1. INTRODUCTORY REMARKS

The rapid expansion of tuna fisheries into previously under-exploited oceanic regions, the extension of national jurisdiction of fisheries by most coastal states and the increase in effort in historic fisheries have placed new demands on the management of tuna resources. The subject of how research can respond most effectively to these changes was recently discussed by an international group of research scientists and administrators (Joseph and Wild 1984). A recommendation of that group was that the movements of tunas and their resulting distributions was one of the key biological problems in the management of tuna fisheries and that this problem was so large that the resources of a single organization were insufficient to make rapid progress in solving it.

In order to conceptualize the problem and to define specific research projects and experimental designs for the study of tuna movement dynamics, three technical workshops were held in 1985. The subjects of discussion were as follows: first workshop, the results and uncertainties in conventional mark and recapture studies of tunas; second, the relation between oceanography and tuna movements; and third, new technologies that might be used to measure tuna movements. In these three workshops experts in various fields participated along with a panel. Different experts participated in each of the three meetings (see List of Experts in Annex), but some panel members were present at all meetings and they wrote the final report.

These meetings were supported jointly by the Inter-American Tropical Tuna Commission (IATTC) and the Southwest Fisheries Center (SWFC) of the U.S. National Marine Fisheries Service. The Office de la Recherche Scientific et Technique Outre-Mer (ORSTOM), France, and the South Pacific Commission (SPC), New Caledonia, also contributed to their organization. We wish to acknowledge all the experts who contributed their time and knowledge and many staff members of the IATTC and SWFC who helped with the conduct of the meeting.

The report does not pretend to make research policy for the tuna research community at large, but it draws attention to the opportunities to expand our knowledge of tuna movements and will facilitate discussion of research approaches.

2. STATEMENT OF THE PROBLEM

2.1 Introduction

Most tuna species in the world's oceans are extremely wide ranging. For many it is known, and for others it is presumed that, within a stock[1], individuals migrate rapidly and broadly, so that in the course of one year they can appear in tropical and temperate waters of the high seas and of several management jurisdictions. Few of these movements are sufficiently documented for the purposes of stock assessment and management, yet under the terms of the recent session of the conference on law of the sea most countries are obligated to develop rational management plans that take into account tuna movements.

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[1] In this document we use the term stock in a purely operational or fishery context. We make no judgement on the degree of genetic interchange, differentiation and isolation which are difficult to measure and have interpretations which are dependent on the resolving power of the measurement technique. Usually fishery stocks are assumed to have similar life history characteristics (growth, spawning location and timing, and mortality) although this need not always be the case, nor is it always known to be the case.

Some of the uncertainties respecting tuna movement and distribution are: 1) timing, extent, directionality and seasonality of movements and, in the case of some species, whether stocks undergo directed or seasonal movements at all, 2) rates of exchange of exploitable adults among management jurisdictions and among vertical and horizontal habitats fished by different gears in the same management jurisdiction, 3) distribution of exploitable adults from individual stocks, 4) duration of residence in an area and probability of return to an area, and 5) underlying relationships between environmental factors and tuna movements and distribution.

As a result of these uncertainties it is difficult to choose catch and effort data that are representative of a stock for purposes of stock assessment and to measure the impact of one fishery's catch on the catch of another fishery. These constraints hinder development of rational fisheries policies to maximize economic returns from the overall resource (and portions of it) that occur within individual management jurisdictions.

In the following seven examples we illustrate how present knowledge of tuna movements has been incorporated into tuna management schemes, and how increased knowledge could lead to improved stock assessment and improved management.

2.2 Eastern Atlantic Yellowfin, *Thunnus albacares*

The status of this stock has been reviewed annually since 1971 by scientists in the Standing Committee for Research and Statistics (SCRS) of the International Commission for the Conservation of Atlantic Tunas (ICCAT).

When the eastern Atlantic surface fishery for yellowfin was operating in the inshore area (Figure 1, upper), the SCRS (ICCAT 1975) concluded that the maximum sustainable yield (MSY) was equal to approximately 50,000 metric tons and that the corresponding optimum effort (60,000 days) was reached by the 1973 fishery (Figure 2). After 1974, the fishery expanded offshore (Figure 1, lower) and effort increased. As a result the MSY estimated by the SCRS changed (Figure 2, upper) to 110,000 metric tons which could be taken with an effort of 240,000 fishing days. Optimum effort was estimated to be four times the earlier estimate.

This apparent contradiction arose because of a lack of knowledge of stock structure and movements. Eastern Atlantic yellowfin probably consist of a single stock, at least for the purpose of management. However, different sizes of yellowfin differ in their geographical distribution and seasonal movement patterns (young fish inshore, older fish offshore; Fonteneau 1982) and mixing is not uniform between adjacent areas (Fonteneau 1982). These factors biased the conclusions of the initial stock assessment, because at that time the fishery did not cover the entire geographic range of the stock, nor did it exploit all vulnerable size classes.

A similar problem also exists in the vertical dimension for the large yellowfin of the eastern Atlantic. On the basis of production model analysis for large yellowfin caught by longline, the SCRS (ICCAT 1973) concluded in the late 1960's that the eastern Atlantic stock of large yellowfin was producing at the MSY (Figure 2, lower). Then a purse seine fishery developed for large yellowfin in the same waters fished by long line. Between 1965 and 1985 the combined catch of large yellowfin by purse seine and longline greatly increased, and the sustained catch of large yellowfin by surface fisheries was 3.4 times the old estimate of MSY! Interestingly, the size of the fish exploited by the two gears was identical and yield-per-recruit analysis showed that the increased catch could not have been a consequence of increased yield per recruit (Fonteneau 1982). The current explanation for these findings is that the surface component of the large yellowfin stock usually does not mix with the deeper

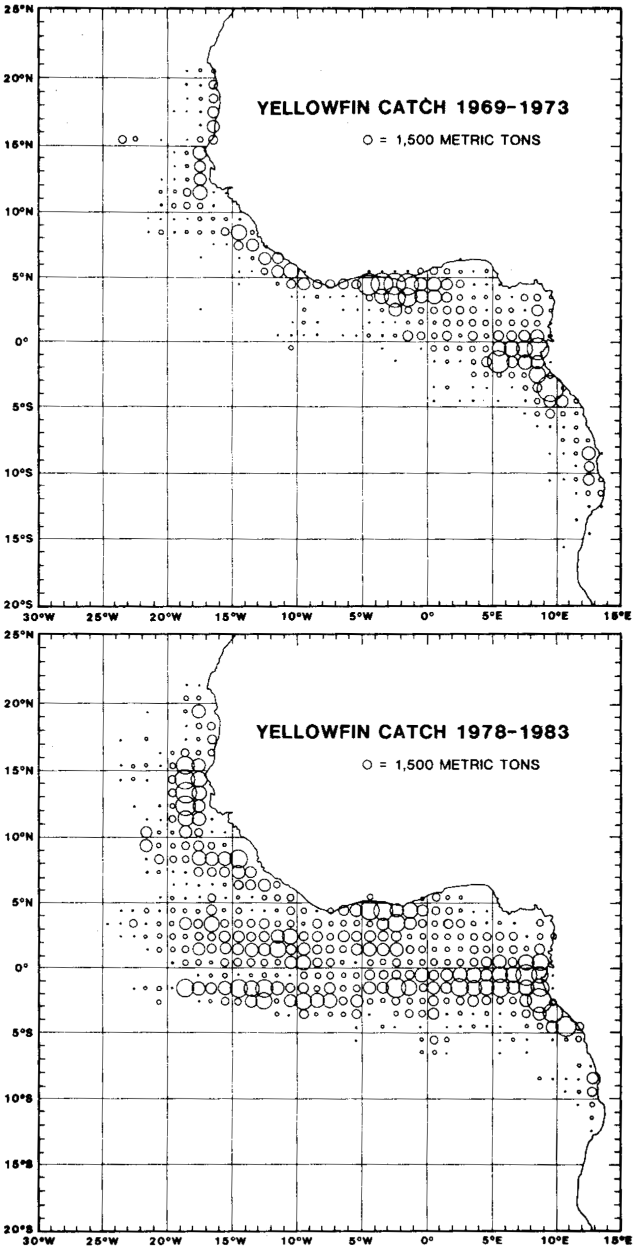


Figure 1. Upper; fishing area in the eastern tropical Atlantic during the early fishery (1962 to 1974), shown by the average yellowfin catches of surface fleets from 1969 to 1973. Lower; fishing area in the eastern tropical Atlantic during the recent fishery shown by the average yellowfin catches of surface fleets from 1978 to 1983. The area of a circle is proportional to the catch. Data are from ICCAT statistical data base.

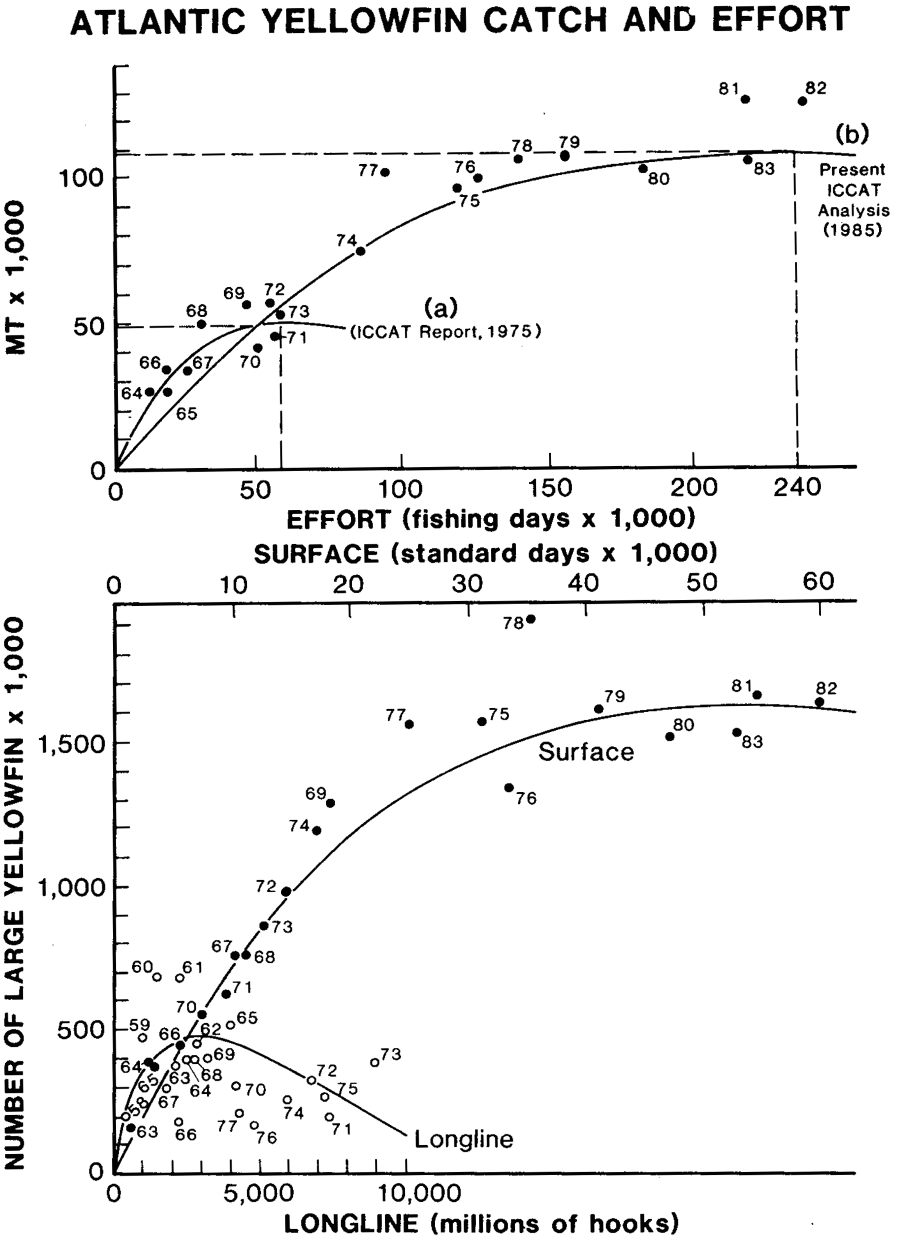


Figure 2. Upper; production model analysis and estimated maximum sustainable yield (MSY) for eastern Atlantic yellowfin tuna, calculated from the 1963-1973 data (ICCAT 1975) and from the 1963-1983 data (present ICCAT analysis). Lower; MSY for large Atlantic yellowfin (in number of fishes calculated for longline fishery (1958 to 1977) and for surface fisheries (1964 to 1983). Data are from ICCAT statistical data base.

component taken by longline vessels in the same area. Clearly, more information is needed on the movement dynamics of Atlantic yellowfin in vertical and horizontal planes before these problems can be solved.

2.3 Northern Atlantic Bluefin, *Thunnus thynnus*

The northern Atlantic bluefin have two spawning grounds, one in the Mediterranean Sea and one in the Gulf of Mexico. The western and eastern Atlantic spawning groups are believed to be separate stocks, although some juveniles and adults of both groups are known to have made trans-Atlantic migrations (ICCAT 1985). The stock in the western Atlantic is thought to be seriously depleted, while the stock in the eastern Atlantic is also thought to be depressed, but to a much lesser extent (ICCAT 1985). If interchange across the ocean is limited and fish always use the spawning ground of their origin, the catches in the western Atlantic should be greatly reduced to permit the western stock to increase. On the other hand, if considerable interchange of reproducing fish exists, then modest curtailment of the fisheries on both groups would be in order.

