainty. These findings have led towards development of fishery-independent movement
estimates (i.e., calculated outside of an estimation model) based on telemetry data alone
(Galuardi et al. 2014). Another lesson taken from simulations was the impact of the tight linkage
between maturity and movement patterns; this linkage makes understanding maturity in the
western population of paramount importance. The recent observation of larval bluefin tuna in the
Slope Sea and suggestion that smaller/younger bluefin tuna may be spawning outside of the Gulf
of Mexico emphasizes the need to understand the relationship between maturity and movement
(Richardson et al. 2016). Finally, simulations demonstrated that movement is the biggest source
of uncertainty in our perception of the bluefin tuna resource; however, the debate regarding a
western high or low recruitment regime will continue to be in issue in the context of modelling
the bluefin tuna resource, given its impact on the perception of productivity. Future operating
models that capture alternative population dynamics including movement, maturity and
recruitment will be a key part of undertaking management strategy evaluation in the future.

Understanding the spatio-temporal scale of bluefin tuna movement in relation to management
units is important for well-informed assessment and effective management. This study
demonstrates that model simulations can provide important insights with respect to the scale of
stock mixing, regions of high mixed stock composition, and can aid in identifying gaps and
uncertainty in knowledge that prevent an accurate view of the resource.

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Table 1. Description of geographic zones represented in the Atlantic bluefin tuna operating model and documentation supporting these regions as unique with respect to patterns in Atlantic bluefin tuna movement, life history stages utilizing these areas, and the dominant gear type(s) used within each region.

1. Gulf of Mexico (GOM, including Straits of Florida and Caribbean Sea)
   i. **Rationale:** Known western population spawning area.
   ii. **Boundaries:** Boundaries are defined by knowledge of spatial extent of western spawning area (ICCAT 2001, Taylor et al. 2011).
   iii. **Life stages present:** Eggs/larvae, juveniles, and adults (Rooker et al. 2007).
   iv. **Fisheries (incidental catch):** Longline.

2. Gulf of St. Lawrence (GSL)
   i. **Rationale:** Assumed to contain western origin fish only.
   ii. **Boundaries:** Boundaries are defined by sampling domain of otolith chemistry data which indicated fish in this region are solely of western origin (Rooker et al. 2008, Taylor et al. 2011).
   iii. **Life stages present:** Juveniles, adolescents, and adults (Rooker et al. 2007).
   iv. **Fisheries:** Rod and reel.

3. Western Atlantic Ocean (WA)
   i. **Rationale:** Assumed to be an area of stock mixing.
   ii. **Boundaries:** The western boundary is defined by knowledge of spatial extent of western spawning area, the Gulf of St. Lawrence and northern extent of the species range. The eastern boundary is defined by the management boundary (45°W, ICCAT 2001, Taylor et al. 2011).
   iii. **Life stages present:** Juveniles, adolescents, and adults (Rooker et al. 2007, 2008).
   iv. **Fisheries:** Rod and reel, longline, purse seine, and harpoon.

4. Central Atlantic Ocean (CA)
   i. **Rationale:** Assumed to be an area of stock mixing.
   ii. **Boundaries:** The western boundary is defined by the management boundary (45°W). The eastern boundary is defined by fact that few fish tagged in the west with electronic tags moved beyond 30°W (ICCAT 2001).
   iii. **Life stages present:** Adolescents and adults (Rooker et al. 2007).
   iv. **Fisheries:** Longline.
5. Eastern Atlantic Ocean (EA)
   i. **Rationale:** Assumed to be an area of stock mixing.
   ii. **Boundaries:** The western boundary is defined by fact that few fish tagged in the west with electronic tags moved beyond 30°W (ICCAT 2001). The eastern boundary is defined by knowledge of spatial extent of the eastern spawning area. The northern boundary is defined by differences in the proportional catch of eastern and western bluefin tuna north and south of this boundary (Block et al. 2005). Recaptures of both eastern (majority) and western (minority) origin fish have been documented in this zone (Block et al. 2005).
   iii. **Life stages present:** Juveniles, adolescents, and adults (Rooker et al. 2007).
   iv. **Fisheries:** Longline, bait boat, trap, and purse seine.

