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EVALUATING THE EFFECT OF ATLANTIC BLUEFIN TUNA MOVEMENT ON THE PERCEPTION OF STOCK UNITS

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SUMMARY

Atlantic bluefin tuna is currently managed as separate eastern and western stocks. However, tagging, genetics, contaminants, and otolith chemistry patterns indicate considerable stock mixing. We developed a simulation model to explore the consequences of bluefin tuna population structure and movement on stock productivity and composition. The analytical framework is a stochastic, age-structured, overlap model that is seasonally and spatially-explicit. The operating model emulates the vital rates, recruitment dynamics, and movement (informed by tagging and otolith chemistry data) of eastern and western spawning populations. Alternate model settings were considered, including using different movement model parameterizations and two prevailing assumptions of recruitment for the western population. The modeled spatial and temporal distribution and relative abundance of eastern and western populations is sensitive to assumptions of recruitment regime and population movement, because they imply different spatio-temporal distributions of the resource and exposure to different fishing mortalities. Simulation results can be used to identify research priorities for assessment and management, to inform the appropriate configurations for spatially-explicit stock assessment models, and to form the foundation for evaluating alternative management scenarios in the context of fish movement.

RÉSUMÉ

Le thon rouge est actuellement géré en deux stocks séparés, l'Est et l'Ouest. Toutefois, les schémas de marquage, de génétique, des contaminants et de la chimie des otolithes indiquent un important mélange entre les stocks. Nous avons mis au point un modèle de simulation afin d'explorer les conséquences de la structure de la population et les mouvements du thon rouge sur la productivité et la composition du stock. Le cadre analytique est un modèle de chevauchement structuré par âge et stochastique qui est saisonnièrement et spatialement explicite. Le modèle opérationnel émule les indices vitaux, les dynamiques de recrutement et le mouvement (calculé au moyen des données de marquage et de la chimie des otolithes) des populations reproductrices de l'Est et de l'Ouest. D'autres configurations du modèle ont été envisagées, incluant l'utilisation de différentes paramétrisations du modèle de mouvement et deux postulats prédominants de recrutement de la population occidentale. La distribution spatio-temporelle modélisée ainsi que l'abondance relative des populations de l'Est et de l'Ouest sont sensibles aux postulats du régime de recrutement et des mouvements de la population, car elles impliquent différentes distributions spatio-temporelles de la ressource et une exposition à diverses mortalités par pêche. Les résultats de la simulation peuvent être utilisés pour identifier les priorités en matière de recherche pour l'évaluation et la gestion, pour apporter des informations aux configurations appropriées pour des modèles d'évaluation des stocks spatialement explicites et pour servir de base à l'évaluation des scénarios de gestion alternatifs dans le contexte du mélange des stocks.

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RESUMEN

El atún rojo del Atlántico se gestiona actualmente como dos stocks separados, un stock oriental y otro occidental. Sin embargo, los patrones de marcado, genéticos, contaminantes y de química de otolitos indican una mezcla considerable de los stocks. Se desarrolló un modelo de simulación para explorar las consecuencias del movimiento y la estructura de la población de atún rojo sobre la productividad y composición del stock. El marco analítico es un modelo solapado, estocástico, estructurado por edad que es estacional y espacialmente explícito. El modelo operativo emula las tasas vitales, la dinámica de reclutamiento y el movimiento (con datos de marcado y de química de otolitos) de las poblaciones reproductoras del este y del oeste. Se consideraron especificaciones del modelo alternativas, incluido el uso de diferentes parametrizaciones del modelo de movimiento y dos supuestos predominantes de reclutamiento para la población occidental. La distribución espacial y temporal modelada y la abundancia relativa de las poblaciones oriental y occidental son sensibles a supuestos de régimen de reclutamiento y movimiento de la población, porque implican diferentes distribuciones espacio-temporales del recurso y la exposición a diferentes mortalidades por pesca. Los resultados de la simulación pueden usarse para identificar prioridades de investigación para las evaluaciones y la ordenación, para aportar información a las configuraciones adecuadas para modelos de evaluación de stock espacialmente explícitos y para servir de base para evaluar escenarios de ordenación alternativos en el contexto del movimiento de los peces.

KEYWORDS

Atlantic bluefin tuna, Stochastic models, Simulation, Migrations, Population structure

1. Introduction

Atlantic bluefin tuna (*Thunnus thynnus*) is a highly migratory species with a distribution that spans the north Atlantic basin. In the past two decades, a suite of research methods have been applied to improve our understanding of bluefin tuna population structure and mixing. The combination of genetics, conventional and electronic tagging, contaminants, and otolith chemistry data supports the idea of at least 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 (Block *et al.* 2005, Carlsson *et al.* 2004, 2007, Boustany *et al.* 2008, Rooker *et al.* 2008a,b, Dickhut *et al.* 2009, Galuardi 2010). Evidence indicates that adult bluefin tuna exhibit a high degree of natal homing (~100%) to their two respective spawning grounds (Mediterranean Sea and Gulf of Mexico, Rooker *et al.* 2008a, b, 2014). However, there is also evidence of extensive population mixing at younger ages that is believed to be related to feeding migrations. Information from satellite and archival tagging confirms that some juveniles and adults make trans-Atlantic migrations (Lutcavage *et al.* 1999, 2001, Block *et al.* 2001, 2005, Galuardi *et al.* 2010, Rooker *et al.* 2014). Furthermore, otolith chemistry data has revealed mixed stock composition of bluefin tuna that depends on the region sampled within the Atlantic, as well as the size/life-stage, and year-class of fish (Rooker *et al.* 2008a, b, 2014, Secor *et al.* in press). Stock mixing rates on foraging grounds in the mid-Atlantic suggest the potential for large contributions (as high as 54%) of eastern-origin fish in western fisheries (Secor *et al.* in press). Increased focus on understanding the movement of this species has revealed complex spatial dynamics that differ between populations and over the lifetime of individuals. Failure to recognize the role of mixing in population and fishery dynamics of bluefin tuna may compromise the accuracy of assessment and effectiveness of management efforts.

The assessment and management of North Atlantic bluefin tuna fisheries requires international cooperation which is coordinated by the International Commission for the Conservation of Atlantic Tunas (ICCAT). Bluefin tuna is currently managed as two stocks, eastern and western, which are assessed separately using virtual population analysis (VPA). Although stock mixing scenarios have been explored (e.g., Porch *et al.* 2001, Taylor *et al.* 2011), they are currently not used to provide advice to management, and recent stock assessments assume no mixing (Anon. 2009, 2013). The abundance of the eastern bluefin tuna stock is estimated to be an order of magnitude greater than the western Atlantic stock (Anon. 2013). Most recently, the spawning stock biomass (SSB) of the eastern stock was estimated to be between 37-89% of the SSB (based on reported catch) needed to support maximum sustainable yield ($SSB_{F0.1}$), and the SSB of the western stock was estimated to be either 140% SSB_{MSY} or 19% SSB_{MSY} under either the low or high recruitment regime assumptions, respectively (Anon. 2013). Thus, both stocks of bluefin tuna may be overfished, and the management focus is on rebuilding stocks to the biomass that can produce MSY (B_{MSY}). Recent strong recruitment, that is apparent in both eastern and western stock assessments (Anon. 2013), and stock mixing is a major uncertainty for informing fisheries management strategies and annual TACs.

The mismatch in the scale of bluefin tuna life history and management (i.e., the stock unit) may have profound implications to the accurate assessment and sustainable management of the species (Kerr *et al.* 2013). Stock mixing violates the 'unit stock' assumption underlying the current assessment approach which applies VPA to separate eastern and western stocks (Anon. 2009, 2013). Since the data collected to inform these separate assessments are likely composed of fish of mixed stock origin, the VPAs confound indices of abundance, catch data, characterization of life history parameters and stock-recruit relationships. Therefore, ignoring stock mixing can potentially result in inaccurate estimates of stock abundance and sustainable yield and misinterpretation of apparent trends in fishery assessment (Kerr *et al.* 2013, Secor 2014). The most recent assessments for Atlantic bluefin tuna support significant differences in relative abundance and productivity between stocks, with the eastern population estimated to be an order of magnitude greater than the western population (Anon. 2013). Because of the much higher abundance of the eastern stock, even low movement rates of eastern origin fish into the western Atlantic will exert considerable influence on the abundance and stock composition of bluefin tuna in this region (NRC 1994). Furthermore, western-origin bluefin tuna that move into the eastern Atlantic may experience considerably higher fishing mortality than is accounted for in the current assessment framework. In general, the harvest of mixed stock aggregations can lead to overfishing of less productive populations and under-fishing more productive populations (Ricker 1958, Cadrin and Secor 2009). In the case of Atlantic bluefin tuna, a combination of overestimated productivity and unaccounted for mortality of the western stock may be responsible for the apparent lack of response of western bluefin tuna to a long-term rebuilding plan (Taylor *et al.* 2011). Understanding the spatio-temporal scale of bluefin tuna movement in relation to management units is important for well-informed assessment and effective management.