Current regulations are based on the assumption that eastern and western Atlantic bluefin constitute separate stocks, and as a consequence quotas apply only to the more seriously depleted western Atlantic fishery. It is not clear that regulations or models that assume no mixing are appropriate since juveniles and adults make trans-Atlantic migrations. Considerably more data from tagging (to measure exchange rates) and estimates of residence times of individual fish using chemical analyses of vertebrae (see section, Reconstruction of Movement Histories from Microconstituents of Mineralized Tissue) may help resolve this issue.

2.4 Southern Bluefin, *Thunnus maccoyii*

Southern bluefin appear to have a circumpolar distribution south of 30° S (Figure 3) but the rates of exchange of bluefin among the different fisheries and fishing areas remain unknown. Tagging and catch data indicate that southern bluefin move south and east from the only known spawning area in the eastern Indian Ocean off the northwest coast of Australia, and appear at progressively older ages (2 through 6 years) in the Western Australia, South Australia, Tasmania and New South Wales fisheries (Murphy and Majkowski 1981) (Figure 4, upper). Bluefin tagged off South Australia have also been recovered well to the west in the Japanese longline fishery off the south coast of Africa (Figure 4, lower). However, the numbers of juvenile bluefin (ages 2-6) that move from Australia in a westerly or easterly direction through the southern ocean, in the area of the west wind drift, are not indicated by the pattern of tag recoveries and longline catch information (Olson 1980). Also unknown are the patterns and frequency of return migrations by bluefin over their 15-20 year life span to the single Indian Ocean spawning area.

The total world catch of southern bluefin has declined from 81,000 metric tons in 1965 to about 35,000 mt in 1984 (Figure 5). Cohort analysis indicates that the world standing stock underwent a dramatic decline from 1960 to the early 1970's and that recruitment had been impaired by low parental stock levels of recent years (Murphy and Majkowski 1981).

The widely distributed Japanese longline fishery (Figure 4, upper, inset) and the Australian surface fisheries for younger fish (Figure 4, upper) take 95% percent of the world harvest of southern bluefin. Australia implemented a management plan for the 1983/1984 fishery to stabilize the level of the southern bluefin stock at the estimated 1980 level of abundance. The plan included an overall catch quota for Australian

SOUTHERN BLUEFIN DISTRIBUTION

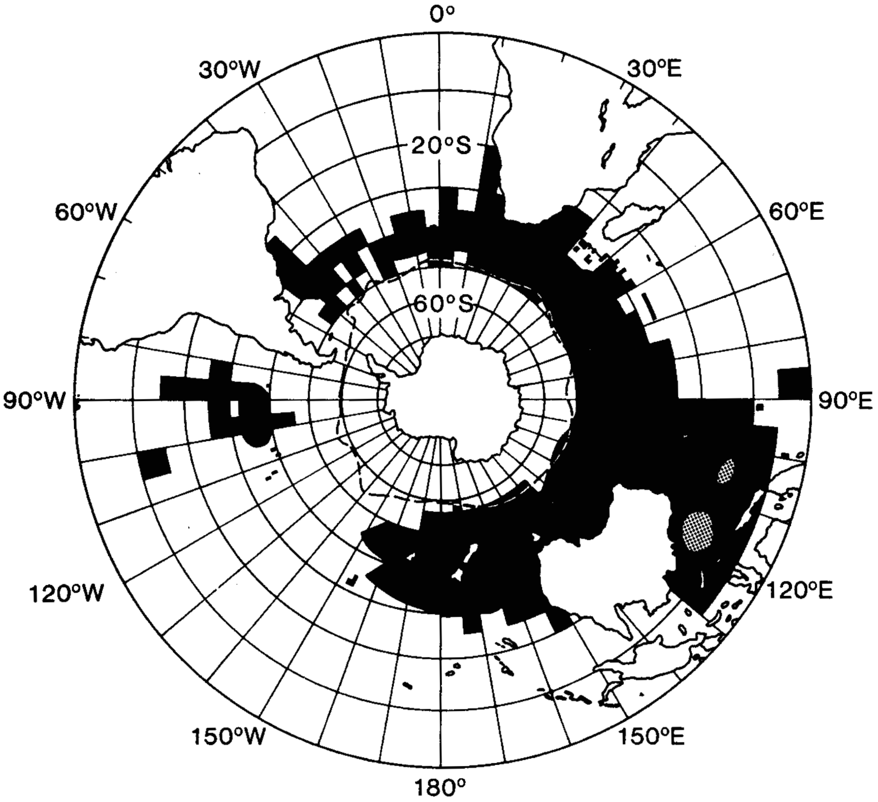


Figure 3. Distribution of southern bluefin tuna (after Harden Jones 1984, with additional data from Shingu 1967 and Hynd 1969 (in 1° areas); Fisheries Agency of Japan 1974, 1975, 1976, 1977, 1978, 1979 (in 5° areas); and Suda 1971, Robins 1963, and Nakamura 1969). The dashed line marks the Antarctic Convergence. The stippling marks the known breeding areas.

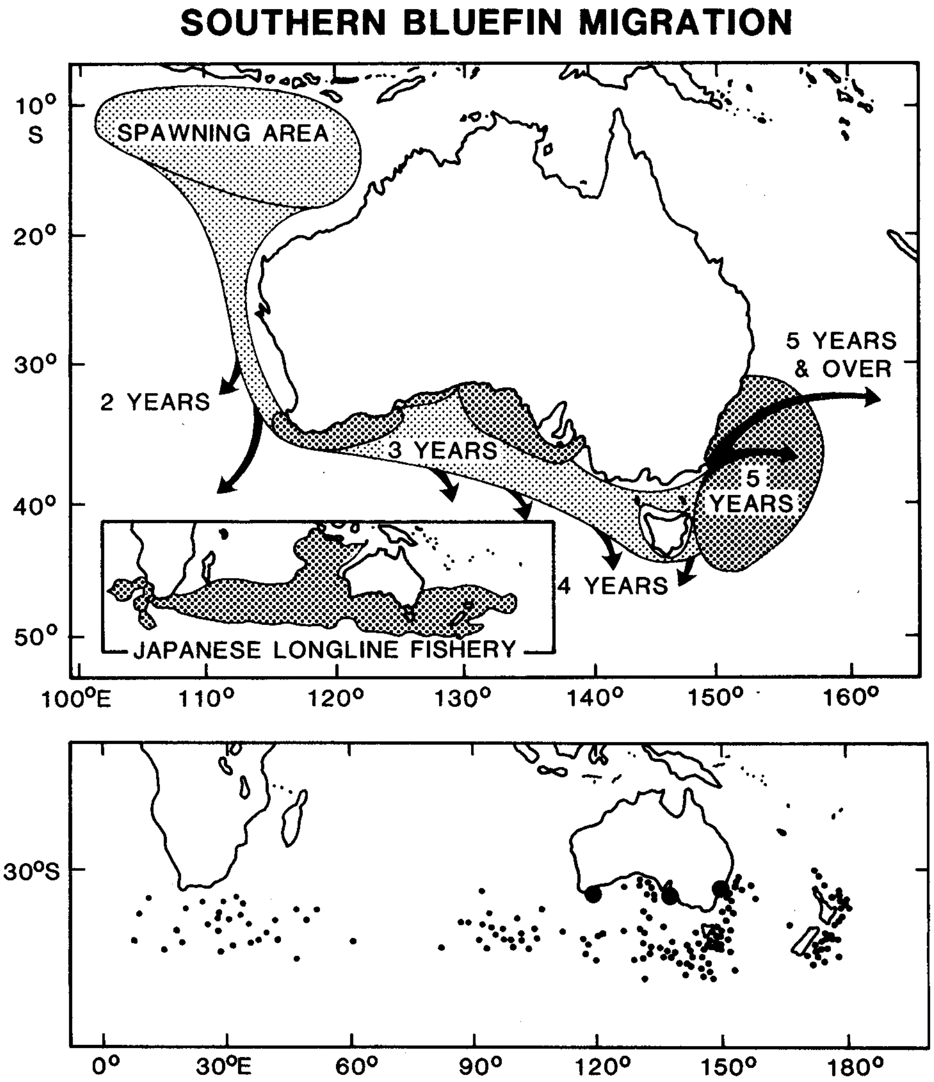


Figure 4. Upper; southern bluefin tuna spawning area and migration pattern off Australia (shown in light stippling). Dark stippling shows the operation areas of the Australian fishery and the Japanese longline fishery (inset). Arrows indicate the direction of fish migration from the Australian fishery. Lower; locations where fish tagged off Western Australia, South Australia, and New South Wales were recaptured after more than one year of liberty (after Murphy and Majkowski 1981).

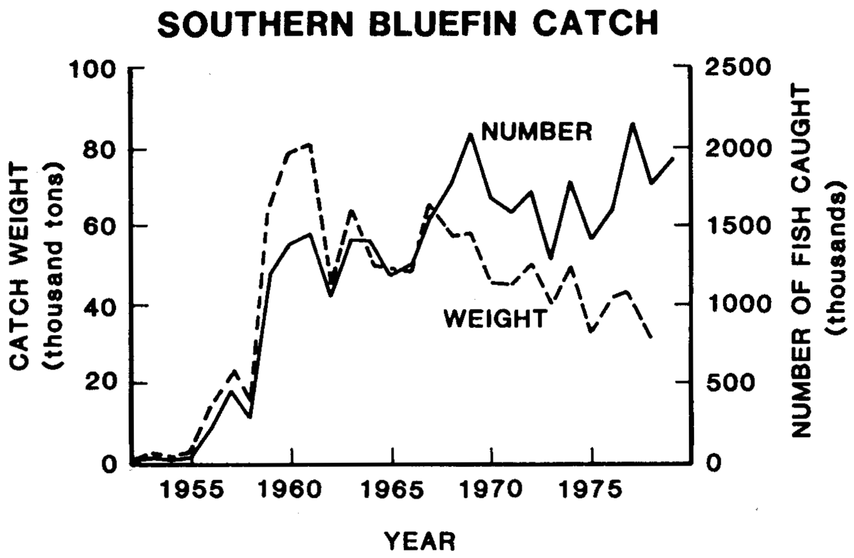


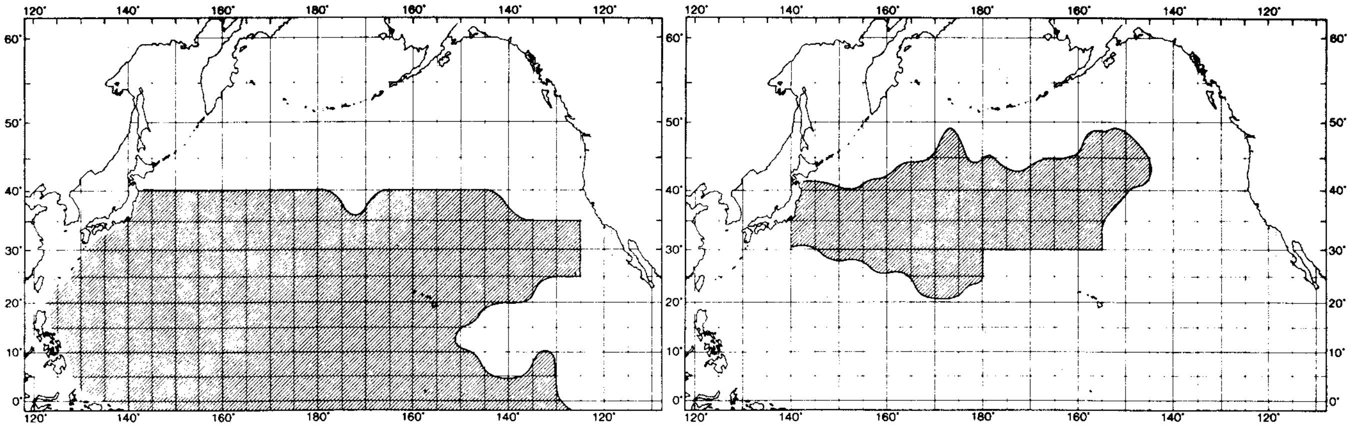
Figure 5. The history of the total catch of southern bluefin tuna (after Murphy and Majkowski 1981).

fisheries of 19,000 metric tons, with specific allocations to fisheries in Western Australia and South Australia (Franklin and Burns 1983). The high-seas longline fishery of Japan has not been placed under catch limits.

Clearly a major uncertainty in assigning catch limits to specific fisheries of southern bluefin is the extent that the catch in any one fishery reduces catches by other fisheries along the bluefin migration route. In addition, migration patterns and frequency of return migrations by bluefin to their Indian Ocean spawning area need to be better defined.

