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Supporting Online Material

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Natal Homing and Connectivity in Atlantic Bluefin Tuna Populations

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Atlantic bluefin tuna populations are in steep decline, and an improved understanding of connectivity between individuals from eastern (Mediterranean Sea) and western (Gulf of Mexico) spawning areas is needed to manage remaining fisheries. Chemical signatures in the otoliths of yearlings from regional nurseries were distinct and served as natural tags to assess natal homing and mixing. Adults showed high rates of natal homing to both eastern and western spawning areas. Trans-Atlantic movement (east to west) was significant and size-dependent, with individuals of Mediterranean origin mixing with the western population in the U.S. Atlantic. The largest (oldest) bluefin tuna collected near the northern extent of their range in North American waters were almost exclusively of western origin, indicating that this region represents critical habitat for the western population.

Harvest strategies for marine fishes depend on fundamental assumptions about their complex life cycles, and management is often based on the "unit stock concept," which relies on the phenomenon of natal homing (return to spawning area) and limited or structured connectivity between populations (*1*). For Atlantic bluefin tuna, these assumptions are important because spawning populations in the western Atlantic are at 10% of the biomass prevailing when industrial fishing began, and recovery is confounded by trans-Atlantic movement across international jurisdictions (*2*). In assessments and management activities, the International Commission for the Conservation of Atlantic Tunas (ICCAT) has assumed that Atlantic bluefin tuna occur as two discrete populations that originate either in the Mediterranean Sea or the Gulf of Mexico; members of either population can undertake trans-Atlantic migrations, but adults will return to natal spawning regions; and trans-Atlantic migrations are relatively small in number, justifying the use of two broad management regions east and west of 45°W longitude. Despite four decades of regulation by ICCAT, bluefin tuna populations remain severely depressed, causing many to question the effectiveness of the current management regime (*3*, *4*). Although recent electronic tagging data demonstrated evidence for spawning site fidelity (i.e., return of adults repeatedly to the same spawning region) (*5*), the degree of natal homing in the populations and rate of exchange between eastern and western populations is unresolved. Without data on population structure and movement, there is no biological rationale for spatially explicit management, and thus rebuilding plans may be predisposed to fail.

Several approaches have been used to examine the population structure of Atlantic bluefin tuna (*2*), of which chemical traces in otoliths (ear stones) have considerable potential for quantifying natal homing and connectivity because otolith material deposited during the first year of life serves as a natural tag of the individual's place of

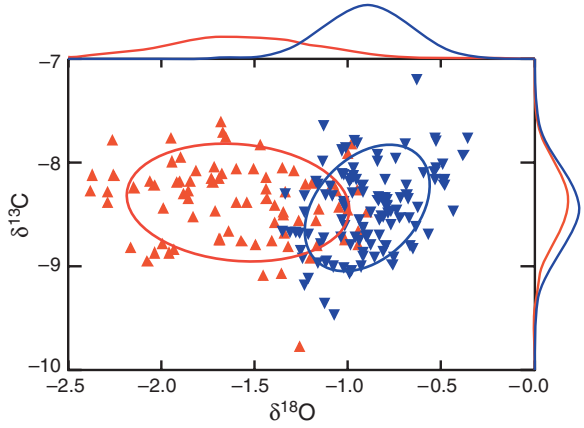

Fig. 1. Otolith $\delta^{13}C$ and $\delta^{18}O$ values for yearling Atlantic bluefin tuna collected from 1999 to 2004 in the eastern Atlantic Ocean/Mediterranean Sea (blue triangles) and western Atlantic Ocean (red triangles). Gaussian bivariate ellipses (one standard deviation of the mean) and normal distribution curves are shown. Yearlings ranged in age from 12 to 18 months. Two regions of the eastern Atlantic Ocean/Mediterranean Sea were sampled over the 6 years: the eastern Atlantic Ocean (Cantabrian Sea; 2000, 2001, and 2002) and the western/central Mediterranean Sea (Ligurian Sea to Adriatic Sea; 1999, 2000, 2002, 2003, and 2004) (n = 113). In the continental shelf waters of the U.S. Atlantic Ocean, yearlings were collected from Maryland to Massachusetts over a 6-year period (n = 81) [see S8 in (*8*)].

