Genetic analysis of the population structure of yellowfin tuna, *Thunnus albacares*, from the Pacific Ocean*

Daniel R. Scoles
Virginia Institute of Marine Science
School of Marine Science, College of William and Mary
Gloucester Point, VA 23062

John E. Graves**
Virginia Institute of Marine Science
School of Marine Science, College of William and Mary
Gloucester Point, VA 23062

Inter-American Tropical Tuna Commission
8604 La Jolla Shores Drive, La Jolla, CA 92037

Abstract.—The genetic basis of the population structure of yellowfin tuna, *Thunnus albacares*, in the Pacific Ocean was investigated with restriction fragment length polymorphism (RFLP) analysis of mitochondrial DNA (mtDNA). Samples of 20 yellowfin tuna were examined from each of five Pacific locations and one Atlantic location. MtDNA analysis with 12 informative restriction endonucleases demonstrated considerable genetic variation, as evidenced by an overall nucleon diversity of 0.84 and a mean nucleotide sequence diversity of 0.91%. Estimates of within-sample variation were remarkably consistent across all six locations. Despite high levels of variation, there was no evidence of genetic differentiation among samples. Common genotypes occurred with similar frequencies in all samples, and, with one exception, all genotypes that were represented by more than one individual occurred at more than one location. We could not reject the null hypothesis that all yellowfin tuna share a common gene pool. Our results are consistent with the alternate hypothesis that there is sufficient gene flow within the Pacific, as well as between the Atlantic and Pacific oceans, to prevent the accumulation of significant genetic differentiation.

Yellowfin tuna (*Thunnus albacares*) occur in the tropical and subtropical oceans and support major commercial fisheries throughout their range (Collette and Nauen, 1983). The economic importance of this species is indicated by high annual catches that have increased from 596,764 metric tons (t) in 1981 to 986,529 t in 1990, of which 66 to 69% were from the Pacific Ocean (FAO, 1992). Recently, purse-seine and longline fisheries in the western Pacific (120°E to about 180°) provided a major share of yellowfin tuna landings, with a catch of 342,921 t in 1990 (Lawson, 1991). In the eastern Pacific (east of 130°W) record landings near 270,000 t occurred in each of the past 3 years[1].

A thorough understanding of yellowfin tuna population structure is necessary for the effective management of this economically important, marine resource. A variety of studies, including tagging, morphometric, fishery statistic and genetic analyses, have been used to infer population structure. However, the proposed population structures differed.

Tagging studies have indicated that movements of yellowfin tuna in the Pacific Ocean tend to be geographically restricted. Fink and Bayliff (1970) analyzed tag return data in the eastern Pacific and proposed a northern and southern group of fish with some exchange between groups. There was very limited westward movement of tagged fish reported in the study; however, as the eastern Pacific fishery expanded westward in subsequent years, several returns were obtained from farther offshore indicating possible mixing between eastern and central Pacific fish (Bayliff, 1984). In the western Pacific tagging studies showed that most individuals remained within the western Pacific region and did not make extensive movements (Itano and Williams, 1992; Lewis, 1992). Although the majority of recaptured yellowfin tuna in all studies showed limited movement, some returns were obtained which demonstrated the potential for fish to move large dis-

[1]Anonymous. 1992. Inter-American Tropical Tuna commission, Annual Report, 1991.

*Contribution No. 1811 of the Virginia Institute of Marine Science.
**To whom reprint requests and correspondence should be addressed.

Manuscript accepted 12 August 1993.
Fishery Bulletin 91:690–698 (1993).

tances and between regions (Fink and Bayliff, 1970; Bayliff, 1984; Itano and Williams, 1992).

Population structure was indicated by investigations of both meristic and morphometric characters which revealed significant differentiation among yellowfin tuna from the eastern, central, and western Pacific regions (Schaefer, 1955; Kurogane and Hiyama, 1957), as well as clinal character variation across the equatorial Pacific (Royce, 1964). Further investigation using discriminant function analysis of morphometric variables suggested mixing occurs between morphologically differentiated northern and southern yellowfin tuna of the eastern Pacific (Schaefer, 1989), as well as across the Pacific (Schaefer, 1991, 1992).

Analysis of fishery data also suggests population structuring of yellowfin tuna within the Pacific. Kamimura and Honma (1963) provided evidence for two or more semi-independent subpopulations based on size composition and catch data of equatorial Pacific yellowfin tuna from longline landings. Suzuki et al. (1978) examined longline and purse-seine length composition data and suggested the existence of semi-independent eastern, central, and western Pacific subpopulations. Additionally, homogeneity within the western Pacific was indicated by the widespread distribution of fish contaminated by radioactivity resulting from the 1954 U.S. nuclear tests at Bikini Atoll (Suzuki et al., 1978).

