

IS ATLANTIC BLUEFIN TUNA A METAPOPOPULATION?

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For Atlantic bluefin tuna fisheries, the linked issues of population structure and mixing remain of paramount significance in optimizing utilization of a species well known for its pan-oceanic migrations. There has been increased scrutiny by scientists and resource representatives of the two stock hypothesis, which guides stock assessments and projections for western Atlantic tuna. The Inter-Sessional Conference of ICCAT on Mixing (September 2001) will address methods to incorporate pan-oceanic migrations by Atlantic bluefin tuna in future stock assessments. A metapopulation framework is considered as a less rigid alternative to the current two stock concept. To date, models of mixing between stocks have been considered under two classifications: 1. *The Diffusion Model*, whereby trans-Atlantic migrants become expatriates, joining the alternate population (true metapopulation) or 2. *The Overlap Model*, where some fraction of each population undertakes a trans-Atlantic migration on an annual and/or ontogenetic basis, but surviving migrants return annually to their natal region (patchy population). Substantial life history differences between Eastern and Western populations favor the idea that Atlantic bluefin tuna is not a true metapopulation. Therefore, the Overlap Model, which stipulates that populations impact each other through ecological rather than genetic interactions currently has more credence than the Diffusion model. The Overlap Model for exchange has considerably less interactive effects between complementary populations than the Diffusion Model because trans-oceanic migrants do not accumulate on the alternate side of the ocean (i.e. survivors return to their natal region on an annual basis). Emigration is a pulsed event in this model, but it seems reasonable that emigration should occur over a protracted period through regions of substantial exploitation. Thus, fishing mortality and emigration probably interact. While subsidy to recruitment from one population to the other has been discounted in favor of the Overlap Model, strong annual numerical subsidy of one system due to recruitment differences can cause over-optimistic projections of past stock abundance and incorrect assessments of future recovery if population membership is not properly taken into account. Alternate or anomalous migration pathways within populations (i.e. contingent structure) of bluefin tuna will not be accommodated easily into metapopulation models until we learn more about the pathways themselves and their determinants. Over the past four years, we have researched the otolith microconstituent approach, which we believe has particular relevance to the problem of mixing and contingent structure.

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Fish Metapopulations

Regulation and control of marine fishes are determined by dispersive and retentive behaviors that serve to counteract a diffusive environment in which habitat resources are heterogeneously distributed. These behaviors are well known, particularly with respect to ontogenetic niche shifts and complex life cycles (Secor 1999). Still, individual and population level variations in migration behaviors have received relatively little attention - this is in part due to the stringent requirement of philopatry (“homing”), a first principle in the unit stock concept (Secor in press). The concept of closed population structure - the unit stock concept - has been fundamental to marine fisheries science for nearly a century. I have argued that anomalous individual migrations - those that diverge from expected ontogenetic circuits of migration - represent modalities, and may confer resiliency in populations where production and mortality risk is related to specific spatial behaviors. These modalities are well documented for retentive and migratory forms of salmon and chars, but have been observed increasingly for taxa of marine and coastal fishes through the use of otolith chemistry (Secor 1999). Groups of individuals with similar migration trajectories are called *contingents* (Table 1), termed initially by Hjort (1914) for such groups that he identified based upon scale morphology.

In metapopulation theory, contingent behavior should be related to intra-population use of heterogeneously distributed habitat. For Hudson River striped bass *Morone saxatilis*, we have observed freshwater, brackish water and ocean contingents (Zlokovitz and Secor 1999; Secor et al. 2001). One could conceive of various natural and anthropogenic influences (a hurricane, a large coastal fishery) that might differentially diminish or increase contingent abundances. A population of contingents can be alternatively described as a “patchy population” (Harrison and Taylor 1997) and represents an important means by which a population adapts to spatial variation in resources (e.g. forage, predation refugia). Thus, patchy populations are systems of energetic or reproductive subsidy that lead to persistence over ecological time scales. Patchiness in resources in time and space leads to variation in migration among contingents. Loss of abundance or production by one contingent can be offset by gains in production by another contingent. Note here that natality (region of spawning) is the same across contingents for a given population. Ray (1997) presented an excellent example of a patchy population: Atlantic menhaden *Brevoortia tyrannus*, in which overall abundance is dependent upon a use of foraging and nursery habitats distributed across numerous estuaries. In past models of exchange rate in Atlantic bluefin tuna, patchy populations correspond to the “overlap” model.