Considerable research has gone into the development of approaches to incorporate stock mixing into Atlantic bluefin tuna stock assessments (e.g., Butterworth and Punt 1994, NRC 1994, Porch *et al.* 2001). The most advanced of these models is the Multi-stock Age-Structured Tag-integrated stock assessment model (MAST). MAST is a recently developed statistical catch-at-age model that integrates stock structure and stock mixing information into a single assessment model (Taylor *et al.* 2011). Taylor *et al.* (2011) used electronic and conventional tagging, catch, and otolith chemistry data to model seasonal matrices of regional stock movements by Atlantic bluefin tuna. The model used bayesian methods for parameter estimation, which permitted simultaneous use of diverse types of data to estimate past abundance trends, movement and fishing rates. Although continued advancement in a two-stock, tag-integrated assessment model is needed, the approach is considered to be developmental for the purpose of providing management advice because simultaneous estimation of movement rates, fishing mortality, selectivity and recruitment remains a challenge, and results are somewhat sensitive to model assumptions and configurations (Taylor *et al.* 2011). However, development of this approach further in the context of an operating model designed to simulate stock mixing can enable exploration of a range of questions relevant to our understanding of population structure and connectivity and its impact on conservation and management goals (Kerr *et al.* 2013).

An advantage of simulation models is their flexibility in accommodating multiple types of information and levels of structural organization (Kerr *et al.* 2014b). Simulation modeling can be used to test a variety of different questions including the performance of alternative data collection and stock assessment approaches. Simulation modeling has been applied to explore the consequences of mis-specification of stock and connectivity for other species. In age-structured simulation models, Kerr *et al.* (2014a) showed that mis-specifying stock structure of Atlantic cod off New England could lead to over estimation of productivity. In the cod case study, modeling the independent dynamics and connectivity of spawning populations resulted in a revised view of the resource with lower SSB and potential yield than indicated by the management unit view. In a similar exercise, Kell *et al.* (2009) observed that the consequences of lumping rather than splitting population components of British Isles herring caused a virtual population assessment model to yield optimistic predictions of the level of overall fishing rates and probability of recovery following depletion.

The goal of this study was to develop an age-structured simulation model for Atlantic bluefin tuna and use it to explore the leading hypotheses of bluefin tuna stock structure and mixing. We aimed to bring biological realism to a dynamic model of bluefin tuna stocks, incorporating the best available science on population structure and movement between the eastern and western populations of bluefin tuna to explore the impact of connectivity on productivity, stability, sustainable yield, and rebuilding goals for bluefin tuna stocks. We examined the implications of different assumptions of productivity for the western population and the impact different methods of estimating movement rates had on results.

2. Methods

The operating model includes two spawning populations, based on eastern and western Atlantic bluefin tuna populations, each with its own unique vital rates and independent recruitment dynamics. The model is a stochastic age-structured (age 1 to 30), 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 (Porch *et al.* 1998, Anon. 2002). Additionally, quarterly time steps were viewed by species experts to be sufficient to capture changes in bluefin tuna movement patterns and the associated fisheries (Anon. 2002).

The spatial strata of the model are informed by 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;** Anon. 2002, Rooker *et al.* 2007, Taylor *et al.* 2011). The strata include the known spawning regions 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**).

2.1 Model Parameters

The values and variances of several model parameters were informed by the most recent ICCAT stock assessments (**Table 2**). Other model parameters were informed by recent peer-reviewed research on movement, mixing, reproductive schedules, and geographic variation in life history traits (**Table 2**).

Length-at-age was estimated from von Bertalanffy growth models, and length-weight relationships were used to estimate weight-at-age of eastern and western bluefin tuna (**Table 2**). The maturity at age schedule for the western stock assumed 50% maturity at age 12 and 100% maturity at age 16 (Diaz and Turner 2007, Anon. 2009). The maturity at age schedule for the eastern stock assumed 50% maturity at age-4 and 100% maturity at age-5 (Mather *et al.* 1995, Anon. 2011). Although alternative estimates of maturity at age are available, the movement rates available from Taylor *et al.* (2011) are conditioned on maturity. Thus, consideration of alternative maturity at age require revised estimates of movement. Natural mortality rates are not well-characterized for bluefin tuna. Natural mortality for bluefin tuna was assumed to be age-independent (M = 0.14 yr^{-1}, Anon 1997, Anon. 2013) based on the current assumption for the western stock assessment (**Table 2**).

A Beverton-Holt stock recruit curve was used to characterize the stock-recruit relationship for western bluefin under the high recruitment scenario (model includes SSB and recruitment data from 1971 to 2008) and a hockey-stick model characterized the relationship under the low recruitment scenario (Anon. 2011; **Table 2**). In the hockey-stick model for the western bluefin tuna, maximum recruitment (*Rmax*) was defined as the geometric mean number of recruits from 1976-2008 (**Table 2**). A hockey-stick stock-recruit relationship was used to characterize the stock-recruit relationship for the eastern stock. Hockey-stick parameters for the eastern stock were estimated as the average spawning stock biomass (SSB threshold) and geometric mean number of recruits (*Rmax*) from 1955-2007 (**Table 2**).

Annual fishing mortality rates by gear type (long-line, purse seine, bait boat, and other), quarter, and zone estimated in the MAST model (average quarterly F for 2008 to 2009) informed simulations of the operating model (**Table 3**; Taylor *et al.* 2011). Because of the difference in modeled zones between MAST and the current model, values of F estimated for zone 4 in MAST were equivalent to F in zones 4, 5, and 6 in this model (**Table 3**). Gear selectivity at age was estimated in the MAST model as a global selectivity across gear types (Taylor *et al.* 2011). Exploitation rate at age by quarter, gear type, and zone ($E_{a,q,g,z}$) was calculated based on Baranov's catch equation.

2.2 Model Initialization

The model was initialized with the number of age-1 recruits for each population in their respective spawning areas (zone 1 for western origin fish and zone 7 for eastern origin fish) and spawning time (quarter 1 in the model) during year 1. Values were based on asymptotic recruitment (R_{max}) estimates for eastern and western stocks (**Table 2**). Abundance at age of bluefin tuna populations in their respective spawning zones during year 1, quarter 1 ($N_{a,q,y,z,p}$) was calculated by

$$N_{a,q_1,y_1,z,p} = N_{a-1,q_1,y_1,z,p} e^{-[M_{a-1} + F_{q_1,g,z}(\gamma_{a-1})]}$$

where M and F are quarterly natural mortality and fishing mortality rates. Abundance at age of bluefin tuna populations in non-spawning zones during year 1, quarter 1 was set equal to zero. Asymptotic recruitment and equilibrium age structure were used to initialize the simulations, because our objectives were long-term projections. However, 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.

2.3 Stochastic Model Structure

Recruitment, or abundance at age-1 in quarter 1, of eastern and western bluefin tuna (under the low recruitment scenario) was calculated using a hockey-stick model

$$N_{a_1,q_1,y,z,p} = \begin{cases} R_{max_p}\varepsilon_{y,p} & if \;\; SSB_{q,y,z,p} \geq SSB_p^* \\ \dfrac{R_{max_p}}{SSB_p^*} SSB_{q,y,z,p}\varepsilon_{y,p} & if \;\; SSB_{q,y,z,p} < SSB_p^* \end{cases}$$

where R_{max_p} is the maximum level of recruitment for each population and SSB_p^* is the spawning biomass threshold that triggers a different response in recruitment. Recruitment of western bluefin tuna under the high recruitment scenario was calculated using a Beverton Holt stock-recruit curve

$$N_{a_1,q_1,y,z,p} = \frac{\alpha_p SSB_{q_1,y,z,p}}{\beta_p + SSB_{q_1,y,z,p}} \varepsilon_{y,p}$$

where α is the maximum number of recruits produced and β controls the rate at which the asymptote, or maximum recruits per spawner, is reached (Beverton and Holt 1957). For stock-recruit calculations only, SSB was calculated at the beginning of the year (i.e., the spawning biomass of bluefin tuna upon their arrival on the spawning ground in quarter 1). The error term (ε) is modeled as a random lognormal variate scaled to approximate recruitment variability observed for each population.

Abundance at age for ages 2 to 30 in quarter 1 is calculated by

$$N_{a,q_1,y,z,p} = N_{a-1,q_4,y-1,z,p} T_{z \to z_{a-1,q_4,p}} e^{-[M+F_{q_4,g,z}(\gamma_{a-1})]}$$

where $T_{z \to z_{a,q,p}}$ is the proportional movement of bluefin tuna from one zone to another zone for each age, quarter, and population.

Abundance at age for ages 1 to 30 in quarters 2 to 4 is calculated by

$$N_{a,q,y,z,p} = N_{a,q-1,y,z,p} T_{z \to z_{a,q-1,p}} e^{-[M+F_{q,g,z}(\gamma_a)]}$$

Spawning stock biomass of eastern and western bluefin tuna in each geographic zone was calculated as a function of the number-at-age, weight-at-age, and maturity-at-age of fish from each population

$$SSB_{q,y,z,p} = \sum_{a=1}^{a=30} N_{a,q,y,z,p} W_{a,p} M_{a,p}$$

Yield of eastern and western bluefin tuna in each geographic zone was calculated as

$$\boldsymbol{Y_{q,y,z,p} = \sum_{a=1}^{a=30} N_{a,q,y,z,p} W_{a,p} E_{a,q,g,z}}$$

2.4 Simulation Scenarios

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). Mean spawning stock biomass (SSB) and yield across geographic zones and quarters and stability (CV_{SSB}) of spawning populations across quarters were calculated for each stock under alternative movement and productivity scenarios.

2.5 Population Movement Scenarios

In the MAST model, movement rates were estimated for two age-groups in non-spawning quarters: 0-7 and 8+ and movement transitions to spawning area during the spawning quarter were given by the maturity-at-age schedule. Two alternative methods of estimating movement rates using the MAST model were used: 1) gravity, and 2) bulk transfer (Taylor *et al.* 2011). The gravity method is a simplification that reduces the number of estimated parameters by estimating an 'attraction' coefficient for each area to derive residence, and movement is derived from 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).

