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STOCK STRUCTURE OF BIGEYE, YELLOWFIN, AND SKIPJACK TUNAS IN THE EASTERN PACIFIC OCEAN

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SUMMARY

Regional fidelity has been demonstrated for bigeye, yellowfin, and skipjack tunas in the eastern Pacific Ocean (EPO), with low levels of mixing expected with stocks in the central and western Pacific Ocean. The scientific information available to elucidate stock structure of these three species in the EPO has been reviewed, evaluated, and compiled in this document. The evidence indicates there are probably northern and southern sub-stocks of bigeye (with separation at about 10°N), based on tagging data; northern and southern sub-stocks of yellowfin (with separation at about 15°N), based on tagging, length-at-maturity, morphometric, and stable nitrogen isotope data; and northern and southern sub-stocks of skipjack (with separation at about 15°N), based on tagging and length-at-maturity data. The spatial extent of those stocks and the levels of mixing are not yet well defined. Stock boundaries most likely oscillate within a few degrees of latitude relative to seasonal and annual variability in oceanographic conditions. Further research is needed to elucidate the extents and interactions of the sub-stocks.

1. INTRODUCTION

Considering the fact that bigeye, yellowfin, and skipjack tunas are widely distributed throughout tropical and sub-tropical waters of the Pacific Ocean (Collette and Nauen, 1983), have the capacity to disperse fairly rapidly throughout their ranges (Hunter *et al*., 1986), and exhibit widespread and protracted spawning (Schaefer, 2001a), it is reasonable to assume they would exhibit little intraspecific stock structure in the eastern Pacific Ocean (EPO). However, it is critical to evaluate this assumption, as failure to detect and account for stock structure in assessments and management of these species could lead to local over-fishing and potentially severe declines (Hutchings, 2000; Pauly *et al*., 2003) or, conversely, to unnecessary restrictions on fishing.

An important consideration in the management of tunas is understanding the distribution of the stocks of fish being exploited and the movement patterns of individuals within those stocks. Stock identification is a critical component in the realistic application of population dynamics models to bigeye, yellowfin, and skipjack tunas in the EPO. The term "stock," as used here, does not necessarily correspond to a genetically-distinct group, but refers to individuals that can be grouped by common phenotypic and life history characteristics within a geographic region; reproductive isolation is not a criterion.

Various stock identification methodologies have been employed for marine fishes (Ihssen *et al.*, 1981; Begg and Waldman, 1999). Most inferences about population structure of tunas in the Pacific Ocean have come from fisheries statistics and from data on tagging, spawning, morphometric and/or meristic characters, parasites as biological markers, immunogenetics, allozyme variation, mitochondrial DNA (mtDNA) or nuclear DNA (nDNA), and elemental composition of otoliths. Each methodology has advantages and disadvantages including how each character set relates differently to the delineation of stocks and their usefulness within stock assessments and fisheries management. Tagging data apparently have the most merit in providing estimates of home range distributions and delineation of stock structure, diffusion rates, and the extent of mixing between regions. However, as several investigators suggest a multi-method approach, which should include a genetic method together with tag-recapture or a phenotypic method (Begg and Waldman, 1999).

Tag release and recapture experiments, utilizing conventional plastic dart tags (PDTs), conducted for several species of tunas in various areas of the world's oceans, have provided valuable information on movements and population structure (Hunter *et al*., 1986; Bayliff, 1993). In recent years tuna-tagging experiments utilizing geolocating archival tags (ATs), have provided significant data toward understanding the spatial dynamics, habitat utilization, and stock structure for the species investigated (Arnold and Dewar, 2001; Gunn and Block, 2001; Block, 2005).

Other stock identification methodologies are, however, important, as they can provide complementary information toward understanding the extent and temporal stability of the stock structure of tunas. Several morphometric and meristic studies have provided results useful for identifying marine fish stocks, including tunas (Winans, 1987; Schaefer, 1992). Investigations of the geographic variation in life history characteristics, including growth and reproductive parameters, have also provided useful information regarding stock structure of tunas (Schaefer, 2001a). Genetic analyses, including mtDNA and nDNA, of tunas have mostly failed to demonstrate differences in the level of genetic heterogeneity for species within ocean basins (Ely *et al*., 2005). The genetic differentiation of stock structure of marine fish has been particularly difficult (Ward, 2000), and for highly-mobile tunas it is more problematic, as long-range movements of a few individuals per generation can result in genetic homogeneity among stocks (Ward, 1995).

The objective of this document was to compile and evaluate the scientific information available to elucidate stock structure of bigeye, yellowfin, and skipjack tunas within the EPO.