While the results of several analyses suggest yellowfin tuna exhibit population structure within the Pacific Ocean, genetic analyses have revealed no significant genetic differentiation. Suzuki (1962) reported that the blood agglutinogen Tg2 occurs in similar frequencies in samples from the Indian Ocean and the eastern Pacific. Additionally, allozyme analysis did not reveal genetic differentiation between samples of yellowfin tuna collected off Hawaii (n=529) and Baja California (n=207) at the polymorphic serum esterase locus, although overall variation was low (Fujino, 1970). Preliminary evidence for frequency differences occurring at two other loci (phosphoglucose isomerase and transferrin A) was reported for both within and between samples of Atlantic and Pacific yellowfin tuna[2,3]. However these loci have not been used to examine population structure.

Our understanding of the population structure of yellowfin tuna in the Pacific Ocean remains problematic. Much evidence is available which suggests that population structure exists, yet genetic analyses did not reveal differentiation among samples collected from distant locations. To further examine the genetic basis of the population structure of Pacific yellowfin tuna we employed restriction fragment length polymorphism (RFLP) analysis of mitochondrial DNA (mtDNA). Because mtDNA evolves rapidly (Moritz et al., 1987; Brown et al., 1979) and displays considerable polymorphism within animal populations (Avise and Lansman, 1983), mtDNA analyses have been useful in revealing population structure within marine fishes (Ovenden, 1990). Using this technique, we demonstrated considerable genetic variability within yellowfin tuna, but we could not reject the null hypothesis that samples share a common gene pool.

Materials and methods

Hearts were taken from 50 yellowfin tuna at each of five Pacific locations and one Atlantic location (Fig. 1); however, only 20 specimens per location were analyzed. Samples from the Pacific were collected during 1990 at Manta, Ecuador (ECU); Revillagigedo Islands, Mexico (MEX); Oahu, Hawaii (HAW); Manus Island, Papua New Guinea (PNG); and New South Wales, Australia (AUS). The sample from the Atlantic was collected during 1991 at Hatteras, North Carolina (ATL). Hearts were dissected within 12 hours of capture and placed on crushed ice. Hearts from fish collected in the Pacific were frozen at –20°C and shipped to the Inter-American Tropical Tuna Commission, La Jolla, CA, where they were stored at –20°C for more than one year before shipment to our laboratory. Hearts from fish collected in the Atlantic were transported on wet ice and frozen at –70°C within four hours of dissection.

MtDNA was purified from 3 g of heart tissue from Atlantic specimens following the CsCl-ethidium bromide gradient centrifugation protocol of Lansman et al. (1981). MtDNA yields averaged about 350 ng of supercoiled mtDNA per g of heart tissue. Aliquots of mtDNA were digested with the following 12 informative restriction endonucleases (Stratagene and BRL) according to the manufacturers' instructions: *Apa*I, *Ava*I, *Ban*I, *Bcl*I, *Bgl*I, *Dra*I, *Eco*RI, *Hin*dIII, *Nci*I, *Pst*I, *Pvu*II and *Xho*I. Restriction fragments were end-labeled with a mixture of all four α-^{35}S-dNTP's by using the Klenow fragment, electrophoresed at 2 volts/cm overnight in 1% agarose gels, and visualized by autoradiography (Sambrook et al., 1989).

Yields of supercoiled mtDNA from Pacific specimens were low, possibly due to sub-optimal storage conditions. For these specimens, mtDNA-enriched genomic DNA was isolated from 4 to 6 g of heart tissue following the protocols of Chapman and Powers (1984), modified by the omission of sucrose step gradients and the

[2]Anonymous. 1977. Inter-American Tropical Tuna Commission, Annual Report, 1976.

[3]Anonymous. 1978. Inter-American Tropical Tuna Commission, Annual Report, 1977.

