Spawning site fidelity in Atlantic bluefin tuna, *Thunnus thynnus*: the use of size-frequency analysis to test for the presence of migrant east Atlantic bluefin tuna on Gulf of Mexico spawning grounds

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Abstract.—The Gulf of Mexico is the only known spawning area for bluefin tuna (*Thunnus thynnus thynnus*) in the western Atlantic. Although it is known from tag recaptures that eastern Atlantic bluefin tuna travel to the western Atlantic, whether or not these fish spawn in the western Atlantic is of critical importance in interpreting the significance of this movement. East Atlantic bluefin tuna mature at a younger age (4–5 yr) and smaller size (45 kg) than western bluefin tuna (8 yr and 135 kg), and tag recaptures indicate that some young fish make the trans-Atlantic swim. Thus the presence of small (<135 kg) bluefin tuna in the Gulf of Mexico during spawning season would constitute evidence that bluefin tuna of east Atlantic origin spawn in the west. We used size-frequency analysis to test the hypothesis that Atlantic bluefin tuna of eastern and western origins mingle on the Gulf of Mexico spawning grounds. We created a simple model to estimate the proportion of small eastern spawning fish that should be found in the Gulf of Mexico catch, assuming a 2% east-to-west transfer rate and complete mixing of eastern and western fish. Using conservative assumptions, the model predicts that between 5% and 10% of the bluefin tuna catch in the Gulf should consist of fish that are less than 135 kilograms in weight, and thus are presumably eastern migrants. We analyzed Gulf of Mexico catch records from 1980 to 1992 for the presence of bluefin tuna less than 135 kg. These small fish represented from 0% to 0.9% of the catch annually, and only 0.3% for the entire period. We conclude that eastern migrant tuna do not mix completely, if at all, with western bluefin tuna on the Gulf of Mexico spawning grounds.

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Atlantic bluefin tuna (*Thunnus thynnus thynnus*) is a highly migratory pelagic species that ranges throughout the Atlantic between 60°N latitude and the equator, although it has not been encountered south of 20°N since the 1960s. Two bluefin tuna breeding sites are known in the North Atlantic: the Gulf of Mexico and the Mediterranean Sea. No other regular spawning site has been identified in the North Atlantic (Richards, 1976; McGowan and Richards, 1989; NRC, 1994). Intensive fisheries exist for bluefin tuna along the North American and European coasts, and to a lesser degree in the high seas of the North Atlantic. Although fish tagged on both sides of the ocean have been recovered on the side opposite from their release, it is not known if bluefin tuna return to their natal spawning ground to reproduce (Turner and Powers, 1995; Cooke and Lankester, 1996). This question is of utmost importance in evaluating the significance of trans-Atlantic movement and the scale at which management must operate to be effective.

The behavior of trans-Atlantic migrating bluefin tuna is unknown, but the possibilities are bounded by two extremes. At one extreme, an emigrant may join the population on the side of the ocean to which it migrates, becoming indistinguishable from the population it joins with respect to the probability, timing, and locale of future life history events, such as maturation, spawning, and migration. At the other extreme, a migrant may always return to its natal side prior to the next spawning season.

These two extremes, and the terms used to describe them, have been the subject of some confusion in the bluefin tuna literature. The permanent transfer of individuals from one side of the Atlantic to the other has been called the "no-memory condition" (Punt and Butterworth, 1995; Powers and Cramer, 1996) or the "diffusion model" (Cooke and Lankester, 1996). The case where migrants always return to their natal side prior to the next spawning season is termed the "overlap model" by Cooke and Lankester (1996). We follow the convention of Cooke and Lankester (1996) and use the terms diffusion and overlap to refer to the two models. We use "transfer rate" to refer to the permanent transfer of an emigrant from one population to the other and "migration rate" to refer generally to the trans-Atlantic movement of individuals. Finally, we use the term "memory" to refer only to an individual's behavior with respect to spawning location, not to other life history attributes. That is, under the diffusion (no-memory) model, a migrant will spawn on the side of the ocean to which it migrates, regardless of its birth location, but will retain other life history attributes such as size or age at maturity.