2. STOCK STRUCTURE

2.1. Bigeye tuna (*Thunnus obesus*)

2.1.1. Catch distribution

Bigeye were caught by purse-seine vessels during 1996-2006 from about 35°N to 25°S (but mostly between about 10°N and 20°S) and from the coast of the Americas west to about 150°W (Anonymous, 2008: Figure A-3). Those catches have been dominated by fish caught in association with floating objects, with small amounts caught in sets on unassociated schools. Bigeye were caught in the EPO by longline vessels during 2000-2004 from about 35°N to 35°S, but primarily in two fairly distinct areas, a southern area between about 10°N and 20°S and from coastal waters to 150°W and a northern area between about 15°N and 35°N and 130° and 150°W (Anonymous, 2008: Figure A-4).

2.1.2. Spawning

Spawning occurs widely across the equatorial Pacific during most months of the year, with the greatest reproductive potential in the EPO, based on apparent maturation, size-frequency, and catch-per-unit-of-effort data (Kikawa, 1966; Nishikawa *et al*. 1985; Miyabe, 1994). In a recent study of reproductive biology of bigeye in the eastern and central Pacific (Schaefer *et al*., 2005), spawning was observed between about 15°N and 15°S and between about 105°W and 175°W, and occurred during most months of the year in which the sea-surface temperatures exceeded about 24°C. However, the sampling coverage in that study was inadequate for a comprehensive description of the spatiotemporal distributions of spawning in the eastern and central Pacific.

2.1.3. Tagging

A total of 19,142 bigeye tuna was captured, tagged, and released with PDTs, and 323 with ATs, in the equatorial EPO during March to May of 2000 and 2002 through 2005, of which 8,246 (43.1%) and 163 (50.5%), respectively, were recaptured and their tags returned (Schaefer and Fuller, 2008). Times at liberty ranged from 1.7 to 1,810.7 d ($\bar{x}$ = 66.5, SE = 1.7). Linear displacements, from release to recapture positions, ranged from 0 to 3,830.1 nm ($\bar{x}$ =299.9, SE = 4.1). Of the 6,562 bigeye at liberty for more than 30 d, 95% were recaptured within 1,017 miles of their release positions. The 95% and 50% utilization distributions, based on 11,585 positions for the combined 98 bigeye AT data sets, from fish at liberty for greater than 30 d, were 1,326,325 km^2 and 60,667 km^2, respectively, and were centered between about 3°N and 5°S and 90°W and 105°W. The tagging data from this study, and a previous study (Schaefer and Fuller, 2002) indicate that bigeye exhibit regional fidelity to this area of very high biological productivity, and suggests a very low level of mixing between the eastern and western Pacific bigeye stocks.

Movements of bigeye inferred from deployments and recoveries of PDTs in the western Pacific (Hampton and Gunn, 1998; Hampton and Williams, 2005; Anonymous, 2008: Figure D-3) and Hawaii (Itano and Holland, 2000), and those from ATs in the western Pacific (Clear *et al*., 2005) also strongly suggest relatively restricted horizontal movements and regional fidelity to geographically-confined areas.

2.1.4. Morphometric and meristic characters

There have apparently been no investigations of geographic differences in morphometric or meristic characters of bigeye in the EPO.

2.1.5. Genetics

The genetic structure of bigeye has been investigated, using of muscle samples collected in selected locations across the Pacific in 1995(Grewe and Hampton, 1998). Genetic analyses of the samples involved the assessment of mitochondrial DNA and nuclear DNA microsatellite allele frequency variation. Initially an evaluation of samples from the two most distant locations, Ecuador and the Philippines, indicated that most alleles at each of eight loci were found in samples from both areas, and there were no significant differences between the samples from those locations. Four loci were then chosen for analyses of all samples collected from each sample location. The overall results of the genetic study did not provide evidence of genetic differentiation of bigeye in the Pacific.

2.1.6. Biological markers

There have apparently been no investigations of potential geographic differences in naturally-occurring biological markers of bigeye in the EPO.

2.1.7. Conclusions

The results of bigeye tagging studies in the eastern and western Pacific Ocean (Anonymous, 2008: Figure D3) demonstrate restricted movements, with very limited mixing of fish between areas separated by distances greater than about 1,000 miles. In the EPO, there appears to be a discontinuity at about 10°N in the catch distribution of longline catches. The bigeye tagging studies recently undertaken in the equatorial EPO demonstrate that movements are restricted primarily to the equatorial region, and no movement from the southern to the northern region of the longline catch distribution was observed. Bigeye within those two regions of the EPO, separated at about 10°N, potentially represent spatially-segregated northern and southern sub-stocks, with little mixing between them.