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origin or nursery habitat (*6*, *7*). We determined the origin of bluefin tuna by means of carbon and oxygen stable isotope ratios ($\delta^{13}C$ and $\delta^{18}O$) in otoliths [see S1 in (*8*)]. Stable isotopes in otoliths and other biogenic carbonates represent a class of chemical tags for which associations with water mass properties are well understood (*9*). Global records of surface water stable carbon and oxygen isotopes indicate these natural markers vary regionally (*10*), and in otoliths these isotopes often serve as natal tags because they reflect water composition differences in nurseries, although fractionation due to kinetic and metabolic effects, particularly for $\delta^{13}C$, can influence isotopic composition (*11*).

The isotopic composition of otoliths from yearling (12 to 18 months of age) bluefin tuna was measured for individuals collected over 6 years (1999 to 2004) from both eastern (Mediterranean Sea/eastern Atlantic Ocean) and western (Gulf of Mexico/U.S. Atlantic Ocean) nurseries (Fig. 1). Otolith composition was distinct between yearlings from eastern and western nurseries [multivariate analysis of variance (MANOVA), $P < 0.01$; based on pooled years], and otolith $\delta^{18}O$ was significantly higher for yearlings from the eastern nursery in five of the years (all except 2001). Mean (SD) otolith $\delta^{18}O$ values for the eastern and western nurseries were –0.89‰ (0.23) and –1.66‰ (0.37), respectively. No significant differences in otolith $\delta^{13}C$ values were observed between eastern and western bluefin tuna in five of the six years sampled (exception 2002, ANOVA, $P < 0.05$) (Fig. 1). Using quadratic discriminant function analysis (QDFA) parameterized with otolith $\delta^{13}C$ and $\delta^{18}O$ values from all year classes, cross-validated classification success to eastern and western nurseries was high (87%), indicating that stable isotopes were useful markers of natal origin for bluefin tuna [see S2 in (*8*)].

Milled cores of otoliths were used to represent the yearling period of school (<60 kg), medium (60 to 140 kg), and giant (>140 kg) category bluefin tuna [see S3 in (*8*)], and maximum likelihood estimates were generated using a mixed-stock algorithm [see S4 in (*8*)] (*12*) to assign individuals to eastern and western nurseries. Although the temporal stability of the primary marker, $\delta^{18}O$, justified the pooling of years for establishing a baseline, temporal variability in otolith core $\delta^{13}C$ or $\delta^{18}O$ values was investigated because our calibration set of juveniles (baseline) did not match our adults. No differences were detected in otolith core $\delta^{18}O$ values between bluefin tuna with birthdates before or during our baseline period in either region, suggesting that the otolith $\delta^{18}O$ composition remained relatively constant over the years investigated [see S5 in (*8*)]. Changes in $\delta^{13}C$ values in otolith cores were detected, and depletion levels for $\delta^{13}C$ were significant and similar to reductions reported in the oceans due to release of CO_2 from the burning of fossil fuels (Suess Effect) (*13*). Otolith core $\delta^{13}C$ values were adjusted to account for such temporal variation, but estimates of origin were comparable to nonadjusted values [see S6 in (*8*)].

Natal homing, defined as the return of spawning adults to their region of origin, was high and remarkably similar for both eastern and western spawning regions: 95.8% for the Mediterranean Sea and 99.3% for the Gulf of Mexico [see S7 in (*8*)]. This work corroborates earlier indications of spawning fidelity from electronic tagging data that showed return migrations of both Mediterranean (*5*) and Gulf of Mexico (*5*, *14*) spawners over multiple years. Additionally, genetic differences have been observed between juveniles collected from the two regions (*15*). Documentation of natal homing in marine vertebrates is rare, and the size of natal areas for bluefin tuna are much larger than in systems where homing is better known (e.g., streams, lakes, and estuaries). Nevertheless, rates of return to eastern and western spawning areas by Atlantic bluefin tuna populations are at the upper end of ranges reported for teleosts, rivaling those of Pacific salmon (*16*). Although we could not document repeat spawning in this particular application, long-term archival tag deployments provide evidence of bluefin tuna returning to the same spawning sites over consecutive years (*2*, *5*).

Estimates of natal origin from otolith chemistry indicate that mixing occurs in North American waters, and our data confirm that U.S.