The permanent transfer of individuals can be considered a migration for dispersal (Greenwood and Harvey, 1982), whereas the overlap model can be assumed to be a feeding migration, and is free of implications for reproductive mixing. One can envision intermediate scenarios combining varying degrees of memory, or philopatry. For example, migrants may remain on the opposite side for a period of years, while either participating in or foregoing spawning, before ultimately returning to their natal side. Furthermore, some migrants may exhibit spawning site fidelity while others may stray, joining previously established spawning populations (e.g. Curry, 1994).

Simulation models have shown that the dynamics of the two populations are potentially very sensitive to even low trans-Atlantic migration rates, particularly for east-to-west transfer (NRC, 1994; Porch et al., 1995; Punt and Butterworth, 1995; Powers and Cramer, 1996) because the average size of the eastern population has been about 6 to 13 times that of the western population over the past 20 years (ICCAT[1,2]; Fig. 1). Recent spawning biomass estimates for the western population are based on catches throughout the fishing area, which includes the entire North Atlantic west of 45°W longitude. If fish of eastern origin are included in these catch statistics but do not spawn in the west Atlantic, then western spawning biomass will be substantially overestimated (Powers and Cramer, 1996; American Fisheries Society[3]).

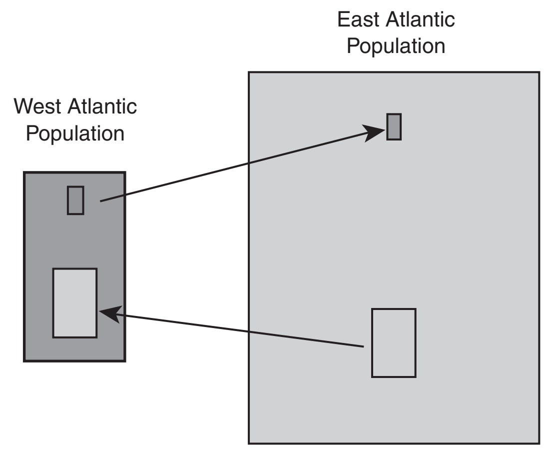

Figure 1

Representation of the effect of migration on the eastern and western populations of bluefin tuna. Migration from the larger eastern population to the west has a larger effect on the western population than does migration from the smaller western population to the east. In this schematic, the eastern population is about six times the size of the western population, and the migration rates are about 1% in each direction.

Determining the spawning site fidelity of iteroparous pelagic species that occur over a wide area of open ocean is difficult. Population differentiation can be inferred from tag-return data, comparisons of life history parameters and morphometric characters, or from genotypic variation. Several studies have attempted to analyze the population structure of Atlantic bluefin tuna with these methods (Calaprice, 1986; NRC, 1994; Cooke and Lankester, 1996).

Several investigators have reviewed and analyzed trans-Atlantic tag returns to estimate rates of migration (NRC, 1994; Punt and Butterworth, 1995; Turner and Powers, 1995; Cooke and Lankester, 1996). These studies have estimated annual migration rates of between 1% and 10% and have considered both diffusion and overlap models. Generally, these studies have sought to find interpretations of tag-return data that agree best with other estimates of population size.

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[1] ICCAT (International Commission for the Conservation of Atlantic Tunas). 1994a. West Atlantic bluefin tuna. Biennial report of the ICCAT Standing Committee on Research and Statistics, 41 p. ICCAT, Estebanez Calderon 3, E-28020, Madrid, Spain.

[2] ICCAT (International Commission for the Conservation of Atlantic Tunas). 1994b. East Atlantic bluefin tuna. Biennial report of the ICCAT Standing Committee on Research and Statistics, 31 p. ICCAT, Estebanez Calderon 3, E-28020, Madrid, Spain.

[3] American Fisheries Society. 1995. Marine Fisheries Section statement on bluefin tuna, 2 p. Am. Fish. Soc., 5410 Grosvenor Lane, Ste. 110, Bethesda, MD 20814-2199.

Punt and Butterworth (1995) estimated west-to-east transfer at about 7% and east-to-west transfer at about 1.5–3%, assuming a diffusion model. They also state that the higher end of the range (3%) suggests a far larger size for the western population than do models that assume no migration. Cooke and Lankester (1996) test both diffusion and overlap models and concluded that the overlap model fits the data better. Under that model, they estimated exchange rates at 7.3% east-to-west and 9.8% west-to-east, but with no statistical difference between the two. Powers and Cramer (1996) examined the implications of a range of migration rates and degrees of spawning site fidelity. Although they made no conclusions about which scenario is most likely, they pointed out the extreme sensitivity of the results to the assumptions.

