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A SIMULATION TOOL TO EVALUATE EFFECTS OF MIXING BETWEEN ATLANTIC BLUEFIN TUNA STOCKS

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SUMMARY

Atlantic bluefin tuna are managed as separate eastern and western stocks. Tagging and otolith chemistry patterns support natal homing with mixing during non-spawning periods. We developed a simulation model for bluefin tuna to explore consequences of leading hypotheses of stock structure and mixing on stock productivity and rebuilding goals. The operating model includes two spawning populations based on western and eastern stocks, each with unique vital rates and independent recruitment. The analytical framework is a stochastic, age-structured, overlap model that is seasonally and spatially-explicit, with seven geographic zones. Spatial model structure and movement patterns were informed by expert consensus. A demonstration, based on stock assessments and published estimates of movement, produced expectations of long-term spawning biomass and yield across geographic zones and seasons that were sensitive to scenario inputs. Such sensitivities suggest that movement rates, fishing mortality, selectivity and recruitment should be simultaneously estimated to avoid conflicting parameter estimates from inconsistent assessment models. Once reliable parameter estimates are available, the modeling framework can provide sufficient flexibility to evaluate alternative management scenarios in the context of stock mixing.

RÉSUMÉ

Le thon rouge de l'Atlantique est géré comme deux stocks distincts : stock de l'Est et stock de l'Ouest. Le marquage et les schémas de la chimie des otolithes appuient le retour vers les frayères avec des échanges pendant les périodes de non-frai. Nous avons développé un modèle de simulation pour le thon rouge afin d'explorer les conséquences que les principales hypothèses sur la structure des stocks et les échanges entre les stocks ont sur la productivité des stocks et les objectifs de rétablissement. Le modèle opérationnel inclut deux populations reproductrices basées sur les stocks Ouest et Est, chacun doté de taux vitaux uniques et d'un recrutement indépendant. Le cadre analytique est un modèle de chevauchement structuré par âge et stochastique qui est saisonnièrement et spatialement explicite, avec sept zones géographiques. La structure spatiale du modèle et les schémas de déplacement ont été convenus par des experts. Une démonstration, basée sur des évaluations de stocks et des estimations publiées de déplacements, a produit des prévisions de biomasse reproductrice à long terme et de production dans l'ensemble des zones géographiques et des saisons qui étaient sensibles aux entrées du scénario. Ces sensibilités suggèrent que les taux de déplacement, la mortalité par pêche, la sélectivité et le recrutement devraient être simultanément estimés afin d'éviter les estimations des paramètres contradictoires à partir de modèles d'évaluation incohérents. Une fois que des estimations de paramètres fiables seront disponibles, le cadre de modélisation pourra fournir suffisamment de flexibilité pour évaluer des scénarios de gestion alternatifs dans le contexte des échanges entre les stocks.

RESUMEN

El atún rojo del Atlántico se gestiona como dos stocks separados, un stock oriental y otro occidental. Los patrones de microquímica de otolitos y marcado respaldan la teoría de la conducta de retorno al lugar de origen con mezcla durante los periodos de no reproducción. Hemos desarrollado un modelo de simulación para el atún rojo con el fin de explorar las

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consecuencias de las principales hipótesis de estructura del stock y mezcla en la productividad del stock y en los objetivos de recuperación. El modelo operativo incluye dos poblaciones reproductoras basadas en los stocks oriental y occidental, cada uno con tasas vitales únicas y reclutamiento independiente. El marco analítico es un modelo superpuesto, estocástico, estructurado por edad, estacional y espacialmente explícito, con siete zonas geográficas. La estructura del modelo espacial y los patrones de movimiento contaron con el acuerdo de los expertos. Una demostración, basada en evaluaciones de stock y estimaciones publicadas de movimiento, produjo previsiones de biomasa reproductora y rendimiento a largo plazo en las zonas geográficas y temporadas que fueron sensibles a las entradas del escenario. Estas sensibilidades sugieren que las tasas de movimiento, la mortalidad por pesca, la selectividad y el reclutamiento deberían estimarse de forma simultánea para evitar entrar en conflicto con estimaciones de parámetros procedentes de modelos de evaluación incoherentes. Cuando se disponga de estimaciones de parámetros fiables, el marco de modelación puede proporcionar una flexibilidad suficiente para poder evaluar escenarios de ordenación alternativos en el contexto de mezcla del stock.

KEYWORDS

Atlantic bluefin tuna, simulation, population dynamics, migrations

1. Introduction

Atlantic bluefin tuna (*Thynnus thynnus*) is a highly migratory species that inhabits the north Atlantic Ocean and adjacent seas. Tagging and otolith chemistry patterns support hypotheses that there are two main spawning locations within the Atlantic: the Mediterranean Sea and Gulf of Mexico (Rooker *et al*. 2008). The two spawning locations appear to support at least two genetic populations, with the eastern Atlantic and Mediterranean stock estimated to be much larger than the western Atlantic stock (ICCAT 2010). Evidence indicates that adult bluefin tuna exhibit a high degree of natal homing within each stock (96% for the Mediterranean Sea and 99% for the Gulf of Mexico, Rooker *et al*. 2008). However, there appears to be a high level of mixing at younger ages that is believed to be related to feeding migrations, and spawning site fidelity to the Gulf of Mexico has been debated (Galuardi *et al*., 2010). Information from satellite and archival tagging confirms that juveniles and adults are capable of trans-Atlantic migrations (Lutcavage *et al*. 1999, 2001, Block *et al*. 2001, 2005, Galuardi *et al*. 2010). Furthermore, otolith chemistry data has revealed a large contribution of smaller, eastern-origin fish to western fisheries (Rooker *et al*. 2008). Increased focus on understanding 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 assessment and management efforts.