Taylor *et al.* (2011) estimated movement rates for a 5 box model; these rates were modified according to the criteria described below to accommodate the new 7 box model structure used in this study. The eastern Atlantic (Zone 4 in the Taylor *et al.* 2011 model) was divided into zones 4, 5, and 6 in the current model and what was previously termed zone 5 (Mediterranean Sea) is now referred to as zone 7. Some movement constraints based on life history stage were imposed. All life stages of eastern origin were allowed to move into the eastern Atlantic (zone 5), however, only juvenile and adolescent fish of western origin were permitted to move into this region (Rooker *et al*. 2007). Only adult eastern origin fish were allowed to move into the northeast Atlantic (zone 6) and western fish were excluded from movement into this region (Rooker *et al.* 2007). In the 7 box model the proportion of residence estimated for zone 4 in Taylor *et al.* (2011) was divided equally into zones 4, 5, and/or 6 (depending on movement constraints by population and life stage). Movement rates for fish in zones 5 and 6 to other zones were identical to rates estimated for zone 4 by Taylor *et al.* (2011).

2.6 Productivity Regime Scenarios

Movement scenarios were run under different assumptions of productivity for the western stock (low and high recruitment regimes). ICCAT has based Maximum Sustainable Yield (MSY) reference points for the western Atlantic bluefin stock using two scenarios of recruitment since 1993(Punt and Butterworth 1995). The high recruitment scenario is based on a Beverton-Holt relationship of the entire series of stock and recruitment estimates, and the low recruitment scenario is based on recruitment estimates since 1976 using a hockey-stick relationship (Anon. 2009, 2011, 2013). The ICCAT SCRS has reported no strong evidence to favor either scenario and concluded that both are reasonable lower and upper bounds on rebuilding potential.

3. Results

The long-term expectations reported here are 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) for the western population. Note that the parameter values associated with these approaches may be inconsistent (e.g., recruitment estimates are likely to be conditioned on movement assumptions), and the long-term expectations may not be realistic. However, these simulations provide insight on the scale and implications of stock mixing.

3.1 Gravity Movement Rates: Low and High Recruitment Regimes

In these scenarios bluefin tuna stock dynamics were simulated using movement rates estimated by the gravity method, assuming a low and high recruitment regime for the western population, and under the condition of status quo fishing mortality. Overall, the magnitude and distribution of long-term SSB and yield differed greatly between eastern and western bluefin tuna spawning populations. Long-term SSB of the eastern population was estimated to be 54 (high recruitment) to 50 (low recruitment) times greater than the SSB of the western population on average across the four quarters of the year (**Table 4**). Long-term annual yield of the eastern population was estimated to be 26 (high recruitment) to 22 (low recruitment) times greater than the yield of the western population (**Table 4**). When the resource is viewed from a management unit perspective (western stock = all fish in zones 1, 2, and 3; eastern stock = all fish zones 4,5,6,7) the western stock is more than twice the total SSB of the western population and the SSB of the eastern stock is slightly lower than that of the eastern population (**Table 4**).

Both high and low recruitment scenarios demonstrated similar patterns in the distribution of eastern and western populations across geographic zones. Simulated biomass and yield were similar under the assumption of high and low recruitment regime. In quarter one, the long-term expectations of spawning stock biomass of the western population was highest in the Gulf of Mexico (zone 1; **Figure 2a, 3a**). This result is a function of the assumption that mature fish return to spawn during quarter one. In the remaining quarters, the long-term SSB of western origin fish was consistently highest in the western Atlantic (zone 3), the central Atlantic (zone 4), and the Gulf of St. Lawrence (zone 2), in order of decreasing biomass (**Figure 2a, 3a**). Western origin fish were also present in the eastern Atlantic (zone 5) at low levels (**Figure 2a, 3a**). Western origin fish were absent from the northeast Atlantic (zones 6) and Mediterranean Sea (zone 7) because of constraints in the model that restricted their movement into these areas. The majority of the long-term yield of western bluefin tuna came from the western and central Atlantic (zones 3 and 4), with moderate contributions from the Gulf of Mexico and eastern Atlantic (zones 1 and 5), and minor contributions from Gulf of St. Lawrence (zone 2; **Figure 2b, 3b**). Long-term yield of the western population was highest in the summer and fall (2^{nd} and 3^{rd} quarters; **Figure 2b, 3b**).

Across quarters, the long-term SSB of eastern population fish was consistently highest in the Mediterranean Sea (zone 7; **Figure 2c, 3c**) and comprised approximately 92% of the basin-wide SSB of the eastern population. Eastern origin fish were present at relative lower levels in the western, central, eastern, and northeastern Atlantic (zones 3, 4, 5, and 6; **Figure 2c, 3c**). Eastern origin fish were absent from the Gulf of Mexico (zone 1) and Gulf of St. Lawrence (zone 2) based on the movement constraints in the model. The long-term yield of eastern origin fish was highest in the Mediterranean Sea (zone 7), with the highest yields occurring during summer (quarter 2; **Figure 2d, 3d**). Yield of eastern origin fish from zones three, four, five and six comprised relatively minor contributions to the total yield of the eastern population (**Figure 2d, 3d**).

Across high and low recruitment scenarios, the population of origin of bluefin tuna spawning biomass and yield in the Gulf of Mexico and Gulf of St. Lawrence (zones 1 and 2) was composed exclusively of western origin fish (**Figure 6a, b, 7a,b**). Bluefin tuna in the northeastern Atlantic (zone 6) and Mediterranean Sea (zone 7) were exclusively eastern origin (**Figure 6a, b, 7a,b**). The SSB in the central and eastern Atlantic (zone 4 and 5) was dominated by eastern origin fish, but there was substantial contribution of western origin to long-term yield of bluefin tuna in these zones (**Figure 6a, b, 7a,b**). The western Atlantic was the zone of highest mixing and simulated stock composition varied across quarters (**Figure 6a, 7a**). The western population comprised between of 15-31% of SSB in the western Atlantic under the high recruitment scenario and 17-33% of SSB under the low recruitment scenario across quarters (**Figure 6a, 7a**). A higher percentage of the yield in the western Atlantic was composed of western origin fish, with 36-61% and 38-64% of the long-term yield comprised of western origin fish under high and low recruitment scenarios respectively (**Figure 6a, 7a**).

3.2 Bulk Transfer Movement Rates: Low and High Recruitment Regime

In these scenarios bluefin tuna population dynamics were simulated using movement rates estimated by the bulk transfer method, assuming a low and high recruitment regime for the western population, and under the condition of status quo fishing mortality. Both high and low recruitment scenarios demonstrated similar patterns in the distribution of eastern and western populations across geographic zones, although the actual biomass and yield was higher under the assumption of a high recruitment regime. Long-term SSB of the eastern population was estimated to be 22 (high recruitment) to 37 (low recruitment) times greater than the western population in the first quarter of the year (**Table 4**). Long-term annual yield of the eastern population was estimated to be 17 (high recruitment) to 28 (low recruitment) times greater across zones compared to the western population (**Table 4**). The stock unit view of the resource would suggest that western stock SSB is either 29% (high recruitment scenario) or 54% (low recruitment scenario) higher and eastern stock SSB is 1% lower compared to the population view of the resource.

In quarter one, the long-term SSB of western origin fish was highest in the Gulf of Mexico (zone 1). However, in quarters two, three and four long-term expectations of spawning stock biomass of western fish were highest in the western Atlantic (zone 3; **Figure 4a, 5a**). This result is attributable to high rates of residency estimated for western origin fish in the western Atlantic and low rates of fish movement to other zones. Western origin fish were absent from zones six (northeast Atlantic) and seven (Mediterranean Sea) based on movement constraints in the model. The majority of the long-term yield of western bluefin tuna came from the western and central Atlantic (zones 3 and 4), with moderate contributions from the Gulf of Mexico and eastern Atlantic (zones 1 and 5), and minor contributions from the Gulf of St. Lawrence (zone 2). Total long-term yield of western origin fish was highest in the summer and fall (2^{nd} and 3^{rd} quarter; **Figure 4b, 5b**).

Across quarters, the long-term SSB of eastern origin fish was consistently highest in the Mediterranean Sea (zone 7; **Figure 4c, 5c**). The long-term SSB in this zone comprised approximately 82% of the total SSB. The biomass of eastern origin fish in the central, eastern, and northeastern Atlantic (zone 4, 5, and 6) was higher based on bulk transfer movement estimates compared to the rates estimated by the gravity method (**Figure 4c, 5c**). Eastern bluefin tuna were present at low levels in the Western Atlantic and absent from the Gulf of Mexico and Gulf of St. Lawrence (zone 1 and 2; **Figure 4c, 5c)**. The long-term yield of eastern origin fish was highest in the Mediterranean Sea (zone 7), with the highest long-term yields occurring during the summer (quarter 2; **Figure 4d, 5d**). The contributions to the total yield of eastern origin fish from zones three, four, five, and six were relatively low, but higher than estimated by the gravity method (**Figure 4d, 5d**).

Similar to gravity rate models, the long-term SSB and yield of bluefin tuna in the Gulf of Mexico and Gulf of St. Lawrence is composed exclusively of western origin fish and long-term SSB in zones six, and seven was composed exclusively of eastern origin fish (**Figure 8a,b 9a,b)**. The percentage of western origin fish that composed SSB in zone three ranged depending on quarter from 43 to 82% under the high recruitment scenario and 31 to 73% under the low recruitment scenario. Overall, western origin fish dominate the composition of the catch in this zone (**Figure 8b, 9b**). The SSB in zones four and five is dominated by eastern origin fish, but there is a substantial contribution of western origin fish to the long-term yield of bluefin tuna in this zone (**Figure 8a, b, 9a, b**).