Eastern and western Atlantic bluefin tuna populations have markedly different life history parameters (Turner, 1994). The western population spawns from mid-April to mid-June (Richards, 1976). Western bluefin tuna sometimes mature as early as age 6 and are considered fully mature by age 8, at a weight of 135 kg (Baglin, 1982; NRC, 1992). The eastern population spawns from June through August (Dicenta and Piccinette, 1980) and matures at an earlier age and smaller size than the western population. Eastern bluefin tuna mature as early as age 3, at a weight of 15 kg (Rodriguez-Roda, 1967; Baglin, 1982), and are fully mature by age 5 (Rodriguez-Roda, 1967; Baglin, 1982; ICCAT[2]).

The contrast in size and age at maturity of western and eastern Atlantic bluefin tuna allows an inferential test of spawning site fidelity. Because the Gulf of Mexico is the only known spawning ground for western Atlantic bluefin tuna, and the vast majority of fish collected in the Gulf are large adults that are present only during and just prior to the spawning season (January–June), we assumed that all bluefin tuna in the Gulf during this time period are there to spawn.

If eastern Atlantic bluefin tuna that migrate to the west mature according to the eastern Atlantic maturation schedule, then the size distribution of bluefin tuna in the Gulf of Mexico should reveal the presence of eastern migrants within the western spawning population. Finding small fish (<135 kg) on the Gulf of Mexico spawning grounds would support the diffusion hypothesis and suggest that trans-Atlantic migrants from the east mix with western fish during spawning. In contrast, the absence of small fish on the Gulf of Mexico spawning grounds would imply that eastern migrants do not spawn in the west, supporting the overlap model and indicating strong spawning site fidelity. We know that small bluefin tuna from the east Atlantic swim west at least occasionally. All tagged eastern Atlantic bluefin tuna recaptured in the west have been small fish (n=19, all captured outside the Gulf), although very few large fish, and relatively few bluefin tuna overall, have been tagged in the east, compared with tagging in the west (NRC, 1994).

Methods

We analyzed the size distribution of bluefin tuna caught in the Gulf of Mexico prior to and during the spawning season (the only time of year when bluefin tuna are present in the Gulf) for fish between the known size of first breeding in the Mediterranean and the known size of first breeding for west Atlantic bluefin tuna. Any individuals smaller than the known size of first spawning in the west would presumably be of eastern Atlantic origin.

A weight-frequency distribution (WFD) of bluefin tuna on the Gulf spawning grounds was constructed by using data reported to National Marine Fisheries Service (NMFS) by the commercial fishing industry operating in the Gulf. This data set included the weight and date of capture for every bluefin tuna legally caught and landed in the Gulf. We used data from 1980 through 1992, because beginning in 1993 only bluefin tuna over 178 centimeters (70 inches) fork length were legally permitted to be retained and sold.[4]

To estimate the proportion of smaller eastern spawning fish expected at a given east-to-west annual transfer rate (i.e. fish remain with the western population), we created a simple model of the number of sexually mature eastern migrants that arrive in the west each year:

$$S^E_y = \sum P_a T^E N^E_{a,y},$$

where S^E_y = the number of age-7 or younger spawning fish of eastern origin arriving in year y;
P_a = the percentage of sexually mature adults in eastern age class a;
T^E = the east-to-west transfer rate; and
$N^E_{a,y}$ = the number in eastern age class a in year y.

East-to-west transfer was modeled as an instantaneous process that occurs prior to the spawning season. The parameter P was taken from the lit-

[4] National Marine Fisheries Service. 1995. Supplemental draft environment impact statement for a regulatory amendment for the western Atlantic bluefin tuna. U.S. Dep. Commer., NMFS, NOAA, Silver Spring, MD, 131 p.