6. Northeast Atlantic Ocean (NEA)
   i. **Rationale:** Assumed to be an area dominated by eastern origin fish, minimal stock mixing
   ii. **Life stages present:** Adults (Rooker et al. 2007; 2008).
   iii. **Boundaries:** The western boundary is defined by fact that few fish tagged in the west with electronic tags moved beyond 30°W (ICCAT 2001). The eastern boundary is defined by the distribution of bluefin tuna. The southern boundary is defined by differences in the proportional catch of eastern and western bluefin tuna north and south of this boundary (Block et al. 2005). Block et al. 2005 indicated no recaptures of western origin fish in this zone.
   iv. **Fisheries:** Longline and purse seine.

7. Mediterranean Sea (MED)
   i. **Rationale:** Known eastern population spawning area.
   ii. **Boundaries:** The boundaries are defined by knowledge of spatial extent of eastern spawning area (ICCAT 2001, Taylor et al. 2011).
   iii. **Life stages present:** Eggs/larvae, juveniles, adolescents, and adults (Rooker et al. 2007, 2008).
   iv. **Fisheries:** Purse seine, longline, handline, and trap.
Table 2. Description of equations in the Atlantic bluefin tuna operating model.

| Eqn. 1 | \( N_{a_{i,1},y,z,p} = \frac{\alpha_p SSB_{q_1,y,z,p}}{\beta_p + SSB_{q_1,y,z,p}} \varepsilon_{y,p} \) |
| Eqn. 2 | \( N_{a_{i,1},y,z,p} = \begin{cases} \frac{R_{max_p} \varepsilon_{y,p}}{SSB^*_p} & \text{if } SSB_{q_1,y,z,p} \geq SSB^*_p \\ \frac{R_{max_p}}{SSB^*_p} SSB_{q_1,y,z,p} \varepsilon_{y,p} & \text{if } SSB_{q_1,y,z,p} < SSB^*_p \end{cases} \) |
| Eqn. 3 | \( N_{a_{q_1,y,z,p}} = N_{a_{-1,q_4,y-1,z,p}} T_{z\rightarrow z'} a_{-1,q_4,p} e^{-[M_q + F_{q,g}x_{y-1}]} \) |
| Eqn. 4 | \( N_{a,q_{-4},y,z,p} = N_{a,q_{-1},y,z,p} T_{z\rightarrow z'} a_{q,p} e^{-[M_q + F_{q,g}x_y]} \) |
| Eqn. 5 | \( SSB_{q,y,z,p} = \sum_{a=1}^{a=29} N_{a,q,y,z,p} W_{a,p} C_{a,p} \) |
| Eqn. 6 | \( Y_{q,y,z,p} = \sum_{a=1}^{a=29} N_{a,q,y,z,p} \frac{F_{q,g}x_y}{M_q + F_{q,g}x_y} \left[ 1 - e^{-\left(M_q + F_{q,g}x_y\right)} \right] W_{a,p} \) |
Table 3. Description of symbols used to denote parameters in Atlantic bluefin tuna operating model.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\alpha_p$</td>
<td>Maximum number of recruits per spawner in Beverton-Holt stock-recruit model</td>
</tr>
<tr>
<td>$\beta_p$</td>
<td>Parameter in Beverton-Holt stock-recruit model that controls the rate at which the asymptote, or maximum recruits per spawner, is reached.</td>
</tr>
<tr>
<td>$C_{a,p}$</td>
<td>Maturity-at-age of a population</td>
</tr>
<tr>
<td>$\varepsilon_{y,p}$</td>
<td>Error term in stock recruitment relationship of a population</td>
</tr>
<tr>
<td>$F_{q,g,z}$</td>
<td>Quarterly gear-specific fishing mortality across geographic zones</td>
</tr>
<tr>
<td>$\gamma_a$</td>
<td>Selectivity of fish at age</td>
</tr>
<tr>
<td>$M_q$</td>
<td>Quarterly natural mortality</td>
</tr>
<tr>
<td>$N_{a,q,y,z,p}$</td>
<td>Number of fish at age, quarter, year, zone, and population</td>
</tr>
<tr>
<td>$R_{\text{max}}^p$</td>
<td>Maximum recruitment of a population in a hockey stick stock-recruit model</td>
</tr>
<tr>
<td>$SSB_{q,y,z,p}$</td>
<td>Spawning stock biomass across quarter, year, zone and population</td>
</tr>
<tr>
<td>$SSB_p^*$</td>
<td>Spawning biomass threshold that triggers a different response in recruitment for a population in a hockey stick stock-recruit model</td>
</tr>
<tr>
<td>$T_{z \rightarrow z',a,q,p}$</td>
<td>Proportional movement of fish from one zone to another zone at age, quarter, and population</td>
</tr>
<tr>
<td>$W_{a,p}$</td>
<td>Weight-at-age of a population</td>
</tr>
<tr>
<td>$Y_{q,y,z,p}$</td>
<td>Yield across quarter, year, zone and population</td>
</tr>
</tbody>
</table>
Table 4. Long-term expectations of average spawning stock biomass and yield of Atlantic bluefin tuna across seasonal quarters from 500 model simulations across alternative scenarios informed by bulk transfer and gravity movement estimates (HR, Young: high recruitment, younger age at maturity; HR, Old: high recruitment, old age at maturity; LR, Young: low recruitment, younger age at maturity; LR, Young: low recruitment, old age at maturity).