Bluefin tuna is currently managed as two stocks, an eastern and western stock. Assessment and management of North Atlantic bluefin tuna fisheries require international cooperation which is coordinated by the International Commission for the Conservation of Atlantic Tunas (ICCAT). The eastern and western stocks are assessed separately using virtual population analysis (VPA). Although stock mixing scenarios have been explored (e.g., Porch *et al*. 2001), they are currently not deemed reliable enough to provide advice to management and the accepted assessment scenarios assume no mixing (ICCAT 2008). Currently, the spawning stock biomass (SSB) of the eastern stock is estimated to be 35% of the SSB needed to support maximum sustainable yield (MSY), and the SSB of the western stock is estimated to be 110 % under low recruitment scenario and 15% under high recruitment scenario of the SSB associated with MSY (ICCAT 2010). 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}). Despite increasingly restrictive management efforts on these stocks in recent years, estimates of biomass do not indicate the anticipated rebuilding.

The apparent failure of bluefin tuna stocks to recover may be attributable to a misperception of the status of the resource due to the assumption of no connectivity in the current assessment and management framework. Stock mixing can give a false impression of local productivity and sustainable yield. For example, migrants from the more abundant eastern stock may supplement the bluefin tuna fishery in the west Atlantic (Rooker *et al*. 2008).

Thus, recognition of the nature and extent of connectivity between populations is critical to understanding how populations will respond to management actions (Cadrin and Secor 2009). Because of the potential impact movement and spatial overlap of bluefin stocks may have on stock perception, there is a critical need for development of tools to incorporate these phenomena into models to better understand local and regional population dynamics and improve management decisions.

Considerable research has gone into examining how inclusion of stock mixing could impact the results of bluefin tuna stock assessments (e.g., Butterworth and Punt 1994, NRC 1994, Porch *et al*. 2001). Butterworth and Punt (1994) and NRC (1994) studied how inclusion of mixing could affect the results of stock assessments for bluefin tuna using a discrete time box-transfer model**.** Porch *et al*. (2001) conducted sensitivity analysis of VPA results to stock mixing using a tag-integrated model of bluefin tuna (VPA 2-box model). Specifically, they explored the impact of two scenarios of mixing, classified as overlap and diffusion. The diffusion model assumed migrants joined the alternate spawning population, whereas the overlap model assumed natal homing or return of migrants to the population of origin to spawn. These studies indicate that including movement between populations in stock assessments can substantially affect estimates of stock size, fishing mortality, and recruitment (Punt and Butterworth 1995; Porch *et al*. 2001). The most sophisticated approach to date is the Multi-stock Age-Structured Tag-integrated stock assessment (MAST) model, which is a statistical catch-at-age model that allows stock mixing, but does not allow fish to move into the spawning grounds of the other stock (Taylor *et al*. 2011).

Simulation modeling is a useful and flexible approach that 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 (e.g., Kerr *et al*. 2010a; In Review). Simulation models can serve as a tool to integrate information gained from multiple approaches to investigating population structure (e.g., genetics, electronic tagging, otolith chemistry, life history traits; Cadrin *et al*. 2005) and permit testing of hypotheses. The generalized model framework is adaptable to incorporation of different levels of organization (i.e., contingents, populations, metapopulations) demographics, and dynamics (Kerr *et al*. 2010a).

The ultimate goal of this study is 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 aim 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 stocks of bluefin tuna to explore the impact of connectivity on productivity, stability, sustainable yield, and rebuilding goals for bluefin tuna stocks. Furthermore, we plan to examine the implications of different assumptions of stock productivity of the western bluefin tuna stock. For this paper, we demonstrate results from one scenario to solicit feedback on model structure and parameter values from participants of the ICCAT Bluefin Tuna Stock Assessment Meeting.

2. Methods

The model is composed of two spawning populations based on western and eastern Atlantic bluefin tuna stocks, each with its own unique vital rates and independent recruitment dynamics. The model is a stochastic age-structured (age 1 to 30), temporally- (quarters) and spatially-explicit (seven geographic zones) overlap model. Consensus from the ICCAT workshop on bluefin mixing (2001) supported the use of an overlap model with discrete spatial and temporal strata as the best approach to model bluefin tuna with greater biological realism. In an overlap model stocks overlap spatially, but exhibit spawning site fidelity (Porch *et al*. 1998). Additionally, quarterly time steps were viewed to be sufficient to capture changes in bluefin movement patterns and the associated fisheries (ICCAT 2001). The spatial strata of the model are informed by information on the distribution, life history, fishery, and management of bluefin tuna and represent the consensus of experts on bluefin tuna mixing (**Table 1**, ICCAT 2001, 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 stocks and five regions where various degrees of spatial overlap occur between stocks (**Figure 1**, **Table 1**). Note that the spatial structure of this model is of a finer scale than the structure used in Taylor *et al.* (2011) in that zone 4 in the Taylor *et al*. model is broken up into zones 4, 5, and 6 in the current model.

2.1 Model Parameters

The values and variances of several model parameters were informed by the most recent ICCAT stock assessments (ICCAT 2010) for the eastern and western stocks (**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-weight relationships were used to estimate weight at age of bluefin tuna stocks ($W_{a,S}$)

$$W_{a,S} = \alpha_S L_{a,S}^{\ \beta_S}$$

where $L_{a,S}$ is length at age for each stock, α_S is a stock-specific proportionality constant and β_S is the allometric coefficient for each stock (**Table 2**). Length at age was estimated from von Bertalanffy growth models with parameters specific to each stock (**Table 2**)

$$L_{a,S} = L_{\infty,S}\left[1 - e^{-k_S(a - a_{0,S})}\right]$$

where $L_{\infty,S}$ is the asymptotic size, k_S defines the rate at which the curve approaches the asymptote, and $a_{0,S}$ is the hypothetical age at which the size of the fish is zero for each stock. 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, ICCAT 2008). 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, ICCAT 1997, 2010). 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 would require revised estimates of movement. Natural mortality rates are not well-characterized for bluefin tuna. Natural mortality rates for young ages were derived from tagging experiments on southern bluefin tuna (ICCAT 2010; **Table 2**).

