

Genetic discontinuity of big fish in a small sea

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There was a time not so long ago when geneticists might have branded the highly migratory Atlantic bluefin tuna (*Thunnus thynnus*) the quintessential panmictic population (1) of the marine world. Because bluefin tuna are designed for mobility and capable of generating millions of offspring per spawning pair (2), migration and gene flow throughout their entire range seemed likely. This would homogenize regional subgroups and cause them to behave, in a statistical sense, like one very large, randomly mating population. In other words, bluefin appeared to fit the null hypothesis that population geneticists make a living trying to reject. Hence, genetic discontinuities should have been hard to find, especially within a small inland sea. In a study in PNAS, Riccioni et al. (3) examine microsatellite loci from contemporary and historical samples of *T. thynnus* and find remarkable evidence (i) that the Mediterranean contains genetically subdivided populations, (ii) that this structure has persisted for nearly 100 years, and (iii) that gene diversity has remained surprisingly intact despite decades of overexploitation and dramatic decline in numbers. These results confirm previous work (4, 5) hinting that *T. thynnus* in the Mediterranean is composed of multiple breeding stocks and raises concern that these newly recognized gene pools are at risk from overfishing.

Atlantic bluefin tuna are migratory giants. Weighing upwards of 600 kg, they traverse the North Atlantic and adjacent seas between feeding and spawning grounds over a 30-year life span (6). Despite great historical abundance, spawning biomass (Fig. 1A) has plummeted over the last four decades (2). The International Convention for the Conservation of Atlantic Tunas, which coordinates management and research of highly migratory tunas, recognizes two populations (Western and Eastern Atlantic stocks) that spawn in the Gulf of Mexico and the Mediterranean Sea and manages them along a line bisecting the mid-Atlantic at the 45th meridian (6). Recently, the nation of Monaco requested that *T. thynnus* be listed under appendix I of the Convention on International Trade of Endangered Species, citing the alarming drop in the Mediterranean stock by 60% in the past 10 years (10).

Marine fish species had once been considered resilient to overexploitation, yet today marine fishery stocks worldwide are in precipitous decline (11). Under a pan-

mictic model, one might assume that the depletion of one local population would be offset by the regular immigration or ongoing larval recruitment from another, both of which are enhanced by high fecundity. This has not always been the case and indicates that population structure could exist. However, analyses of neutrally evolving markers (mitochondrial DNA or microsatellites) have often failed to reject the null hypothesis, leaving behind conclusions that marine fish had little population structure to manage (12) or that genetic techniques failed to resolve the structure that was there (13).

Riccioni et al. note little loss of gene diversity in the Mediterranean.

To complicate matters more, evidence of genetic differentiation was often suspect and considered an artifact of high fecundity. Great reproductive success of only a few individuals could cause genetic variance (F_{ST} 's) to fluctuate widely each generation (commonly called "genetic sweepstakes") (14) such that differences one year should not be expected the next. In the study in PNAS (3), the authors include historical samples from juveniles and adults—insightfully preserved by Masimo Sella in the early part of the last century—to confirm that the differences that they find in Atlantic bluefin tuna inhabiting the Mediterranean Sea are temporally stable, and not a variable artifact.

Riccioni et al. (3) show that spatial differences between Atlantic bluefin sampled in the Adriatic and Tyrrhenian seas have persisted for nearly a century. Genetic differences between these two regions have been reported in other species (15), including red mullet (*Mullus barbatus*), anchovies (*Engraulis encrasicolus*), and striped sea bream (*Lithognathus mormyrus*). Given the Atlantic bluefin's reputation for wanderlust, it is odd that it would join a list of lesser vagile species with a similar geographic pattern. However, the eastern and western basins of the Mediterranean differ in temperature, salinity, and circulation. Oceanographically speaking, these basins are considered partially isolated along the

straits of Sicily and Messina (7) as shown in Fig. 1B.

Bluefin are known to spawn in the Balearic and Tyrrhenian seas on the Mediterranean's western side and in the Ionian and possibly Levantine seas to the east (4, 5). Spawning in the Adriatic is unknown. Plotted onto Fig. 1B are migration tracks from two Atlantic bluefin (8, 9) tagged off North Carolina (roughly 7400 km away). After crossing the Atlantic Ocean, the bluefin pass through the Straits of Gibraltar where their tracks show remarkable salmon-like homing behavior to eastern and western Mediterranean spawning grounds located less than 500 km apart.