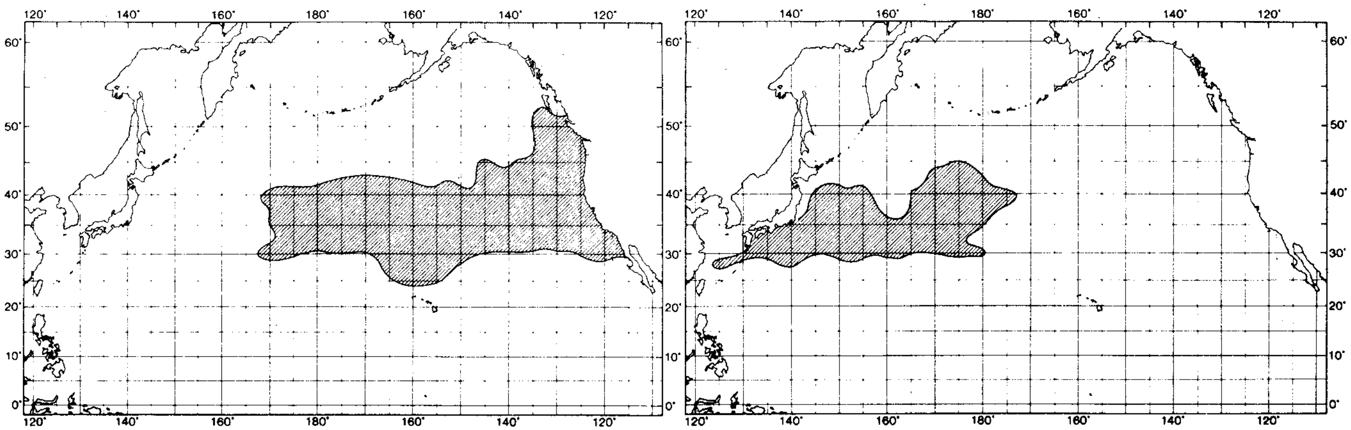
2.5 North Pacific Albacore, *Thunnus alalunga*

A growing body of evidence (Brock 1943; Laurs and Lynn 1977; Laurs and Weatherall 1981) indicates that albacore in the North Pacific are not as homogeneous as previously assumed (Clemens 1961; Otsu and Uchida 1963). Results from recent tagging suggest that north Pacific albacore may consist of two stocks that have different migratory patterns (Laurs et al. 1979). Fish belonging to a proposed northern north Pacific stock migrate between the eastern and western north Pacific, resulting in an interchange of fish of unknown magnitude between the U.S. fishery north of 40° N, the Japanese live bait and gillnet fisheries, and the Asian longline fisheries west of 180° (Figure 6). Fish belonging to the proposed southern north Pacific stock have a different migration route than those of the northern north Pacific stock. These fish enter the U.S. fishery south of 40° N and the longline fisheries east of 180°. Only a small proportion of the proposed southern north Pacific stock appears to migrate between the eastern and western Pacific to enter the Japanese fisheries. Also, during a particular fishing season, little exchange of albacore exists between the proposed northern and southern stocks that are exploited by the U.S. fishery. There is, however, a small amount of interannual exchange. An analogous situation to that posed above may also exist for albacore in the north Atlantic Ocean (Delaporte 1982).



1980 JAPANESE LONGLINE

1981 JAPANESE GILLNET



1983 U. S. SURFACE FLEET

1979 JAPANESE POLE & LINE

Figure 6. Catch areas of the four major fisheries for North Pacific albacore (from Majors et al. 1984).

Tagged north Pacific albacore recaptured off the coast of North America north of 40° N and in the western north Pacific off the coast of Japan grow more slowly than those recovered off the coast of north America south of 40° N (Laurs and Wetherall 1981). The differences in growth rate were consistent with differences in length frequencies of albacore caught north and south of 40° N (Brock 1943; Laurs and Lynn 1977).

Clearly, the situation for north Pacific albacore is complex and dynamic, with each stock's contribution to each fishery varying from year to year. Some evidence exists that such variation is directly linked to changes in oceanographic conditions (Laurs pers. comm.). Confirmation that more than one stock was present in north Pacific albacore fisheries would have important consequences for stock assessment, fishery evaluation, management policy, and development of accurate catch forecasting systems. Thus further work is needed on movements of albacore to clarify stock structure and migratory exchange.

2.6 Eastern Pacific Yellowfin, Thunnus albacares

In 1961 the Inter-American Tropical Tuna Commission (IATTC) proposed a catch quota of 83,000 short tons of yellowfin to conserve the stock in the eastern Pacific. No boundaries for the stock were defined and no regulation resulted. In 1962, the Commission defined a Yellowfin Regulatory Area (CYRA) (Figure 7) which included all areas of the eastern Pacific where the surface fishery existed and a large offshore area where no fishery existed except in the vicinity of a few distant islands (IATTC 1963:15). In the mid and late 1960's many newly-constructed large purse seiners began to fish further offshore and in 1968 they began to fish outside the CYRA. Within a few years some had extended their operations as far west as 150° W, making it possible to better establish the western boundary of the CYRA. Subsequent tagging of yellowfin inside and outside the CYRA (Bayliff 1979) showed relatively little interchange of fish across the boundary, but these data were of relatively poor quality because of low tag return rates and lack of year-round fishing both inside and outside the CYRA. Length-frequency studies have shown that the fish outside the CYRA tended to be larger than those inside the CYRA (IATTC 1985: Figures 13 and 14). After the fishery had been regulated for several years it became apparent that little fishing existed in some of the more remote portions of the CYRA and several of these were designated as "experimental areas" (Figure 7) where unrestricted fishing was permitted experimentally.

No international regulations for yellowfin fishing have existed in the eastern Pacific since 1979. If and when regulations are required, a need will exist to better define size-specific movements of yellowfin within and outside the CYRA. Experimental areas will probably continue to be designated so that regulations can be adjusted in accordance with the latest knowledge of yellowfin movement.

2.7 South Pacific Skipjack, Katsuwonus pelamis

Prior to the program of the South Pacific Commission (SPC) on abundance and movements of skipjack in the central and western Pacific, two-stock (Fujino 1972, 1976) and five-stock (Sharp 1978) hypotheses of skipjack stock structure in the Pacific existed. On the basis of geographical distributions presented for these stocks, the two hypotheses had been used to support the management policies of particular groupings of countries (Kearney pers. comm.). Several of the proposed stock boundaries fell within the SPC (Figure 8) and IATTC (Figure 7) areas, and many skipjack tagged by these agencies were recovered after crossing the boundaries (SPC 1981) proposed by Fujino and Sharp. A clinal hypothesis of stock structure (Richardson 1983) seems a reasonable alternative to the "isolated" stock hypotheses of Fujino and Sharp. The clinal hypothesis is

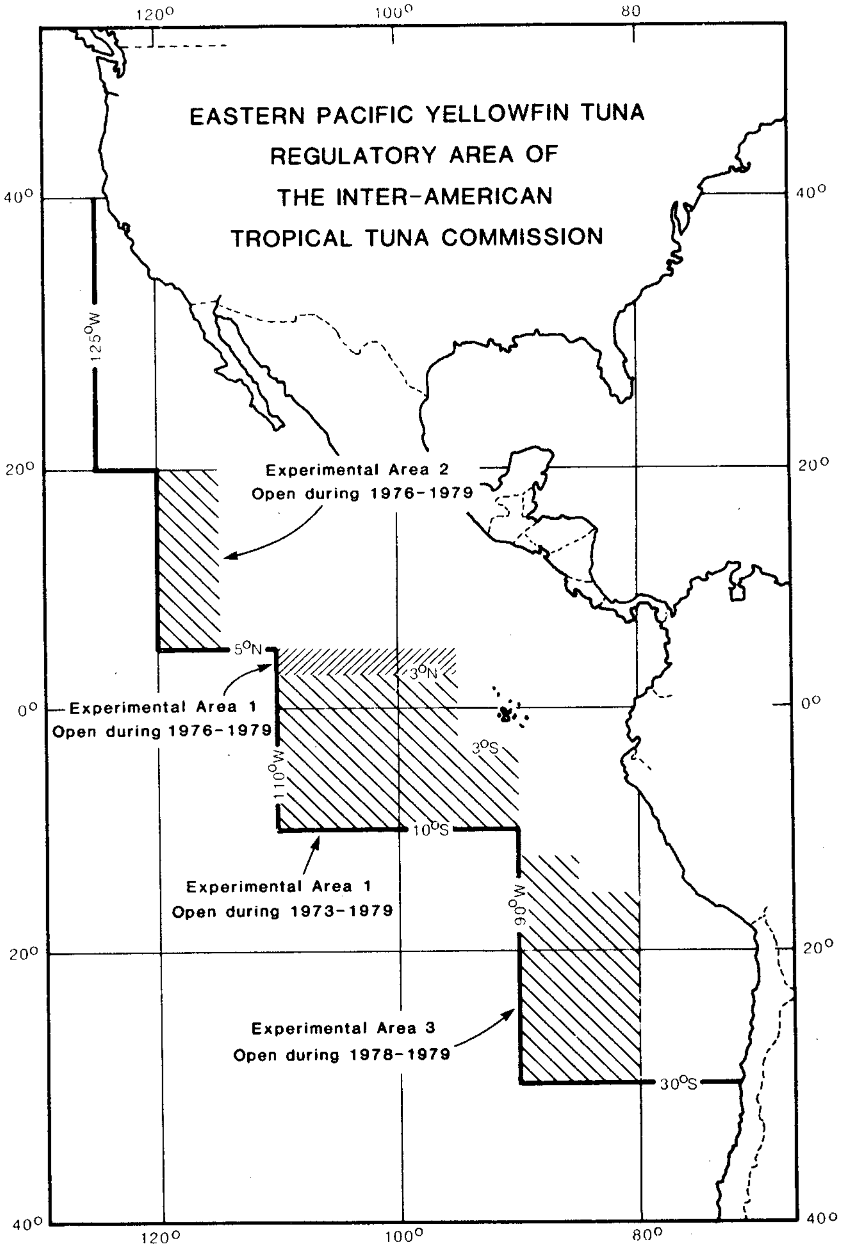


Figure 7. The eastern Pacific yellowfin tuna regulatory area of the Inter-American Tropical Tuna Commission (from IATTC 1985). The heavy line is the outer boundary of the CYRA.

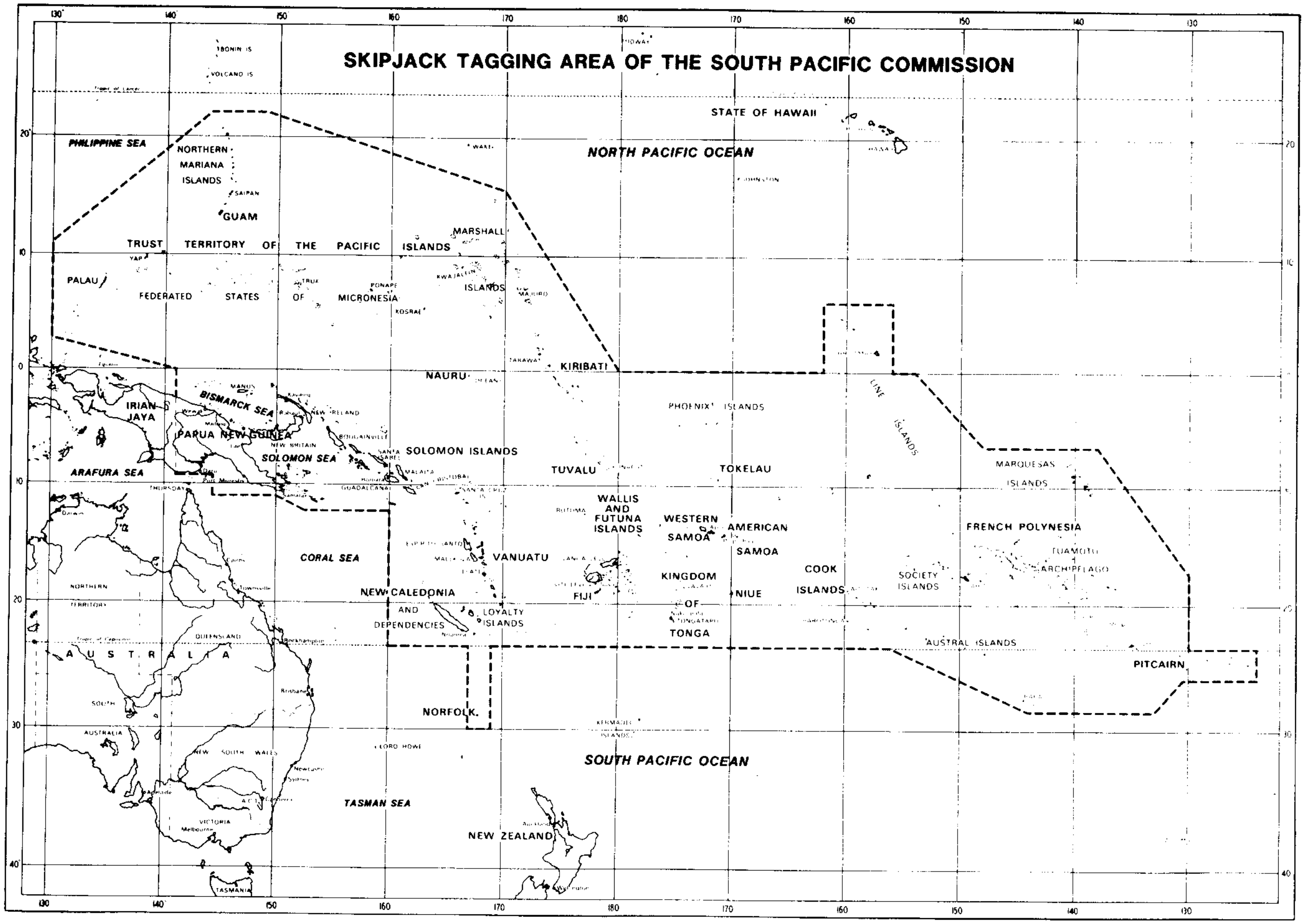


Figure 8. The skipjack tagging area of the South Pacific Commission (from Kleiber et al. 1983).

supported by the tagging results and a variety of new evidence, including sampling for tuna juveniles and states of sexual maturation (Argue et al. 1983), blood electrophoretic sampling and tagging skipjack from the same schools (SPC 1980, 1981), and analysis of skipjack growth (Sibert et al. 1983).

Unfortunately all lines of research on stock structure of Pacific skipjack had deficiencies (Argue et al. 1986). In the case of tagging data, not knowing the route that skipjack traversed between release and recovery meant that the range and pattern of skipjack movement could not be inferred with great confidence. For example, many fish at large for long periods were recovered near their release locations. These fish may have migrated extensively and then returned (or homed) to the release site or the recaptured fish were local residents and did not migrate at all. Clearly, much greater confidence could be placed on interpretations of tag recovery data if the paths traversed by skipjack were known. Such information would be useful in defining stocks and detecting the effect of one skipjack fishery on another.