erature, and is 0 for ages 0–3, 0.5 for age 4, and 1 for ages 5 and beyond (Baglin, 1982; ICCAT[2]). We assumed that any migrant of age 8 or greater would be the same size as western spawning fish and would not be distinguishable from western spawning fish of the same size (Cort, 1991; Turner et al., 1991; Table 1). We used a transfer rate T of 2% per year, east-to-west. This rate is at the low range of published estimates. In this initial test, we did not consider fish less than age 4 that could have migrated to the west as immature fish in prior years and then reached age 4 and maturity in the current year. Thus, our estimate of the expected number of spawning fish of eastern Atlantic origin in the western Atlantic should represent a minimum estimate and provide a conservative test for the presence of eastern migrants. $N^E_{a,y}$ was taken from yearly age-specific population estimates supplied by NMFS from a run of the ADAPT virtual population analysis (VPA) program with 2% east-to-west and a 1% west-to-east transfer rates, assuming no memory. Note that the population estimates from this VPA run resulted in poor fits to the indices of abundance used to tune the VPA.[5] We used these population estimates because they provided a conservative test of our assumptions.

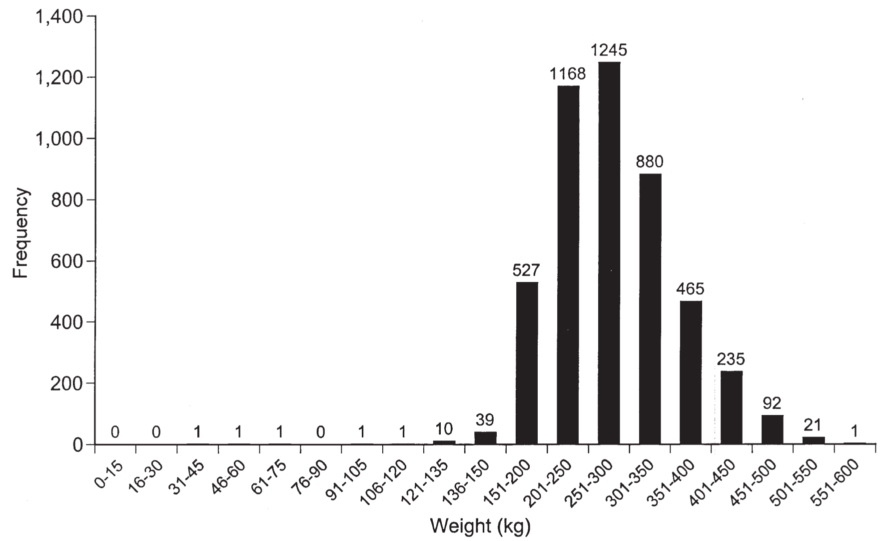

Figure 2

Weight-frequency distribution of bluefin tuna caught in the Gulf of Mexico between 1980 and 1992. The numbers over the bars indicate the total number of fish caught in the weight interval indicated.

Table 1

Estimated length at age for eastern (Cort, 1991) and western (Turner et al., 1991) Atlantic bluefin tuna.

	Length (cm)	
Age (yr)	East	West
1	53.4	48.6
2	77.0	73.8
3	98.4	97.0
4	118.0	118.5
5	135.8	138.4
6	152.1	156.8
7	166.9	173.7
8	180.4	189.4

Results and discussion

Bluefin tuna smaller than the accepted size at first spawning of western fish are very rare in the Gulf. Catches of fish less than 135 kg ranged from 0% to 0.9% of annual catch from 1980 to 1992 and averaged 0.3% over the entire period (Table 2). A complete weight frequency distribution is presented in Figure 2.

These percentages are not consistent with the low end of published migration rate estimates under the diffusion model. That is, if 2% of each age class migrated from east to west and joined the western population, we would expect to see many more small fish, i.e. fish of eastern origin, spawning in the west. (Recall that the diffusion, or no-memory model, implies that the migrant does not "remember" its natal spawning ground but does "remember" its maturation schedule.) The model predicts that between 8483 and 14,655 sexually mature migrants smaller than 135 kg would have arrived each year in 1980–92. We compared these numbers with the numbers of sexually mature fish estimated for the west from the

[5] Porch, C. 1995. National Marine Fisheries Service, Southeast Fisheries Science Center, 75 Virginia Beach Drive, Miami, FL 33149. Personal commun.