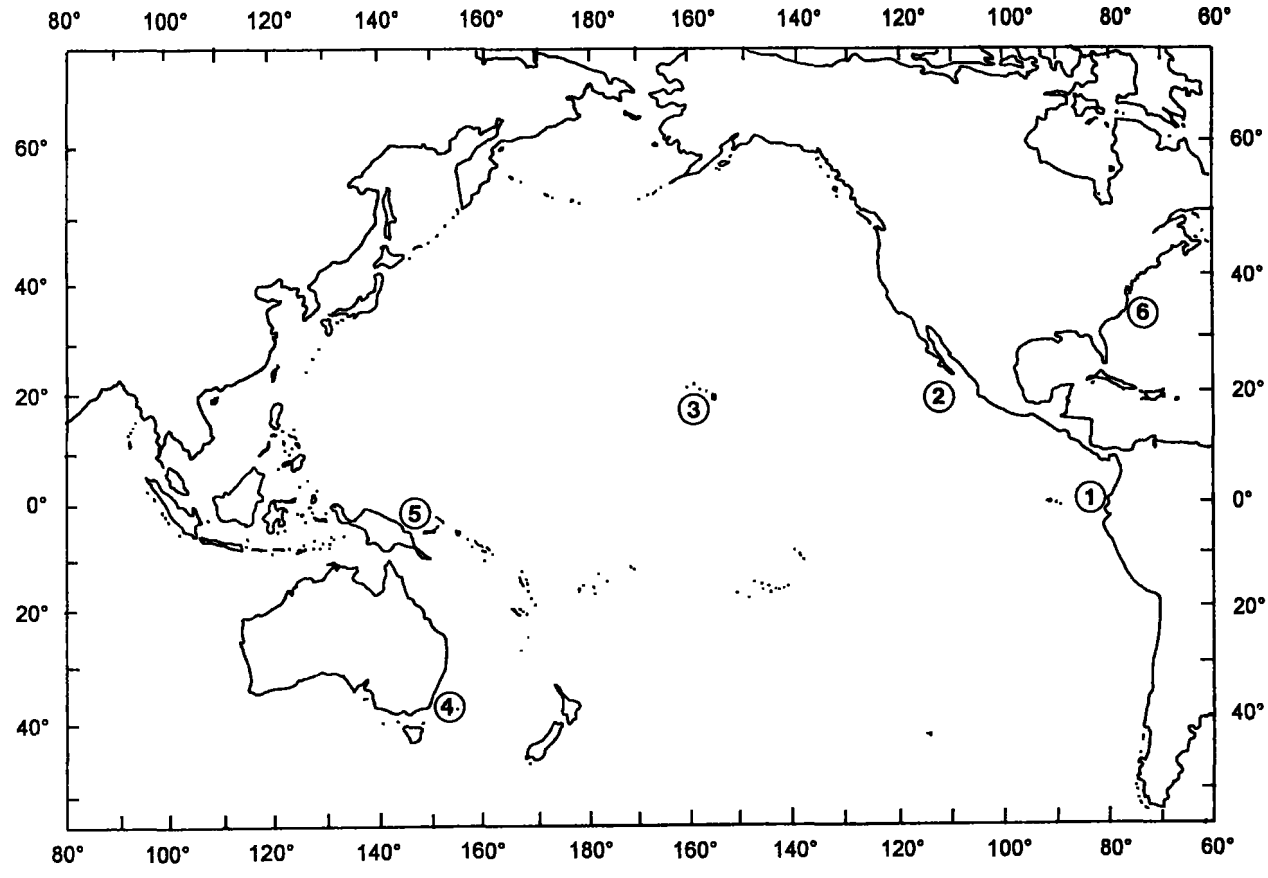

Figure 1

Thunnus albacares. Location of sampling sites used in this analysis: (1) Manta, Ecuador (ECU); (2) the Revillagigedo Islands, Mexico (MEX); (3) Oahu, Hawaii (HAW); (4) New South Wales, Australia (AUS); (5) Manus Island, Papua New Guinea (PNG); and (6) Hatteras, North Carolina (ATL).

use of 1.5% sodium dodecyl sulfate for mitochondrial lysis. Following restriction enzyme digestion and horizontal agarose gel electrophoresis, DNA fragments were transferred to nylon membranes by Southern transfer (Sambrook et al., 1989) and immobilized by long-wave UV irradiation. Prehybridization was conducted for two hours at 42°C in 50% formamide, 5× SSC, 5× Dendhardt's solution, 0.025 mM $NaPO_4$, pH 6.5, and 100 µg/mL heat denatured calf thymus DNA. Probe DNA (mtDNA purified from extra specimens from the Atlantic) was nick-translated to incorporate biotin-7-dATP (BRL), and separated from unincorporated nucleotides by size exclusion chromatography. One µg of probe was added to the prehybridization solution for each 200 cm^2 blot and allowed to hybridize overnight at 42°C. Following post-hybridization washes (Sambrook et al., 1989), mtDNA fragments were visualized with the BRL BluGene Non-Radioactive Nucleic Acid Detection Kit.

A 12-letter composite mtDNA genotype, indicating the fragment pattern for each restriction enzyme, was developed for each individual. Estimates of nucleon diversity (h) for each sample and for the pooled samples were computed following Nei (1987). Nucleotide sequence divergences among genotypes were estimated by using the site method of Nei and Li (1979). Estimates of nucleotide sequence diversity (p) within each sample, and mean nucleotide sequence divergences among samples (corrected for within-sample diversities) were computed following Nei (1987). Nucleotide sequence divergences were clustered by the unweighted pair-group method with arithmetic means (UPGMA) by using the average linkage algorithm of the SPSS-X statistical package (Norusis, 1988). Values of G_{st}, a measure of heterogeneity between samples, were estimated from sample genotype frequencies (Nei, 1987), and values of N_em, the absolute number of migrants between samples, were determined from the relation

$N_em = (1/G_{st} - 1)/2$ (Birky et al., 1983; Nei, 1987). Chi-square analysis was conducted by using the Monte-Carlo method of Roff and Bentzen (1989) with 1000 randomizations of the data to evaluate heterogeneity of genotype frequencies among samples without combining rare genotypes.