Fig. 1B illustrates the challenge in accurately assessing stock sizes of distinct bluefin populations. Eastern Mediterranean fish must cross western Mediterranean waters to reach their spawning grounds; if caught en route, they will be counted as part of the wrong population for stock assessments. The same issue confronts the western Atlantic (Gulf of Mexico-spawning) stock. A proportion of *T. thynnus* tagged off the coast of North Carolina belongs to the Mediterranean-spawning stock, and their presence in the western Atlantic catch can artificially inflate biomass estimates (16). One way to overcome this challenge is through the use of microsatellite markers. Multilocus genetic profiles characterizing each bluefin stock could make it possible to assign individuals to their population of origin. Such work could enable better accounting of migrating individuals captured in regions of population overlap as it has with salmonids (17).

Finally, despite of lower biomass, Riccioni et al. (3) note little loss of gene diversity in the Mediterranean. However, even in fish populations that have undergone more extensive declines than those documented here (e.g., Newfoundland cod, 75–99%), it is not always possible to observe bottlenecks in genetic data (18).

Atlantic bluefin tuna have long been a challenge for population geneticists. At first

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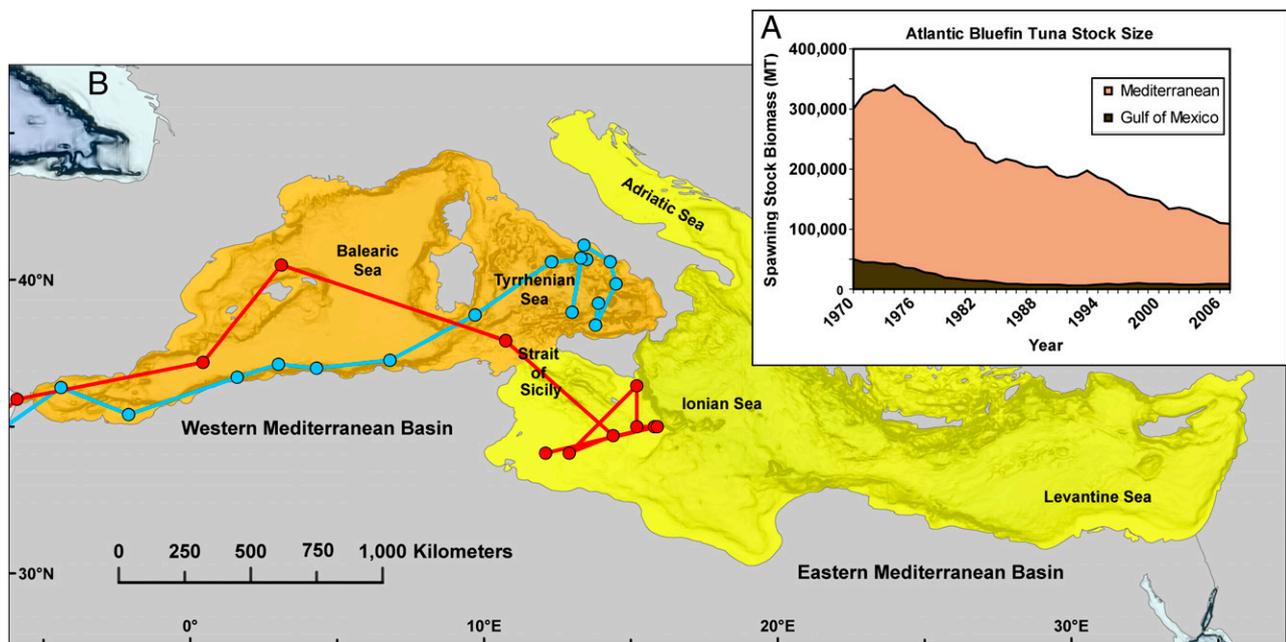


Fig. 1. (A) Decline over time of Atlantic bluefin tuna biomass in the Mediterranean- and Gulf of Mexico-spawning stocks (2). MT, metric tons. (B) Map of the Mediterranean Sea divided into eastern (yellow) and western (orange) basins with relevant subseas labeled (7). Blue (8) and red (9) lines are tracks of *T. thynnus* migrating into the Mediterranean Sea carrying electronic tags deployed off North Carolina.

glance, they appear to be unproductive research choices. But a closer look reveals a fine-scale structure. Although development of faster-evolving markers such as microsatellites has undoubtedly helped to resolve population structure in highly migratory fishes, better experimental design and elimination of mixed samples have played a more important role. Additional technologies (forensics, electronic

tags, otolith microchemistry) combined with genetics will soon rewrite the dogma surrounding highly migratory marine fish and pave the way for geneticists to finally make significant contributions to the management and conservation of these fisheries. Decades ago, Sewall Wright (19) wrote, “There are species which appear to breed so nearly at random throughout

their whole range. . .” But he added, “This is probably unusual.”

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