Stock-recruit relationships for the western stock were characterized under high and low recruitment regimes. A Beverton-Holt stock recruit curve was used to characterize the western stock-recruit relationship under the high recruitment scenario and a hockey-stick model characterized the relationship under the low recruitment scenario (ICCAT 2010; **Table 2**). A hockey-stick stock-recruit relationship was used to characterize the stock-recruit relationship for the eastern stock. Hockey-stick parameters were estimated as the average spawning stock biomass (SSB threshold) and geometric mean number of recruits (*Rmax*) from 1955-2007 (**Table 2**).

Fishing mortality by gear type (long-line, purse seine, bait boat, and other), quarter, and zone was reported in Taylor *et al.* (2011). Average fishing mortality values from 2008 to 2009 where used in the model (values for zone 4 in the Taylor *et al.* (2011) model were used for zones 4, 5, and 6 in this model; **Table 3**). Gear selectivity at age was derived from values in Legault and Restrepo (1998) and Fromentin and Bonhommeau (2010). Note that the gear types used in the estimation of selectivity and fishing mortality were not an exact match. Exploitation rate at age by quarter, gear type, and zone ($E_{a,q,g,z,S}$) was calculated based on Baranov's catch equation

$$E_{a,q,g,z,S} = \frac{F_{q,g,z}\gamma_{a,g,S}}{F_{q,g,z}\gamma_{a,g,S} + M_{a,S}} 1 - e^{-M_{a,S} - F_{q,g,z}(\gamma_{a,g,S})}$$

where $F_{q,g,z}$ is the fishing mortality by quarter, gear, and zone, $\gamma_{a,g,S}$ is age-specific gear selectivity by stock, and $M_{a,S}$ is age-specific natural mortality by stock.

2.2 Model Framework

2.2.1. Model Initialization

The number of fish at age in each stock, zone, and quarter during year 1 was calculated to fully initialize the model. The model was initialized with the number of age-1 recruits for each stock in their respective spawning areas (zone 1 for western stock fish & zone 7 for eastern stock fish) and time (quarter 1) during year 1. Values were based on asymptotic recruitment (R_{max}) estimates for eastern and western stocks (western stock: low recruitment scenario; **Table 2**). Abundance at age of bluefin tuna stocks in their respective spawning zones during year 1, quarter 1 ($N_{a,q1,y1,z,S}$) was calculated by

$$N_{a,q_1,y_1,z,S} = N_{a-1,q_1,y_1,z,S}\, e^{-M_{a-1,S} - \sum_{g=1}^{g=4} F_{q_1,g,z,S}(\gamma_{a-1,S})}$$

Abundance at age of bluefin tuna stocks in non-spawning zones during year 1, quarter 1 was set equal to zero. Abundance at age in year 1, quarters 2 to 4 was calculated as

$$N_{a,q,y_1,z,S} = \sum_{z=1}^{z=7} N_{a,q-1,y_1,z,S}\, C_{z \to z_{a,q-1,S}}\, e^{-M_{a,S} - \sum_{g=1}^{g=4} F_{q-1,g,z,S}(\gamma_{a,S})}$$

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

2.2.2. Stochastic Model Structure

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

$$N_{a_1,q_1,y,z,S} = \begin{cases} R_{\max_S}\varepsilon_{y,S} & \text{if } SSB_{y,q_1,z,S} \geq SSB^*_S \\ \dfrac{R_{\max_S}}{SSB^*_S} SSB_{y,q_1,z,S}\varepsilon_{y,S} & \text{if } SSB_{y,q_1,z,S} < SSB^*_S \end{cases}$$

where $R_{\max_S}$ is the maximum level of recruitment for each stock and SSB^*_S is the spawning biomass threshold specific to each stock that triggers a different response in recruitment. For stock-recruit calculations only, SSB is calculated at the beginning of the year (i.e., the spawning stock 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 stock. Recruitment of the western bluefin tuna stock under the high recruitment scenario was calculated using a Beverton Holt stock-recruit curve

$$N_{a_1,q_1,y,z,S} = \frac{\alpha_S SSB_{y,q_1,z,S}}{\beta_S + SSB_{y,q_1,z,S}}\varepsilon_{y,S}$$

where α_S is the maximum number of recruits produced and β_S controls the rate at which the asymptote, or maximum recruits per spawner, is reached (Beverton and Holt 1957).

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

$$N_{a,q_1,y,z,S} = \sum_{z=1}^{z=7} N_{a-1,q_4,y-1,z,S} C_{z\to z_{a-1,q_4,S}} e^{-M_{a-1,S} - \sum_{g=1}^{g=4} F_{q4,g,z,S}(\gamma_{a-1,S})}$$

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

$$N_{a,q,y,z,S} = \sum_{z=1}^{z=7} N_{a,q_{-1},y,z,S} C_{z\to z_{a,q-1,S}} e^{-M_{a,S} - F_{q-1,z}(\gamma_{a,S})}$$

Spawning stock biomass of bluefin tuna stocks 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 stock

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

Yield of bluefin tuna stocks in each geographic zone was calculated for each stock

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

2.3. Simulation

A series of 500 stochastic model runs, each conducted over a 150-year time period, will be performed for each model scenario (only the last 100 years were used in analyses to allow simulations to approach a dynamic equilibrium). Mean productivity (SSB) and yield across geographic zones and quarters and stability (CV_{SSB}) of stocks across quarters will be calculated for each stock under alternative stock connectivity and productivity scenarios. For this paper, one 'baseline' scenario (specified below) is presented for demonstration.

