LETTER

REPLY TO SAFINA AND WALTER ET AL.: Multiple lines of evidence for size-structured spawning migrations in western Atlantic bluefin tuna

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Walter et al. (1) and Safina (2) raise numerous concerns regarding our study (3). Specifically, they question our conclusions that (*i*) a majority of spawning occurs outside the Gulf of Mexico, (*ii*) western North Atlantic bluefin tuna mature earlier than currently estimated, and (*iii*) additional spawning locations and younger age at maturity mean that the western Atlantic bluefin tuna are less vulnerable to anthropogenic impacts, including exploitation.

There are two alternative hypotheses regarding the life history of western Atlantic bluefin tuna: (*i*) a late-maturing stock (age of 9+ y) that spawns only in the Gulf of Mexico and (*ii*) an early-maturing stock (age of 4–5 y) that spawns in multiple locations during age-structured migrations (3). The hypothesis that western Atlantic bluefin tuna spawn only in the Gulf of Mexico is refuted by our finding of very young larvae in the Slope Sea; the assertion that these larvae were spawned off the Bahamas or in the Gulf of Mexico is not supported by oceanographic studies. The hypothesis that western Atlantic bluefin tuna mature at the age of 9 y or older is refuted by direct reproductive studies. We encourage those individuals interested in determining the value of this evidence to read the maturity studies cited in our work (4, 5), as well as the study by Mather et al. (6), rather than relying on the edited quote in the letter of Safina (2). Previously, the absence of younger fish (<9 y of age) in the Gulf of Mexico (i.e., the only known spawning ground) was used as indirect evidence for an older age at maturity and to question the direct reproductive studies (7, 8). With the discovery of a Slope Sea spawning ground, this indirect argument is no longer valid.

Our conclusion that a majority of spawning occurs outside the Gulf of Mexico is based on the conclusion of a lower age at maturity; our analysis of tagging data; and estimates of total mortality, including values from the stock assessment model used by Walter et al. (1). A central component of this analysis, the proportion of fish migrating to the Gulf of Mexico by size (or age), is remarkably consistent across four separate datasets: two independent electronic tagging datasets (3, 8) and analyses of two fisheries-dependent longline catch datasets (7, 9). Abundance of larvae in the Slope Sea compared with the Gulf of Mexico provides secondary support for the conclusion; the referenced collection of larvae in other areas outside the Gulf of Mexico (10, 11) provides additional support. We understand that this conclusion is challenging, and we thus provided numerous sensitivity analyses for readers to evaluate this claim, including one consistent with age at maturity and mortality from the current stock assessment.

Based on our findings supporting a lower age at maturity and spawning in areas outside the Gulf of Mexico, we conclude that western Atlantic bluefin tuna are less vulnerable to anthropogenic impacts than previously thought. Formal assessments of species vulnerability involve evaluating intrinsic species attributes, population trends, and extrinsic factors (e.g., climate change, oil spills), along with the uncertainty in each. The Convention on International Trade in Endangered Species (CITES) standard lists a set of intrinsic vulnerability factors, the first two of which are as follows: (*i*) "life history (e.g., low fecundity, slow growth rate of the individual, high age at first maturity, long generation time)" and (*ii*) "low absolute numbers or biomass or restricted

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area of distribution" (at any life stage) (12). According to these criteria, an additional spawning ground, younger age at maturity, and larger mature population all reduce vulnerability. Further, the analyses presented by Walter et al. (1) and the International Commission for the Conservation of Atlantic Tunas (ICCAT) (13) indicate that lowering the age at maturity within the stock assessment model reduces the maximum decline in spawning stock biomass over the observed 1970–2013 period from an >80% decline (age of 12–16 y at maturity), to an ∼74% decline (age of 9 y at maturity), to an ∼66% decline (age of 4–5 y at maturity). A lower rate of decline in the face of fishing is one definition of lower vulnerability.

Safina (2) raises the possibility that the Slope Sea is an eastern Atlantic stock spawning ground. This statement further questions the central Atlantic stock separation line that forms the basis of Atlantic bluefin tuna assessment and management. Stock boundaries should encompass the spawning grounds of a population. We do not believe that this explanation is the most likely one for currently available data; however, as we state in our paper, "to fully evaluate bluefin tuna population structure, biological samples from spawning fish and larvae collected in the Slope Sea need to be included in future analyses."

The available data support the hypothesis that bluefin tuna in the western Atlantic have size-structured spawning migrations across a wide latitudinal range. As Walter et al. (1) state in the conclusion of their letter, further testing of this model will require additional research using multiple techniques. Longline sampling of adult fish in the Slope Sea for studies of reproduction and population structure is a top priority. We also agree with Walter et al. (1) that larval surveys and analyses should be designed that allow for the implementation of the larval production method (14) in both the Slope Sea and the Gulf of Mexico. This approach can provide an independent rigorous comparison of the relative magnitude of spawning in the two regions. Finally, as with the testing of the Gulf of Mexico-only spawning hypothesis, exploratory sampling is critical to answering whether there are other undocumented spawning grounds that may further change our perception of the life history of this species.

The process by which we engage in bluefin tuna science is important. We emphasize the benefits of advancing collaborative scientific approaches that value the insights of fishermen, many of whom had deduced Slope Sea spawning from their own observations. Furthermore, the highly migratory nature and oceanic habitat of bluefin tuna require that multiple types of sampling and data across a wide geographic range be used to address even the most basic life history questions. Improving and implementing open access standards for all types of data will accelerate progress in understanding bluefin tuna life history.

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