Several analytical models (Kleiber et al. 1984; Sibert 1984) have been developed to quantify interactions between skipjack fisheries using the tag and recovery data collected by the SPC. Interactions were found to be negligible between locally based fisheries in the 200-mile zones of Papua New Guinea, Solomon Islands, Fiji, and New Zealand (SPC 1984a). Results for Japanese distant-water pole-and-line fisheries in the waters of the Republic of Palau, the Commonwealth of the Northern Marianas, the Federated States of Micronesia, and the Marshall Islands (countries where the north equatorial counter current is the dominant oceanographic feature) were more equivocal. There was some indication that skipjack moved in sequence, from west to east through pole-and-line fisheries that operated in the vicinity of the north equatorial counter current. Some estimates of interaction for these fisheries were quite high (SPC 1984).

Subsequent to this work the skipjack catch increased greatly and the distribution of fishing effort changed as more and more purse-seiners entered the fishery and distant-water pole-and-line vessels began to be phased out. Although the early tagging results suggested that there was not much interaction between pole-and-line fisheries, there was concern that these data did not accurately represent the situation, where purse-seine, pole-and-line and artisanal fisheries operated together. There was also concern that seasonal and directed movements of skipjack might not have been detected in the original tagging study due to inadequacies of experimental design.

On a finer scale, the purse-seine, local artisanal and local pole-and-line fisheries have come to depend heavily on anchored fishery aggregation devices that concentrate surface tunas and apparently make them more vulnerable to hook-and-line gear. The available conventional tagging data provide little information on the optimum distribution and numbers of devices to employ to maximize catches and minimize costs. Ultrasonic tracking of skipjack holds promise for solving this problem.

The skipjack resource is of great economic importance to the small countries of the central and western Pacific (Kearney 1979), and considerable fishing pressure exists in their waters as well as in international waters. Their combined 200-mile zones cover over one half of the ocean area west of 175° E. If it is found that large numbers of skipjack consistently move through a series of fishing areas in seasonal sequence and that fisheries at the end of the series are most severely affected by low catch rates, then such a finding would have important consequences for developing fishery policy in this region. This clearly is an area where further research on skipjack movement is warranted.

2.8 Atlantic Bigeye, *Thunnus obesus*

In the eastern Atlantic, bigeye tuna are exploited by fisheries in widely separated areas from the equator to temperate waters. Each fishery takes a different size class of bigeye: very small bigeye (<5 kg) are taken by bait boat and purse-seine in the Gulf of Guinea; 5 to 15 kg bigeye are caught by bait boat in tropical waters off Senegal and Mauritania; and large bigeye (>15 kg) are captured by longline and bait boat in temperate waters, such as those off the Canary Islands and off the Azores (ICCAT 1984a; Figure 9).

It is assumed that bigeye migrate from their equatorial spawning area to foraging areas that end in temperate waters (ICCAT 1984). During this migration they pass through 200-mile zones of many countries (and through international waters), where they are exploited by different gears. In each of these fisheries the estimates of yield per recruit will, of course, differ since parameters of growth and mortality differ in each zone (Pereira 1984). Rational management of the bigeye resource must take into account these movements and associated changes in productivity as bigeye move through fisheries with different harvest levels.

2.9 Conclusions

The new Law of the Sea has placed an obligation on coastal- and distant-water fishing nations to develop rational management plans for harvesting exploitable fishery resources. The seven examples described here illustrate how weaknesses in the understanding of distribution and movement of the principal tuna species have constrained development of rational management policy for many fisheries.

These weaknesses are often revealed when it is necessary to develop management plans or select catch and effort data that is representative of the stock after the fishery has expanded into a new area. This problem has become particularly important for management of depressed bluefin stocks. Another problem area is the quantification of interchange of fish between fisheries in different management jurisdictions and between gear types in the same jurisdiction. This area is presently of great importance to management of the yellowfin, Pacific skipjack and southern bluefin stocks, and will take on increasing importance with all tuna stocks as fisheries expand. On a finer scale, interchange of tuna among fish aggregating devices needs to be determined to optimize deployment strategies.

To make a fundamental advance in resolving these uncertainties and the other management problems we have discussed will require better information on the movement dynamics of tunas. Fishery-independent estimates of distribution and movement of exploitable adults are needed, as is knowledge of internal (physiological) and external (environmental) mechanisms governing their movement that could improve the predictability of movements. These issues are considered in the next sections.

3. PRESENT APPROACHES

In this section we discuss the research approaches and technologies presently used to describe the migrations and movements of tunas and to study the mechanisms underlying them. We describe the use of fishery information and mark and recapture data to measure tuna movements, discuss the movements of tunas in relation to oceanographic conditions, describe how a synthesis of existing data might expand our knowledge of movements, and discuss the use of a relatively new technique, ultrasonic telemetry. In this process, we attempt to identify the benefits and limitations of specific technologies and point out ways traditional approaches can be used in the future to expand our knowledge of tuna movements.

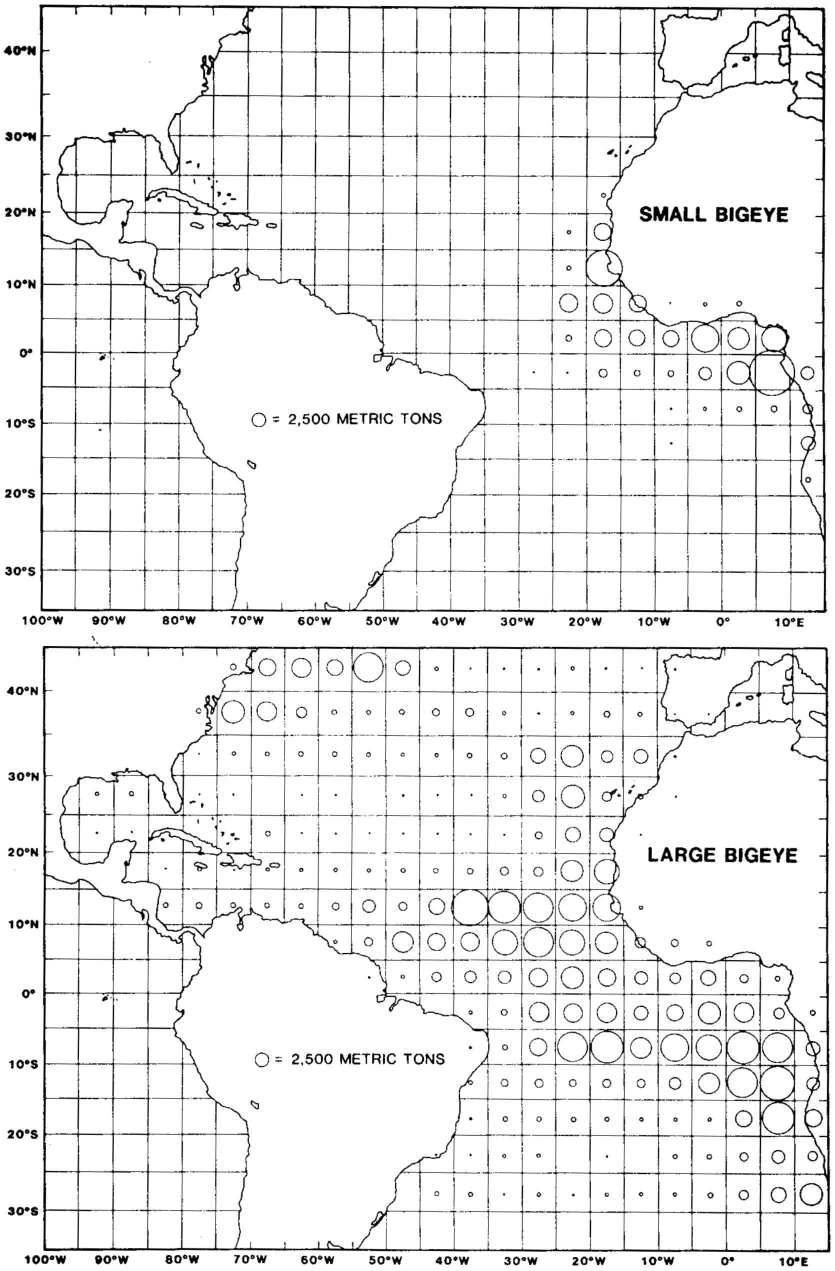


Figure 9. Upper; average catch of small bigeye (≤ 15 kg) by purse-seiners from 1975 to 1982. Lower; average catch of large bigeye (> 15 kg) by longliners from 1975 to 1982. The area of a circle is proportional to the catch. Data from ICCAT statistical data base.

3.1 Tuna Movements From Fishery Information

Many examples exist of the movements of tuna originally inferred from fishery statistics and later confirmed with tagging. The oldest reference is probably that of Aristotle (1910) who described fairly accurately the migrations of the Mediterranean bluefin tuna 20 centuries ago, using the spatial and temporal distribution of the catches. More recently, hypotheses regarding the movements of Atlantic yellowfin were made from catch and catch and effort data from surface and longline fisheries (Richards 1969; Honma and Hisada 1971) before any tagging was done.

Reasonable hypotheses for the movements of most of the world's tuna stocks can be inferred from fishery data provided: 1) the fisheries exploit most of the stock -- sizes and distribution; 2) reasonably good catch and length frequency data (small time and area resolution) are available; and 3) the species show consistent annual distribution patterns (true for most tunas).

Although changes in the vulnerability to capture may be misinterpreted as migration, in general fishery statistics are still useful for formulating hypotheses about tuna migrations. The relatively "recent" development of more active and powerful techniques, such as tagging and telemetry, will not replace, but rather complement, this traditional approach, and fishery statistics will remain an important source of information for the studying of the movements of tuna in relation to their environment because of the extensive data available and wide geographic coverage. Improved precision of the data, which in some cases permits analysis on a temporal scale of days, and a spatial scale of minutes of latitude and longitude (Fonteneau 1978) offer new opportunities for the study of tuna movements using fishery statistics. Improved computer facilities and graphical displays will facilitate such analyses. New work can be done on size-specific movements as length data become available.

3.2 Marking and Recapture of Tunas

Analysis of the recoveries of marked tunas combined with fishery information has provided most of our knowledge of tuna migrations and movements. However, the greatest advances have been made when mark and recapture data were combined with other information, such as larval distributions and the results of length-frequency analyses and biochemical and morphometric studies (Argue et al. 1983; Bayliff 1983). The method of marking and recapture also provides estimates of natural and fishing mortality, growth, stock structure, and schooling behavior, as well as defining migrations and exchange rates among fisheries, making it one of the most powerful methods for acquiring information needed for tuna management.

3.2.1 Mark and Recapture Methodology

Tags have been applied to tunas caught by baitboats, trollers, sport-fishing boats, purse seiners, traps, and other gear. About 607,000 tunas have been marked with conventional tags, mostly from baitboats. Streamer tags were used during the 1950's, but these were replaced during the 1960's by dart tags with nylon or steel heads, the latter being used for larger tunas captured by recreational fishermen and tagged while in the water. Most of the tunas that have been tagged have been skipjack or yellowfin tuna, but substantial numbers of all the important species have been tagged. The largest number of fish tagged in one day on a single vessel was 3,689 (skipjack, mean length 48 cm; Argue and Kearney 1983). The tags are usually returned by fishermen, unloaders, and cannery workers who receive modest rewards for returning tags and in some cases chances to win substantial cash prizes in drawings held at the end of the year (ICCAT

1983: 218-219). In many cases, employees of fishery organizations make daily visits to tuna unloading areas to collect the tags found by the workers.

3.2.2 **Movements**

Past studies of the transoceanic movements of bluefin tuna illustrate the crucial role of mark and recapture data and the importance of ancillary information used to interpret such data. Godsil and Byers (1944) concluded from an analysis of anatomical characteristics that two species of northern bluefin existed in the north Pacific, but this hypothesis was later rejected when fish tagged in the eastern Pacific were recaptured in the western Pacific and vice versa (Clemens and Flittner 1969). Similarly, the eastern and western Atlantic bluefin were considered separate species (Ginsburg 1953) until subsequent tagging showed that transoceanic migrations in both directions existed (Mather and FAO, 1972). In the north Pacific, bluefin spawning occurs only in the vicinity of Japan (Bayliff 1980), indicating all fish in the eastern Pacific have migrated across the ocean. On the other hand, in the Atlantic, transoceanic spawning migrations cannot be inferred because larval data indicate spawning occurs on both sides of the Atlantic (Mediterranean Sea and the Gulf of Mexico). Recent analyses of the chemical composition of the vertebrae seem to indicate that only a minority of bluefin cross the Atlantic Ocean (Calaprice 1986).

Tagging experiments indicate that during the annual migration of albacore across the northeastern Pacific to North America virtually no interchange exists between albacore north and south of 40°N latitude and only a low rate of interchange across that boundary occurs at other times (Laurs 1983). Other studies (Laurs and Wetherall 1981) indicate that the growth rates of fish from the two areas differ.

Mark and recapture studies have also shown that considerable mixing of yellowfin exists in the Pacific Ocean. Yellowfin seem to move long distances less frequently (Fink and Bayliff 1970; Bayliff 1979) than do bluefin or albacore, and little or no evidence of homing exists for yellowfin. Nevertheless studies of the distribution of adults and larvae, sexual maturity, length frequencies, and tag returns of yellowfin suggest that three stocks may exist in the Pacific (Suzuki et al. 1978).