Table 2

Comparison of the number and proportion of spawning fish less than 135 kg actually caught in the Gulf of Mexico from 1980 to 1992 and predictions on the basis of a hypothesized 2% annual trans-Atlantic transfer rate. The number of small spawning fish observed is significantly less than the predicted number (χ^2=353, P<0.0001). Data in columns 2 and 3 from NMFS ADAPT VPA with 2% east-to-west and 1% west-to-east transfer rates and no memory; columns 4 and 5 are unpublished data, NMFS.

Year	Western population age 8 or greater	Predicted migrant spawning fish	Number of bluefin tuna <135 kg caught in the Gulf	Total bluefin tuna caught in the Gulf	Actual proportion of catch in the Gulf <135 kg	Predicted proportion of catch in the Gulf <135 kg
1980	97,824	10,745	0	19	0	0.099
1981	97,698	9,732	0	255	0	0.091
1982	88,781	9,402	0	228	0	0.096
1983	96,739	8,483	0	316	0	0.081
1984	92,440	8,691	0	320	0	0.086
1985	83,659	10,623	0	429	0	0.113
1986	89,444	13,151	1	395	0.003	0.128
1987	106,182	14,561	3	474	0.006	0.121
1988	117,440	14,655	3	516	0.006	0.111
1989	134,585	13,035	1	273	0.004	0.088
1990	167,115	10,631	4	469	0.009	0.060
1991	191,036	8,525	1	596	0.002	0.043
1992	260,192	9,436	1	399	0.003	0.035

ADAPT VPA run supplied by NMFS (Table 2). Table 2 shows that, if the no-memory assumption is correct and the trans-Atlantic transfer rate is at least 2%, we would expect about 5% to 10% of fish spawning in the west to be smaller than 135 kg. (Note that for this comparison to be valid, either all mature fish in the west and all small migrant spawning fish must go to the Gulf of Mexico to spawn or the same proportion of each group must go there each year.) In fact, only 0% to 0.3% of fish on the Gulf spawning grounds between 1980 and 1992 weighed less than 135 kg (Fig. 3), significantly less than predicted (χ^2=353, P<0.0001). Of 4688 fish for which NMFS has recorded weights, 15 were less than 135 kg, and 10 of those were between 120 and 135 kg (Fig. 2).

Note that this analysis considered only newly arrived migrants each year, and ignored the possible accumulation of sexually mature migrants from previous years that had not yet reached 135 kg. The continued presence of prior migrants would have raised the expected number of small spawning fish. Even without the cumulative effect of small migrants, the actual proportion of small spawning fish in the Gulf catch was about 5–10% of that predicted by the model with a 2% transfer rate. Higher transfer rates would imply that even greater numbers of small spawning fish should appear in the Gulf.

It is clear from our results that small bluefin tuna are not present among spawning fish in the Gulf of Mexico in the numbers that would be expected for even the lowest of hypothesized trans-Atlantic transfer rates. Our interpretation is that young adult bluefin tuna of eastern origin seldom or never spawn in the Gulf of Mexico and presumably do not contribute significantly to the spawning biomass of the western population. There are at least three possible alternatives: 1) eastern migrants may either delay spawning in the west until they reach 135 kg or remain in the east until they reach 135 kg, making them indistinguishable from western spawning fish; 2) migrant eastern tuna may be spawning in the west but not in the Gulf of Mexico; or 3) small migrants may be spawning in the Gulf but are avoiding detection or are being under-reported.

Size and age at maturity

If size and age at maturity are environmentally determined, then eastern migrants might follow the west Atlantic maturity schedule and thus be undetected with our methods. For example, changes in size and age at maturity may be a response to differences in interspecific or intraspecific population density. A lower population density reduces competition for food and increases per capita food intake, resulting in faster growth. When experiencing such low inter- or intraspecific population densities and enhanced growth, fish may mature at about the same size but would attain this size at a younger age (Trippel, 1995). However, for bluefin tuna, the reported dif-