4. Discussion

The goal of this study was to develop an operating model for Atlantic bluefin tuna that incorporated the current state of knowledge of bluefin tuna population structure and movement patterns. Through simulation of this model, under different assumptions, we explored the implications of population structure and mixing on our perception of the resource and the mixed origin nature of bluefin tuna across the Atlantic basin. The model simulations also aided in identifying gaps and uncertainty in knowledge that prevent an accurate view of the resource.

Simulations of the operating model indicated considerable mixed stock composition of the mature tuna biomass and yield in the western Atlantic (Zone 3), with lower levels of mixing in the central Atlantic (Zone 4), and limited mixing in the eastern Atlantic (Zone 5). The modeled stock composition in the western Atlantic (zones 3) was most sensitive to the method of estimating population movement (gravity vs. bulk transfer methods). This is a region of uncertainty in terms of modeled stock composition, as well from direct measures of stock composition based on otolith chemistry with samples from different regions of the western Atlantic (zone 3) and different years yielding varying estimates of stock composition (Rooker *et al.* 2008, Rooker *et al.* 2014, Secor in press). This suggests that this region is a dynamic region of stock mixing in the Atlantic Ocean and further resolution of spatial and temporal variability of mixing in the western Atlantic could improve characterization of stock mixing in this zone.

Results from operating model simulations demonstrate that explicitly modeling stock mixing altered our perception the distribution of the resource in space and time and may have profound implications to Atlantic bluefin tuna assessment and management. When we view the resource through the management unit lens (western stock unit = zones 1,2, and 3, eastern stock unit = zones 4, 5, 6, and 7) and compare this with our population-view we find that the management unit view slightly underestimated the SSB of eastern origin fish and profoundly overestimated the SSB of western origin fish. Migrants from the more abundant eastern population supplement the bluefin tuna spawning biomass and fishery in the western Atlantic. Western origin fish are also caught in the eastern fishery, this represents unaccounted for fishing mortality on the western population. Recognition of the nature and extent of this connectivity between eastern and western populations will be critical to understanding how these populations respond to alternative management actions. The misperception of the status of the western resource may be a key factor in the slower than predicted rebuilding of this stock. Because of the impact movement and spatial overlap of bluefin populations have on stock perception, there is a critical need for further development of the operating model approach to better understand population dynamics and to serve as a test bed for evaluating alternative management measures.

4.1 Model Sensitivities

The magnitude and distribution of productivity and yield of western and eastern bluefin tuna populations was sensitive to the interaction between fish movement across geographic zones and fishing mortality experienced within each zone. Thus, estimated movement rates and movement constraints in the model should be critically evaluated to ensure they represent reality. Further investments into estimating movement and stock composition are needed to address this sensitivity. It is important to note that movement rates estimated by Taylor *et al.* (2011) during the spawning quarter are linked to the maturity schedule for the stock. Thus, the choice of maturity schedule can also have a large impact on estimates of spawning stock biomass of bluefin tuna. Currently, the assumed age at 100% maturity of western origin fish (age 16) is much older than that assumed for the eastern origin fish (age 5). Other studies suggest that a younger age at maturity may be more appropriate (Lutcavage pers. comm.). For example, the current stock assessment assumes an age at 100% maturity of nine years for the western stock and considers values as young as six or as old as sixteen (Anon. 2011). Alternative maturity schedules may be particularly important to estimation of productivity for bluefin tuna stocks. Integrated modeling of both eastern and western Atlantic bluefin stocks also illustrates the need for consistency in determining life history parameters (e.g., maturity, natural mortality, form of stock-recruitment relationships). Similar to the association between assumed maturity schedules and estimated movement rates, fishing mortality and selectivity are also associated with perceived movement rates. For example, fishing mortality, selectivity and movement rates are simultaneously estimated by Taylor *et al.* (2011). Furthermore, given the substantial amount of mixing suggested from the baseline simulation scenario, estimates of recruitment are also likely to be conditional on mixing assumptions. Therefore, further developments in simulations should be coordinated with advancements in spatially-explicit estimation models so that the operating model has maturity, movement, fishing mortality and selectivity parameters that are mutually consistent. One promising option is to estimate movement directly from telemetry observations for input to spatially-explicit stock assessment models.

This model is also subject to some of the same uncertainties in life history parameters that are found in the current stock assessment framework. In addition to uncertainty in maturity schedules, there is uncertainty in estimates of natural mortality and stock recruit relationships for bluefin tuna stocks. Thus, improved information on life history of each bluefin tuna stock, will increase the accuracy of this simulation model.

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Table 1. Description of spatial strata utilized in bluefin tuna model.

1. **Gulf of Mexico (including Straits of Florida and Caribbean Sea)**: assumed to be western spawning area
    a. *Life stages present:* Eggs/larvae, juveniles, and adults (Rooker *et al.* 2007)
    b. *Boundaries:* Boundaries are defined by knowledge of spatial extent of western spawning area (Anon. 2001, Taylor *et al.* 2011).

2. **Gulf of St. Lawrence:** assumed to contain primarily western origin fish
    a. *Life stages present:* Juveniles, adolescents, and adults (Rooker *et al.* 2007)
    b. *Boundaries:* Boundaries are defined by sampling domain of otolith chemistry data which indicated fish in this region are of western origin (Rooker *et al.* 2008, Taylor *et al.* 2011).
3. **Western Atlantic Ocean**: assumed to be mixed-stock area
    a. *Life stages present:* Juveniles, adolescents, and adults (Rooker *et al.* 2007)
    b. *Boundaries:* The western boundary is defined by knowledge of spatial extent of western spawning area. The eastern boundary is defined by the management boundary (45°W, Anon. 2002, Taylor *et al.* 2011).
4. **Central Atlantic Ocean**: assumed to be mixed-stock area
    a. *Life stages present:* Adolescents, adults (Rooker *et al.* 2007)
    b. *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 (Anon. 2002).
5. **Eastern Atlantic Ocean**: assumed to be mixed-stock area
    a. *Life stages present:* Juveniles, adolescents, and adults (Rooker *et al.* 2007)
    b. *Boundaries:* The eastern boundary is defined by tagging information (see description for zone 4). The western boundary is defined by knowledge of spatial extent of eastern spawning area. The northern boundary is defined by large differences in the proportional catch of western and eastern bluefin tuna to the north and south of this boundary. Block *et al.* 2005 indicated recaptures of eastern (majority) and western (minority) origin fish in this zone.
6. **Northeast Atlantic Ocean**: assumed to be mixed-stock area
    a. *Life stages present:* Adults (Rooker *et al.* 2007)
    b. *Boundaries:* The eastern boundary is defined by tagging information (see description for zone 4). The western boundary is defined by the distribution of bluefin tuna. The southern boundary is defined by large differences in the proportional catch of western and eastern bluefin tuna to the north and south of this boundary. Block *et al.* 2005 indicated no recaptures of western origin fish in this zone.
7. **Mediterranean Sea**: assumed to be eastern spawning area.
    a. *Life stages present:* Eggs/larvae, juveniles, adolescents, and adults (Rooker *et al.* 2007)
    b. *Boundaries:* The boundaries are defined by knowledge of spatial extent of eastern spawning area (Anon. 2002, Taylor *et al.* 2011).

Table 2 Summary of input parameters to bluefin tuna operating model and sources of information.

Parameter		Value	Sources
Length-weight relationship			
	West	a=0.00002861, b=2.929	Parrack and Phares 1979, ICCAT 2010
	East	a=0.0000295, b=2.899	Rey and Cort Unpubl, ICCAT 2010
Von Bertalanffy growth model			
	West	k=0.089, linf= 315, t0= -1.13	Restrepo et al. 2009, ICCAT 2010
	East	k= 0.093, linf= 319, t0=-0.97	Cort 1991, ICCAT 2010
Maturity Schedule			
	West	50% maturity at age 12, 100% maturity at age 16	Diaz and Turner 2007, ICCAT 2008
	East	50% maturity at age 4, 100% maturity at age 5	Mather et al. 1995, ICCAT 1997, 2010
Natural Mortality (quarterly)			
	West East	Age-independent natural mortality, M = 0.14 yr-1	Anon 1997, ICCAT 2012
Stock-recruit relationship			
	West	Low recruitment scenario: Rmax = 84,363; SSb Hinge = 12,236, Standard Error of Random Deviations = 0.37 High recruitment scenario: Alpha = 432,982; Beta =61,344, Standard Error of Random Deviations = 0.37	ICCAT 2010, S. Calay pers. comm
	East	Rmax = 1,889,896; SSb Hinge = 215,584, CV of recruitment = 0.43	Estimated as described in the text.

Table 3. Fishing mortality (yr^{-1}) by gear type (LL: long-line, PS: purse seine, BB: baitboat, and other), quarter, and zone (Taylor *et al.* 2011).