<p>| | | | | | | | | | | |
|---------------------|-----------------------------------|---------|----------|-----------|----------|-----------|        |         |        |         |
| Gravity Movement    | High recruit, Younger maturity    | Q1      | 1,169,926| 1,148,344 | 107,867  | 106,825   | 5,590  | 5,972   | 1,002  | 928     |
|                     | Q2                                | 1,104,404| 1,064,083| 101,638   | 118,620  | 21,428    | 23,663 | 1,348   | 489    |
|                     | Q3                                | 1,055,000| 1,011,265| 96,112    | 116,556  | 9,118     | 10,898 | 1,002   | 680    |
|                     | Q4                                | 1,013,540| 955,306   | 91,822    | 133,117  | 4,632     | 5,359  | 329    |
|                     | Q1                                | 1,166,824| 1,148,344 | 107,867  | 106,825   | 5,590  | 5,972   | 1,002  | 928     |
|                     | Q2                                | 1,101,506| 1,040,455| 101,638   | 118,620  | 21,428    | 23,663 | 1,348   | 489    |
|                     | Q3                                | 1,052,138| 994,217   | 81,551    | 101,557  | 9,175     | 9,929  | 845    | 653    |
|                     | Q4                                | 1,010,996| 991,483   | 77,818    | 74,015   | 4,504     | 5,392  | 295    |
|                     | Q1                                | 1,165,943| 1,138,389 | 36,204    | 36,525   | 5,574     | 5,944  | 336    | 312    |
|                     | Q2                                | 1,100,634| 1,041,414| 34,113    | 65,643   | 21,363    | 22,901 | 452    | 299    |
|                     | Q3                                | 1,051,395| 986,049   | 32,258    | 70,578   | 9,090     | 9,834  | 640    | 463    |
|                     | Q4                                | 1,010,074| 928,022   | 30,819    | 92,711   | 4,618     | 4,937  | 259    | 230    |
|                     | Q1                                | 1,165,984| 1,144,308| 31,767    | 31,283   | 5,575     | 5,955  | 326    | 293    |
|                     | Q2                                | 1,100,708| 1,035,736| 30,428    | 52,684   | 21,368    | 22,664 | 335    | 415    |
|                     | Q3                                | 1,051,373| 988,345   | 29,256    | 51,880   | 9,170     | 9,625  | 304    | 425    |
|                     | Q4                                | 1,010,259| 968,624   | 27,917    | 43,678   | 4,502     | 4,936  | 325    | 176    |
| Bulk Transfer Movement | High recruit, Younger maturity  | Q1      | 1,183,559| 1,162,945| 122,877  | 121,657   | 5,672  | 6,060   | 1,142  | 1,058   |
|                     | Q2                                | 1,118,669| 1,067,455| 115,502   | 142,128  | 21,176    | 23,568 | 1,767   | 723    |
|                     | Q3                                | 1,069,231| 1,038,045| 109,560   | 142,841  | 8,673     | 10,029 | 1,836   | 988    |</p>
<table>
<thead>
<tr>
<th>Quarter</th>
<th>High recruit, Older maturity</th>
<th>Low recruit, Younger maturity</th>
<th>Low recruit, Older maturity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Q4</td>
<td>1,027,532</td>
<td>976,863</td>
<td>105,204</td>
</tr>
<tr>
<td>Q1</td>
<td>1,183,829</td>
<td>1,198,985</td>
<td>57,084</td>
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<tr>
<td>Q2</td>
<td>1,118,926</td>
<td>1,133,146</td>
<td>53,771</td>
</tr>
<tr>
<td>Q3</td>
<td>1,069,541</td>
<td>1,082,854</td>
<td>50,951</td>
</tr>
<tr>
<td>Q4</td>
<td>1,027,901</td>
<td>1,027,868</td>
<td>48,850</td>
</tr>
<tr>
<td>Q1</td>
<td>1,177,510</td>
<td>1,150,148</td>
<td>38,837</td>
</tr>
<tr>
<td>Q2</td>
<td>1,112,954</td>
<td>1,040,583</td>
<td>36,506</td>
</tr>
<tr>
<td>Q3</td>
<td>1,063,769</td>
<td>1,014,916</td>
<td>34,628</td>
</tr>
<tr>
<td>Q4</td>
<td>1,022,284</td>
<td>961,568</td>
<td>33,251</td>
</tr>
<tr>
<td>Q1</td>
<td>1,187,171</td>
<td>1,193,883</td>
<td>26,168</td>
</tr>
<tr>
<td>Q2</td>
<td>1,122,090</td>
<td>1,127,695</td>
<td>24,649</td>
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<tr>
<td>Q3</td>
<td>1,072,567</td>
<td>1,077,567</td>
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<tr>
<td>Q4</td>
<td>1,030,811</td>
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Figure Captions