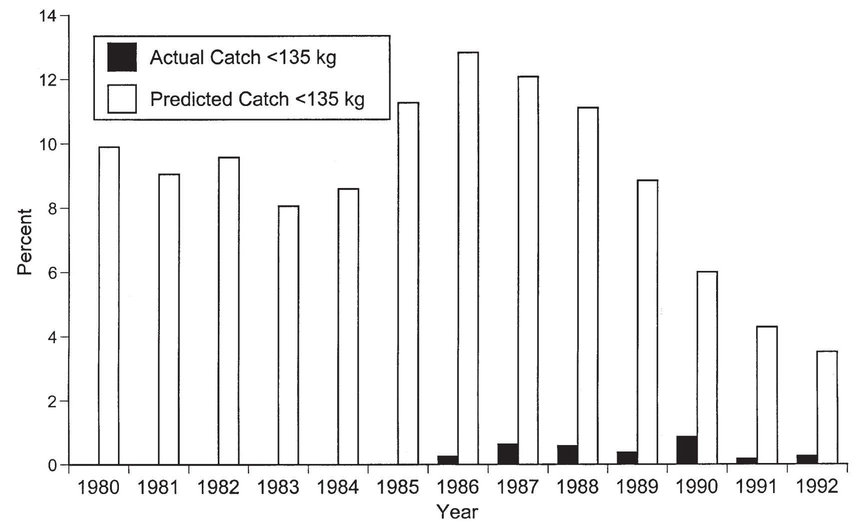

Figure 3

Comparison of actual catch of bluefin tuna less than 135 kg in the Gulf of Mexico between 1980 and 1992 and catch predicted with a 2% annual eat-to-west transfer rate and the diffusion model.

ference in size and age at maturity between east and west Atlantic populations does not appear related to differences in growth rate because recent growth models indicate little difference between populations (Cort, 1991; Turner et al., 1991; Table 1).

Similarly, if differences in age or size at maturity are affected by environmental conditions, for example temperature, we would expect this effect to be manifested primarily by changes in growth rate. Again, the similarity in growth rate between east and west Atlantic bluefin tuna suggests that environmental conditions are unlikely to explain the difference in size and age at maturity.

Alternatively, if age at maturity is a heritable trait, then a long period of size-selective fishing mortality could shift genotype frequencies in the population because few late-maturing fish are likely to survive to reproduce (Trippel, 1995), resulting in a younger age or smaller size at maturity, or both (Policansky, 1993; Trippel, 1995). Experiments with guppies indicate that increased mortality (as through fishing) selects for earlier maturity at smaller size (Reznick, 1993). Bluefin tuna in the east Atlantic has a longer history of exploitation and a much larger population than west Atlantic bluefin tuna. Assuming that the very large difference in population sizes results in a comparable difference in stock density, then an eastern bluefin tuna with a genetic propensity to mature at or before age 5 in the east Atlantic should, upon migrating to the west Atlantic, find itself in a relatively resource-rich, lower-density environment, which should certainly not delay maturation or inhibit spawning. Thus, although genetic effects are difficult to establish, such a large difference in size and age at maturity as between east and west Atlantic bluefin tuna is unlikely to be a result of density-dependent or environmental differences. Further, it seems unlikely that a sexually mature five- or six-year-old east Atlantic bluefin tuna would revert to immaturity upon migrating to the west Atlantic, and then remain immature for two or three years until finally spawning at age eight.

Another possible explanation for these results is that the size-at-maturity data on which this analysis depends are incorrect. In fact, Clay (1990) criticized both the Baglin (1982) and Rodriguez-Roda (1967) studies, citing small sample sizes and inadequate temporal and spatial coverage. As Clay (1990) pointed out, the Rodriguez-Roda (1967) study dealt with fish that were on their way to the spawning grounds and thus may have over-estimated the percentage of small, mature fish in the total population. Although this is a valid criticism, it is worth noting that the collection of Rodriguez-Roda also contained immature fish, implying that not all fish in his sample were on their way to the spawning grounds.

Further, although our method clearly relies on the assumption that bluefin tuna of eastern origin first spawn at a smaller size than western fish, only a small proportion of age classes 4 through 7 need be mature for our results to prevail. We investigated the sensitivity of our model to a ten-fold reduction in the maturity parameter P (i.e. to 0.05 on age-4 and 0.1 on ages 5 through 7) and found that small bluefin tuna would still be significantly rarer (chi-square test, $P<0.005$) in the Gulf than predicted under the diffusion model with a 2% east-to-west transfer rate, given our assumptions.

Finally, for the purpose of this study, we have made the most conservative assumption, i.e. that any bluefin tuna (except larvae) found in the Gulf of Mexico is spawning. Thus, it is possible that some of the smaller bluefin tuna in the Gulf of Mexico landing records were not actually spawning fish, or were of west Atlantic origin, or both.