Area	**Gear Type**	**Quarter**			
Zone 1		**1**	**2**	**3**	**4**
	LL	0.009	0.006	0.000	0.000
	PS	0.000	0.000	0.000	0.000
	BB	0.000	0.000	0.000	0.000
	Other	0.000	0.000	0.000	0.000
	Total	**0.010**	**0.006**	**0.000**	**0.001**
Zone 2	LL	0	0	0	0
	PS	0	0	0	0
	BB	0	0	0	0
	Other	0	0	0.00677	0.00248
	Total	**0.000**	**0.000**	**0.007**	**0.002**
Zone 3	LL	0.001	0.001	0.000	0.002
	PS	0.000	0.000	0.002	0.000
	BB	0.000	0.000	0.000	0.000
	Other	0.000	0.005	0.007	0.001
	Total	**0.001**	**0.006**	**0.009**	**0.003**
Zone 4, 5, & 6	LL	0.002	0.054	0.013	0.020
	PS	0.001	0.003	0.001	0.001
	BB	0.001	0.037	0.042	0.005
	Other	0.001	0.003	0.005	0.001
	Total	**0.005**	**0.098**	**0.061**	**0.027**
Zone 7	LL	0.001	0.011	0.001	0.001
	PS	0.004	0.013	0.010	0.004
	BB	0.000	0.000	0.000	0.000
	Other	0.001	0.002	0.001	0.001
	Total	**0.005**	**0.025**	**0.012**	**0.005**

Table 4. Comparison of long-term expectations of spawning stock biomass (mT) and yield from model simulations under different movement model parameterizations (gravity, bulk transfer) and two prevailing assumptions of recruitment for the western population (high, low). Results are summarized for population of origin and stock unit.

		Gravity Movement Rates		**Bulk Transfer Movement Rates**	
		High recruitment	**Low recruitment**	**High recruitment**	**Low recruitment**
Spawning Biomass (mT)	Western Population	16,454	17,960	38,410	22,539
	Eastern Population	891,280	889,953	846,385	844,040
	Western Stock	37,259	38,408	49,630	34,668
	Eastern Stock	870,475	869,505	835,166	831,911
Yield (mT)	Western Population	1,309	1,444	2,176	1,283
	Eastern Population	33,811	33,763	36,179	36,081
	Western Stock	789	840	1,390	876
	Eastern Stock	34,331	34,367	36,965	36,488

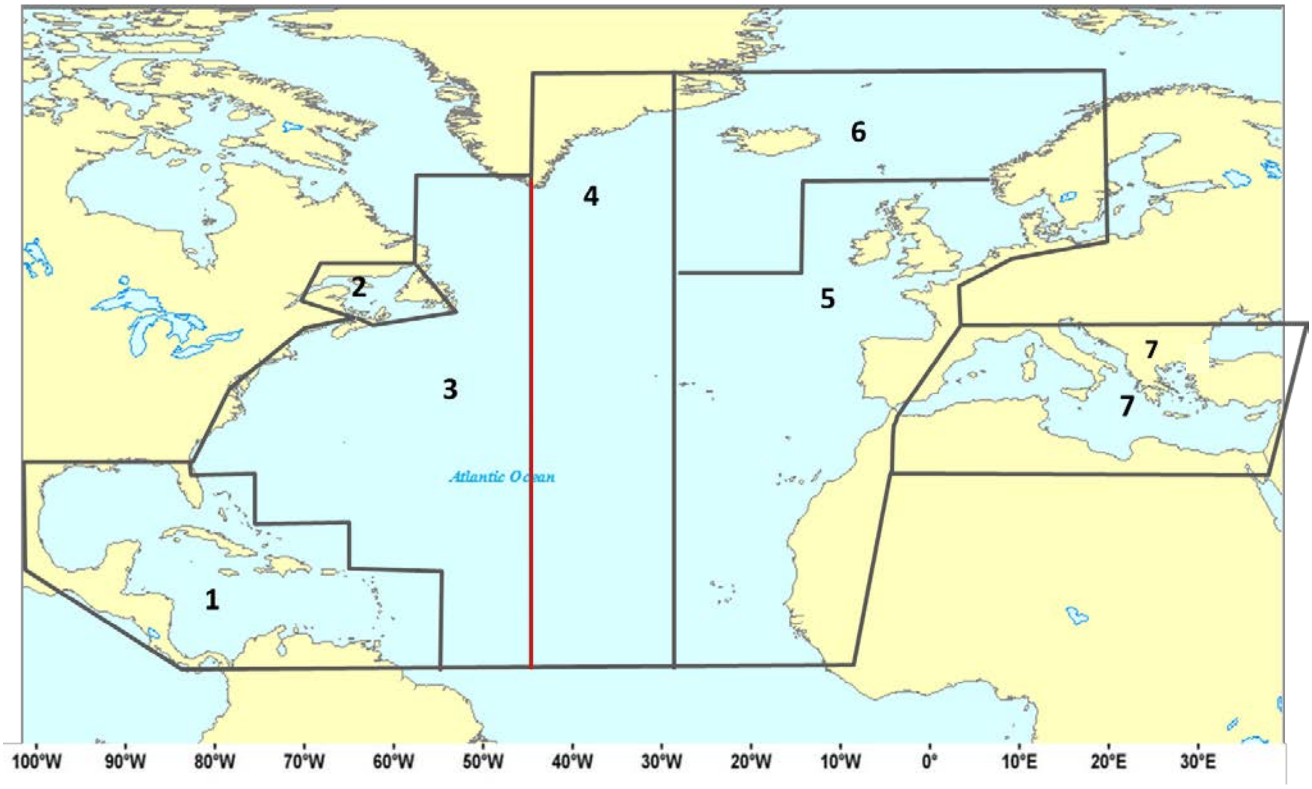

Figure 1. Spatial structure utilized in bluefin tuna model (modified from Taylor *et al.* 2011). The spatial strata defined by Taylor *et al.* 2011 were modified according to the consensus of experts on bluefin tuna mixing (Anon. 2002, Rooker *et al.* 2007).

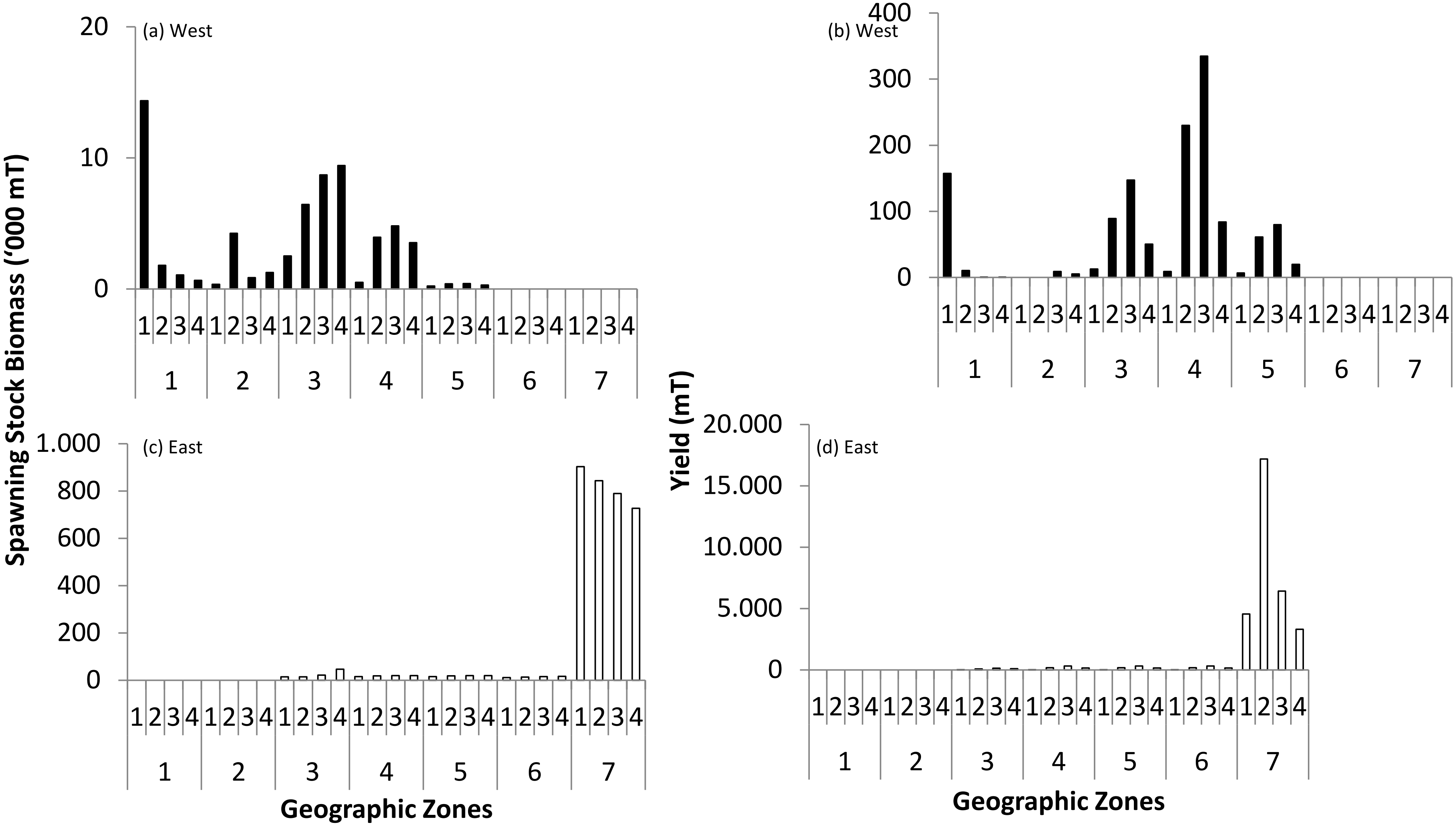

Figure 2. Gravity movement rates, high recruitment scenario: Spawning stock biomass and yield (mt) of western (a, b) and eastern (c,d) bluefin tuna populations across geographic zones (1-7) and quarters (1-4).