2.2. Yellowfin tuna (*Thunnus albacares*)

2.2.1. Catch distribution

Yellowfin were caught by purse-seine vessels during 1996-2006 from about 30°N to 20°S and from the coast of the Americas west to about 150°W (Anonymous, 2008: Figure A-1. Those catches have been dominated by fish caught in association with dolphins, followed by sets on unassociated fish, with much smaller amounts from fish caught in association with floating objects. Yellowfin were caught by longline vessels during 2000-2004 from about 30°N to 45°S but primarily in the southeastern Pacific between about 10°S and 30°S and from the coast of South America to about 150°W (Anonymous, 2008: Figure A-4).

2.2.2. Spawning

Yellowfin spawning occurs over vast areas of the Pacific Ocean and throughout the year in the warm northern equatorial waters, but in the more northern or southern regions it is restricted to periods when the sea-surface temperatures exceed 24°C (Schaefer, 2001a). In the EPO, where spawning occurs all year around between 0° and 20°N, the proportions of reproductively-active females are positively correlated with fluctuations in sea-surface temperatures (Schaefer, 1998). The expansion of suitable spawning habitat for yellowfin in the EPO with the northward and southward movements of the 24°C surface isotherms into the subtropical regions north of 20°N and south of 0° during the northern and southern hemisphere summer months, and the apparent movement of yellowfin into these regions and subsequent spawning, is possibly the mechanism which generates, in some years, two observed cohorts about 6 months apart in the yellowfin length-frequency data for the population (Schaefer, 1998).

Yellowfin mature at lesser sizes off Central America than in the northern areas off southern Baja California, the southern part of the Gulf of California, and the Revillagigedo Islands (Schaefer and Orange, 1956; Orange, 1961). Additional research to evaluate relationships between age, growth, and maturation in yellowfin and potential geographic variation in those relationships has been conducted (Schaefer, 1998). The growth rates for the fish from the southern area are apparently greater than those for fish from the northern area (where sea-surface temperatures are significantly cooler) until the fish are just under 3 years of age, at which time it decreases. Earlier onset of maturation was observed in the southern area.

2.2.3. Tagging

Tagging studies on yellowfin throughout the EPO, utilizing PDTs, have indicated that movements of tagged fish at liberty for more than 30 days tend to be restricted to less than 1,000 miles of their release positions (Schaefer *et al*., 1961; Fink and Bayliff, 1970; Bayliff and Rothschild, 1974; Bayliff, 1979, 1984; Anonymous, 2007). These studies indicate regional fidelity to areas of tagging, with little exchange of fish between the northern and southern regions of the EPO. Joseph *et al*., (1964) stated that yellowfin is not a far-ranging species, and that the majority of recovered fish had been caught within 200 miles of the area of release, based upon 55,737 yellowfin tagged during 1952 to 1962 and a total of 6,086 recoveries. Hunter *et al*., (1986: Figure 10) provided data on distances traveled by yellowfin released in the EPO that were at liberty for various time intervals, indicating that almost all fish free 31 to 180 days, and also those free for more than 180 days, had been caught within 750 miles of the area of release. Schaefer (1967) reported that movement patterns of yellowfin within the EPO from tag recoveries "indicate that it is not inhabited by a single rapidly intermixing population. It appears that there may be at least two sub-populations, with an approximate boundary near 15°N latitude." Fink and Bayliff (1970) also noted the presence of "two main groups" north and south of about 15°N, but stated that "there is considerable intermingling among the fish of the two groups."

In a recent study of yellowfin movements and behavior, utilizing ATs implanted in fish during 2002 and 2003 and released off Baja California, Mexico, the most probable movement paths for 20 of the fish at liberty for 154 or more days indicated that 19 (95%) remained within 900 miles of their release locations (Schaefer *et al*., 2007).

The results from yellowfin tagging studies in the EPO, using both PDTs and ATs, indicate restricted movements and regional fidelity to areas of tagging and release. Similar conclusions were reached from recent evaluations of extensive data for tagging with PDTs in the western and central Pacific Ocean (WCPO) (Sibert and Hampton, 2003).

2.2.4. Morphometric and meristic characters

Analyses of morphometric data from yellowfin collected from various locations in the EPO to assess geographic and temporal variation of morphometric characters indicated significant differences between fish sampled from north and south of 15°N-20°N (Schaefer, 1989). The results clearly demonstrated geographic variation in morphometric characters of yellowfin in the EPO, suggesting differences between the life histories of the northern and southern groups.