Alternative spawning grounds

Our results might also be otabined if small migrant tuna of eastern origin spawn elsewhere in the west other than the Gulf of Mexico. A recently discovered concentration of medium and large tuna off the coast of North Carolina from January through April caused speculation that perhaps this concentration represents another spawning area. However, the lack of gonad development in a sample of seventeen fish (weighing between 65 and 183 kg) suggested that these fish were unlikely to spawn in the year they were captured and were probably immature (Belle[6]).

Several other workers have searched for evidence of bluefin tuna spawning in the west Atlantic. Mather et al. (1995) reported finding ripening small fish but no larvae. If the overlap hypothesis does prevail, then these potentially mature but nonspawning smaller fish may be eastern migrants that although capable of spawning, will return to the Mediterranean before actually doing so. McGowan and Richards (1989) reported on the sporadic presence of larvae in the Gulf Stream as far north as North Carolina but concluded that most larvae found in the Gulf Stream were either advected out of the Gulf or spawned by tuna exiting the Gulf. Furthermore, they stated that conditions are poor for larval development in the Gulf Stream and that the occasional occurrence of larvae there does not indicate an additional spawning ground. On the matter of alternative spawning grounds, the National Research Council concludes that “extensive searching has detected only two spawning localities: the Gulf of Mexico and the Mediterranean Sea” (NRC, 1994, p. 18).

Underreporting or low catchability

Two other possibilities for the lack of small bluefin tuna in the Gulf of Mexico catch are that they are present in the Gulf of Mexico and are either being caught but not recorded, or are not being caught owing to a lack of appropriate fishing effort. To test for the first possibility, we acquired records of all bluefin tuna recorded by longline observers in the Gulf of Mexico during 1993–95. Of 31 bluefin tuna recorded by observers for which actual or estimated weights were recorded, all were greater than 135 kg. We also reviewed ICCAT data for the Japanese longline fishery in the Gulf of Mexico for the period 1973 to 1981 and found that only 58 records out of 14,530 (0.4%) were for fish under 180 cm (135 kg). These data are particularly significant in light of the fact that there were no regulations concerning the retention and sale of small bluefin tuna during this period as there have been in recent years. Therefore, the Japanese would have had no incentive to intentionally misidentify or underreport small bluefin tuna. Mather et al. (1995), after reviewing longline catches in the Gulf and Caribbean prior to 1973, found only fish larger than 185 cm. They also reported very young bluefin tuna (less than 2 kg) in the Gulf of Mexico from July into November (Mather et al., 1995); fish presumably spawned a few months earlier. Similarly, Hisada and Suzuki (1982) presented length-frequency distributions of Japanese longline catches from the Gulf of Mexico which appear to show essentially no fish smaller than 200 cm.

The possibility that small bluefin tuna are present in the Gulf but are not being caught cannot be completely eliminated. However, there is a considerable accumulation of evidence that suggests that this is highly unlikely. For example, although there currently is no directed fishery for either small or large bluefin tuna in the Gulf, there is a widespread, year-round yellowfin tuna (*Thunnus albacares*) longline fishery. This fishery targets yellowfin tuna of the same size as the small bluefin tuna of east Atlantic origin that we hypothesize would be present in the Gulf if the diffusion model is correct. This fishery does have a bycatch of bluefin tuna, none of which have ever been recorded by observers as less than 175 cm.[7]

Furthermore, longline operations in the northwest Atlantic do catch small bluefin tuna, indicating that they are potentially vulnerable to this gear. Cramer and Turner[8] reported length frequencies for observer data from the U.S. longline fishery in the northwest Atlantic from 1992 to 1995, showing that over 30% of fish hooked were less than 150 cm straight fork length (Fig. 4). Similarly, catch data from the Japanese northwest Atlantic longline fishery in the 1970s and 1980s show that the catch dominated by bluefin tuna between 100 and 150 cm in several years (Fig. 8 in Hisada and Suzuki, 1982). Although failure to catch a given species or size class in an area can never rule out its presence, given the extent and diversity of fishing activity in the Gulf, it is unlikely that any significant aggregation of small bluefin tuna

[6] Belle, S. 1996. Biological sampling of bluefin tuna off Cape Hatteras, North Carolina. Final report to the New England Aquarium Corporation (NOAA requisition no. 43AANF503279), Boston, MA, 12 p.