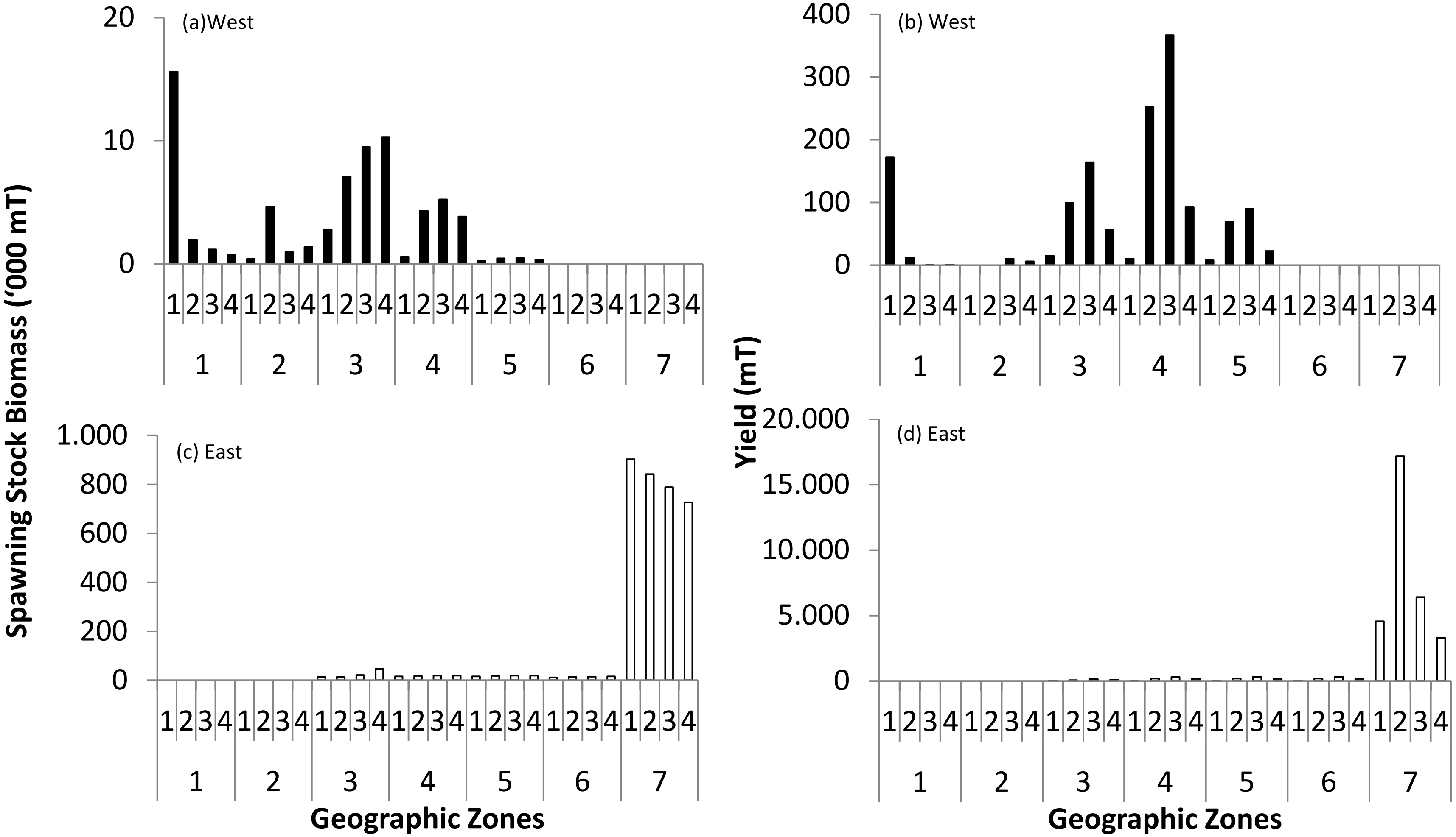

Figure 3. Gravity movement rates, low recruitment regime scenario: Spawning stock biomass and yield (mt) of western (a, b) and eastern (c,d) of bluefin tuna populations across geographic zones (1-7) and quarters (1-4).

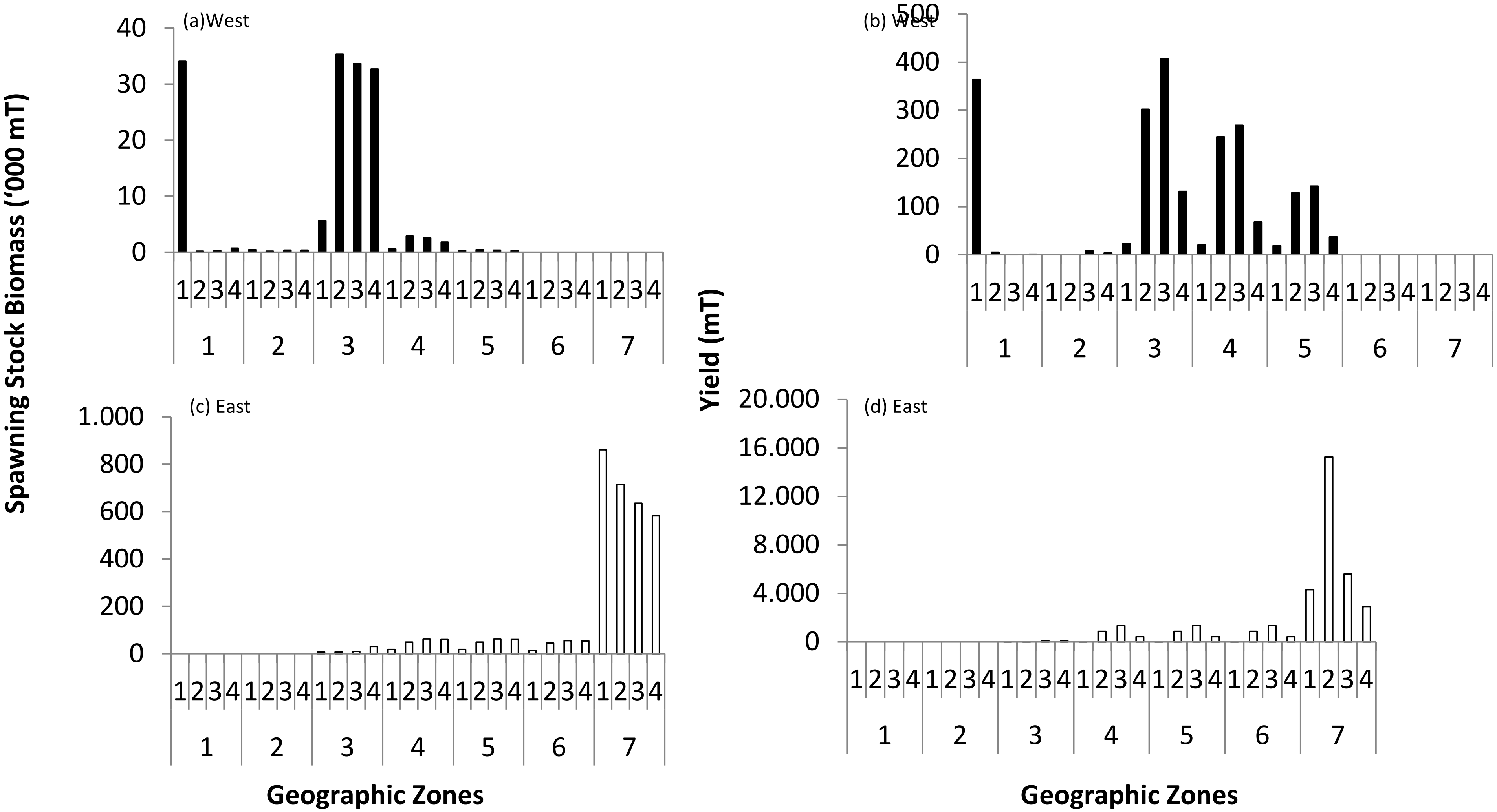

Figure 4. Bulk transfer movement rates, high recruitment scenario: Spawning stock biomass and yield (mt) of western (a, b) and eastern (c,d) bluefin tuna populations across geographic zones (1-7) and quarters (1-4).