Considerable mixing of skipjack exists in the Pacific Ocean. Skipjack, like yellowfin, move long distances less frequently (Fink and Bayliff 1970; Kleiber et al. 1983) than do bluefin or albacore, but their migration from the eastern to the central and western Pacific as the fish approach maturity (IATTC 1983: 32-33) suggests homing. Extensive ichthyoplankton surveys have produced few skipjack larvae in the eastern Pacific, and large skipjack make up a much higher portion of the catch in the central relative to the eastern Pacific. These facts have led investigators to believe that the skipjack in the eastern Pacific are hatched from eggs spawned in the central and western Pacific (Rothschild 1965).

The net distances traveled by yellowfin tagged in the eastern Pacific and skipjack tagged in the western Pacific after 0-30,31-180, and more than 180 days at liberty are shown in Figure 10. It is obvious that many of the fish moved considerable distances from the locations of release. Most of the tagging took place in areas where fishing effort was heavy. If the fishing effort were evenly distributed in the Pacific Ocean there probably would have been fewer returns of fish which had moved short distances and more returns of fish which had moved long distances.

An important uncertainty is the extent that the apparent dispersion of fish from a tagging site is an actual representation of their movement

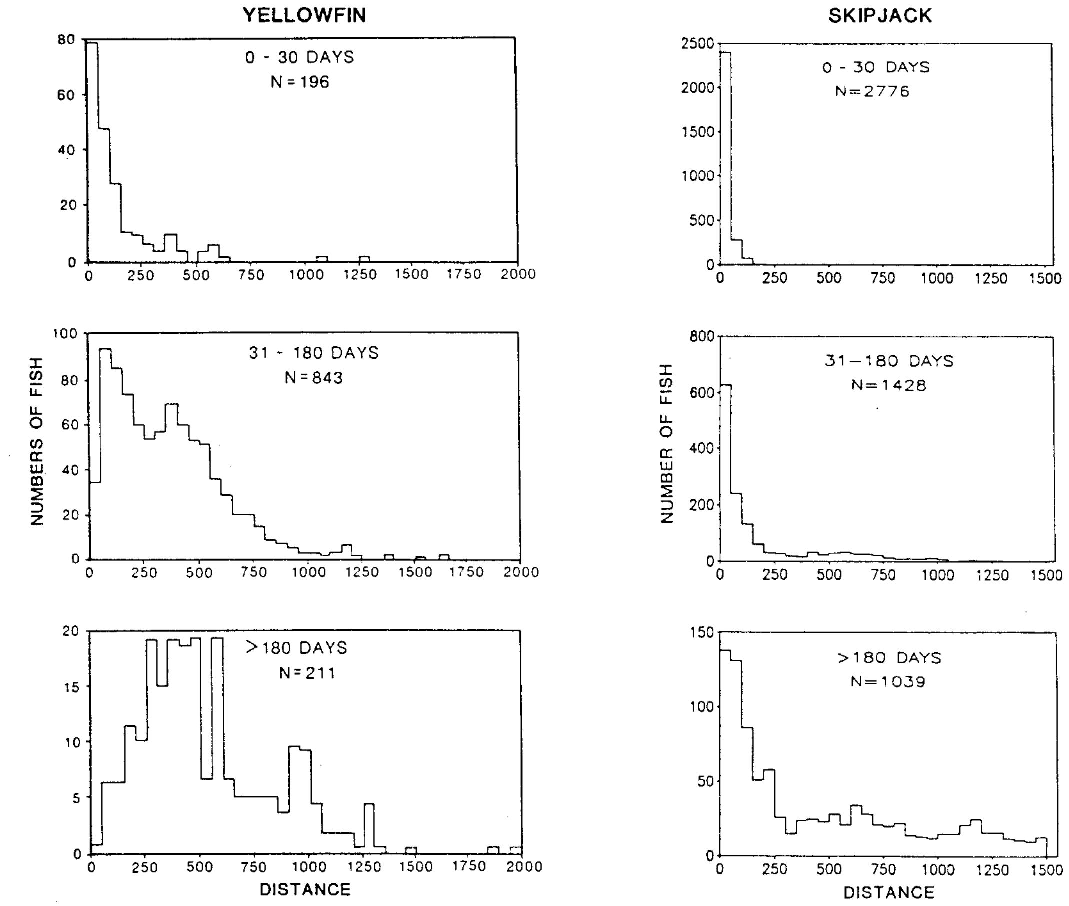


Figure 10. Net distances, in nautical miles, traveled by purse seine-caught yellowfin tagged in the eastern Pacific during 1968-1978 (W.H. Bayliff, pers. comm.) and baitboat-caught skipjack tagged in the western Pacific during 1977-1980 (after Ke[illegible]y 1983). One yellowfin, not shown in the figure, was recaptured 2,765 miles from the point of release after 138 days at liberty.

rather than an artifact of the present marking and return system. Obviously many of the biases and constraints in mark and recapture technology could lead to erroneous conclusions about the movements of tuna. These are discussed in more detail in subsequent sections. Clearly, better knowledge of the actual paths followed by the fish for extended periods is needed before these issues can be resolved.

3.2.3 Return Rates

The percentage of tags that are recovered and returned varies widely among and within species, as indicated in Table 1.

Table 1

Percentages of tags returned.

Species	Area	Years	Total percentages of return Min	Max	Mean	Reference
Yellowfin	Eastern Pacific	1959-1964	2.7	65.3	21.6	Fink and Bayliff, 1970
Skipjack	Eastern Pacific	1959-1964	2.3	43.9	8.1	Fink and Bayliff, 1970
Skipjack	Western and central Pacific	1977-1980	0.0	13.9	4.4	SPC, 1984b
Northern bluefin	Western Atlantic	1954-1971	0.0	44.2	23.6	Mather and working party, 1972
Albacore	Eastern Pacific	1971-1978	2.0	8.5	5.4	Laurs and Weatherall, 1981

The great majority of the marked yellowfin and skipjack that have been recaptured were at liberty less than one year, whereas a substantial fraction of marked albacore and bluefin have been recaptured after over one year. In fact, the record time at liberty for a tagged tuna is for a southern bluefin that remained at large for nearly 18 years (Anonymous 1981). The decline in recoveries of marked tunas with time varies not only among species, but also within species. For example, among skipjack fisheries, the decline in recoveries is steepest in the eastern Pacific, intermediate in the eastern Atlantic, and most gradual in the southwestern Pacific (Figure 11). Skipjack from the eastern Pacific migrate to the central and western Pacific prior to spawning, but are seldom recovered by the minor fisheries in those areas (IATTC 1983: 32-33), whereas the southwestern Pacific includes both major fisheries and several major skipjack spawning areas (Argue et al. 1983).

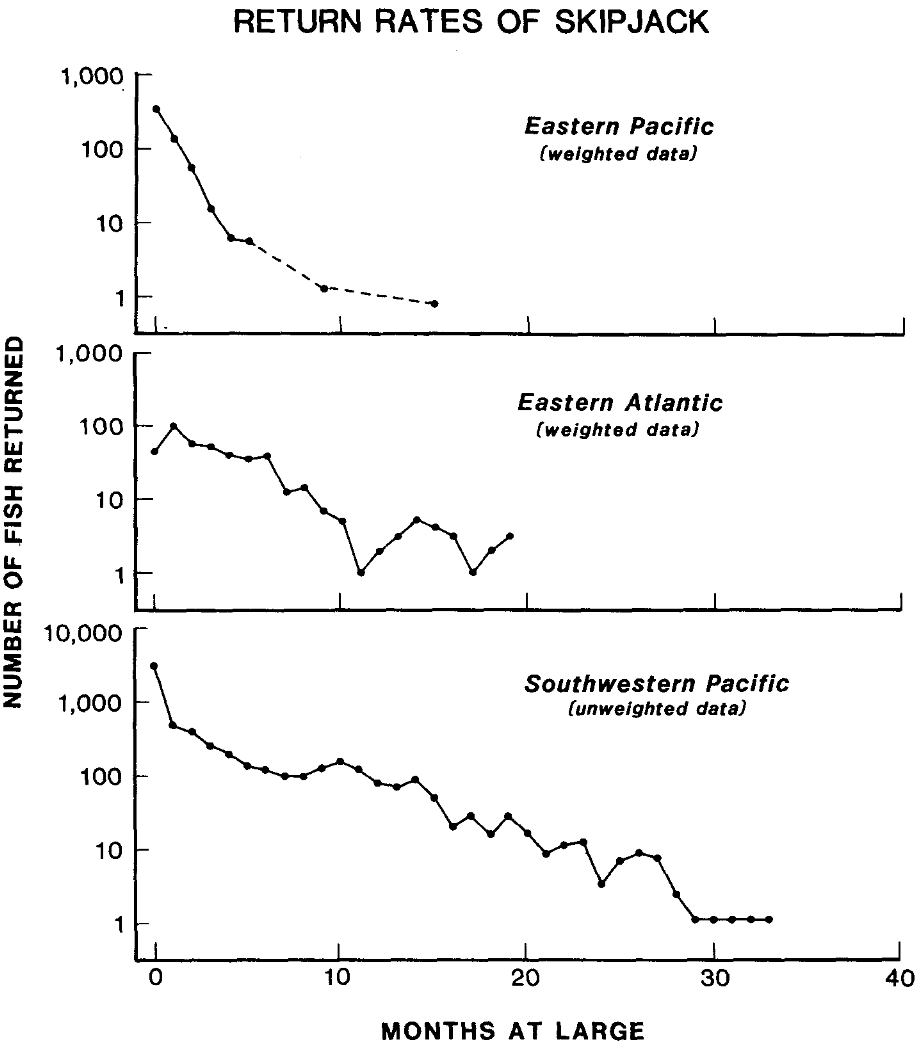


Figure 11. Catch curves for tagged skipjack in the eastern Pacific (Bayliff 1977), eastern Atlantic (Bard et al. 1983), and southwestern Pacific (Kleiber et al. 1983).

3.2.4 Uncertainties and Limits of Conventional Mark-Recapture Technology

Substantial numbers of several species of tuna are caught at sizes in excess of 50 kg, but because of technical problems tunas larger than about 20 kg are seldom tagged. Some tunas tagged when they were small were recovered after having grown considerably, but such events are rare because of high rates of fishing and natural mortality. Thus many small fish must be tagged to ensure the recovery of even a few large ones. For example, in the eastern Pacific surface fishery for yellowfin (where the annual coefficients of natural and fishing mortality are about 0.8 and 0.7, respectively), if 1,000 yellowfin were tagged, one would expect a return of about 363 (36%) of the tags in the first year, 81 (8%) in the second, 18 (2%) in the third, 4 (<1%) in the fourth, and 1 in the fifth. The observed recovery rates, however, after the first year are even lower than those predicted from the natural and fishing mortality rates. Of 13,598 yellowfin tagged off Baja California during 1957-1963, 6,621 tags (49%) were returned in the first year (May-April), but only 73 (1%) were returned in the second year, only 2 (<1%) during the third year, and none thereafter (Bayliff 1971). High vulnerability to capture shortly after tagging, lesser vulnerability to capture of larger fish, and shedding of the tags may be responsible for the differences between the observed and expected returns.

The attrition rate of tag recoveries can be considered as the reduction in the tagged stock with time due to natural and fishing mortality, tag shedding, mortality caused by the tags, growth out of vulnerability to the fishery, and emigration (Kleiber et al. 1983). Ideally, it would be useful to partition attrition into, at least, natural mortality, emigration, and other losses. Cayré, Diouf, and Fonteneau (1986) have estimated the instantaneous rate of mortality due to carrying tags for skipjack. Although no attempt to partition the attrition rates into those classes has been entirely successful (Sibert 1984), some possible research approaches discussed later in this report might ultimately make this problem more tractable.

A number of other problems exist in the interpretation of mark and recapture data in addition to lack of understanding of the relative role of the various factors that affect the attrition rate of tagged fish. It is difficult to be certain that tagged fish are truly representative of a study area, as usually only one or a few vessels are used to capture tunas for tagging, and the released fish may not quickly mix within the study area. In addition, vessels often do not fish in all areas occupied by the stock, and this distorts the apparent movements as indicated by the recapture data. Some adjustments can be made by dividing the numbers of recoveries by the fishing effort in the recovery areas (Bayliff 1979). A more accurate adjustment would be to adjust the recoveries for fishing effort over the actual path followed by the fish between release and recovery, but this is not possible using existing approaches.

The recovery of tags is an additional problem, as some of the finders of tagged tunas do not return the tags or furnish poor data. Bard et al. (1983), tagged freshly-caught dead fish and placed them in the wells of fishing vessels at sea. They estimated that about 70 percent of the skipjack they tagged were returned by unloaders and cannery workers. However, tags attached to freshly-caught fish may be more easily knocked off and lost during loading and unloading than tags attached to fish which had been tagged and released weeks, months, or years previously.

3.2.5 Directed and Random Movements

Harden Jones (1968) recognized three types of "migratory movements": drifting with the currents, random locomotory movements, and oriented locomotory movements. In a later paper (Harden Jones 1984) he stated, "I use the word migration in the sense of coming and going with the seasons on a regular basis." Jones (1956 and 1966), using physical diffusion models, derived equations for calculating the directed (V) and random (A^2) components of the movements of a group of tagged fish, and Bayliff and Rothschild (1974) derived a crude method for adjusting the return data for uneven distribution of fishing effort. In the strictest sense, the movement is not random unless V is equal to zero, which has never been the case in any tuna study. The central issue is to determine why V is not equal to zero. Four explanations exist for apparent nonrandom movement, and each is discussed below.