[7] Lee, D. 1996. National Marine Fisheries Service, Southeast Fisheries Science Center, 75 Virginia Beach Drive, Miami, FL 33149. Personal commun.

[8] Cramer, J., and S. C. Turner. 1996. Standardized catch rates for bluefin tuna, *Thunnus thynnus*, from the U.S. pelagic longline fishery in the northwest Atlantic. ICCAT working document SCRS/96/69.

there would have been entirely missed.

Finally, we tested the sensitivity of our results to a range of selectivities of longline gear set in the Gulf of Mexico. With selectivities on fish smaller than 135 kg ranging from 0 to 1 (where the selectivity on fish greater than 135 kg is 1), the sensitivity analysis indicated that at selectivities greater than about 0.13, small fish were significantly less abundant (chi-square test, $P<0.05$) in the catch in the Gulf than would be expected given our assumptions and a 2% east-to-west transfer rate.

Future research on this topic must seek to address both the annual rate of trans-Atlantic movement as well as the degree of philopatry exhibited by migrants to achieve a full understanding of the population dynamics of east and west Atlantic bluefin tuna. Currently, there are studies underway to identify nuclear and mitochondrial DNA markers that may have variations specific to east and west populations (Graves et al., 1995). Examinations of otolith chemistry (microconstituent analysis) may provide information on stock differentiation and mixing rates, and researchers are currently deploying archival tags on bluefin tuna caught in the west Atlantic, primarily off Cape Hatteras, North Carolina.[9,10] These tags will record geolocation data and, if recovered, should yield a complete record of each fish's movement since its release. Finally, additional studies on the maturation schedules of fish in the east and west are still needed.

Clearly, it will take years before these studies yield sufficient information on transfer rates and philopatry to provide robust management advice. The depleted state of bluefin tuna populations worldwide, and in the west Atlantic particularly (Safina, 1993), make these issues of considerable practical importance. Until such time as these questions are answered definitively we believe that spawning site fidelity should be assumed and the stocks managed accordingly.

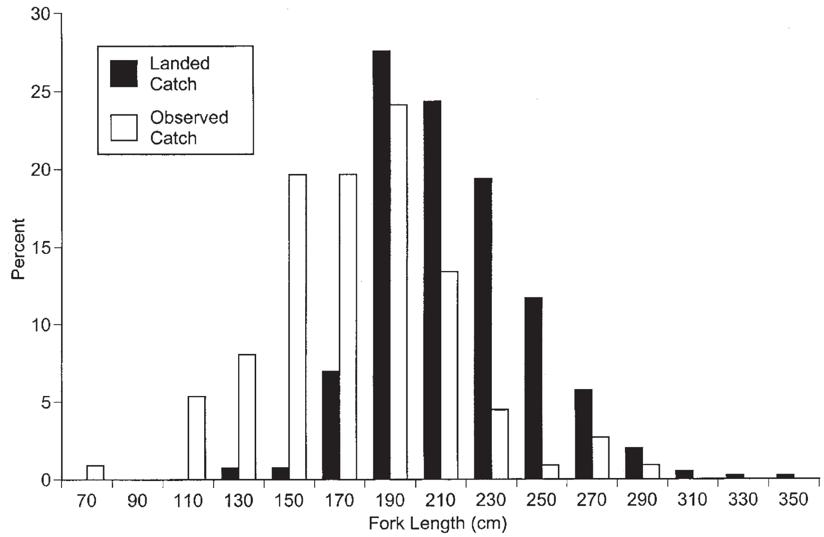

Figure 4

Length-frequency distributions of bluefin tuna caught on longlines in the northwest Atlantic (landings, n=403) and measured by observers on longline vessels (observer, n=112) between 1992 and 1995 (see Footnote 7 in the main text).

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[9] Prince, E. 1996. National Marine Fisheries Service, Southeast Fisheries Science Center, 75 Virginia Beach Drive, Miami, FL 33149. Personal commun.

[10] Block, B. 1997. Hopkins Marine Station, Stanford University, Oceanview Boulevard, Pacific Grove, CA 93950-3094. Personal commun.

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