2.3.1. Status Quo Model

This model assumes eastern and western stocks are separate with no movement or overlap between them (i.e., the scenario assumed in the separate eastern and western stock assessments). These scenarios are essentially long-term projections of the dynamics assumed and estimated for the separate stocks (ICCAT 2010).

2.3.2. Stock Mixing Scenarios

Stock connectivity scenarios were developed; scenarios utilized movement rates estimated by three different methods: 1) gravity method (Taylor *et al.* 2011), 2) bulk transfer method (Taylor *et al.* 2011), and 3) proportional movement based on electronic tags (B. Galardi pers. comm.). The gravity method is a simplification that reduces the number of estimated parameters by estimating probability of residence in each area and distributing the remaining movement probability evenly among other areas, with some ontogenetic constraints based on expert opinion. The bulk transfer method is more statistically demanding, because it estimates probabilities of all movements among areas. The reliability of results from gravity and bulk transfer methods may not reflect actual movements of Atlantic bluefin tuna, because movement estimates from the gravity method are somewhat arbitrary (i.e., movements may not be evenly distributed among areas), and bulk transfer estimates of movement may not be well estimated because models may be over-parameterized. The third movement scenario was more empirically derived from tagging observations, primarily from tagging in western areas to contrast model estimates.

Taylor *et al*. (2011) provided movement rates for a 5 box model; these rates were modified according to the criteria described below to accommodate the 7 box model structure used in this study.

Movement Rates to Zone 5:

- Western stock: Juvenile and adolescent fish (≤ age 8) were allowed to move into zone 5.
- Eastern stock: Juvenile, adolescent, and adult fish were allowed to move into zone 5.

Movement Rates to Zone 6:

- Western stock fish were excluded from movement into zone 6
- Eastern stock: Only adult fish (≥ age 5 [age at 100% maturity]) were allowed to move into zone 6.

In the 7 box model the estimated residency rate for Taylor *et al*. (2011) zone 4 was divided equally into zones 4 and 5 or zones 4, 5, and 6 depending on stock 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).

2.3.3. Productivity Regime Scenarios

The status quo and stock mixing scenarios will be run under different assumptions regarding productivity of the western stock. The baseline model run presented in this paper assumes a low recruitment regime for the western stock (based on recruitment patterns in 1990 and 2000s). The alternative scenario will assume a high recruitment regime for the western stock (based on recruitment patterns in 1970 and 1980s).

3. Results for Demonstration Scenario

Movement Rates: Gravity Method
Recruitment Regime of Western Stock: Low
Management: Status quo fishing mortality

The long-term expectations reported here are conditional on the assumed parameter values under the scenario of status quo fishing mortality, 'gravity' estimates of movement, and 'low recruitment' for the western stock. ***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.*** Overall, the magnitude and distribution of long-term SSB and yield differed greatly between eastern and western bluefin tuna stocks under this scenario. Long-term SSB of the eastern and western stocks in the first quarter of the year averaged 646,459 mt and 18,979 mt, respectively, and decreased across quarters due to the fishing and natural mortality experienced throughout the year (**Figure 4**). Long-term annual yield of the eastern stock was 1,555 mt and western stock was 215 kt (**Figure 4**). The eastern bluefin tuna stock exhibited slightly higher stability or lower CV_{SSB} (CV_{SSB} ranged 0.3 to 0.16) than the western bluefin tuna stock (CV_{SSB} ranged 0.3 to 0.21).

Long-term expectations of spawning stock biomass of the western stock was highest in zone one (Gulf of Mexico), quarter one (**Figure 2a**). This result is a function of the assumption that mature fish return to zone one to spawn during quarter one. During the remaining quarters, the long-term SSB of western stock fish was consistently highest in zone three (western Atlantic), four (central Atlantic), and two (Gulf of St. Lawrence), in order of decreasing biomass (**Figure 2a**). The contribution of western stock fish in zone five (eastern Atlantic) to the long-term SSB of the stock was minor. This was due to the movement constraint that permitted only young fish (≤ 8 years), of which only a small portion were considered mature, to enter this area. Western stock fish were absent from zones six (northeast Atlantic) and seven (Mediterranean Sea), because constraints in the model that restricted their movement into these areas. The majority of the long-term yield of western stock bluefin tuna came from zones three and four, with minor contributions from zones one, two, and five. Total long-term yield of the western stock was highest in the third quarter (**Figure 2b**).

Across quarters, the long-term SSB of eastern stock fish was consistently highest in zone seven (Mediterranean Sea; **Figure 3a**). The long-term SSB in this zone comprised approximately 87% of the total SSB. This concentration of biomass was a function of high residency rates specified within this zone in movement rates estimated by the gravity method. Eastern stock fish were present at lower levels in zones three, four, five, six (**Figure 3a**). Eastern stock fish were absent from zones one and two based on the movement constraints in the model. The long-term yield of eastern stock fish was highest in zone seven, with the highest long-term yields occurring during quarter two (**Figure 3b**). Minor contributions to the total yield of eastern stock fish came from zones three, four, five, and six.

In the context of the movement rates in this scenario, the long-term SSB and yield of bluefin tuna in zones one and two is composed exclusively of western stock fish and long-term SSB in zones five (with very minor contribution from west), six, and seven is composed of eastern stock fish (**Figure 4a, 4b**). Zones three and four are dominated by eastern stock fish, but there is substantial contribution of western fish to long-term SSB and yield of bluefin tuna in these zones. The eastern stock comprises an average of 77% of the SSB and 53% of the yield of bluefin tuna in zone three (**Figure 4**). The eastern stock also dominants the long-term SSB and yield of bluefin tuna in zone four, however there is a contribution of western stock fish (16% of SSB and 33% of yield on average).