First, if fish were tagged near a coastline the recapture data would probably show that fish had moved offshore and parallel to the coast in both directions and that the center of abundance of the recaptures was further offshore than the center of abundance of the releases. This does not indicate, except in the strictest sense, that the movement of the fish was non-random. In fact, the same pattern would result if dye molecules were injected near the edge of a barrier.

Second, the fish might encounter concentrations of food by moving randomly, and by random movement remain there until the food was nearly exhausted. This behavior would produce values of V greater than zero, but few investigators would classify this behavior as directed movement.

Third, fish are able to sense gradients in physical, chemical, and biological properties of the environment and follow such gradients to a richer food environment. In some cases these movements may be related to irregular environmental events and in others to such regular seasonal events as warming and cooling of the surface water in temperate regions. In the latter case the tuna could be orienting to navigational cues (gradients in the earth's magnetic field, or angle of a celestial body) rather than gradients in food abundance or other properties that determine the suitability of the habitat. According to the definition of Harden Jones (1984), such seasonal movements would be migrations, regardless of the mechanisms involved.

Fourth, some fish, such as bluefin and albacore, make spectacular seasonal movements, but the factors controlling these movements are much less well understood than such seasonal events as the movement of skipjack into temperate New Zealand waters in the spring and out of those waters in the fall. Homing, defined by Gerking (1953) as "the return to a place formerly occupied instead of going to other equally probable places", seems to be involved here.

Ideally, in the development of a model using tag recovery data one might first subtract such effects as proximity to land, then non-seasonal effects such as patchy distribution of food, and finally easily-understood seasonal effects such as poleward movement during the spring and the reverse during the fall. This would leave homing effects as the residual. Considerable interest exists in this subject, especially for skipjack in the Pacific Ocean (SPC 1981). Present data may not be adequate for such an analysis but some of the research approaches we propose in subsequent sections may make such an approach practical in the future.

In general, the ratio of V to A^2 would be expected to be greater for highly-migratory species, such as bluefin and albacore, than for species without evident well-defined movements. Unfortunately, no estimates of V or A^2 are available for bluefin or albacore, but such data for yellowfin and skipjack, from Bayliff (1984), are shown in Table 2. In every case the $(V\times1000)/A^2$ value is greater for skipjack than for yellowfin, indicating that the movements of skipjack in the eastern Pacific are more directed than those of yellowfin.

3.2.6 **Integrity of Schools**

Skipjack do not appear to remain in the same schools for long periods of time. During the first 1 to 3 months after release fish tagged in the eastern Pacific Ocean at the same location on the same date are not randomly mixed with untagged fish in the same area, but by the fourth month random mixing has taken place (IATTC 1984: 33-36). Present evidence for south Pacific skipjack also indicates that schools do not maintain their integrity for long periods (Kleiber and Argue, MS); this evidence includes analyses of western Pacific data for instances of multiple recoveries of tagged skipjack from the same school recaptured on the same date, and

Table 2

Estimates of V and A^2 for yellowfin and skipjack (from Bayliff 1984).

		Yellowfin			Skipjack		
Region	Year	V	A^2	Vx1000 A^2	V	A^2	Vx1000 A^2
Colombia	1981	0.5	835	0.6	2.9	426	6.8
Gulf of Panama	1959	1.4	776	1.8	1.4	449	3.1
Gulf of Panama	1961	2.9	2065	1.4	2.8	1816	1.5
Gulf of Panama	1981	0.6	232	2.6	1.1	293	3.8
S. Central America	1979	0.8	2719	0.3	2.4	2678	0.9
S. Central America	1980	0.7	479	1.5	1.7	985	1.7
S. Central America	1981	1.9	2180	0.9	4.1	779	5.3
N. Central America	1979	2.3	3821	0.6	4.5	2406	1.9

studies of data for rare blood serum alleles. Analyses of this type have not been performed for other species, but anecdotal evidence suggests that the schools of other species of tunas do not retain their integrity for long periods.

3.2.7 Additional Mark and Recapture Studies

A large fraction of the data on marking and recapture in the files of various fishery agencies has not been fully analyzed. Analyses have not been completed in some cases because the investigations have only begun, but in others the work could be done if money and manpower were allocated. In addition, little tagging of tunas has been done in some regions, such as the Indian Ocean and Philippines-Indonesia region, and relatively few individuals of bigeye in the Pacific Ocean and *Euthynnus* spp. and *Auxis* spp. in any ocean have been tagged. Bigeye are of great commercial importance in the eastern Pacific Ocean, but as nearly all are caught with longline gear, large-scale tagging is impractical using present technology. (This is not the case in the Atlantic Ocean where bigeye tagging can be easily conducted.) *Euthynnus* and *Auxis* are currently of only minor commercial importance in most areas, but this is likely to change. Large-scale tagging of these two genera is presently impractical except in a few areas such as Japan, the Philippines, Senegal, and Indonesia, where they are relatively heavily exploited.

3.3 Tunas and Their Ocean Environment

3.3.1 Introduction

Oceanic environmental variables and processes that affect tunas vary spatially and temporally over a large array of time and space scales in three dimensions. Sette (1961) stressed that to understand and eventually model the effects of the ocean environment on fish populations, information on the "changing ocean" and on average ocean conditions is needed. The "changing ocean" is caused by variations of the interaction at the ocean surface between air and sea: wind stress, heat exchange, precipitation, evaporation, and advection.

Tunas differ in their environmental and habitat requirements and these requirements change over their life history. Yellowfin, skipjack and bigeye are restricted to tropical waters, whereas albacore and bluefin are found in temperate seas. Juvenile stages of skipjack and albacore live in shallower depths than adults and migrate more extensively.

The mechanisms that link the ocean environment to tuna movement are not well defined or understood. In some cases ocean conditions are believed to act directly on the biology of the tunas, while in other cases the relationship with ocean conditions is indirect through their forage. The distributional limits of various species may be set by specific oceanographic properties acting directly on the physiology and/or behavior of individuals in the population. For example, albacore apparently are not able to thermoregulate effectively at temperatures below about 10°C (Graham and Dickson 1981), and this may be why the species is usually not found in waters cooler than 10°C. Variations in the availability of tunas within their distributional limits may not be linked with ocean conditions acting directly on the tunas, but rather indirectly through the distribution and abundance of forage organisms. For example, the availability of tunas within their distributional range is usually greatest in the vicinity of oceanic fronts where food abundance is high (Uda 1973, Laurs and Lynn 1977, Laurs et al. 1984). To identify the optimal approach for studying this multivariate three-dimensional system is a major challenge. We discuss here the status of knowledge of the relationship between tuna movement and the environment and possible directions of future research.

3.3.2 **Limits**

A focus of much of the past work on tuna movements and distributions has been on physical characteristics of the habitat at the extremes of horizontal and vertical distributions of tunas. This work has been reviewed most recently by Sund et al. (1981) and documentation for much of the following can be found in their publication. Correlations, which have been well described in the literature, exist between tuna catches and the physical environmental barriers indicated by sea-surface temperatures, mixed layer depth, and oxygen concentration. The principal evidence of the effect of temperature on tuna distribution has been the seasonal expansion and contraction of the range of surface-caught fish at the periphery of their ranges and this expansion and contraction correspond fairly well to sea-surface isotherm displacements (Blackburn 1965; Champagnat and L'homme 1970; Cayré et al. 1974). In the same statistical sense temperature and possibly oxygen also establish vertical habitat limits for tunas. Such statistical evidence of the extremes of the potential habitat of tunas has proven to be quite useful for fishery operations, but much more detailed cause and effect relationships which would forecast movement are lacking.

In the past, the thermocline was thought to represent a limit to vertical distribution of tunas. This relationship is in part based on work relating purse seine fishing success with thermocline depth (Green 1967). Also, skipjack occur in many areas of tropical seas where they are not available to surface gear (Sharp 1978), their presence being indicated by their larvae (Nishikawa et al. 1985) and by anecdotal evidence of bird flocks feeding on forage driven to the surface by feeding fish. Such observations have led some to believe that this subsurface existence provides a refuge from surface fishing gear. Recent results from tuna tracking studies show that tuna spend much of their time within the thermocline (Yonemori 1982; Laurs and Dotson, in prep.) and suggest that tuna are "creatures of the thermocline". In fact, the thermocline may not act as a barrier, but rather determine the degree of vulnerability of tunas to surface and subsurface fishing gear. When the thermocline is shallow the fish are more vulnerable to surface fishing gear and vice versa. Also, longline fishing successs is markedly higher when hooks are set in the thermocline rather than at depths above it (Laurs and Dotson, MS).

The concept of limits in the distribution of tunas is indicated in acoustic tracking studies which were conducted to investigate the vertical distribution of tunas, although this concept has not been strongly supported by laboratory work (Matsumoto et al. 1984). Laboratory work indicates that kawakawa (Euthynnus affinis) penetrate oxygen or thermal barriers for a food award, and these barriers are far more extreme than fishery correlates would predict (Matsumoto et al. 1984). Lethal limits exist in the ocean; in the central North Pacific (Figure 12) at 11°N lat., oxygen concentrations of only 0.5 ml/l occur within 100 m of the surface. Partial pressures of oxygen below 50% of saturation or temperatures below 10°C are lethal for albacore (Graham and Laurs 1982; Graham and Dickson 1981). Lethal limits are probably seldom significant in the mortality of tunas as the fish would retreat before they became lethal. Some anecdotal evidence indicates that direct effects of temperature might occasionally be the final cause of death. Tracking studies indicate that injured tuna, swimming too slowly to maintain hydrostatic equilibrium, slowly glide into colder water which causes them to swim even slower, increasing their rate of descent into ultimately fatal conditions. Perhaps this is the manner in which starving tuna die. Future work should emphasize using the high technology of acoustic tracking and archival tagging along with concurrent measurements of the ocean using observations made from ships and satellites. Data resulting from these types of studies should aid understanding of the oceanic limits and habitats of tuna.

3.3.3 **Forage**

Striking differences exist in tag recovery rates or in CPUE between regions and seasons suggesting differences in local concentration or vulnerability of tuna to the fishery or both. Dramatic variations in catch rates are common in tunas, indicating the crucial role of the environment in concentrating tunas and affecting their availability to surface fisheries. Future investigations, therefore, must be concerned with discovering the "crucial" environmental mechanisms.

When aggregations of tunas occur near the surface along edges of oceanic provinces and other oceanic fronts, usual explanations are that tuna forage is more abundant or more available in such localities or that the sharp thermal or salinity gradients constitute physiological barriers to tuna movement. The latter argument has not been supported by the experimental findings. On the other hand, the well known correspondence between tuna catch and ocean productivity, illustrated in Figures 13a and 13b (for Atlantic tuna fisheries), indicates that such aggregations are related to the availability of forage. Forage abundance or availability becomes the crucial environmental variable for explaining the abundance of tunas in such areas (Stretta et al. 1975), yet no adequate quantitative assessments of the abundance of forage exist. It seems essential that forage or a reliable index of it be measured in such areas to confirm this hypothesis. Such indices should account for the vertical migrations of mesopelagic organisms (King and Iverson 1962) as well as epipelagic organisms. Acoustic methods and midwater trawls seem promising in this regard. In addition to direct measurement of forage, a reliable and easily measurable index of forage abundance is needed.

Prediction of forage abundance may depend on identification of the appropriate time lag between the onset of a productivity event and tuna catches. The time lags vary with region, times of year and other variables. For example, different scenarios exist for the different

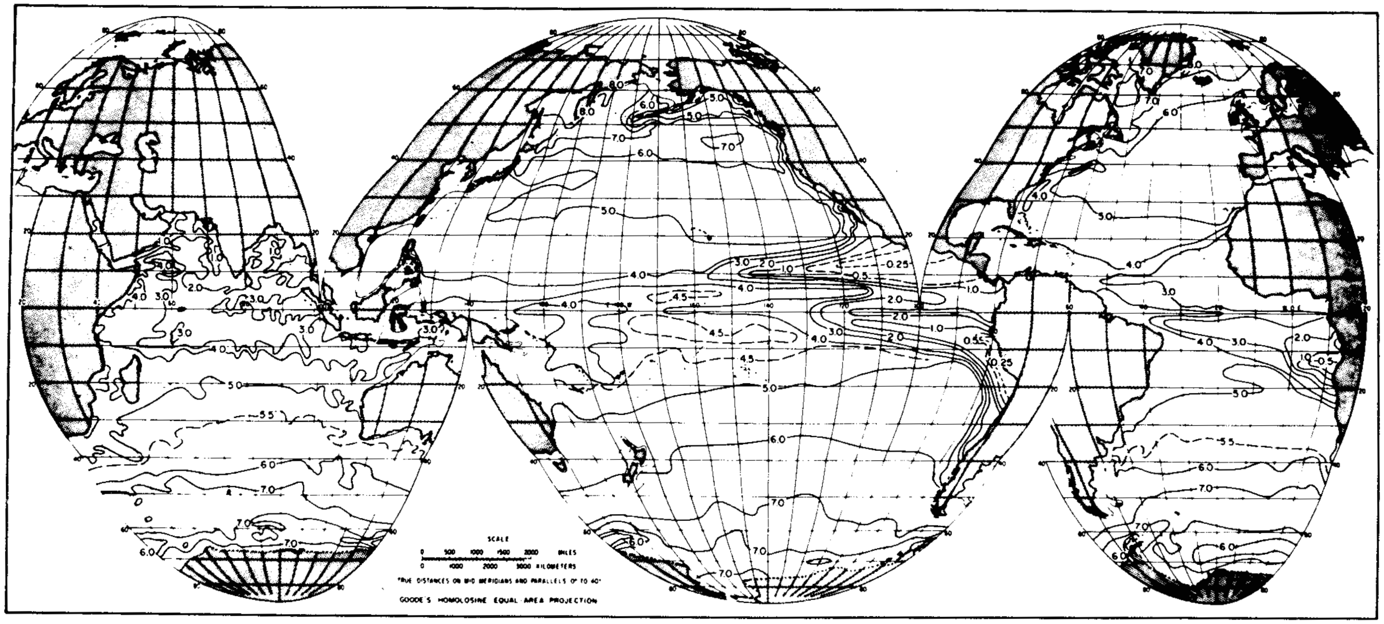


Figure 12. Distribution of dissolved oxygen (ml/l) at 100 m in the world ocean (from Reid et al. 1978).