Further research (Schaefer 1991; 1992) has shown morphometric and meristic differences among fish from the eastern, central, and western Pacific, and also latitudinal differences for fish from both the eastern and western Pacific. Although there is annual variability in the morphometric characters, the results demonstrated that the stocks examined are morphometrically distinguishable and that their phenetic relationships reflect their geographic origin (Schaefer, 1992). Geographic variation observed in morphometric characters and gill raker counts of yellowfin from northern and southern regions of the EPO results from restricted movements, limited mixing, and environmental variation (Schaefer, 1992).

2.2.5. Genetics

There have been several genetic studies across the Pacific, none of which showed statistically-significant geographic variation. A study based on mitochondrial DNA, comparing samples across the Pacific from five spatially-isolated locations and one from the Atlantic, reported considerable variation, but no differences among samples (Scoles and Graves, 1993). Further genetic analyses of yellowfin samples from the Pacific, using mitochondrial DNA, provided limited evidence of genetic heterogeneity between eastern Pacific and the central and western Pacific samples (Ward *et al*., 1994).

Microsatellites are reportedly a powerful tool, with high resolution, for discrimination of genetic differences among fish populations (O'Conell and Wright, 1997). A recent genomic study utilizing microsatellite variation has provided some preliminary evidence of the presence of discrete northern and southern populations, separated by the equator, in the EPO (Diaz-Jaimes and Uribe-Alcocer, 2006). The authors caution, however, that the spatial differentiation observed may be due to temporal variation or non-random sampling, and their preliminary results need to be corroborated through further studies incorporating larger sample sizes and temporal replicates.

2.2.6. Biological markers

Studies of the stable nitrogen isotopes of yellowfin suggest limited movements in the EPO. The stable isotope values from the muscle tissue of a yellowfin reflects its food and nutrient sources during a previous period of time, the length of which is determined by the rates of tissue turnover. Furthermore, the isotope values are a function of not only what species of prey it ate, but also the locations at which it consumed the prey. The isotope values measured in the muscle of yellowfin exhibited a similar geographical trend, to those of copepods, a proxy for the base of the food web, in the EPO, increasing gradually over a meridional south to north range of almost 35 degrees (Popp *et al*., 2007). These observations show that spatial trends in stable nitrogen isotopes at the base of the food web are mirrored in the muscle of yellowfin, implying limited movements over the 6-8 months prior to capture.

2.2.7. Conclusions

The results from tagging experiments, along with investigations of geographic variation in length at maturity, morphometrics, and stable nitrogen isotopes of yellowfin in the EPO, demonstrate restricted movements, with fidelity to northern and southern regions of the EPO. Yellowfin within those two regions of the EPO, separated at about 15°N, probably represent spatially-segregated northern and southern sub-stocks with limited mixing between them. Furthermore, the results of tagging studies, utilizing PDTs and/or ATs, indicate very limited mixing between areas separated by distances greater than about 1,000 miles.

2.3. Skipjack tuna (***Katsuwonus pelamis***)

2.3.1. Catch distribution

Skipjack were caught by purse-seine vessels during 1996-2006 from about 35°N to 25°S and from the coast of the Americas west to about 150°W (Anonymous, 2008: Figure A-2). Those catches have been dominated by sets on unassociated fish and fish caught in association with floating objects, with much smaller amounts caught in association with dolphins. The catches of unassociated fish occurred mostly between about 5°N and 5°S and from the coast to about 95°W. The catches of fish associated with floating objects takes place primarily between 5°N and 15°S and from the coast to about 115°W. Small amounts of skipjack are caught with longline gear (Anonymous, 2008).

2.3.2. Spawning

Spawning of skipjack occurs throughout the year in tropical waters, and seasonally in subtropical waters, in the Pacific Ocean (Schaefer, 2001a). Early research on the reproductive biology of skipjack in the EPO indicated spawning off Central America, off Baja California, Mexico, and near the Revillagigedo Islands (Schaefer and Orange, 1956; Orange, 1961). It was concluded from these studies that in the EPO skipjack spawning occurs mainly offshore. It was later assumed, however, that skipjack did not reproduce in the EPO, but migrated to the central Pacific to spawn (Rothschild, 1965). This hypothesis has been recently tested, and the results indicate that significant spawning of skipjack, 50 cm or greater in length, occurs in areas of the EPO where sea-surface temperatures are equal to or greater than 24°C, but appears to be more concentrated offshore, west of 95°W longitude (Schaefer, 2001b). The extensive compilation of data on larval scombrids by Nishikawa *et al.* (1985) also indicates that there is widespread spawning of skipjack east of 150°W between 10°S and 10°N, mostly west of 110°W.

Skipjack were found to mature at lesser sizes off Central America than in the northern areas off southern Baja California, Mexico (Schaefer and Orange, 1956; Orange, 1961), indicating geographic variation, most likely from limited mixing and environmental variation.