**Figure 1.** Geographic zones represented in the Atlantic bluefin tuna operating model (see Table 1 for a full description of zones), including GOM: Gulf of Mexico, GSL: Gulf of St. Lawrence, WA: western Atlantic Ocean, CA: central Atlantic Ocean, EA: eastern Atlantic, NEA: northeast Atlantic, and MED: Mediterranean Sea.

**Figure 2.** Fishing mortality by gear type (LL: long-line, BB: bait boat, PS: purse seine, and Other), seasonal quarters (1-4), and geographic zones (GOM: Gulf of Mexico, GSL: Gulf of St. Lawrence, WA: western Atlantic Ocean, CA: central Atlantic Ocean, EA: eastern Atlantic, NEA: northeast Atlantic, and MED: Mediterranean Sea). Values are based on averaged quarterly F values for 2008 and 2009 estimated from the MAST model (Taylor et al. 2011). Because of the difference in modeled zones between MAST and the current model, values of F in the central, eastern, and northeast Atlantic were all set equivalent to values of F estimated for the eastern Atlantic in MAST. Asterisks indicate zero fishing mortality within the specific quarter and zone.

**Figure 3.** Spawning stock biomass and yield (mT) of western (a, c) and eastern (b, d) Atlantic bluefin tuna populations across seasonal quarters (1-4) and geographic zones (GOM: Gulf of Mexico, GSL: Gulf of St. Lawrence, WA: western Atlantic Ocean, CA: central Atlantic Ocean, EA: eastern Atlantic, NEA: northeast Atlantic, and MED: Mediterranean Sea). Movement rates were estimated using the gravity method and the model was simulated under alternative recruitment regimes (high and low) and assumptions of maturity at age (younger and older) for the western bluefin tuna population. Note that y-axes differ by an order of magnitude between eastern and western populations.
Figure 4. Mixed stock composition of spawning biomass and yield of Atlantic bluefin tuna in regions of mixing (WA: western Atlantic Ocean, CA: central Atlantic Ocean, EA: eastern Atlantic) across seasonal quarters (1-4). The gravity method was used to estimate movement under alternative assumptions of recruitment (high, low) and maturity (younger maturity, older maturity) for western bluefin tuna.

Figure 5. Spawning stock biomass (a) and yield (b) of western and eastern populations and stocks across quarters (1-4). The gravity method was used to estimate movement under alternative assumptions of recruitment (high, low) and maturity (younger maturity, older maturity) for western bluefin tuna.