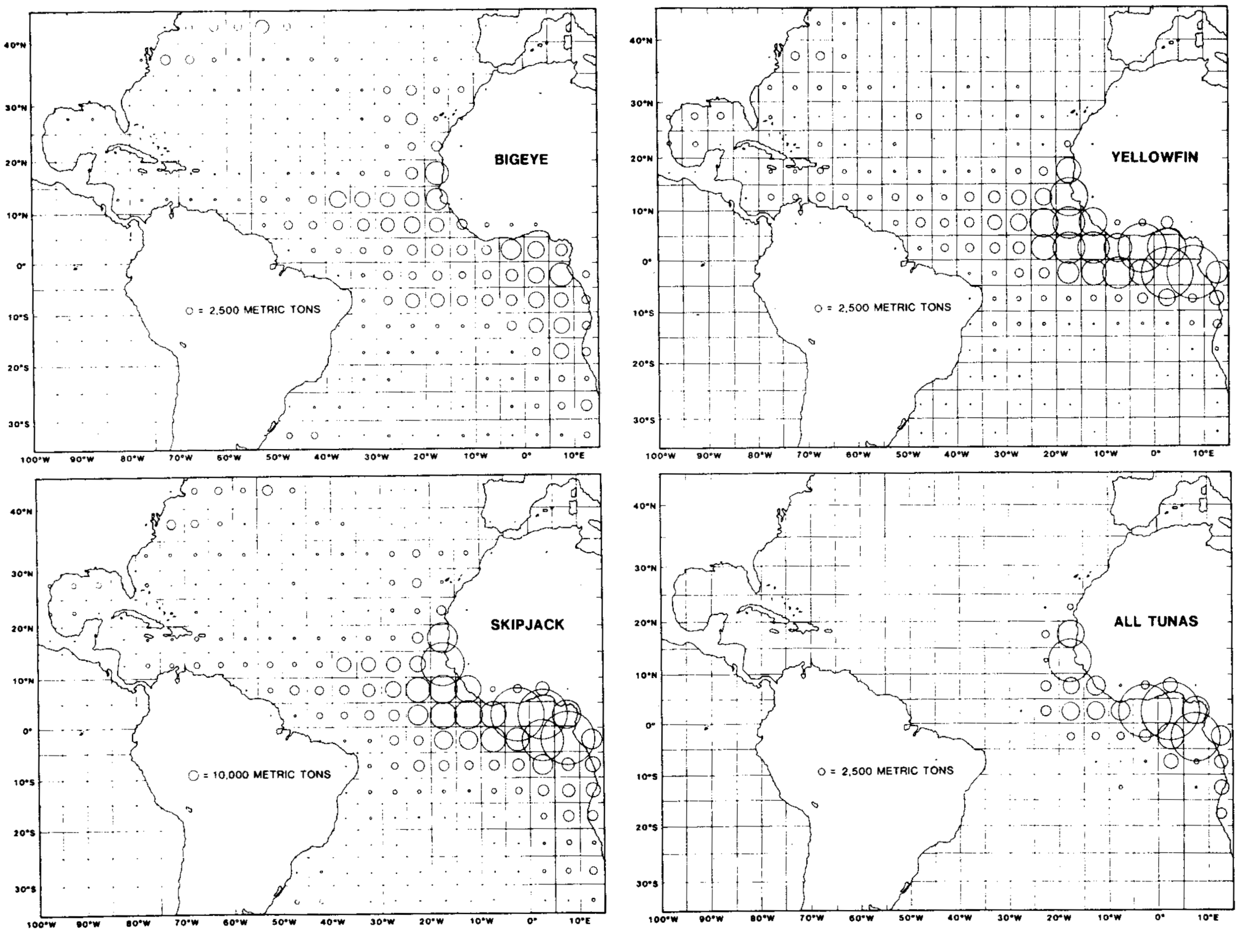


Figure 13a. Average catch of bigeye, yellowfin, skipjack tuna, and all tuna summed by 5° areas. The area of a circle is proportional to catch (prepared from ICCAT data base).

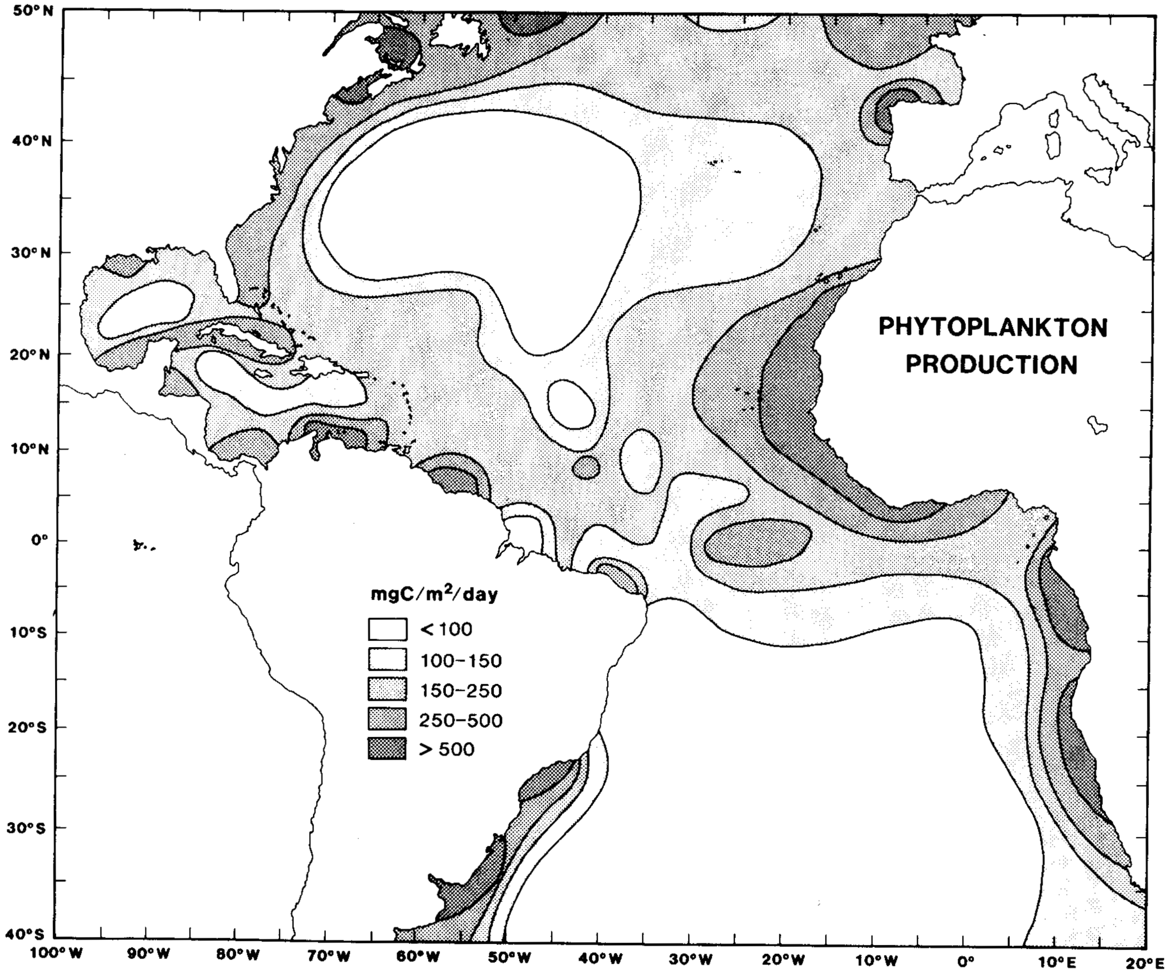


Figure 13b. Average phytoplankton production (after Koblentz-Mishke et al. 1970; FAO 1972).

frontal areas in the eastern Atlantic; each region of the African coast shows a somewhat different rate of development (J.-M. Stretta, unpublished data). The onset of a typical event (rising of nutrients into the euphotic zone) occurs 4-6 weeks prior to the development of a fishery in the region (J.-M. Stretta, unpublished data).

3.3.4 **Processes**

Wind-driven advection and mixing are principal physical processes that determine forage production and distribution. On the largest scales, zones of convergent and divergent flow occur consistently.

Divergent zones are biologically productive because nutrients are brought vertically to the euphotic layer, but organisms are dispersed laterally. Proximate convergent zones can collect this production. On somewhat smaller scales of time and space, wind-driven convergent and divergent flow along coastlines creates special environments for tuna and forage. Usually tunas avoid upwelling (divergent) zones but frequent the downwelling (convergent) fronts usually found seaward of upwelling sources. This is presumably due to the higher forage associated with such fronts. Convergent fronts also are produced where colder or more saline water meets warmer or less saline water. At 3-5°N, cold water from the equatorial upwelling meets warm countercurrent water and slides downward. The process is expressed as a series of thermal fronts encountered in this region, especially in the eastern half of the Pacific Ocean basin. River plumes, such as those of the Columbia and Amazon Rivers, have frontal zones due to lateral impingement of saline waters on fresher water of the plume.

The converging effect of the wind stress distribution causes the thermocline to deepen (usually called downwelling) and tends to have low productivity. Examples are the central areas of the large ocean gyres where the thermocline is deep and the water is highly transparent. Temperature and/or salinity fronts are found around the periphery of these central areas. For example, in the Hawaiian region a salinity front moves seasonally north-southward into the island region. Associated with this frontal movement is the seasonal movement of skipjack into range of the local fishery (Seckel 1972). Similarly, high catches of skipjack in the western Pacific seem to be correlated with the 35 ^{o}/oo isohaline. Presumably the higher catches are due to aggregation of skipjack on forage produced in convergence zones which are marked at the surface by the 35 ^{o}/oo isohaline (Donguy et al. 1978).

Eddy motions also create convergent or divergent flow, depending on flow direction and Coriolis deflection. Cyclonic eddies produce divergent flow and tend to produce higher production in their centers, such as the Costa Rican Dome. Recent evidence (Tranter et al. 1983) indicates that biotic enrichment can occur at edges of anticyclonic eddies. Demonstrably different organism ensembles occur in eddies of both types (Wiebe et al. 1976; Backus et al. 1969).

On a smaller scale, fronts or convergences can also be produced by the interaction of the wind-driven surface flow with ocean currents, or they can be the result of eddying water motion. In all cases forage organisms are redistributed, diverged or converged by these water movements.

3.3.5 **Fronts and Visibility**

In the albacore fishing grounds at the border of the North Pacific Ocean, the fish concentrate in the vicinity of ocean fronts. These fronts are associated with: current systems and other features in the western Pacific (Uda 1973); coastal upwelling (Laurs et al. 1977; Laurs et al. 1984); and the Columbia River plume in the eastern Pacific (Owen 1968;

Pearcy and Mueller 1970). The migration patterns and fishing success for albacore in the central North Pacific are also related to oceanic frontal structure associated with the North Pacific Transition Zone (Laurs and Lynn 1977 and Lynn 1984). Similarly, skipjack and yellowfin do not enter the green water of coastal upwelling areas in the Gulf of Guinea and the Gulf of Panama but remain in the clear oceanic water along the edge of the front. In addition, phytoplankton stocks and production are highest on the Costa Rican Dome (about 9°N, 89°W), while zooplankton is more abundant and tuna catch highest along the edges (F. Miller, unpublished data, IATTC, La Jolla, CA, USA).

This pattern in the distribution of tunas along coastal fronts has led to the hypothesis that tunas do not enter the more turbid coastal waters because lower visibility reduces foraging efficiency; they remain along the edges of such habitats where the visibility remains high and capture prey from the coastal habitat as they stray into clearer water. An alternative explanation is that prey become concentrated in the front and are therefore more abundant than in either the coastal upwelled water or the offshore water. We believe sufficient data exist on the vision of fishes and underwater visibility to develop an optimal foraging model to test the visibility hypothesis.

3.3.6 **Movements**

Some evidence exists that variations in oceanographic conditions affect the timing of the onset of migration of albacore from one part of the North Pacific to another, and affect the rates of migration and routes that the fish follow during migrations. For example, the timing of the emigration of fish in the western North Pacific appears to be determined by conditions associated with the Kuroshio Current system (R.M. Laurs pers. comm.). Emigration from the eastern Pacific is not understood, nor have its relationships with ocean conditions been defined, except in general terms of seasonal cooling of the ocean (Flittner 1968). The routes followed by albacore on their migrations across the North Pacific are believed to be associated with the Transition Zone (McGary et al. 1961) and mid-ocean frontal structure (Laurs and Lynn 1977). The migration rates and aggregations of albacore in the mid-ocean are markedly influenced by the degree of frontal structure development (Laurs and Lynn 1977). Variation in oceanographic conditions might have similar effects on the well-defined spawning migrations of Atlantic and Pacific northern bluefin.