Results

Analysis of mtDNA from 120 yellowfin tuna with 12 restriction enzymes revealed a total of 34 genotypes, comprising 83 unique fragments. The most common genotype consisted of 52 fragments, representing a survey of 304 bp, or about 1.8% of the mtDNA genome. The mean size of the yellowfin tuna mtDNA genome, determined from the most common restriction fragment profiles for each of the 12 restriction enzymes, was 16,549 ± 309 bp (SD).

RFLP analysis of yellowfin tuna mtDNA demonstrated considerable variation. While four restriction enzymes, *Ava*I, *Dra*I, *Hin*dIII, and *Xho*I, showed no variation, the remaining eight revealed two to seven restriction morphs each. Of the 34 genotypes, two were represented by 20 or more individuals, five were represented by four or more individuals, and 20 genotypes occurred only once (Table 1). Within-sample nucleon diversities were high and showed little variation among samples, ranging from 0.82 to 0.86, with a value of 0.84 for the pooled samples (Table 2). Mean nucleotide sequence diversities were also high, ranging

Table 1

Distributions of mtDNA genotypes among samples of yellowfin tuna, *Thunnus albacares*. Letters represent fragment patterns produced by the following enzymes (left to right): *Eco*RI, *Hin*dIII, *Pst*I, *Dra*I, *Ava*I, *Pvu*II, *Nci*I, *Ban*I, *Bcl*I, *Bgl*I, *Xho*I, and *Apa*I. A description of fragment sizes is available upon request.

	mtDNA genotype	Sampling location						
		ECU	MEX	HAW	AUS	PNG	ATL	Total
1	AAAAAAAAAAAA	7	6	7	8	8	7	43
2	BAAAAAAAAAAA	2	5	3	4	3	3	20
3	BAAAAABAAAAA	3	—	1	—	1	1	6
4	AAAAAAAAECAA	1	1	—	2	—	2	6
5	AAAAAAAABAAA	—	—	—	1	1	2	4
6	AAAAAABAEAAA	1	—	1	—	—	1	3
7	AAAAAABABAAA	2	1	—	—	—	—	3
8	AABAAAAAAAAA	—	2	—	1	—	—	3
9	AAAAAAABAAAA	—	—	1	—	1	—	2
10	AAAAAAAABBAA	—	—	1	1	—	—	2
11	BAAAAAAAAAAB	—	—	1	—	—	1	2
12	BAAAAAAACAAA	—	—	1	—	1	—	2
13	AAAAAAAAEAAF	—	1	—	—	1	—	2
14	AAAAAABAAAAA	—	—	2	—	—	—	2
15	AAAAAAAAAAAB	—	—	—	1	—	—	1
16	AAAAABAAAAAA	—	—	—	—	—	1	1
17	AAAAAAAAAAAC	—	—	—	—	1	—	1
18	AAAAAAAAAAAD	—	—	—	—	1	—	1
19	AAAAAAAAFAAA	—	—	—	—	1	—	1
20	AAAAAAAAAAAF	—	—	1	—	—	—	1
21	AABAAAAABAAA	—	—	—	—	—	1	1
22	BABAAAAAAAAA	—	—	1	—	—	—	1
23	AAAAAABAAAAE	—	—	—	1	—	—	1
24	AAAAAAAADAAB	—	—	—	—	1	—	1
25	CAAAAABAAAAA	1	—	—	—	—	—	1
26	AABAAAAAAAAG	1	—	—	—	—	—	1
27	AABAAAAAEAAA	1	—	—	—	—	—	1
28	AAAAAABAAAAB	—	1	—	—	—	—	1
29	BAAAAAAAAAAD	—	1	—	—	—	—	1
30	BAAAAAAABBAA	—	1	—	—	—	—	1
31	BAAAAABABAAA	—	1	—	—	—	—	1
32	BAAAAABAGAAA	1	—	—	—	—	—	1
33	AAAAAABAADAA	—	—	—	—	—	1	1
34	AAAAAAACFEAA	—	—	—	1	—	—	1
Total		20	20	20	20	20	20	120

Table 2
Genetic variation within samples of yellowfin tuna, *Thunnus albacares*, expressed as nucleon diversity (h) and percent nucleotide sequence diversity (p).

Sampling location	Nucleon diversity (h)	Nucleotide sequence diversity (p) %
ECU	0.863	1.04
MEX	0.863	0.955
HAW	0.868	0.799
AUS	0.816	0.905
PNG	0.837	0.737
ATL	0.863	0.917
Pooled	0.840	0.907

from 0.74% to 1.04%, and 1.04% for the pooled samples (Table 2).

Despite the high level of within-sample variation, there was little evidence for genetic differentiation among the six sampling sites. The two most common genotypes (1 and 2) were observed at all locations at similar frequencies (30–40%, 10–25%, respectively; Table 1). Of the 12 other genotypes that occurred in more than a single individual, 11 were found in two or more samples, and only one (genotype 14) occurred in a single sample, represented by two individuals.