Figure 6. Spawning stock biomass and yield (mt) of western (a, c) and eastern (b, d) Atlantic bluefin tuna populations across seasonal quarters (1-4) and geographic zones (GOM: Gulf of Mexico, GSL: Gulf of St. Lawrence, WA: western Atlantic Ocean, CA: central Atlantic Ocean, EA: eastern Atlantic, NEA: northeast Atlantic, and MED: Mediterranean Sea). Movement rates were estimated using the bulk transfer method and the model was simulated under alternative recruitment regimes (high and low) and assumptions of maturity at age (younger and older) for the western bluefin tuna population. Note that y-axes differ by an order of magnitude between eastern and western populations.

Figure 7 Mixed stock composition of spawning biomass and yield of Atlantic bluefin tuna in regions of mixing (WA: western Atlantic Ocean, CA: central Atlantic Ocean, EA: eastern Atlantic) across seasonal quarters (1-4). The bulk transfer method was used to estimate movement under alternative assumptions of recruitment (high, low) and maturity (younger
maturity, older maturity) for western bluefin tuna.

**Figure 8.** Spawning stock biomass (a) and yield (b) of western and eastern populations and stocks across seasonal quarters (1-4). The bulk transfer method was used to estimate movement under alternative assumptions of recruitment (high, low) and maturity (younger maturity, older maturity) for western bluefin tuna.
Figure 1
Figure 2
Figure 3

Time (quarters)
Geographic Zone

Spawning Stock Biomass ('000 mT)

Yield ('000 mT)
Figure 4
Figure 5
Figure 6

Time (quarters)

Geographic Zone

https://mc06.manuscriptcentral.com/cjfas-pubs
Figure 7

- High recruit, younger maturity
- Low recruit, younger maturity
- High recruit, older maturity
- Low recruit, older maturity

- SSB (mT)
- Yield (mT)

- WA
- CA
- EA

West
East
Figure 8

The figure shows the values of West SSB ('000 mT) and East SSB ('000 mT) for different maturity stages (Younger and Older) and recruit levels (High and Low) for both West and East populations and stocks.

For West SSB ('000 mT):
- High recruit, Younger maturity
- High recruit, Older maturity
- Low recruit, Younger maturity
- Low recruit, Older maturity

For East SSB ('000 mT):
- High recruit, Younger maturity
- High recruit, Older maturity
- Low recruit, Younger maturity
- Low recruit, Older maturity

The data points are represented using different markers (circles, squares, triangles) for each maturity and recruit level.
### Movement Matrices estimated using the MAST model (Taylor et al 2011).
Eastern pop. = unit 1, Western pop. = unit 2, spawning quarter=1, spawning zones = 1 (Gulf of Mexico) & 7 (Mediterranean Sea)

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https://mc06.manuscriptcentral.com/cjfas-pubs
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https://mc06.manuscriptcentral.com/cjfas-pubs
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2 0.44760600 0.00002510 0.00012687 0.9522420 0 0 0
3 0.00385973 0.00206493 0.98298500 0.0110899 0 0 0
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,, quarter = 4, age = 23, unit = 2
zone
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2 0.30210400 0.00001640 0.33649100 0.3613890 0 0 0
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6 0.00000000 0.00000000 0.00000000 0.0000000 0 0 0
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,, quarter = 1, age = 24, unit = 2
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2 1 5.08e-12 1.31e-14 1.31e-14 0 0 0
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3  0.00461983  2.44094e-03  0.96123300  0.0317067  0  0  0
4  0.03781710  1.41130e-02  0.00004300  0.9480270  0  0  0
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**Note:** Each block of data represents the statistics for a specific quarter, age, and unit combination.
### Quarter 3, Age 29, Unit 2

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Eastern pop. = unit 1, Western pop. = unit 2, spawning quarter = 1, spawning zones = 1 (Gulf of Mexico) & 7 (Mediterranean Sea)