2.3.3. Tagging

There is a large volume of information on skipjack movements in the WCPO (Kearney, 1983). Although there were numerous long-distance movements of individual tagged skipjack observed, the overall percentage of recoveries having displacements of greater than 200 miles was only 17%, and there are few probable migration routes revealed from the recovery of tagged skipjack tuna (Wild and Hampton, 1994). Furthermore, when considering skipjack tuna on a Pacific-wide basis, particularly the areas of tagging operations in the WCPO, it was concluded that skipjack did not appear to migrate toward specific areas for feeding or spawning but appeared to move in more or less random directions within broad limits (Hunter *et al.,* 1986). There have been no recoveries in the EPO from skipjack tagged in the WCPO. The assumed eastward migration routes of juveniles described in the skipjack migration model (Rothschild, 1965) lack validation, and hypothesis about the energetic advantages of migration to the EPO using the North Equatorial Countercurrent and the Equatorial Undercurrent (Williams, 1972) are unsubstantiated.

Numerous tagging studies have also been conducted in the EPO to investigate movements of skipjack tuna (Schaefer *et al*., 1961; Fink and Bayliff, 1970; Bayliff, 1984). It appears from these studies that skipjack show some consistency of directed movement in the near-shore regions off Central America and northern South America. In the northern region around the Revillagigedo Islands and the west coast of Baja California, there is a northern and then a southern movement of the fish between 20°N and 30°N in response to the seasonal movements of the 20°C surface isotherm between about May and December. Hunter *et al*., (1986: Figure 10) provided data on distances traveled by skipjack liberated in the EPO that were at liberty for various time intervals, indicating that almost all fish free 31 to 180 days had been caught within 250 miles of the points of release. A considerable portion of those at liberty for more then 180 days, however, had moved more than 250 miles from the points of release. Although limited, there was some movement of fish reported between the northern and southern areas of the fishery in the EPO. However, from well over 100,000 skipjack tagged in the EPO and several thousand returns, only 27 skipjack have been recovered in the central or western Pacific, and 21 of those were recaptured around the Hawaiian Islands (Bayliff, 1988: Appendix 2). Of those fish recovered, 19 were tagged off Baja California, 4 off the Revillagigedo Islands, 2 off Clipperton Island, and 1 well offshore at about 4°N and 119°W. Only 1 skipjack tagged in the near-shore waters off Central America, within the area of the primary fishery, has been recovered in the central Pacific around Hawaii. Before the recovery of this tagged skipjack there was no evidence from tagging that fish of the southern group move to the central Pacific.

Recent tagging of skipjack with PDTs in the equatorial EPO, concurrently with bigeye and yellowfin tagging described above, provides useful comparative information on linear displacements of the tagged fish, determined from release and recapture positions. The overall distributions of the recaptures for the skipjack, bigeye, and yellowfin tunas tagged in similar locations illustrate similar latitudinal and longitudinal ranges of dispersion (Anonymous, 2007). After 30 days at liberty, 95 percent of the recaptured skipjack were within 1,350 miles of their release positions, and 93% were recaptured within 1,000 miles of those positions.

Too much emphasis has been placed on long-range movements of a few tagged skipjack. The tagging data for skipjack supports only offshore-onshore movements and north-south movements in the EPO. Similar conclusions were reached from recent evaluations of extensive skipjack data for tagging with PDTs in the western and central Pacific (Sibert and Hampton, 2003).

2.3.4. Morphometric and meristic characters

A morphometric study has shown significant differences between skipjack from the EPO and the central Pacific (Hawaii and French Polynesia) (Hennemuth, 1959). These differences could indicate a low level of mixing of skipjack between the central Pacific and the EPO.

2.3.5. Genetics

Genetic studies on skipjack samples across the Pacific, using isozymes have demonstrated an east-west cline in a serum esterase allele (Fujino, 1976; Richardson, 1983; Fujino, 1996). Differences were also demonstrated in esterase allele frequencies in samples from the Atlantic, Indian, and Pacific Oceans by Fujino (1981). However, mtDNA analyses of small numbers of skipjack samples from the Pacific and Atlantic appeared nearly identical (Graves *et al*., 1984). Also, no genetic differentiation was observed between reasonable sample sizes of Atlantic and Pacific skipjack or between skipjack samples from the eastern and western Pacific Ocean using DNA isolation, mtDNA D-loop region amplification, and nucleotide sequence analyses methodologies (Ely *et al*., 2005).

2.3.6. Biological markers

The chemical composition of skipjack otoliths collected from the EPO and Hawaii were analyzed using electron-beam microprobe technology (Ianelli, 1993). Chemical analyses of the early growth zones on those otoliths were found to be similar.