True metapopulations are systems of genetic subsidy that lead to persistence over multi-generational time scales. Typically, metapopulations are conceived as insurance systems against local extinction. A given local population receives a stream of colonizers from other populations, offsetting risk of local extinction and indeed, extinction of the entire metapopulation. Metapopulations are defined by exchange, which must involve deviations by individuals in both migration and spawning: a behavior known as “straying.” Philopatry (“homing”) and straying initially seem to be diametrically opposed behaviors. Still, viewed in terms of metapopulation persistence and growth, it is clear that both behaviors are necessary (Olivieri and Gouyan 1997). Straying, a minority behavior, permits initial exchange or colonization; subsequent homing, the more probable behavior, increases the chance that a straying event is effective in subsidizing the recipient population or colonizing new environments. An interesting issue is how contingent behaviors are related to metapopulation structure. One could consider individuals within dispersive contingents as those more likely to emigrate to other populations (Secor 1999). Metapopulation structure would be especially relevant to coastal open systems where homing and retentive mechanisms are expected to be less effective than for anadromous fishes.

Metapopulation structure might seem esoteric, were it not for anthropogenic forces that have collapsed the time scale of processes that control marine fishes. Populations that are reduced through lost or fragmented habitat require increased levels of subsidy by individuals from habitats that remain productive. High rates of exploitation in more productive patches or sub-populations (sources) can have disproportionate effects on less productive segments of the population or the entire metapopulation (Crowder et al. 2000; Tuck and Possingham 2000). A principal hurdle in applying metapopulation concepts to marine fishes is measurement of individual exchange rates that transfer genes and energy among local populations (Campana et al. 1999; Thresher 1999; Thorrold et al. 2001).

Bluefin Tuna Metapopulation Models

Due in part to increased evidence of trans-Atlantic migrations (Lutcavage et al. 1998; 2001), there has been increased scrutiny by scientists and resource representatives of the two stock hypothesis, which guides stock assessments and projections for western Atlantic tuna (Magnuson et al. 1994). In addition, there is strong sentiment by commercial and recreational sectors of the U.S. bluefin tuna fishery (Chase et al. 2001) that high rates of exploitation of small tuna in the Eastern Atlantic and Mediterranean Ocean are curtailing the recovery of Western stock bluefin tuna, despite stringent harvest limits that have been promulgated upon North American fisheries.

The Inter-sessional Conference of ICCAT on Mixing (September 2001) will address methods to incorporate pan-oceanic migrations by Atlantic bluefin tuna in future stock assessments under the current two stock concept. Here, I encourage participants to consider metapopulation theory as a means to develop more implicit spatial models of exchange for Atlantic bluefin tuna. To date, models of mixing between stocks have been considered under two classifications (Figure 1): 1. *The Diffusion Model*, whereby trans-Atlantic migrants become expatriates, joining the alternate population (true metapopulation) or 2. *The Overlap Model*, where some level of trans-Atlantic migration occurs on an annual and/or ontogenetic basis, but migrants return annually to their natal region (patchy population). These models represent spatially realistic metapopulation models, where vital rates and interactions between populations are specified. The NRC report (Magnuson et al. 1994) provides an example of the Diffusion Model, which is developed for two linked populations:

$$N_{w, a+1, t+1} = N_{w,a,t} \exp[-(M+F_{w,a,t})](1-T_w) + N_{e,a,t} \exp[-(M+F_{e,a,t})](T_e)$$

and

$$N_{e, a+1, t+1} = N_{e,a,t} \exp[-(M+F_{e,a,t})](1-T_e) + N_{w,a,t} \exp[-(M+F_{w,a,t})](T_w)$$

where N_e and N_w are eastern and western Atlantic populations, a is age, t is year, M and F are natural and fishing mortality and T is rate of transoceanic migration (assumed to be irreversible). A similar but more elaborate and potentially useful model was developed for American lobster by Fogarty (1998). Applying the notation above:

$$N_{w, a+1, t+1} = N_{w,a,t} \exp[-(M+F_{w,a,t})](1-T_{wA}) + \mathcal{F}_w(N_{t-r})(1-T_{wJ}) + \mathcal{F}_e(N_{t-r})(T_{eJ}) + N_{e,a,t} \exp[-(M+F_{e,a,t})](T_{eA})$$

and

$$N_{e, a+1, t+1} = N_{e,a,t} \exp[-(M+F_{e,a,t})](1-T_{eA}) + \mathcal{F}_e(N_{t-r})(1-T_{eJ}) + \mathcal{F}_w(N_{t-r})(T_{wJ}) + N_{w,a,t} \exp[-(M+F_{w,a,t})](T_{wA})$$

where transoceanic migration rates are now specified for juveniles (J) or adults (A). In addition, stock-recruitment functions are included as $\mathcal{F}_{e,w}(N_{t-r})$ for each sub-population. The populations show complementary behaviors - if one population has a net loss the other one will have a net gain. The NRC model is explicitly driven by supplied estimates of abundance at different times and ages as well

as parameters for migration and mortality rates, but does not include productivity differences between the sub-populations (Figure 1). There is considerable evidence that the eastern sub-population is many fold more productive than the western one. The elaboration in Fogarty's model is useful in that separate stock-recruitment relationships (i.e. with differing replacement rates and carrying capacities) can be considered in populations linked through migration rates. Further, the model considers migration rates that vary with ontogeny.

Nemerson et al. (2000) used a variant of the NRC approach to evaluate the underlying assumption of the Diffusion Model. Past demographic studies show large differences in age and size at maturity between the eastern (age~4 years; FL~130 cm) and western (age~8 years; FL~200 cm) populations. Based upon modeled (irreversible) contribution rates of juveniles from the Eastern Atlantic Ocean and Mediterranean Sea, fish <135 kg (i.e. young adults of the eastern sub-population) should represent 5-10% of the spawning stock in the Gulf of Mexico. Nemerson et al. (2000) compiled available landings data and showed that observed fractions attributable to these smaller fish on the spawning grounds were <1%. Age and size at maturation are fundamental life history traits that have been given little attention in stock mixing. It seems unlikely that such large differences in life history attributes would be maintained if there was substantial straying between sub-populations. There is also some reason to speculate that millennia of exploitation in the Mediterranean Sea vs. only decades of exploitation in the western Atlantic Ocean would result in a lower age at maturity and associated higher replacement rates (Nemerson et al. 2000). Substantial life history differences favor the idea that Atlantic bluefin tuna is not a true metapopulation. Therefore, the Overlap Model, which stipulates that populations impact each other through ecological rather than genetic interactions currently has more credence than the Diffusion Model.

The Overlap Model for exchange has considerably less interactive effects between complementary populations than the Diffusion Model because trans-oceanic migrants do not accumulate on the alternate side of the ocean. Each year, a fixed fraction will randomly migrate from one population to the other as a discrete pulse (Porch et al. 2001). At the end of that year, remaining emigrants will return to their natal region and another randomly drawn fraction will instantaneously emigrate to the alternate side of the ocean. These fractions can be stipulated to vary by year and age-class, but the concept of pulsed and random contributions from one side of the ocean to the other remains the same. Porch et al. (2001) showed that the overlap model can be derived in essentially the same form as the NRC model, only that abundance was modeled according to fishery region (eastern or western Atlantic Oceans) rather than sub-population.

The Overlap Model could be elaborated to consider non-independence between F and T. These would seem to be competing processes, particularly if emigration is not pulsed, and requires tuna to migrate through regions where substantial exploitation occurs. Geographic and fishery differences between the Mediterranean Sea and the western Atlantic Ocean would indicate that the interaction between F and T also differs between regions. As with the NRC model, the Overlap Model does not explicate large production differences between the eastern and western populations. These production differences have not been placed in a quantitative framework in lieu of a formal stock assessment (e.g. determination of a stock-recruitment relationship) for the eastern population. While subsidy to recruitment from one sub-population to the other has been largely discounted due to evidence for population structure (see above), strong subsidy of one system to the other due to recruitment differences can cause over-optimistic projections of past stock abundance and incorrect assessments of future recovery if the population membership is not properly taken into account.