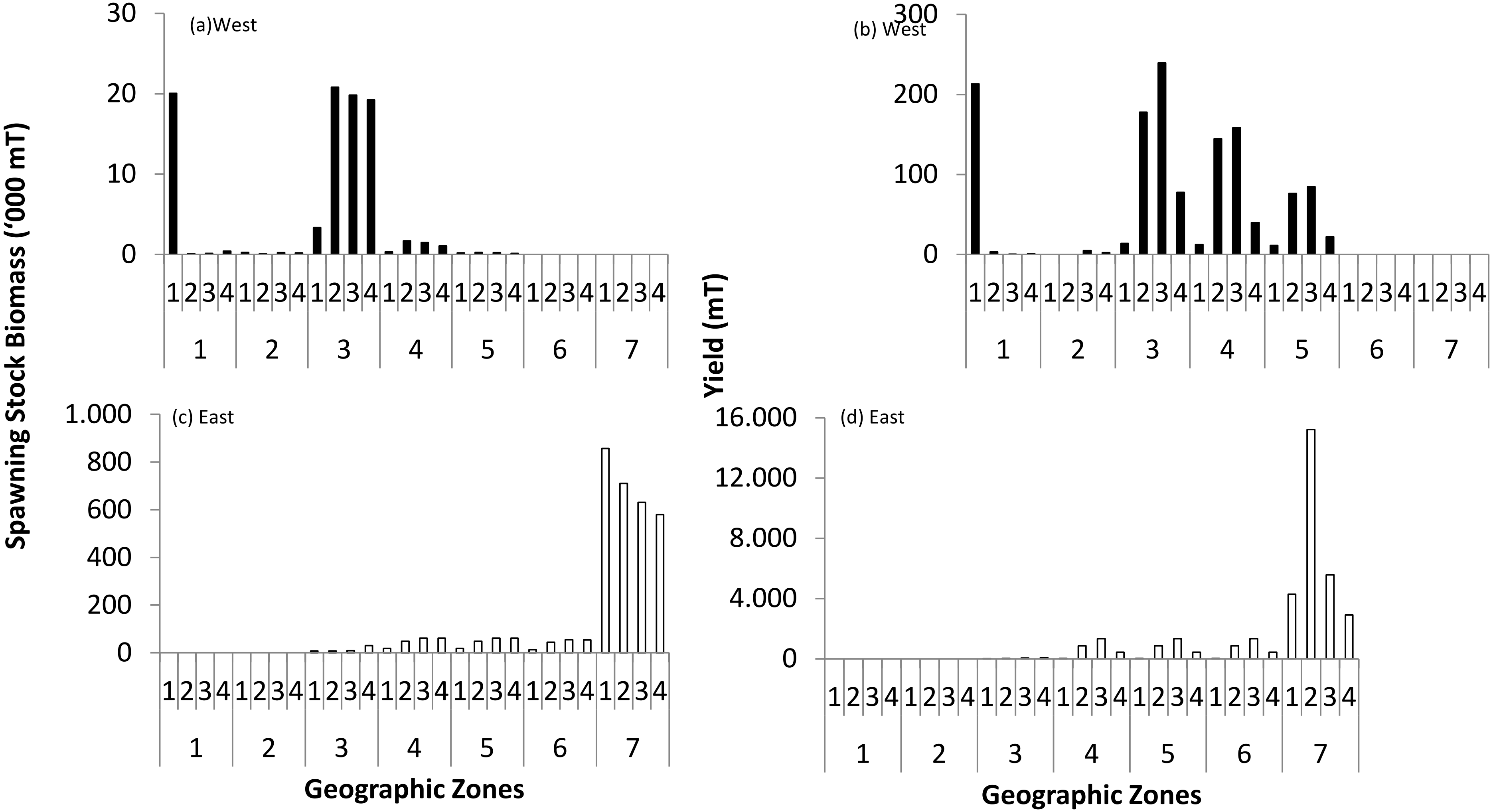

Figure 5. Bulk transfer movement rates, low recruitment scenario: Spawning stock biomass and yield (mt) of western (a, b) and eastern (c,d) bluefin tuna populations across geographic zones (1-7) and quarters (1-4).

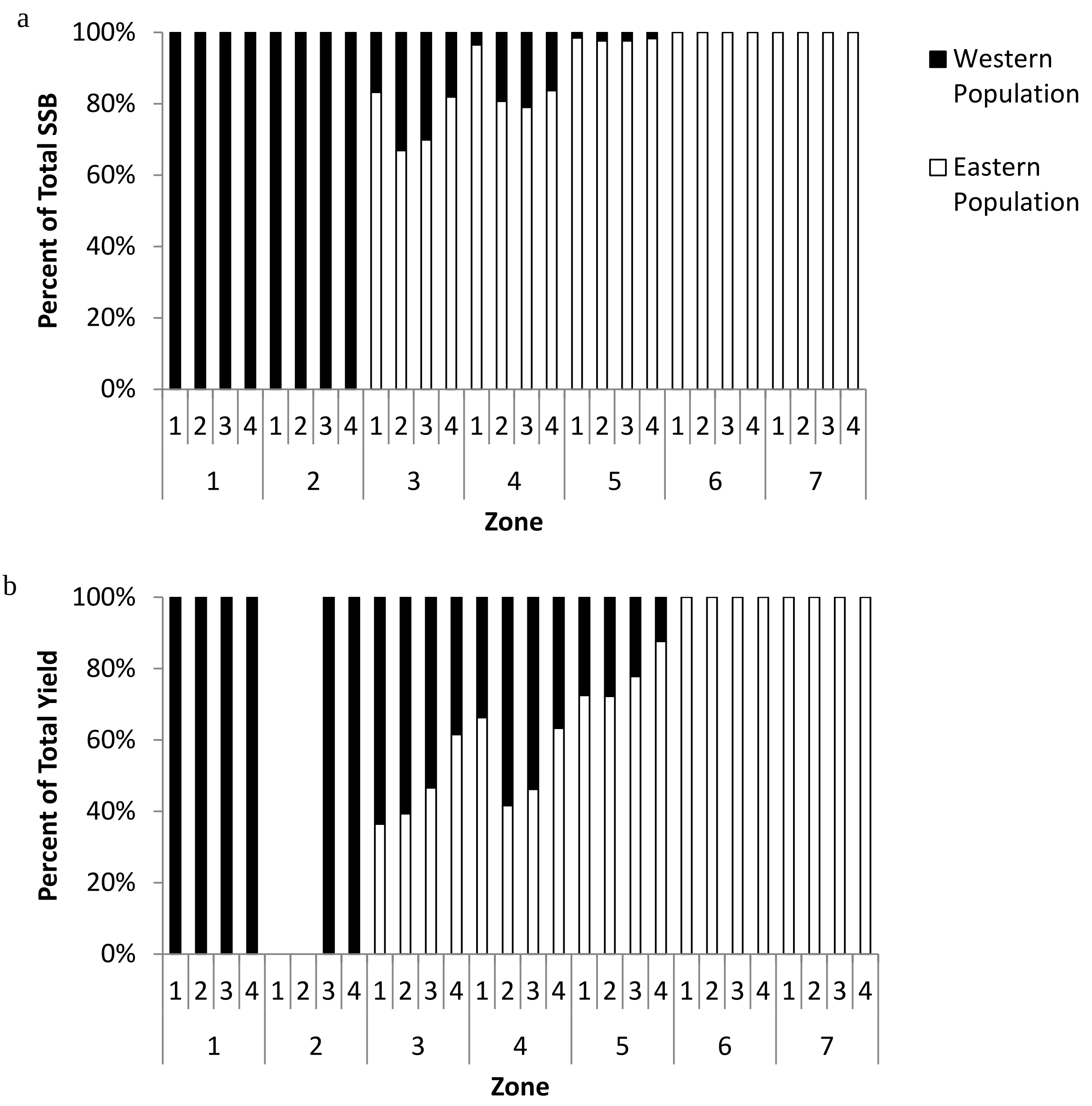

Figure 6. Gravity movement rate, low recruitment scenario: a) Percent composition of equilibrium spawning stock biomass across geographic zones (1-7) and quarters (1-4). b) Percent composition of equilibrium yield (mt) across geographic zones (1-7) and quarters (1-4).

a

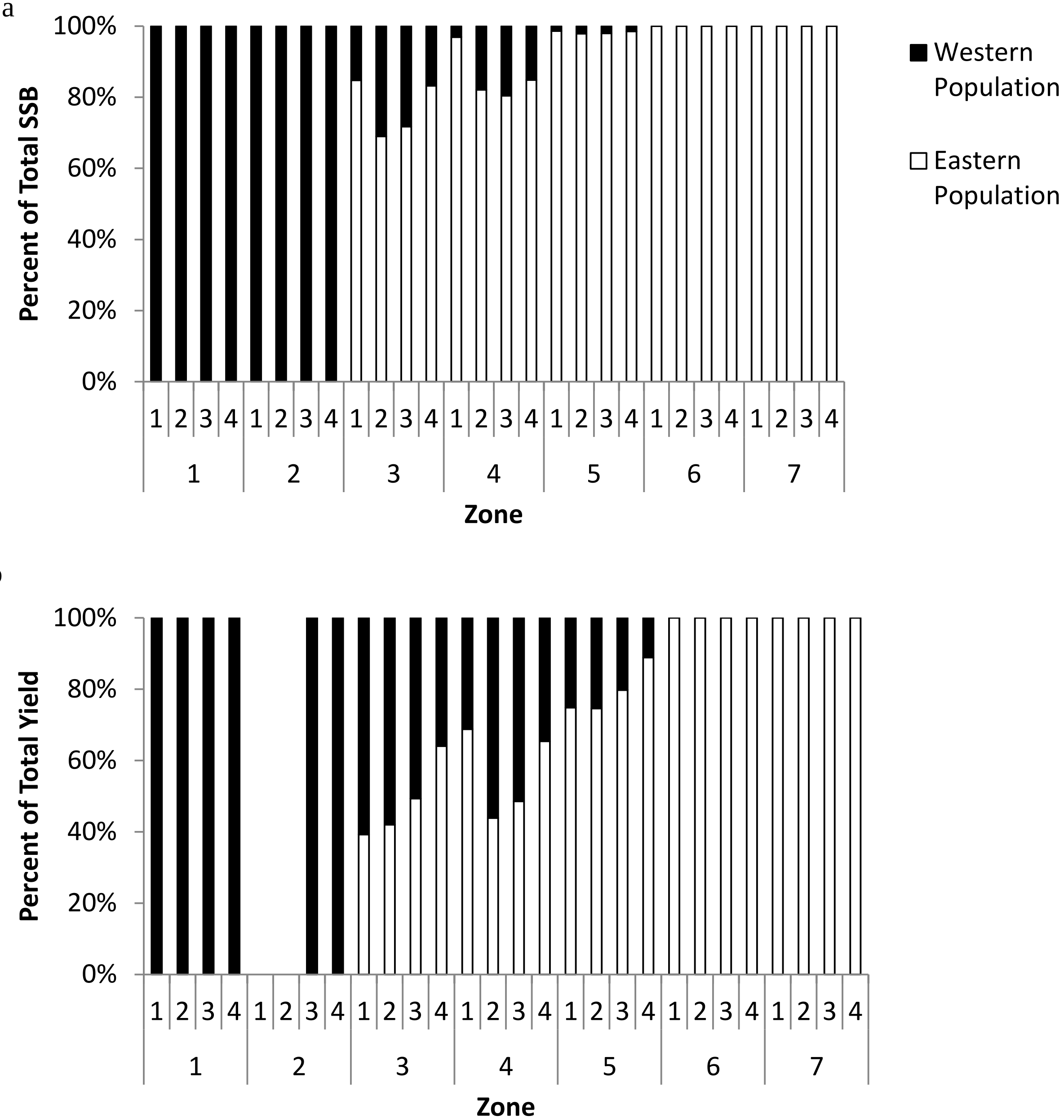

Figure 7. Gravity movement rates, high recruitment scenario: a) Percent composition of equilibrium spawning stock biomass across geographic zones (1-7) and quarters (1-4). b) Percent composition of equilibrium yield (mt) across geographic zones (1-7) and quarters (1-4).