Pairwise estimates of corrected nucleotide sequence divergences between samples (including the Atlantic) were low, ranging from 0.012% to 0.104%, with a mean pairwise divergence of 0.04%. Similarly, estimates of G_{st} were low, ranging from 0.011 to 0.025, and values of N_em were correspondingly high, ranging from 19.5 to 44.5 females per generation. No clear pattern of phylogeographic structure was revealed in cluster analyses of nucleotide sequence divergences among mtDNA genotypes or sampling locations. Chi-square analysis of heterogeneity among samples was not significant, as randomizations of the data into six samples were more heterogeneous than the observed genotypic distributions 581 of 1000 times (P=0.581).

To determine an appropriate number of individuals to examine from each location and the number of restriction enzymes to employ, we compared levels of genetic variation and differentiation revealed by a pilot study of 12 individuals per location with 5 enzymes with larger analyses of up to 20 individuals per location with 12 enzymes (Table 3). Levels of variation were influenced more by increasing the number of enzymes surveyed than the number of individuals. Increasing the number of enzymes increased the number of genotypes, the nucleon diversities, and, to a lesser extent, nucleotide sequence diversities. Analysis of a greater number of individuals per location had little effect on diversity estimates with either 5 or 12 enzymes, although the ranges of within-sample diversities among locations decreased as more individuals were analyzed.

Increasing the number of individuals or the number of enzymes had little effect on levels of genetic differentiation. No significant differences were found in the distributions of genotypes among locations in Roff and Bentzen (1989) chi-square tests (Table 3). Furthermore, increasing the number of individuals in the 12 enzyme analysis did not increase the frequencies of genotypes unique to a location. Instead, many unique genotypes in the analysis of 12 individuals occurred in other locations as a greater number of individuals were used. Because increasing sample sizes from 12 to 20 individuals did not reveal greater spatial partitioning of genetic variation, we decided that 20 individuals was an appropriate sample size.

Discussion

Population structure is typically manifested as the spatial or temporal partitioning of genetic variation. Therefore, to demonstrate if population structure exists, a technique must first reveal a reasonable level of genetic variation. RFLP analysis of mtDNA revealed considerable genetic variation in yellowfin tuna. The overall nucleon diversity and mean nucleotide sequence diversity (0.84 and 0.91%, respectively) are in the up-

Table 3
Pooled percent nucleotide sequence diversities (p) and nucleon diversities (h), and respective ranges (in parentheses) among samples obtained by varying the numbers of restriction enzymes and individuals of yellowfin tuna, *Thunnus albacares*, per sampling location. Probabilities of significance result from Roff and Bentzen's (1989) chi-square analysis with 1000 randomizations of the data. The five enzymes selected for the pilot study were *Eco*RI, *Hin*dIII, *Pst*I, *Dra*I, and *Ava*I.

Design	Number of genotypes	Nucleon diversity (h)	Nucleotide sequence diversity (p) (%)	Prob.
5 enzymes 12 individuals	6	0.496 (0.41–0.64)	0.705 (0.49–0.90)	0.960
5 enzymes 20 individuals	6	0.509 (0.42–0.63)	0.714 (0.62–0.91)	0.845
12 enzymes 12 individuals	27	0.829 (0.76–0.94)	0.907 (0.66–1.22)	0.975
12 enzymes 20 individuals	34	0.840 (0.82–0.87)	0.907 (0.74–1.04)	0.581

per ranges reported for marine fishes (Avise et al., 1989; Ovenden, 1990; Gold and Richardson, 1991) including other large, pelagic fishes (Table 4).

Genetic variability in tuna species has also been demonstrated by sequence analysis of a 307-base-pair region of the mitochondrial cytochrome *b* gene of bluefin tuna, *Thunnus thynnus*; bigeye tuna, *T. obesus*; albacore, *T. alalunga*; and yellowfin tuna (Bartlett and Davidson, 1991). The sequence data presented for 33 yellowfin tuna result in a nucleon diversity of $h = 0.28$, a value that is considerably lower than the nucleon diversity of 0.84 obtained in our study. Although nucleon diversity values are greatly influenced by the number of base pairs surveyed (Nei, 1987), the number examined in this study and in Bartlett and Davidson (1991) were very close (304 and 307, respectively). This difference in nucleotide sequence diversity may reflect a slower evolutionary rate for the mitochondrial cytochrome *b* gene relative to the entire mtDNA genome.

Significant genetic differentiation among yellowfin tuna from geographically distant locations was not found. Corrected nucleotide sequence divergences averaged only 0.04%, indicating that the mean difference between two genotypes randomly chosen from any two samples was essentially the same as the difference between two genotypes randomly drawn from the same sample. The frequencies of the two most common genotypes were similar among all locations, and an overall chi-square test for heterogeneity was non-significant. Furthermore, nucleon diversities and nucleotide sequence diversities were similar among locations, although uniformity in the latter estimates was less pronounced.

Table 4

Genetic variation within selected pelagic species determined by RFLP analysis of mtDNA employing 11–13 informative enzymes. Variation is expressed as nucleon diversity (h) and percent nucleotide sequence diversity (p).