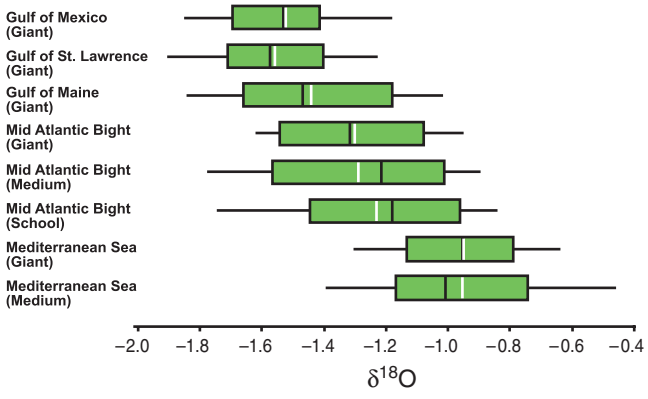

Fig. 2. Box plots showing otolith core $\delta^{18}O$ values of school (<60 kg), medium (60 to 140 kg), and giant (>140 kg) category Atlantic bluefin tuna from spawning areas (Mediterranean Sea, Gulf of Mexico), and foraging areas (Gulf of St. Lawrence, Gulf of Maine, Mid Atlantic Bight). Interquartile range (25th and 75th percentile) is shown by extent of boxes, and error bars represent 10th and 90th percentiles. Median (50th percentile) and mean values are shown in boxes as black and white lines, respectively. Collection dates: Mediterranean Sea (2003 to 2007), Gulf of Mexico (2004, 2007), Gulf of St. Lawrence (2006 to 2007), Gulf of Maine (1996, 1998), Mid Atlantic Bight (1997 to 2000).

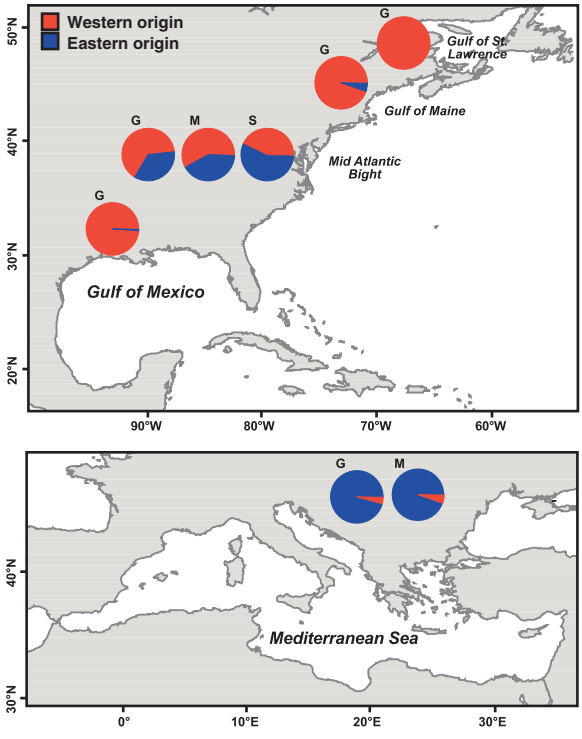

Fig. 3. Estimates of natal origin for school (S), medium (M), and giant (G) category Atlantic bluefin tuna from spawning areas (Mediterranean Sea, Gulf of Mexico) and foraging areas (Gulf of St. Lawrence, Gulf of Maine, Mid Atlantic Bight). Contribution rates (percentages) were determined by comparing milled otolith cores (corresponds to yearling period) to a baseline sample from eastern and western nurseries (east + west = 100%). Assignment to either eastern or western nursery was based on maximum likelihood estimations. Standard deviations (SD) were expressed as percentages of estimated proportions. Size classes were approximated based on weight or age (actual or derived from length): giant (>140 kg, ≥ age 10 years), medium (60 to 140 kg, age 5 to 9 years), and school (<60 kg, < age 5 years) category bluefin tuna. Percentage contribution of "western population" and standard deviation (SD) around estimated proportion per region and size category: Gulf of Mexico [giant: 99.3% (SD 1.7%), $n = 42$]; Mediterranean Sea [giant: 4.2% (SD 3.1%), $n = 94$; medium: 4.2% (SD 4.4%), $n = 38$]; Gulf of St. Lawrence [giant: 100% (SD 0.0%), $n = 38$]; Gulf of Maine [giant: 94.8% (SD 5.3%), $n = 72$]; Mid Atlantic Bight [giant: 64.9% (SD 21.9%), $n = 12$; medium: 55.7% (SD 10.4%), $n = 56$; school: 42.6% (7.2%), $n = 86$].