4. Discussion

The simulation model was designed to incorporate the current state of knowledge of bluefin tuna life history and movement patterns. The demonstrated output presents one scenario (i.e., 'low recruitment' in the western stock, gravity estimates of movement, status-quo fishing mortality rates). Other scenarios (e.g., the 'high recruitment' option for the western stock; bulk transfer movement estimates with greater emigration from the Mediterranean) are expected to produce substantially different long-term expectations of SSB and yield. Such simulations can help us to evaluate how spatial overlap of stocks may impact our perception of the resource. The model can also aid in identifying gaps and uncertainty in knowledge that prevent an accurate view of the resource. Once the operating model is deemed valid, and specific movement scenarios are agreed upon by experts to be realistic, the model may be useful in informing temporal and spatial harvest targets in management of eastern and western bluefin tuna stocks for developing rebuilding plans and determining optimal harvest rates.

Currently, bluefin tuna stock assessments assume no mixing between eastern and western stocks. The output of this movement scenario demonstrates that stock mixing alters the way that assessments represent stock status. Due to the difference in relative abundance between eastern and western stocks, it is particularly important to quantify immigration of eastern origin fish to the western Atlantic, because this can profoundly impact estimation of abundance of the western bluefin tuna stocks. This movement scenario suggests that zone three (western Atlantic), which under the current management unit framework is considered to be composed entirely of western stock fish, is expected to be composed primarily of eastern stock fish in the long-term (based on the scenario of status quo fishing patterns, low recruitment in the western stock and gravity model estimates of movement). This demonstration illustrates that misperception of stock mixing may lead to inaccuracy in the assessment of western bluefin tuna.

The magnitude and distribution of productivity and yield of western and eastern bluefin tuna stocks is highly 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. 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 stocks. Currently, the assumed age at 100% maturity of the western stock (age 16) is much older than that assumed for the eastern stock (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 (ICCAT 2010). 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). Our operating model includes the more informative selectivity by fleet from Legault and Restrepo (1998), which may not correspond with the fishing mortalities and movements estimated in conjunction with the constant, aggregate selectivity assumed 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.

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.

Long-term expectations of SSB from the simulated scenario are greater than the SSB associated with MSY for the eastern stock of bluefin tuna and less than the SSB associated with MSY for the western stock. Long-term SSB of the western stock is similar to the medium-term (i.e., 2010) projections from Taylor *et al*. (2011). However, long-term SSB of the eastern stock is greater than their medium-term projections, and more similar to Taylor *et al*.'s (2011) estimates for the 1990s. The long-term expectations are strongly influenced by the high probability of residence in zone 7 (Mediterranean Sea) estimated by Taylor *et al*. (2011), where fishing mortality is much less than zone 4,5,6 (central and eastern Atlantic).

Our results illustrate that implications of stock mixing should be considered in stock assessment and fishery management. For example, most fleets represent a mixed-stock fishery, and regulations on the fleets affect both stocks. Therefore, management actions should be coordinated among stocks and fleets to meet management objectives.

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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 stock 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 stock spawning area (ICCAT 2001, Taylor *et al*. 2011).
2. **Gulf of St. Lawrence:** assumed to contain primarily western-stock 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. **Northwest Atlantic Ocean**: assumed to be mixed-stock are**a**
    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 eastern stock spawning area. The eastern boundary is defined by East/West Management boundary (45° meridian, ICCAT 2001, 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 East/West Management boundary (45° meridian). The eastern boundary is defined by fact that few fish tagged in the west with electronic tags moved beyond 30°W (ICCAT 2001).
5. **Southeast 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 the fact that few fish tagged in the west with electronic tags moved beyond 30°W (ICCAT 2001). The western boundary is defined by knowledge of spatial extent of western stock 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 the fact that few fish tagged in the west with electronic tags moved beyond 30°W (ICCAT 2001). 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 stock 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 stock spawning area (ICCAT 2001, Taylor *et al*. 2011).

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

Parameter		Value	Sources
Length-weight			
	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			
	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 1: 0.1225, age 2: 0.06, age : 0.06, age 4: 0.06, age 5:0.06, age 6:0.05, age 7:0.04375, age 8:0.0375, age 9:0.03125, ages 10-30: 0.025	vector based on tagging experiments on southern bluefin tuna, ICCAT 1997, 2010
Stock-recruit			
	West	Hockey-stick "Low recruitment" Model: Rmax = 84,363; SSb Hinge = 12,236, Standard Error of Random Deviations = 0.37 Beverton and Holt " High Recruitment" Model: Alpha = 432,982; Beta = 61,344, Standard Error of Random Deviations = 0.37	ICCAT 2010, S. Calay pers. comm
	East	Hockey-stick Model: Rmax = 1,889,896; SSB Hinge = 215,584, CV of recruitment = 0.43	Estimated from data in ICCAT 2010

Table 3. Fishing mortality (yr^{-1}) by gear type (LL: long-line, PS: purse seine, BB: bait boat, 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. Gear selectivity (LL: long-line, PS: purse seine, BB: bait boat, and other) for eastern (Fromentin and Bonhommmeau 2010) and western stocks of bluefin tuna (Legault and Restrepo 1998). Selectivity values were kept the same for the western stock ages 10+ and eastern stock ages 19+. The selectivity for eastern stock fish by bait boats was used for the western stock.