Species	Nucleon diversity (h)	Nucleotide sequence diversity (p) (%)
Thunnus albacares[1] (Yellowfin Tuna)	0.84	0.91
Thunnus alalunga[2] (Albacore Tuna)	0.60	0.31
Tetrapturus audax[3] (Striped Marlin)	0.74	0.54
Tetrapturus albidus[3] (White Marlin)	0.70	0.35
Makaira nigricans[3] (Blue Marlin)	0.86	1.99
Istiophorus platypterus[3] (Sailfish)	0.62	0.87

[1]This study.
[2]Graves and Dizon (1989) and Graves, unpublished data.
[3]Graves and McDowell, in press.

The apparent genetic homogeneity of yellowfin tuna is consistent with the hypothesis that there is genetic exchange among locations. Rare mtDNA genotypes had low frequencies of occurrence (Table 1), characteristic of high gene flow (Slatkin, 1985), a situation similar to that found in other species for which high gene flow is suggested: American eel, *Anguilla rostrata* (Avise et al., 1986); marine catfishes, Ariidae (Avise et al., 1987); weakfish, *Cynoscion regalis* (Graves et al., 1992a); and bluefish, *Pomatomus saltatrix* (Graves et al., 1992b). Low pairwise estimates of G_{st} (0.011–0.025) also indicated homogeneity in yellowfin tuna and gave rise to high N_em values (>19) which are consistent with high rates of gene flow among regions (Birky et al., 1983).

The absence of genetic differentiation between Pacific and Atlantic samples of yellowfin tuna is similar to that reported for other vagile pelagic species. RFLP analysis of mtDNA of skipjack tuna, *Katsuwonus pelamis*, and of albacore from the Atlantic and Pacific oceans revealed modest amounts of within-sample variation, but no significant differentiation was found between Atlantic and Pacific conspecifics (Graves et al., 1984; Graves and Dizon, 1989). Similarly, RFLP analysis of mtDNA of the pelagic dolphin, *Coryphaena hippurus*, revealed no significant differentiation between samples from the Atlantic and Pacific oceans[4]. However, spatial partitioning of genetic variation occurs in at least some pelagic fishes. Significant genetic differentiation was shown between Atlantic and Pacific blue marlin, *Makaira nigricans*, by direct sequence analysis of the mitochondrial cytochrome *b* gene (Finnerty and Block, 1992) and RFLP analysis of mtDNA (Graves and McDowell, in press). Similarly, differentiation was found among striped marlin samples, *Tetrapturus audax*, and sailfish, *Istiophorus platypterus*, from the Pacific Ocean by RFLP analysis of mtDNA (Graves and McDowell, in press).

There are several characteristics of yellowfin tuna which could promote gene flow among locations. Yellowfin tuna are distributed circumtropically (Collette and Nauen, 1983) and occur around the Cape of Good Hope in the southern summer (Talbot and Penrith, 1962). Tagging studies demonstrated that adults are capable of traveling large distances between Pacific regions (Fink and Bayliff, 1970; Bayliff, 1984; Itano and Williams, 1992), and are capable of undergoing trans-Atlantic crossings (Bard and Scott, 1991). The existence of suitable spawning areas throughout the

[4]Carol Reeb, University of Hawaii, pers. commun. April 1992.

tropical oceans, suggested by circumtropical occurrence of larvae (Nishikawa et al., 1985), would permit unobstructed gene flow throughout the species' distribution.

Both genetic and morphological analyses revealed considerable variation in yellowfin tuna; however, genetic analyses indicated that differentiation does not occur. Evidence that morphological characters are environmentally influenced was provided by comparison of our data to the morphological differentiation found in Schaefer (1991, 1992). In our analysis, 20 fish from four locations (Ecuador, Mexico, Hawaii, and Australia) were the same as those used in Schaefer's studies. Although no genetic differences were found among these locations, morphometric characters and gill-raker counts differed significantly, which we conclude is the result of phenotypic plasticity. The finding of greater morphological variability among Pacific samples than occurred between the Atlantic and Pacific (Schaefer and Walford, 1950) also supports the hypothesis that phenotypic plasticity is the cause of morphological differentiation in the Pacific.

The null hypothesis that yellowfin tuna in the Pacific Ocean share a common gene pool could not be rejected in this analysis. Our results were consistent with the alternate hypothesis that yellowfin tuna maintain sufficient gene flow among areas to prevent the accumulation of significant genetic differentiation. As theoretical models indicate that very low levels of migration (only a few individuals per generation) are needed to prevent genetic differentiation among large populations (Allendorf and Phelps, 1981; Hartl and Clark, 1989), the present data indicate only that some minimal amount of exchange is occurring. Other approaches are necessary to quantify the amounts of mixing among regions and to judge more accurately whether or not separate stocks should be distinguished for management purposes.

Acknowledgments

Kurt Schaefer either directly collected or arranged collection of all specimens from the Pacific. Antony Lewis and Ziro Suzuki kindly made regional literature available for our use. William Bayliff, Mark Chittenden, Bruce Collette, Edward J. Heist, and Kurt Schaefer critically reviewed the manuscript.