commercial and recreational fisheries are composed of both populations of bluefin tuna (Fig. 2). A large fraction of the school (57.4%) and medium (44.3%) category bluefin tuna present in the U.S. waters of the Mid Atlantic Bight were from the eastern population, and we observed that the occurrence of eastern bluefin tuna in the Mid Atlantic Bight decreased with increasing size (age) (Fig. 3). Our estimates of trans-Atlantic exchange were significantly higher than previous reports from conventional tags (*3*) and demonstrated substantial intermingling of individuals from eastern and western populations in U.S. waters, a finding supported with recent evidence from electronic tags (*5*). In contrast, giant category bluefin tuna collected from northern U.S (Gulf of Maine) and Canadian (Gulf of St. Lawrence) fisheries were almost entirely of western origin (94.8% and 100%, respectively). The mechanism(s) responsible for differences in stock composition of bluefin tuna samples from Mid Atlantic Bight (mixed populations) and Gulf of Maine/Gulf of St. Lawrence (western population) waters appears related to size (age) or reproductive state. The majority of our sample from the Mid Atlantic Bight was composed of adolescent bluefin tuna (<5 years of age), and tagging studies have demonstrated that young bluefin tuna are more likely to display trans-Atlantic movements that are linked to foraging than are adults (*2*). Ontogenetic shifts in dispersive behaviors often occur for marine vertebrates displaying natal homing, with exploratory movements associated with foraging decreasing at the onset of breeding (*17*, *18*). Similarly, our finding of stock homogeneity of giants (>140 kg, >10 years of age) in the Gulf of Maine and Gulf of St. Lawrence, and increasing contributions from the western population with age in the Mid Atlantic Bight, suggests that movement becomes more limited and structured after bluefin tuna become sexually mature.

Significant trans-Atlantic mixing of eastern adolescents on western foraging areas emphasizes the connectivity of Atlantic bluefin tuna populations. Under the current assessment framework that assumes limited mixing, a high degree of exchange evident from chemical signatures in otoliths indicates that past abundances of western Atlantic bluefin tuna may have been overestimated, particularly at younger age classes. In addition, exchange rates reported here show that U.S. fisheries for bluefin tuna appear dependent, to some extent, on recruits from the Mediterranean Sea. Because the eastern population is at least an order of magnitude higher in abundance than the western population (*19*), it is unlikely that west-to-east movement of adolescents from the western population contribute significantly to Mediterranean and other eastern Atlantic fisheries. Of greater concern is that adolescents from the western population show similar eastward dispersive behaviors across the 45°W management boundary. If this occurs at rates observed here for eastern adolescents, the smaller, less productive western population will be disproportionately affected by higher fishing rates in the eastern management zone.

The disparity between the eastern and western population sizes and the continued decline of the western stock suggests that some added level of protection is needed to ensure the sustainability of the smaller western component. Natal homing rates reported here were remarkably high to both regions and clearly show that the contribution of eastern adults to the western spawning area is inconsequential. Thus, spawning adults in the Gulf of Mexico appear to be entirely of western origin, and this region should be given high priority for conservation. High connectivity between foraging areas in the Gulf of Maine/Gulf of St. Lawrence and the Gulf of Mexico was also observed, signifying that this region of the northern Atlantic represents critical refugia for western giants. Due to the condition of the western population, a more conservative rate of exploitation of bluefin tuna, inclusive of eliminating bycatch in the Gulf of Mexico, will be required for the recovery of this population.

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Supporting Online Material

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Fig. S1
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Glia Are Essential for Sensory Organ Function in *C. elegans*

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Sensory organs are composed of neurons, which convert environmental stimuli to electrical signals, and glia-like cells, whose functions are not well understood. To decipher glial roles in sensory organs, we ablated the sheath glial cell of the major sensory organ of *Caenorhabditis elegans*. We found that glia-ablated animals exhibit profound sensory deficits and that glia provide activities that affect neuronal morphology, behavior generation, and neuronal uptake of lipophilic dyes. To understand the molecular bases of these activities, we identified 298 genes whose messenger RNAs are glia-enriched. One gene, *fig-1*, encodes a labile protein with conserved thrombospondin TSP1 domains. FIG-1 protein functions extracellularly, is essential for neuronal dye uptake, and also affects behavior. Our results suggest that glia are required for multiple aspects of sensory organ function.

Glia, the largest cell population in vertebrate nervous systems, are implicated in processes governing nervous system development and function (*1*). However, the functions of few glial proteins are characterized. Astrocytic glia are often positioned near synapses and can respond to and participate in synaptic activity (*2*, *3*), influencing the response of postsynaptic cells to presynaptic stimulation (*4*).

Sensory neurons convert environmental stimuli into neuronal activity, and their receptive endings are often associated with glia, such as retinal pig-

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