a

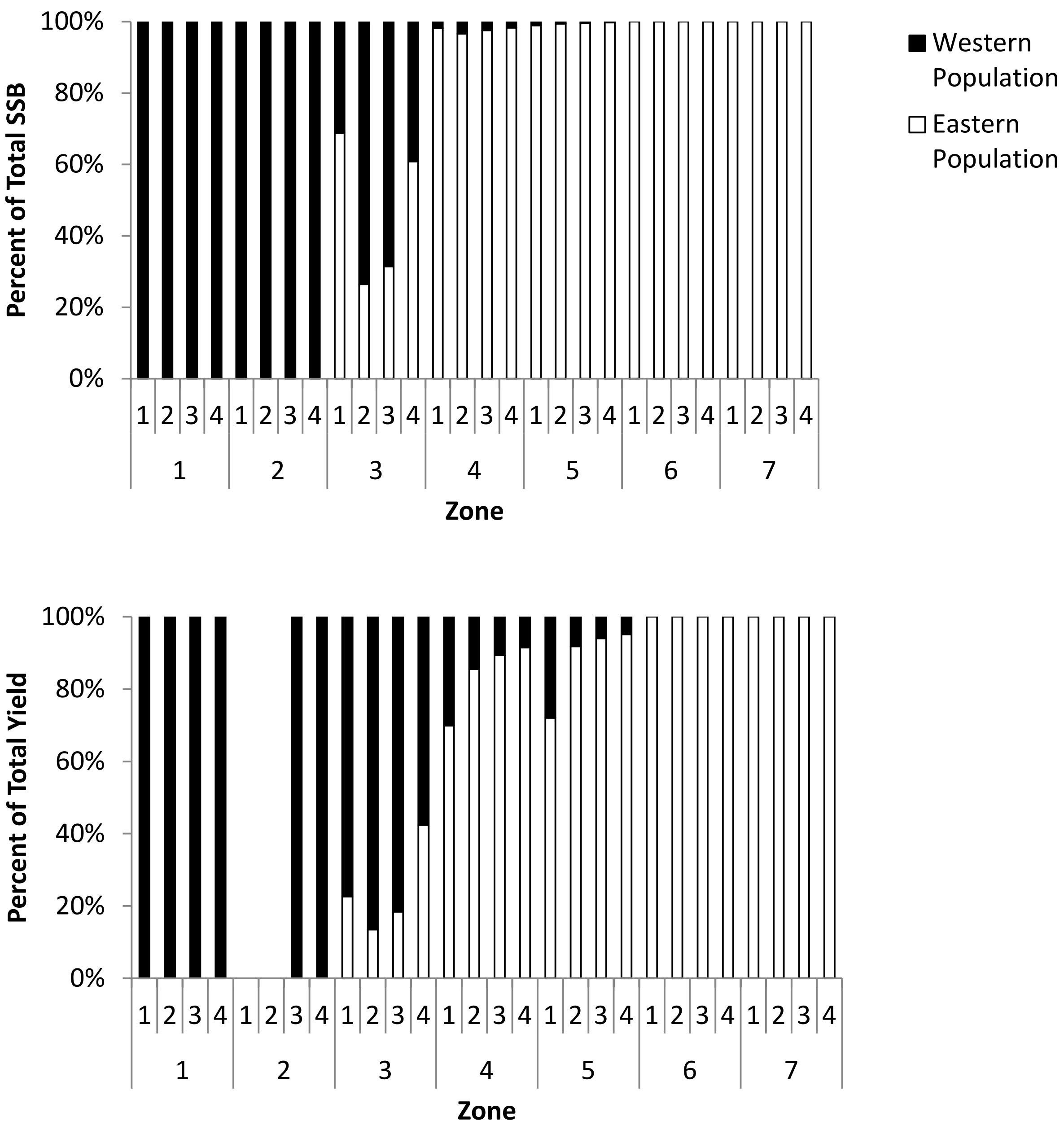

Figure 8. Bulk transfer movement rates, low recruitment scenario: a) Percent composition of equilibrium spawning stock biomass across geographic zones (1-7) and quarters (1-4). b) Percent composition of equilibrium yield (mt) across geographic zones (1-7) and quarters (1-4).

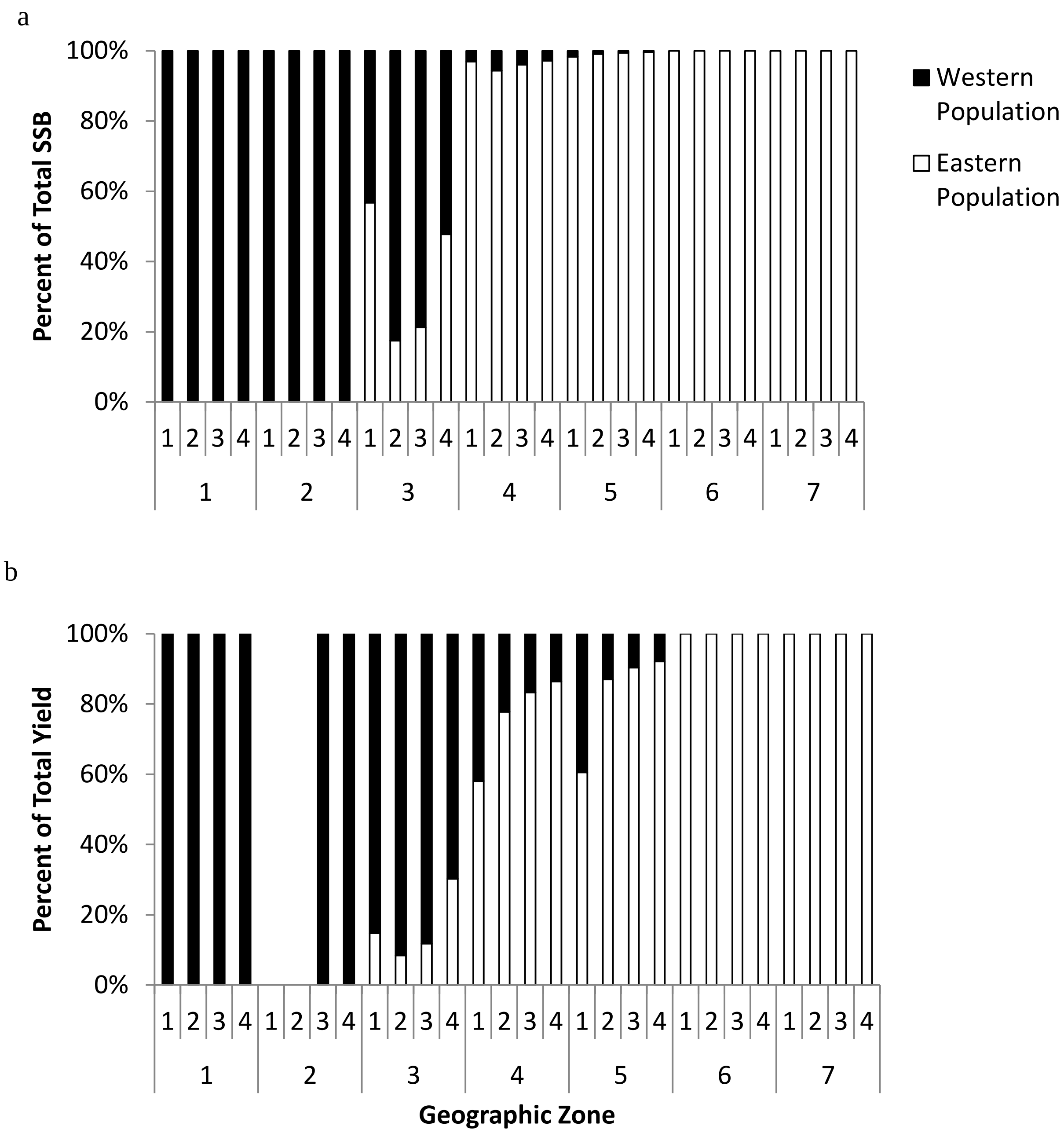

Figure 9. Bulk transfer movement rates, high recruitment scenario: a) Percent composition of equilibrium spawning stock biomass across geographic zones (1-7) and quarters (1-4). b) Percent composition of equilibrium yield (mt) across geographic zones (1-7) and quarters (1-4).