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https://mc06.manuscriptcentral.com/cjfas-pubs
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Canadian Journal of Fisheries and Aquatic Sciences
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3 0 0 0.000000000 0.000000000 0.000000000 0.000000000 0.000000000
4 0 0 0.000000000 0.000000000 0.000000000 0.000000000 0.000000000
5 0 0 0.000000000 0.000000000 0.000000000 0.000000000 0.000000000
6 0 0 0.000000000 0.000000000 0.000000000 0.000000000 0.000000000
7 0 0 0.000000000 0.000000000 0.000000000 0.000000000 0.000000000

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quarter = 1, age = 25, unit = 1

zone

zone 1 2 3 4 5 6 7
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2 0 0 0 0 0 0 0
3 0 0 0 0 0 0 1
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quarter = 2, age = 25, unit = 1

zone

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2 0 0 0.000000 0.0000000 0.0000000 0.0000000 0.0000000 0.0000000
3 0 0 0.974641 0.0082069 0.0082069 0.0082069 0.0007387
4 0 0 0.438810 0.1764533 0.1764533 0.1764533 0.0318300
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quarter = 3, age = 25, unit = 1

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quarter = 4, age = 25, unit = 1

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Canadian Journal of Fisheries and Aquatic Sciences
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Thus, quarter = 2, age = 2, unit = 2

Thus, quarter = 3, age = 2, unit = 2

Thus, quarter = 4, age = 2, unit = 2

Thus, quarter = 1, age = 3, unit = 2

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3  0.0193382  0.0824851  0.8325880  0.0327943  0.0327943  0  0
4  0.0663658  0.7876890  0.0141584  0.0658935  0.0658935  0  0
5  0.0663658  0.7876890  0.0141584  0.0658935  0.0658935  0  0
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3  0.64565  0.0048343  0.3446810  0.0024172  0.0024172  0  0
4  0.64565  0.0597455  0.0597455  0.1174295  0.1174295  0  0
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2  0.2494070  0.3786190  0.1535070  0.1092340  0.1092340  0  0
3  0.0651801  0.0812293  0.7993560  0.0271176  0.0271176  0  0
4  0.4844040  0.1093480  0.0753687  0.1654400  0.1654400  0  0
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3  0.281312  0.0362411  0.5671370  0.0124794  0.0124794  0  0
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3 0.00535689 5.31433e-03 0.959209000 0.0301202 0 0 0
4 0.05839930 5.66370e-02 0.000040200 0.8849240 0 0 0
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zone          1           2           3         4 5 6 7
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3 0.00388466 0.001870280 0.983549000 0.0106958 0 0 0
4 0.01860600 0.007104100 0.054638000 0.9196520 0 0 0
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3 7.44e-18 2.07e-16 7.44e-18 0 0 0 0 0
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, quarter = 2, age = 28, unit = 2

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3 0.00388466 0.001870280 0.983549000 0.0106958 0 0 0
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, quarter = 1, age = 29, unit = 2

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### Movement Matrices estimated using the MAST model (Taylor et al. 2011).

- Eastern pop. = unit 1, Western pop. = unit 2,
- spawning quarter = 1, spawning zones = 1 (Gulf of Mexico) & 7 (Mediterranean Sea)

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6 0 0 0.1793100 0.213793667 0.213793667 0.213793667 0.1793100
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7 0 0 0.00421207 0.001404023 0.001404023 0.001404023 0.9915760

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6 0 0 1.32e-08 7.333333e-10 7.333333e-10 7.333333e-10 1
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https://mc06.manuscriptcentral.com/cjfas-pubs
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7 0 0 0.00421207 0.001404023 0.001404023 0.001404023 0.99157600

zone
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https://mc06.manuscriptcentral.com/cfjas-pubs
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, , quarter = 3, age = 29, unit = 1

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Canadian Journal of Fisheries and Aquatic Sciences
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### Movement Matrices estimated using the MAST model (Taylor et al. 2011).