Literature cited

Allendorf, F. W., and S. Phelps.
1981. Use of allelic frequencies to describe population structure. Can. J. Fish. Aquat. Sci. 38:1507–1014.

Avise, J. C., and R. A. Lansman.
1983. Polymorphism of mitochondrial DNA in populations of higher animals. *In* M. Nei and R.K. Koehn (eds.), Evolution of genes and proteins, p. 147–164. Sinauer, Sunderland, MA.

Avise, J. C., G. S. Helfman, N. C. Saunders, and L. S. Hales.
1986. Mitochondrial DNA differentiation in North Atlantic eels: population genetic consequences of an unusual life history pattern. Proc. Natl. Acad. Sci. USA 83:4350–4354.

Avise, J. C., C. A. Reeb, and N. C. Saunders.
1987. Geographic population structure and species differences in mitochondrial DNA of mouthbrooding marine catfishes (Ariidae) and demersal spawning toadfishes (Batrachoididae). Evolution 41:991–1002.

Avise, J. C., B. W. Bowen, and T. Lamb.
1989. DNA fingerprints from hypervariable mitochondrial genotypes. Mol. Biol. Evol. 6:258–269.

Bard, F. X., and E. L. Scott.
1991. Sept traversées transatlantiques d'albacores marqués. Thons migrateurs ou sédentaires? (SCRS/89/23, YYP/89/1). *In* Report of the ICCAT Yellowfin Year Program. ICCAT Coll. Vol. Sci. Papers XXXVI:205–222.

Bartlett, S. E., and W. S. Davidson.
1991. Identification of *Thunnus* tuna species by the polymerase chain reaction and direct sequence analysis of their mitochondrial cytochrome *b* genes. Can. J. Fish. Aquat. Sci. 48:309–317.

Bayliff, W. H.
1984. Migrations of yellowfin and skipjack tuna released in the central portion of the eastern Pacific Ocean, as determined by tagging experiments. IATTC Internal Rep. 18, 107 p.

Birky, C. W. Jr., T. Maruyama, and P. Fuerst.
1983. An approach to population and evolutionary genetic theory for genes in mitochondria and chloroplasts, and some results. Genetics 103:513–527.

Brown, W. M., M. George Jr., and A. C. Wilson.
1979. Rapid evolution of animal mitochondrial DNA. Proc. Natl. Acad. Sci. USA 76:1967–1971.

Chapman, R. W., and D. A. Powers.
1984. A method for the rapid isolation of mitochondrial DNA from fishes. Maryland Sea Grant College Program Tech. Rep. UM-SG-TS-84-01, 11 p.

Collette, B. B., and C. E. Nauen.
1983. FAO species catalogue. Vol. 2: Scombrids of the world: an annotated and illustrated catalogue of tunas, mackerels, bonitos and related species known to date. FAO Fish. Synop. 125, 137 p.

FAO (Food and Agriculture Organization of the United Nations).
1992. Yearbook of fisheries statistics. Catches and landings, 1990. Yearb. Fish. Stat., Vol. 70.

Fink, B. D., and W. H. Bayliff.
1970. Migrations of yellowfin and skipjack tuna in the eastern Pacific Ocean as determined by tagging experiments, 1952–1964. Inter-Am. Trop. Tuna Comm. Bull. 15:1–227.

Finnerty, J. R., and B. A. Block.
1992. Direct sequencing of mitochondrial DNA detects highly divergent haplotypes in blue marlin (*Makaira nigricans*). Mol. Mar. Biol. and Biotechnolog. 1:206–214.

Fujino, K.
1970. Immunological and biochemical genetics of tunas. Trans. Am. Fish. Soc. 99:152–178.

Gold, J. R., and L. R. Richardson.
1991. Genetic studies in marine fishes. IV. An analysis of population structure in the red drum (*Sciaenops ocellatus*) using mitochondrial DNA. Fish. Res. 12:213–241.

Graves, J. E., and A. E. Dizon.
1989. Mitochondrial DNA sequence similarity of Atlantic and Pacific albacore tuna (*Thunnus alalunga*). Can. J. Fish. Aquat. Sci. 46:870–873.

Graves, J. E., and J. R. McDowell.
1993. Genetic analysis of population structure. International Commission for the Conservation of Atlantic Tunas (ICCAT) special billfish workshop publication, SCRS/92/50. ICCAT, Madrid, in press.

Graves, J. E., S. D. Ferris, and A. E. Dizon.
1984. Close genetic similarity of Atlantic and Pacific skipjack tuna (*Katsuwonus pelamis*) demonstrated with restriction endonuclease analysis of mitochondrial DNA. Mar. Biol. 79:315–319.

Graves, J. E., J. R. McDowell, and M. L. Jones.
1992a. A genetic analysis of weakfish *Cynoscion regalis* stock structure along the mid-Atlantic coast. Fish. Bull. 90:469–475.