2.3.7. Conclusions

The results from tagging experiments, along with investigations of geographic variation in length at maturity of skipjack in the EPO, demonstrate restricted movements, with fidelity to northern and southern regions of the EPO. The results of tagging studies indicate low levels of mixing between areas separated by distances greater than about 1,000 miles. Skipjack within regions of the EPO, separated at about 15°N, probably represent spatially-segregated northern and southern sub-stocks with limited mixing between them.

LITERATURE CITED

Anonymous. 2008. Tunas and billfishes in the eastern Pacific Ocean in 2006. Fishery Status Report 5. Inter-Amer. Trop. Tuna Comm.: 155 p.

Anonymous. 2007. Inter-American Tropical Tuna Commission Quarterly Report for October-December 2006 (http://www.iattc.org/PDFFiles2/IATTCq064ENG.pdf).

Arnold, G., and H. Dewar. 2001. Electronic tags in marine fisheries research: a 30-year perspective. In: Sibert, J.R., Nielsen, J.L. (eds) Electronic tagging and tracking in marine fisheries. Kluwer, Dordrecht. The Netherlands, pp 7-64.

Bayliff, W.H. 1979. Migrations of yellowfin tuna in the eastern Pacific Ocean as determined from tagging experiments initiated during 1968-1974. Inter-Amer. Trop. Tuna Comm., Bull. 17: 447-506.

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. Inter-Amer. Trop. Tuna Comm., Intern. Rep. 18: 107 p.

Bayliff, W.H. 1988. Growth of skipjack, *Katsuwonus pelamis*, and yellowfin, *Thunnus albacares*, tunas in the eastern Pacific Ocean, as estimated from tagging data. Inter-Amer. Trop. Tuna Comm., Bull. 19: 307-385.

Bayliff, W.H. 1993. An indexed bibliography of papers on tagging of tunas and billfishes. Inter-Amer. Trop. Tuna Comm., Spec. Rept. 8: 91 pp.

Bayliff, W.H., and B.J. Rothschild. 1974. Migrations of yellowfin tuna tagged off the southern coast of Mexico in 1960 and 1969. Inter-Amer. Trop. Tuna Comm., Bull. 16: 1-64.

Begg, G.A., and J.R. Waldman. 1999. An holistic approach to fish stock identification. Fish. Res. 43: 35-44.

Block, B.A. 2005. Physiological ecology in the 21st century: Advancements in biologging science. Integr. Comp. Biol. 45:305-320.

Clear, N.P., K. Evans, J.S. Gunn, S. Bestley, K. Hartmann, and T. Patterson. 2005. Movement of bigeye tuna (*Thunnus obesus*) determined from archival tag light-levels and sea surface temperatures. In: Migration and habitat preferences of bigeye tuna, *Thunnus obesus*, on the east coast of Australia. CSIRO Report FRPC 1999/109: 19-46.

Collette, B.B. and C.E. Nauen. 1983. 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.

Diaz-Jaimes, P. and M. Uribe-Alcocer. 2006. Spatial differentiation in the eastern Pacific yellowfin tuna revealed by microsatellite variation. Fish. Sci. 72: 590-596.

Ely, B., J. Vinas, J.R. Alvarado Bremer, D. Black, L. Lucas, K. Covello, A.V. Labrie, and E. Thelen. 2005. Consequences of the historical demography on the global population structure of two highly migratory cosmopolitan marine fishes: the yellowfin tuna (*Thunnus albacares*) and the skipjack tuna (*Katsuwonus pelamis*). Evol. Bio. 5: 19.

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-Amer. Trop. Tuna Comm., Bull. 15: 1-227.

Fujino, K. 1976. Subpopulation identification of skipjack tuna specimens from the southwestern Pacific Ocean. Bull. Jap. Soc. Sci. Fish. 42: 1229-1235.

Fujino, K. 1981. Genetic diversity of skipjack tuna in the Atlantic, Indian, and Pacific Oceans. Bull. Jap. Soc. Sci. Fish. 47: 215-222.

Fujino, K. 1996. Genetically distinct skipjack tuna subpopulations appeared in the central and western Pacific Ocean. Fish. Sci. 62: 189-195.

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.

Grewe, P.M. and J. Hampton. 1998. An assessment of bigeye (*Thunnus obesus*) population structure in the Pacific Ocean, based on mitochondrial DNA and DNA microsatellite analysis. University of Hawaii, Joint Institute for Marine and Atmospheric Research Contribution 98-320, 29 p.

Gunn, J. and B. Block. 2001. Advances in acoustic, archival, and satellite tagging of tunas. In: Tuna physiology, ecology, and evolution. B.A. Block and E.D. Stevens (eds) San Diego (California): Academic Press, pp. 167-224.