Eastern pop. = unit 1, Western pop. = unit 2,
spawning quarter = 1, spawning zones = 1 (Gulf of Mexico) & 7 (Mediterranean Sea)

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, quarter = 2, age = 7, unit = 1

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1 0 0 0.00000000 0.00000000 0.00000000 0.00000000 0.999749
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3 0 0 0.95895600 0.00684063 0.00684063 0.00684063 0.0205219
4 0 0 0.20976600 0.19348967 0.19348967 0.19348967 0.2097660
5 0 0 0.20976600 0.19348967 0.19348967 0.19348967 0.2097660
6 0 0 0.20976600 0.19348967 0.19348967 0.19348967 0.2097660
7 0 0 0.03866010 0.01288670 0.01288670 0.01288670 0.9226800

, quarter = 3, age = 7, unit = 1

zone
zone 1 2 3 4 5 6 7
1 0 0 0.00000000 0.00000000 0.00000000 0.00000000 0.999749
2 0 0 0.00000000 0.00000000 0.00000000 0.00000000 0.999749
3 0 0 0.92207200 0.01298803 0.01298803 0.01298803 0.0389641
4 0 0 0.22802600 0.18131633 0.18131633 0.18131633 0.2280260
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6 0 0 0.22802600 0.18131633 0.18131633 0.18131633 0.2280260
7 0 0 0.00635445 0.00211815 0.00211815 0.00211815 0.9872910

, quarter = 4, age = 7, unit = 1

zone
zone 1 2 3 4 5 6 7
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2 0 0 0.00000000 0.00000000 0.00000000 0.00000000 0.999749
3 0 0 0.96339800 0.00610030 0.00610030 0.00610030 0.0183009
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5 0 0 0.26029400 0.15980367 0.15980367 0.15980367 0.2602940
6 0 0 0.26029400 0.15980367 0.15980367 0.15980367 0.2602940
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, quarter = 1, age = 8, unit = 1

zone
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5 0 0 0.00023808 3.380833e-05 3.380833e-05 3.380833e-05 0.999600
6 0 0 0.00023808 3.380833e-05 3.380833e-05 3.380833e-05 0.999600
7 0 0 0.00032823 3.766667e-06 3.766667e-06 3.766667e-06 0.999600

, quarter = 2, age = 8, unit = 1

zone
zone 1 2 3 4 5 6 7
1 0 0 0.00000000 0.00000000 0.00000000 0.00000000 0.00000000
zone
zone 1 2 3 4 5 6 7
1 0 0 0.0000000 0.0000000 0.0000000 0.0000000 0.0000000 0.0000000
2 0 0 0.9589560 0.0068406 0.0068406 0.0068406 0.0205219 0.0000000
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4 0 0 0.2097660 0.1934897 0.1934897 0.1934897 0.2097660 0.2097660
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6 0 0 0.2097660 0.1934897 0.1934897 0.1934897 0.2097660 0.2097660
7 0 0 0.0386601 0.0128867 0.0128867 0.0128867 0.0128867 0.9226800

zone
zone 1 2 3 4 5 6 7
1 0 0 0.0000000 0.0000000 0.0000000 0.0000000 0.0000000 0.0000000
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6 0 0 0.2097660 0.1934897 0.1934897 0.1934897 0.2097660 0.2097660
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zone
zone 1 2 3 4 5 6 7
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zone
zone 1 2 3 4 5 6 7
1 0 0 0.0000000 0.0000000 0.0000000 0.0000000 0.0000000 0.0000000
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zone
zone 1 2 3 4 5 6 7
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2 0 0 0.9589560 0.0068406 0.0068406 0.0068406 0.0205219 0.0000000
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Canadian Journal of Fisheries and Aquatic Sciences
zone
zone 1 2 3 4 5 6 7
1 0 0 0.00000000 0.00000000 0.00000000 0.00000000 0.00000000
2 0 0 0.00000000 0.00000000 0.00000000 0.00000000 0.00000000
3 0 0 0.92207200 0.01298803 0.01298803 0.01298803 0.0389641
4 0 0 0.22802600 0.18131633 0.18131633 0.18131633 0.22802600
5 0 0 0.22802600 0.18131633 0.18131633 0.18131633 0.22802600
6 0 0 0.22802600 0.18131633 0.18131633 0.18131633 0.22802600
7 0 0 0.00635445 0.00211815 0.00211815 0.00211815 0.9872910