Graves, J. E., J. R. McDowell, A. M. Beardsley, and D. R. Scoles
1992b. Stock structure of the bluefish *Pomatomus saltatrix* along the mid-Atlantic coast. Fish. Bull. 90:469–475.

Hartl, D. L., and A. G. Clark.
1989. Principles of population genetics. 2nd, rev. ed. Sinauer, Sunderland, MA.

Itano, D. G., and P. G. Williams.
1992. Analysis of yellowfin tagging data and related information collected by the Skipjack Survey and Assessment Programme. SPC Tuna and Billfish Assessment Programme (TBAP) Tech. Rep. 28, 39 p.

Kamimura, T., and M. Honma.
1963. Distribution of the yellowfin tuna *Neothunnus macropterus* (Temminck and Schlegel) in the tuna longline fishing grounds of the Pacific Ocean. FAO, Fish. Rep. 6:1299–1328.

Kurogane, K., and Y. Hiyama.
1957. Morphometric comparison of the yellowfin taken from the equatorial Pacific. Jap. Soc. Sci. Fish. Bull. 23:388–393.

Lansman, R. A., R. O. Shade, D. F. Shapira, and J. C. Avise.
1981. The use of restriction endonucleases to measure mitochondrial DNA sequence relatedness in natural populations. III. Techniques and potential applications. J. Mol. Evol. 17:214–226.

Lawson T.
1991. Status of tuna fisheries in the SPC area during 1990, with annual catches since 1952. SPC Tuna and Billfish Assessment Programme (TBAP) Tech. Rep. 27, 73 p.

Lewis, A. D.
1992. Stock structure of Pacific yellowfin—a review. W. Pacific Yellowfin Tuna Res. Group Workshop; Honolulu, Hawaii, No. 7, 13 p.

Moritz, C., T. E. Dowling, and W. M. Brown.
1987. Evolution of animal mitochondrial DNA: relevance for population biology and systematics. Ann. Rev. Ecol. Syst. 18:269–292.

Nei, M.
1987. Molecular evolutionary genetics. Columbia Univ. Press, New York, 512 p.

Nei, M., and W.-H. Li.
1979. Mathematical model for studying genetic variation in terms of restriction endonucleases. Proc. Natl. Acad. Sci. 76:5269–5273.

Nishikawa, Y., M. Honma, S. Ueyanagi, and S. Kikawa.
1985. Average distribution of larvae of oceanic species of scombroid fishes, 1956–1981. Far Seas Fish. Res. Lab., S Ser., 12, 99 p.

Ovenden, J. R.
1990. Mitochondrial DNA and marine stock assessment: a review. Aust. J. Mar. Freshwater Res. 41:835–53.

Norusis, M. L.
1988. SPSS-X advances statistics guide. 2nd ed. SPSS Inc., Chicago, IL.

Roff, D. A., and P. Bentzen.
1989. The statistical analysis of mitochondrial DNA polymorphisms: chi-square and the problem of small samples. Mol. Biol. Evol. 6:539–545.

Royce, W. F.
1964. A morphometric study of yellowfin tuna *Thunnus albacares* (Bonnaterre). U.S. Fish Wildl. Serv. Fish. Bull. 63:395–443.

Sambrook, J., E. F. Fritsch, and T. Maniatis.
1989. Molecular cloning, a laboratory manual, 2nd ed. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, New York.

Schaefer, K. M.
1989. Morphometric analysis of yellowfin tuna, *Thunnus albacares*, from the eastern Pacific Ocean. Inter-Am. Trop. Tuna Comm. Bull. 19:387–427.
1991. Geographic variation in morphometric characters and gill-raker counts of yellowfin tuna *Thunnus albacares* from the Pacific Ocean. Fish. Bull. 89:289–297.
1992. An evaluation of geographic and annual variation in morphometric characters and gill-raker counts of yellowfin tuna, *Thunnus albacares*, from the Pacific Ocean. Inter-Am. Trop. Tuna Comm. Bull. 20:133–163.

Schaefer, M. B.
1955. Morphometric comparison of yellowfin tuna from southeast Polynesia, Central America, and Hawaii. Inter-Am. Trop. Tuna Comm. Bull. 1:89–136.

Schaefer, M. B, and L. A. Walford.
1950. Biometric comparisons between yellowfin tunas (*Neothunnus*) of Angola and the Pacific coast of Central America. U.S. Fish and Wildl. Serv. Fish. Bull. 51:425–443.

Slatkin, M.
1985. Rare alleles as indicators of gene flow. Evolution 39:53–65.

Suzuki, A.
1962. On the blood types of yellowfin and bigeye tuna. Am. Nat. 96:239–246.

Suzuki, Z., P. K. Tomlinson, and M. Honma.
1978. Population structure of Pacific yellowfin tuna. Inter-Am. Trop. Tuna Comm. Bull. 17:273–441.

Talbot, F. H., and M. J. Penrith.
1962. Tunnies and marlins of South Africa. Nature 193:558–559.