	Western Stock			**Eastern Stock**			
Age	LL	PS	Other	LL	PS	BB	Other (trap)
1	0.02	0.25	0	0.03	0.38	0.63	0
2	0.1	0.57	0.01	0.05	1	1	0.01
3	0.27	0.55	0.03	0.05	0.88	0.46	0
4	0.4	0.26	0.04	0.04	0.46	0.25	0.02
5	0.45	0.12	0.07	0.05	0.27	0.15	0.05
6	0.56	0.1	0.13	0.09	0.21	0.08	0.08
7	0.79	0.25	0.35	0.17	0.2	0.05	0.13
8	1	0.87	0.71	0.31	0.78	0.04	0.21
9	0.98	1	1	0.45	0.3	0.04	0.35
10	0.68	0.29	0.84	0.64	0.51	0.04	0.5
11				0.8	0.8	0.04	0.72
12				0.81	0.53	0.05	0.77
13				1	0.39	0.09	0.94
14				1	0.42	0.13	1
15				1	0.44	0.21	0.98
16				0.75	0.52	0.29	0.94
17				0.79	0.55	0.29	0.75
18				0.71	0.54	0.35	0.75
19				0.79	0.6	0.22	0.5

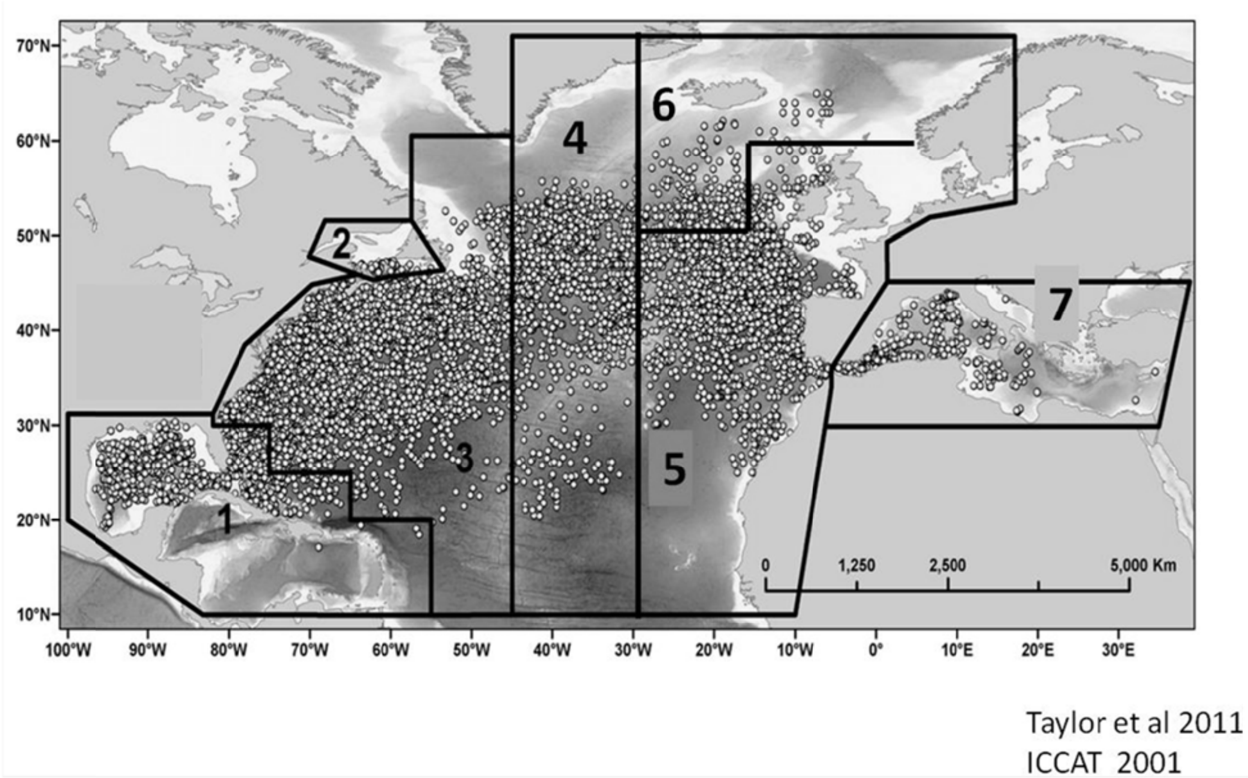

Figure 1. Spatial structure utilized in bluefin tuna model (modified from Taylor *et al*. 2011). The spatial strata defined by Taylor *et al*. 2011 were modified according to the consensus of experts on bluefin tuna mixing (ICCAT 2001, Rooker *et al*. 2007).