, , quarter = 4, age = 14, unit = 1

zone
zone 1 2 3 4 5 6 7
1 0 0 0.00000000 0.00000000 0.00000000 0.00000000 0.00000000
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3 0 0 0.96339800 0.006100300 0.006100300 0.006100300 0.0183009
4 0 0 0.26029400 0.159803667 0.159803667 0.159803667 0.26029400
5 0 0 0.26029400 0.159803667 0.159803667 0.159803667 0.26029400
6 0 0 0.26029400 0.159803667 0.159803667 0.159803667 0.26029400
7 0 0 0.02764550 0.009215167 0.009215167 0.009215167 0.9447090

, , quarter = 1, age = 15, unit = 1

zone
zone 1 2 3 4 5 6 7
1 0 0 0.00000000 0.00000000 0.00000000 0.00000000 0.00000000
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, , quarter = 2, age = 15, unit = 1

zone
zone 1 2 3 4 5 6 7
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2 0 0 0.00000000 0.00000000 0.00000000 0.00000000 0.00000000
3 0 0 0.92207200 0.01298803 0.01298803 0.01298803 0.0389641
4 0 0 0.22802600 0.18131633 0.18131633 0.18131633 0.22802600
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6 0 0 0.22802600 0.18131633 0.18131633 0.18131633 0.22802600
7 0 0 0.00635445 0.00211815 0.00211815 0.00211815 0.9872910

, , quarter = 3, age = 15, unit = 1

zone
zone 1 2 3 4 5 6 7
1 0 0 0.00000000 0.00000000 0.00000000 0.00000000 0.00000000
2 0 0 0.00000000 0.00000000 0.00000000 0.00000000 0.00000000
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6 0 0 0.20976600 0.193489667 0.193489667 0.193489667 0.20976600
7 0 0 0.03866010 0.012886700 0.012886700 0.012886700 0.9226800

, , quarter = 4, age = 15, unit = 1

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zone 1 2 3 4 5 6 7
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Canadian Journal of Fisheries and Aquatic Sciences

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, quarter = 4, age = 20, unit = 1

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| zone 5 | 0 | 0 | 0.228026000 | 0.181316330 | 0.181316330 | 0.181316330 | 0.228026000 |
| zone 6 | 0 | 0 | 0.228026000 | 0.181316330 | 0.181316330 | 0.181316330 | 0.228026000 |
| zone 7 | 0 | 0 | 0.006354450 | 0.002118150 | 0.002118150 | 0.002118150 | 0.987291000 |

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| zone 5 | 0 | 0 | 0.260294000 | 0.159803667 | 0.159803667 | 0.159803667 | 0.260294000 |
| zone 6 | 0 | 0 | 0.260294000 | 0.159803667 | 0.159803667 | 0.159803667 | 0.260294000 |
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| zone 4 | 0 | 0 | 0.2097660 | 0.193489667 | 0.193489667 | 0.193489667 | 0.2097660 |
| zone 5 | 0 | 0 | 0.2097660 | 0.193489667 | 0.193489667 | 0.193489667 | 0.2097660 |
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zone 1 2 3 4 5 6 7
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2 0.000000 0.0000681 0.4999660 0.4999660 0 0 0
3 0.000000 0.0211470 0.9577060 0.0211470 0 0 0
4 0.000000 0.000000 0.1810020 0.8189980 0 0 0
5 0.000000 0.000000 0.000000 0.000000 0 0 0
6 0.000000 0.000000 0.000000 0.000000 0 0 0
7 0.000000 0.000000 0.000000 0.000000 0 0 0

, quarter = 4, age = 14, unit = 2

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3 0.00e+00 0.0124185 0.975163 0.0124185 0 0 0
4 0.00e+00 0.1558190 0.155819 0.6883620 0 0 0
5 0.00e+00 0.000000 0.000000 0.000000 0 0 0
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7 0.00e+00 0.000000 0.000000 0.000000 0 0 0

, quarter = 1, age = 15, unit = 2

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2 1 6.15e-08 1.40e-10 1.40e-10 0 0 0
3 1 2.21e-09 5.73e-08 2.21e-09 0 0 0
4 1 2.59e-09 2.59e-09 5.66e-08 0 0 0
5 0 0.00e+00 0.00e+00 0.00e+00 0 0 0
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3 0.000000 0.025097 0.949806 0.025097 0 0 0
4 0.000000 0.000000 0.0943494 0.905651 0 0 0
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