Hampton, J. and J. Gunn. 1998. Exploitation and movements of yellowfin tuna (*Thunnus albacares*) and bigeye tuna (*T. obesus*) tagged in the north-western Coral Sea. Mar. Freshwater Res., 49: 475-489.

Hampton, J. and P. Williams. 2005. A description of tag-recapture data for bigeye tuna (*Thunnus obesus*) in the western and central Pacific Ocean. Inter. Comm. Conser. Atlan. Tunas, Coll. Vol. Sci. Pap., 57: 85-93.

Hennemuth, R.C. 1959. Morphometric comparison of skipjack from the central and eastern tropical Pacific Ocean. Inter-Amer. Trop. Tuna Comm., Bull. 3: 239-304.

Hunter, J.R., A.W. Argue, W.H. Bayliff, A.E. Dizon, A. Fonteneau, D. Goodman, and G.R. Seckel. 1986. The dynamics of tuna movements: an evaluation of past and future research. FAO Fish. Tech. Pap., 277: 78 p.

Hutchings, J.A. 2000. Collapse and recovery of marine fishes. Nature 406: 882-885.

Ianelli, J.N. 1993. Studies on the population structure of skipjack tuna Katsuwonus pelamis in the central and eastern Pacific Ocean. Ph.D. Thesis. University of Washington, Seattle. 215 p.

Ihssen, P.E., H.E. Booke, J.M. Casselman, J.M. McGlade, N.R. Payne, and F.M. Utter. 1981. Stock identification: materials and methods. Can. J. Fish. Aquat. Sci. 38: 1838-1855.

Itano, D.G. and K.N. Holland. 2000. Movement and vulnerability of bigeye (*Thunnus obesus*) and yellowfin tuna (*Thunnus albacares*) in relation to FADs and natural aggregation points. Aquat. Living Res. 13: 213-223.

Joseph, J., F.G. Alverson, B.D. Fink, and E.B. Davidoff. 1964. A review of the population structure of yellowfin tuna, *Thunnus albacares*, in the eastern Pacific Ocean. Inter-Amer. Trop. Tuna Comm., Bull. 9: 53-112.

Kearney, R.E. 1983. Assessment of the skipjack and baitfish resources in the central and western tropical Pacific Ocean: a summary of the Skipjack Survey and Assessment Programme. South Pacific Commission: 37 pp.

Kikawa, S. 1966. The distribution of maturing bigeye and yellowfin and an evaluation of their spawning potential in different areas in the tuna longline grounds in the Pacific. Nankai Reg. Fish. Res. Lab., Rep. 23: 131-208.

Miyabe, N. 1994. A review of the biology and fisheries for bigeye tuna, *Thunnus obesus*,

in the Pacific Ocean. FAO Fish. Tech. Pap. 336: 207-243.

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.

O'Conell, M. and J.M. Wright. 1997. Microsatellite DNA in fishes. Rev. Fish Biol. Fish,7: 331-363.

Orange, C.J. 1961. Spawning of yellowfin and skipjack in the eastern tropical Pacific, as inferred from studies of gonad development. Inter-Amer. Trop. Tuna Comm., Bull. 5: 459-526.

Pauly, D., J. Alder, E. Bennet, V. Christensen, P. Tyedmers, and R. Watson. 2003. The future of fisheries. Science 302: 1359-1361.

Popp, B.N., B.S. Graham, R.J. Olson, C.C.S. Hannides, M.J. Lott, G.A. Lopez-Ibarra, F. Galvan-Magana, and B. Fry. 2007. Insight into the trophic ecology of yellowfin tuna, Thunnus albacares, from compound-specific nitrogen isotope analysis of proteinaceous amino acids. *In* Dawson, T.E., and R.T.W. Siegwolf (eds.), Stable Isotopes as Indicators of Ecological Change. Elsevier-Academic Press, Terrestrial Ecology Series, San Diego: 173-190.

Richardson, B.J. 1983. Distribution of protein variation in skipjack tuna (*Katsuwonus pelamis*) from the central and south-western Pacific. Aus. Jour. Mar. Fresh. Fish. 34: 231-251.

Rothschild, B.J. 1965. Hypothesis on the origin of exploited skipjack tuna (*Katsuwonus pelamis*) in the eastern and central Pacific Ocean. U.S. Fish. Wildl. Serv., Spec. Sci. Rep. Fish. 512: 20 p.

Schaefer, K.M. 1989. Morphometric analysis of yellowfin tuna, *Thunnus albacares*, from the eastern Pacific Ocean. Inter-Amer. Trop. Tuna Comm., Bull. 19: 387-427.