a

b

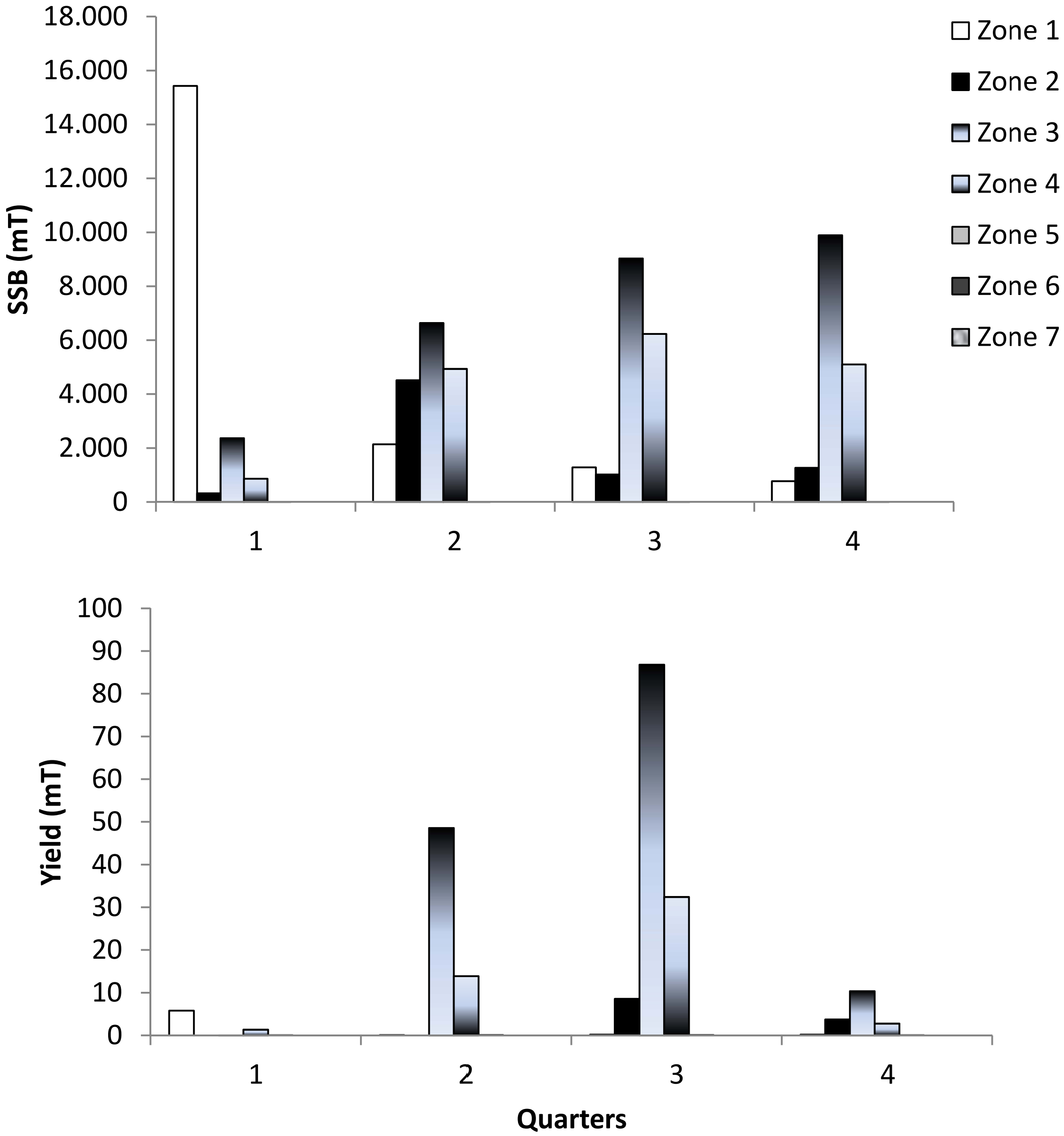

Figure 2. a) Equilibrium spawning stock biomass (mt) of western stock bluefin tuna across geographic zones (1-7) and quarters (1-4). b) Equilibrium yield (mt) of western stock bluefin tuna across geographic zones (1-7) and quarters (1-4). Note that the parameter values associated with these approaches may be inconsistent (e.g., recruitment estimates are likely to be conditioned on movement assumptions), and the long-term expectations may not be realistic.