Migration Anomalies and Contingent Structure in Bluefin Tuna

Tunas often show anomalous occurrences, where migrations are highly variable and apparently related to the effects of climate change, ocean circulation and related changes in prey distribution (Povlina 1990; Kimura et al. 1997). The high maintenance demands by tunas engender a higher dependence on exploratory behaviors to attain sufficient energy. Bluefin tuna are peculiar among

tunas in having a temperate distribution and in the Atlantic Ocean historically bluefin tuna ranged between Brazil and Norway. Since the 1980s, bluefin have not been harvested at the “frontiers” of their range (but see high latitude record by DeMetrio et al. 2001). Fonteneau and Soubrier (1996) speculated that previous frontier fisheries for bluefin tuna occurred on unique segments of the population. These exploratory contingents may have been lost because they were more vulnerable to the effects of exploitation.

Recent efforts to understand spawning migrations by adult Atlantic bluefin tuna through the use of electronic tags and satellite telemetry has uncovered an unexpected migration trajectory: large adults tagged in the fall in the North Atlantic Bight were recorded several months later - during spawning season - in the mid-Atlantic Ocean near the Azores (Lutcavage et al. 1999). While spawning activity has not been documented outside the Gulf of Mexico/Florida Straits and Mediterranean Sea, another spawning region cannot be ruled out, particularly considering the spawning behavior of Pacific bluefin tuna, which spawns in the ocean basin and in two marginal sea (Okiyama 1974, 1979; Rooker et al. In press, b). Alternatively, the group may represent a here-to-for underappreciated migration pathway undertaken by either (both?) population(s).

Alternate migration pathways within populations (i.e. contingent structure) of bluefin tuna will not be accommodated easily into mixing models until we learn more about the pathways themselves and their determinants. In the example shown in Figure 1, this issue would correspond to understanding the relative contribution of Eastern and Western Atlantic nurseries to three different mixed stock fisheries. Contingent behaviors could indicate that current mixing models will need to be modified to reflect variations in ontogenetic patterns of trans-oceanic migration. In addition, it seems reasonable to expect that some “vagrant” juveniles and adults do not return to natal regions on an annual basis. Still, this is all speculation until contingent behaviors are better described. There is a clear priority within ICCAT to develop empirical methods to measure mixing rates and transatlantic migrations. In response to this priority, we have researched the otolith microconstituent approach, which we believe has particular relevance to the problem of mixing and contingent structure (Secor et al. 1998, in Review; Rooker et al. In Press, a, b; in Review).

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Table 1. Terms used in this paper.

Contingent: Set of individuals that share seasonal or ontogenetic migration pathways (Hjort 1914; Secor 1999).

Otolith microconstituents: Set of trace elements (<10 ppt) occurring in otoliths. Multivariate sets of micro-constituents define **elemental fingerprints** that can be used to determine nursery of origin (Campana 1999).

Population: reproductively isolated group of fish. Here defined by nursery/spawning regions (Sinclair 1988).

Population/Metapopulation structure: Network of contingents or populations that are linked by migration (from Hanski and Simberloff 1997).

Stock: Definition is dependent on application (Booke 1981). Here, stock refers to accessible (fishable) portions of population(s) (Russell 1931; Secor 1999).

Stock structure: apportionment of stock according to population (nursery of origin) (from Waldman et al. 1997).

Figure 1. Conceptual diagrams of metapopulation structures for Atlantic bluefin tuna. **A.** Representation of impact of mixing under from Nemerson et al. (2000) depicting important productivity differences between eastern and western Atlantic populations. Note that $T_{e,w}$ (transatlantic migration) is the same fraction of either population. **B.** Metapopulation construct for mixed fisheries (stocks) in W., Mid-, and E. Atlantic Ocean. Contingents are cohorts that have similar migration pattern and are represented by ovals that link stocks to nursery/spawning habitats. Note that this metapopulation concept does not include migrations that link spawning habitats. Such migrations define a true metapopulation; that presented here is for a patchy population.