Schaefer, K.M. 1991. Geographic variation in morphometric characters and gill-raker counts of yellowfin tuna, *Thunnus albacares*, from the Pacific Ocean. U.S. Nat. Mar. Fish. Serv., Fish. Bull. 89: 289-297.

Schaefer, K.M. 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-Amer. Trop. Tuna Comm., Bull. 20: 135-163.

Schaefer, K.M. 1998. Reproductive biology of yellowfin tuna (*Thunnus albacares*) in the eastern Pacific

Ocean. Inter-Amer. Trop. Tuna Comm., Bull. 21: 205-272.

Schaefer, K.M. 2001a. Reproductive biology of tunas. *In* Block, B.A. and E.D. Stevens (eds.). Tuna: Physiology, Ecology and Evolution. Fish Physiology, Academic Press, San Diego, Vol. 19: 225-270.

Schaefer, K.M. 2001b. Assessment of skipjack tuna (*Katsuwonus pelamis*) spawning activity in the eastern Pacific Ocean. U.S. Nat. Mar. Fish. Serv., Fish. Bull., 99: 343-350.

Schaefer, K.M. and D.W. Fuller. 2002. Movements, behavior, and habitat selection of bigeye tuna (*Thunnus obesus*) in the eastern equatorial Pacific, ascertained through archival tags. U.S. Nat. Mar. Fish. Ser., Fish. Bull. 100: 765-788.

Schaefer, K.M., D.W. Fuller, and N. Miyabe. 2005. Reproductive biology of bigeye tuna (*Thunnus obesus*) in the eastern and central Pacific Ocean. Inter-Amer. Trop. Tuna Comm., Bull. 23: 1-31.

Schaefer, K.M., D.W. Fuller, and B.A. Block. 2007. Movements, behavior, and habitat utilization of yellowfin tuna (*Thunnus albacares*) in the northeastern Pacific Ocean, ascertained through archival tag data. Mar. Biol. 152: 503-525.

Schaefer, K.M. and D.W. Fuller. 2008. Horizontal movements of bigeye tuna (*Thunnus obesus*) in the eastern Pacific Ocean, as determined from conventional and archival tagging experiments initiated during 2000-2005. Inter-Amer. Trop. Tuna Comm., Bull.: in review.

Schaefer, M.B. 1967. Some new trends in investigation of tunas in the Pacific Ocean. Proc. Symp. Scombroid fishes, Part 3. Mar. Biol. Assoc. India, Symp. Ser. 1: 1160-1172.

Schaefer, M.B. and C.J. Orange. 1956. Studies on the sexual development and spawning of yellowfin (*Neothunnus macropterus*) and skipjack (*Katsuwonus pelamis*) in three areas of the eastern Pacific Ocean, by examination of gonads. Inter-Amer. Trop. Tuna Comm., Bull. 1: 281-349.

Schaefer, M.B., B.M. Chatwin, and G.C. Broadhead. 1961. Tagging and recovery of tropical tunas, 1955-1959. Inter-Amer. Trop. Tuna Comm., Bull. 5: 341-455.

Scoles, D.R. and J.E. Graves. 1993. Genetic analysis of the population structure of yellowfin tuna, *Thunnus albacares*, from the Pacific Ocean. U.S. Nat. Mar. Fish. Ser., Fish. Bull. 91: 690-698.

Sibert, J. and J. Hampton. 2003. Mobility of tropical tunas and the implications for fisheries management. Mar. Pol. 27: 87-95.

Ward, R.D., N.G. Elliott, P.M. Grewe, and A. Smolenski. 1994. Allozyme and mitochondrial DNA variation in yellowfin tuna (*Thunnus albacares*) from the Pacific Ocean. Mar. Biol. 118: 531-539.

Ward, R.D. 1995. Population genetics of tunas. Jour. Fish. Biol. 47: 259-280.

Ward, R.D. 2000. Genetics in fisheries management. Hydrobiol. 420: 191-201.

Wild, A. and J. Hampton. 1994. A review of the biology and fisheries for skipjack tuna, *Katsuwonus pelamis*, in the Pacific Ocean. FAO Fish. Tech. Pap. 336: 1-51.`

Williams, F. 1972. Consideration of three proposed models of the migration of young skipjack tuna (*Katsuwonus pelamis*) into the eastern Pacific Ocean. U.S. Nat. Mar. Fish. Serv., Fish. Bull. 70: 741-762.

Winans, G.A. 1987. Using morphometrics and meristic characters for identifying stocks of fish. *In* H.E. Kumpf, R.N. Vaught, C.B. Grimes, A.G. Johnson, and E.L. Nakamura (editors), Proceedings of the Stock Identification Workshop. Panama City Beach, Florida, 5-7 November 1985: 25-62.