a

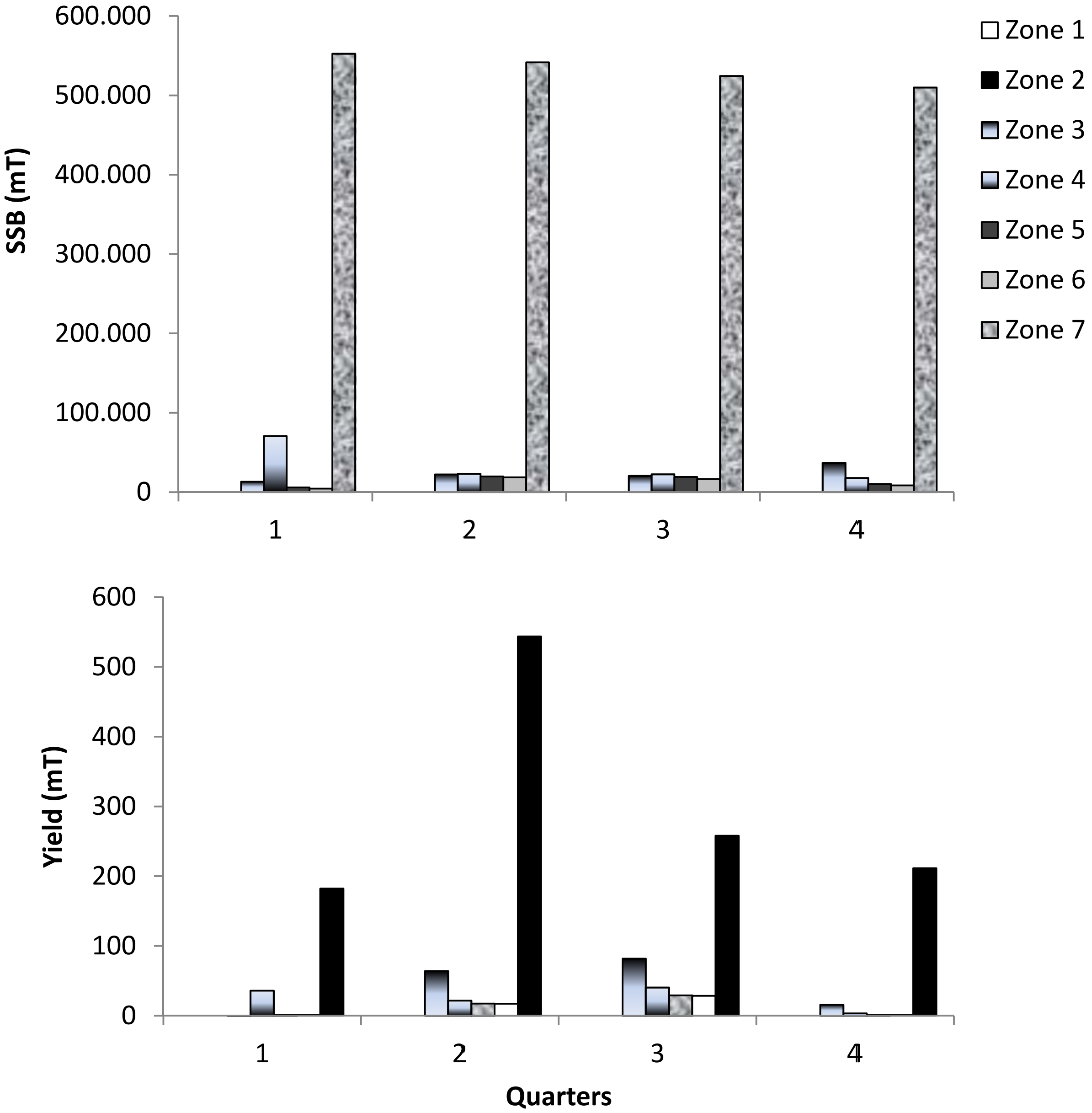

Figure 3. a) Equilibrium spawning stock biomass (mt) of eastern stock bluefin tuna across geographic zones (1-7) and quarters (1-4). b) Equilibrium yield (mt) of eastern stock bluefin tuna across geographic zones (1-7) and quarters (1-4). Note that the parameter values associated with these approaches may be inconsistent (e.g., recruitment estimates are likely to be conditioned on movement assumptions), and the long-term expectations may not be realistic.

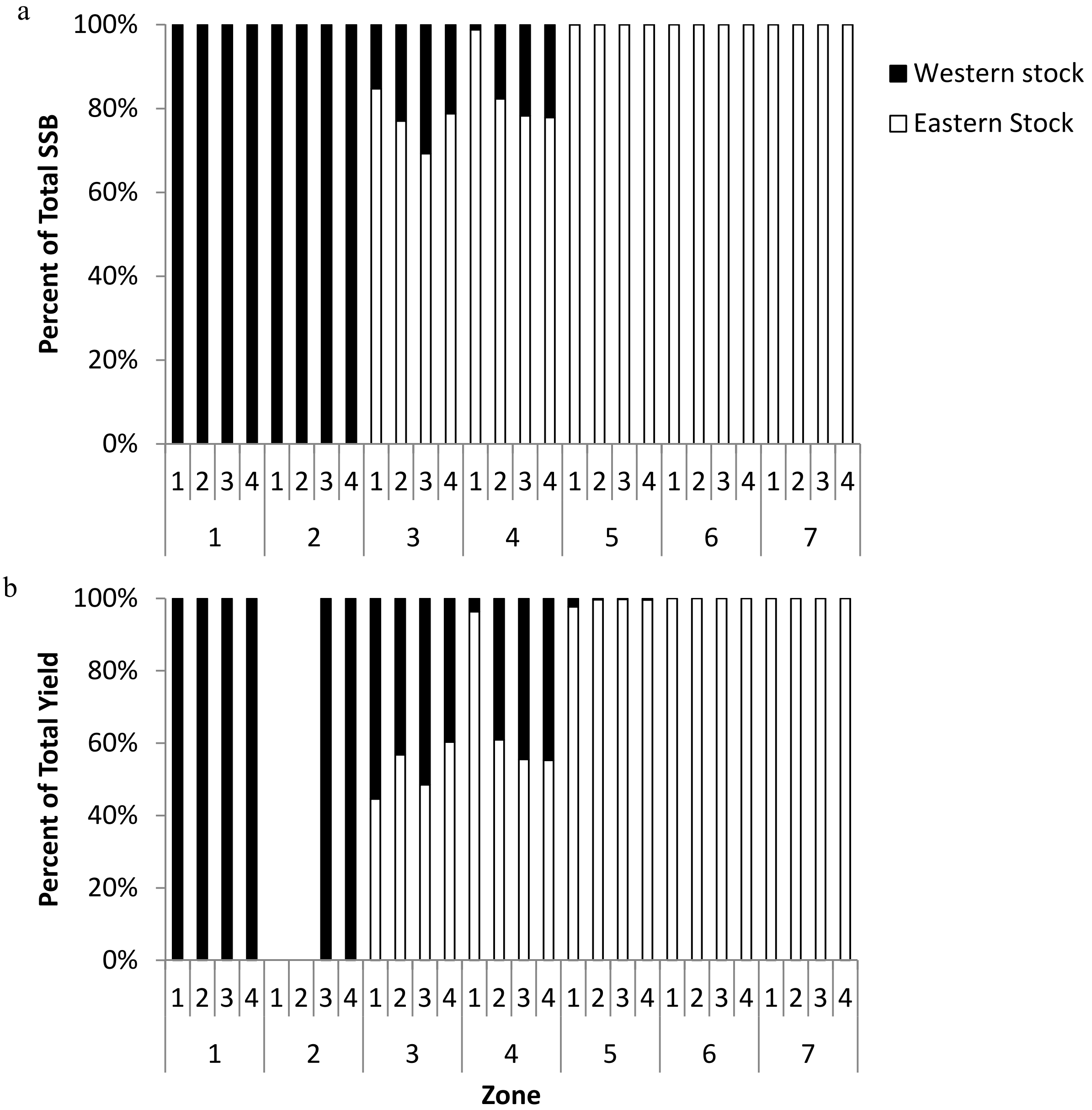

Figure 4. a) Percent composition of equilibrium spawning stock biomass across geographic zones (1-7) and quarters (1-4). b) Percent composition of equilibrium yield (mt) across geographic zones (1-7) and quarters (1-4). Note that the parameter values associated with these approaches may be inconsistent (e.g., recruitment estimates are likely to be conditioned on movement assumptions), and the long-term expectations may not be realistic.