Much less is known of the migrations of skipjack and yellowfin, and even less is known of the effect of variation of oceanic conditions on their migratory patterns. In fact, some stocks appear to be more nomadic than migratory. In the eastern Atlantic skipjack follow a predictable route, apparently moving from one area of high productivity to another along the African coast (ICCAT 1984 ; Figure 14). They then seem to disappear from the coastal fishery, probably moving offshore along the equator. However, the seasonal movements may be more related to changes in forage availability than to an inherent migrational cycle. In contrast, the extensive tagging work on the South Pacific skipjack indicated no consistent patterns of movement, although fisheries in the region show a seasonal pattern. Broad trends must exist but they could not be resolved due to seasonal movement of the tagging vessel (Lewis 1981; Argue and Kearney 1982). The short-term (30 days or less) recoveries of skipjack indicated only dispersion, whereas over longer periods the tagging data show somewhat more directional consistency (A.W. Argue, unpublished data). As before, this indicates that the scale of movement is a critical consideration in studies of movements. Movements considered on a monthly basis may appear random, but with longer periods, patterns may emerge showing a net directional component. In other words, a fixed geographic coordinate system may be inappropriate for tuna, since a fish can follow the same inherent rules in such a system without following the same path.

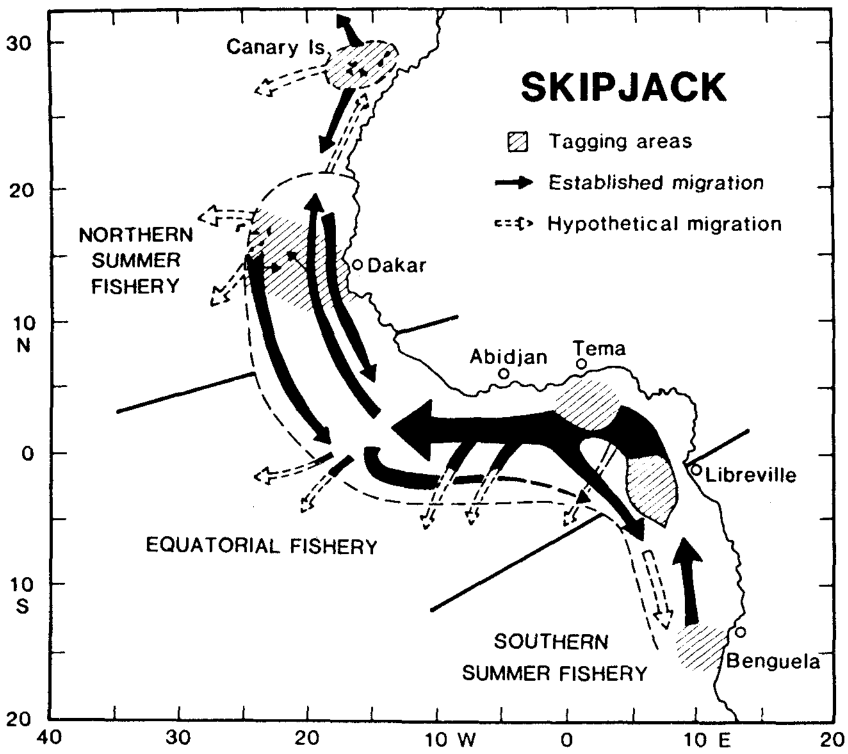


Figure 14. Migration pattern for skipjack tuna in the eastern Atlantic from International Skipjack Year Program tagging experiments (ICCAT 1984). Solid arrows depict observed movement of fish from tagging areas. Open arrows depict possible movements, not yet confirmed by tagging.

Other boundaries exist in the ocean that could be used as coordinates relative to which tuna distributions could be described. Moving frontal zones with which the tuna are associated is one such example.

Water motion affects fish during migration, but passive or selective transport (Arnold and Cook 1984) by currents has yet to be identified as the mechanism used by tuna in any of their migratory routes, although a number of such mechanisms have been postulated. Examples include the transport of skipjack young to the eastern tropical Pacific (Seckel 1972; Williams 1972), and movement of southern bluefin to their spawning grounds in the South Pacific and transport of their juveniles to Australian waters (Harden Jones 1984). The dispersive element in the short-term recoveries of marked skipjack and other tunas might also be related to water movements. If the fish were foraging in a limited area, they could be dispersed by the eddy motion of the water. The effects of water motion should be included in all studies of tuna movement or migration until it can be demonstrated that they are negligible.

The regular transoceanic movements of the temperate tunas suggest that tuna have the ability to navigate. Walker et al. (1984) have postulated a possible compass and piloting mechanism. In addition, yellowfin tagged off

Hawaii return to fish attraction devices on a regular basis and at about the same time of day (Holland et al. in press). The inherent navigational component of movements is not a key management issue in most tuna stocks because if it exists it is equivalent to the known average pattern. What we need to know is how to predict the anomalies from the average pattern. On the other hand, if a channeling of movements existed as a result of navigation cues, or transport by currents, it could have direct management implications.

3.3.7 Opportunities for Cooperative Studies

Major new initiatives in oceanography have started and are planned for the remainder of this century. These initiatives will provide new understanding of ocean structures and processes and provide opportunities for interdisciplinary studies. The Tropical Oceans, Global Atmosphere (TOGA) international program began in 1985. This program will lead directly into the World Ocean Circulation Experiment (WOCE) which is scheduled to begin in 1990. The first is particularly pertinent to studies related to tropical tunas. The latter program will make use of vast arrays of observations including those obtained from new satellite sensors measuring wind stress and sea level. It is probable that, when the programs are completed, the variability of the equatorial current systems and the thermocline depth can be modeled and predicted. As a result, more detailed information about ocean structure, ocean currents, frontal developments and distributions will become available.

Drifting buoys that can be tracked by satellites provide a new opportunity to study tuna movements as they are related to currents. The buoys could be deployed during a tagging cruise and the dispersive element of the water as reflected by both surface and subsurface buoys could be compared to the apparent dispersion of fish indicated from short-term or longer-term recoveries of tags. This experiment would test the hypothesis that variation in the headings or dispersion of short-term recoveries of marked tuna is related to transport by currents. This approach could be integrated with the TOGA program since, as part of TOGA, an extensive expendable bathythermograph observational program is in progress. Information, so far unavailable, will be obtained about the subsurface temperature structure and its month-to-month changes in the tropical Atlantic and Pacific.

In short, a wealth of environmental data will soon be available for the study of tuna movement dynamics. The data can be used to test hypotheses regarding movements using existing movement data. In addition, the programs provide a data field around which international sea experiments on tuna movements could be designed. Physical oceanographers are receptive to making their studies interdisciplinary, and funding agencies favor cooperative work. Cooperation must be sought with the oceanographers and their funding agencies to establish such an interdisciplinary program. Steps should be taken to combine fishery research objectives with those of international oceanography and to ensure that the wealth of incoming oceanographic data will be in a form useful for interpreting tuna movements. However, more data on actual paths of tunas must be obtained before any major advances can be expected in the dynamics of tuna movements, or before the wealth of environmental data can be fully utilized in the interpretations of movements.

3.3.8 Research Approaches

We need to forecast from physical data where tunas will be, their numbers, and their vulnerability to fishing gear. If their food distribution can be described and predicted or if habitats which are more likely to be selected by tunas can be described and predicted, then the distribution of tunas could be described and predicted. Thus, a model is added that describes the process of movements and then forecasts movements on the basis of the driving variables. Such a model would have great value where the fishery is composed of a mosaic of national jurisdictions. A model similar to this is being developed for North Pacific albacore (P. Kleiber pers. comm).

Powerful statistical techniques have recently been employed to identify tuna-environment relationships in the eastern tropical Atlantic (Mendelssohn and Roy 1986). These techniques involve multivariate, time series models that use temporal and spatial distributions of tuna, catch rates, and environmental properties such as sea-surface temperatures, mixed layer or thermocline depths, and wind stress. These models identify significant environmental properties, show phase relationships in cyclical fisheries, and identify lags between oceanographic events and increased catches. This type of model is most easily applied when obvious correlations exist between environmental conditions and catch, but the processes are not identified.

Research planning must consider whether funds should be expended to understand relationships between environment and movements or identify correlations. In the past, management needs seemed satisfied by the latter approach, but no consensus exists among experts on the preferred approach. One view was that it was preferable to link tuna movements to the environment by establishing cause and effect relationships, because past correlations have ultimately broken down. The alternative view was that such linkages were difficult to establish and difficult to apply to real fishery problems and that the proper approach was to become more sophisticated in measurement of the environment and tuna movements; then the correlations would hold. The latter view supports large-scale measurements and broad project objectives, whereas the former view would lead to a series of smaller-scale and highly focused investigations designed to test specific hypotheses. Examples are testing how movement rates vary with forage patterns and physiological state or how visibility affects foraging patterns. Extensive use of ocean measurements made by satellite should be most beneficial in such work.

The development of a major program on movement dynamics of tunas must address the issue of scales. Most management issues are large scale (5,000-10,000 km), whereas the events that affect movement on a daily basis are of smaller scale (50 km). The approaches to integrate these fundamental differences in scale will be a key issue in the development of a program on tuna movements.

3.4 Reexamination of Tuna Movement Data

This section addresses the importance of reexamining existing data as a prelude to developing a major research program on tuna movement. Much information on movement has been collected in the last 30 years for the six principal tuna species (skipjack, yellowfin, albacore, bigeye, northern bluefin, and southern bluefin). The primary data include conventional tag and recovery data and catch and effort data; secondary data include oceanographic and climatic data, data pertaining to stock identification, size and age of the catch, diet, reproduction and general ecology and biology of adults and juveniles. The approximate numbers of tag releases for each species in the world's oceans (Pacific, Atlantic and Indian Oceans) is roughly proportional to the distribution of current world catch (Tables 3 and 4).

Table 3

Approximate numbers of tag releases for the principal tuna species (from Bayliff, Fonteneau, and Kearney, pers. comm.).

Ocean:	Atlantic	Indian	Pacific	Total
Skipjack	35,000	0	280,000	315,000
Yellowfin	14,000	0	140,000	154,000
Albacore	6,000	0	25,000	31,000
Bigeye	8,000	0	1,000	9,000
Northern bluefin	23,000	0	15,000	38,000
Southern bluefin	-	0	60,000	60,000
Total	86,000	0	521,000	607,000
Percent	14.2	0	85.8	100.0

Table 4

The 1979 world catch in metric tons of the principal tuna species (from Joseph 1983).

Ocean:	Atlantic	Indian	Pacific	Total
Skipjack	87,714	32,662	578,309	698,685
Yellowfin	144,159	60,649	379,222	584,309
Albacore	74,325	12,233	114,696	201,254
Bigeye	33,060	31,632	121,684	186,376
Northern bluefin	13,330	-	20,108	33,438
Southern bluefin	7,629	18,142	7,109	32,880
Total	360,217	155,318	1,221,128	1,736,663
Percent	20.7	8.9	70.3	100.0

New lines of research could be explored through further analyses of existing tag recovery, catch-effort, oceanographic, climatic and other data. Investigators could attempt the following: identification of hydrographic and climatic features that have the greatest impact on movement and concentration of tunas; examination of seasonality in fisheries as it relates to movements of tuna (from catch-effort and tag recovery data); examination of directionality of tuna movements and of interaction among tuna fisheries (cooperative examination of tag recovery and catch-effort data); analysis of tag recoveries in relation to the size (age) of tuna in the fishery at the time the tags were recovered; cooperative examination of tag recapture data, oceanographic data and data on forage items (from diet samples), which might be indicative of tuna movement among ocean domains; and comparative studies of species and stocks.

With further analysis of existing data, the research proposed in this report could be refined, as could development of specific research hypotheses. On the other hand, without combining data from various regions and international and national agencies, exploration of existing data could prove misleading. For example, when blood electrophoretic data for Pacific skipjack included only those samples collected by the United States and Japan (Figure 15), it was hypothesized that skipjack in the Pacific comprised several subpopulations (stocks). When samples collected by the South Pacific Commission were included (Figure 16), it was concluded that clinal population structure was a reasonable alternative hypothesis. Tag and recovery data provide an example of how examination of large data sets can change conceptual models. If one examined only skipjack tag and recovery data collected by Japan in the central and western Pacific (Figure 17, upper), one would define the extent of skipjack movement much differently than if one had also examined the South Pacific Commission data (Figure 17, lower) and the Inter-American Tropical Tuna Commission data (Figure 18, upper). In Figure 18 (lower), which combines the long-distance movements from all three data sets, it can be seen that there is exchange of skipjack among each of the study areas although only a limited portion of the stock may make such extensive movements.

To a large extent tagging data cannot be analyzed without catch and effort data. Such data are usually confidential when used at the level of an individual vessel, but need not be so when vessels or vessel trips are not identifiable. To make the proper interpretations of results from integrated analysis of movement and fishery data one must have considerable experience with the fisheries. The same could be said of the integrated analysis of movement and oceanographic data. Agencies such as ICCAT are at an advantage in this regard because they maintain data bases on tagging and fishery statistics for several countries in an area that covers the range of most stocks of Atlantic tunas. The scientists associated with ICCAT thus have the benefit of a) complete sets of data, and b) the experience necessary to analyse the data. Similar regional systems are being established in the Indian Ocean by the Indo-Pacific Tuna Development and Management Programme (IPTP) and in the Western Pacific Ocean.

Clearly the benefits of a coordinated analysis of existing data are substantial. An important first step in development of an international research program on tuna movement would be to make available historic tagging data for analysis with fishery and oceanographic data. Cooperative analysis of these data could yield relationships not previously identified that in turn would affect structure and cost of a new research program.

3.5 Ultrasonic Telemetry

Deployment of ultrasonic transmitters on free-ranging tunas has provided nearly all present information on smaller-scale, horizontal and vertical movements. Investigators have followed tunas so equipped for up to 8 days, successfully tracking skipjack, yellowfin, bigeye, northern bluefin and albacore. A successful track--that is, a reported track--usually lasts over 5 hours, as shorter ones generally are not reported.

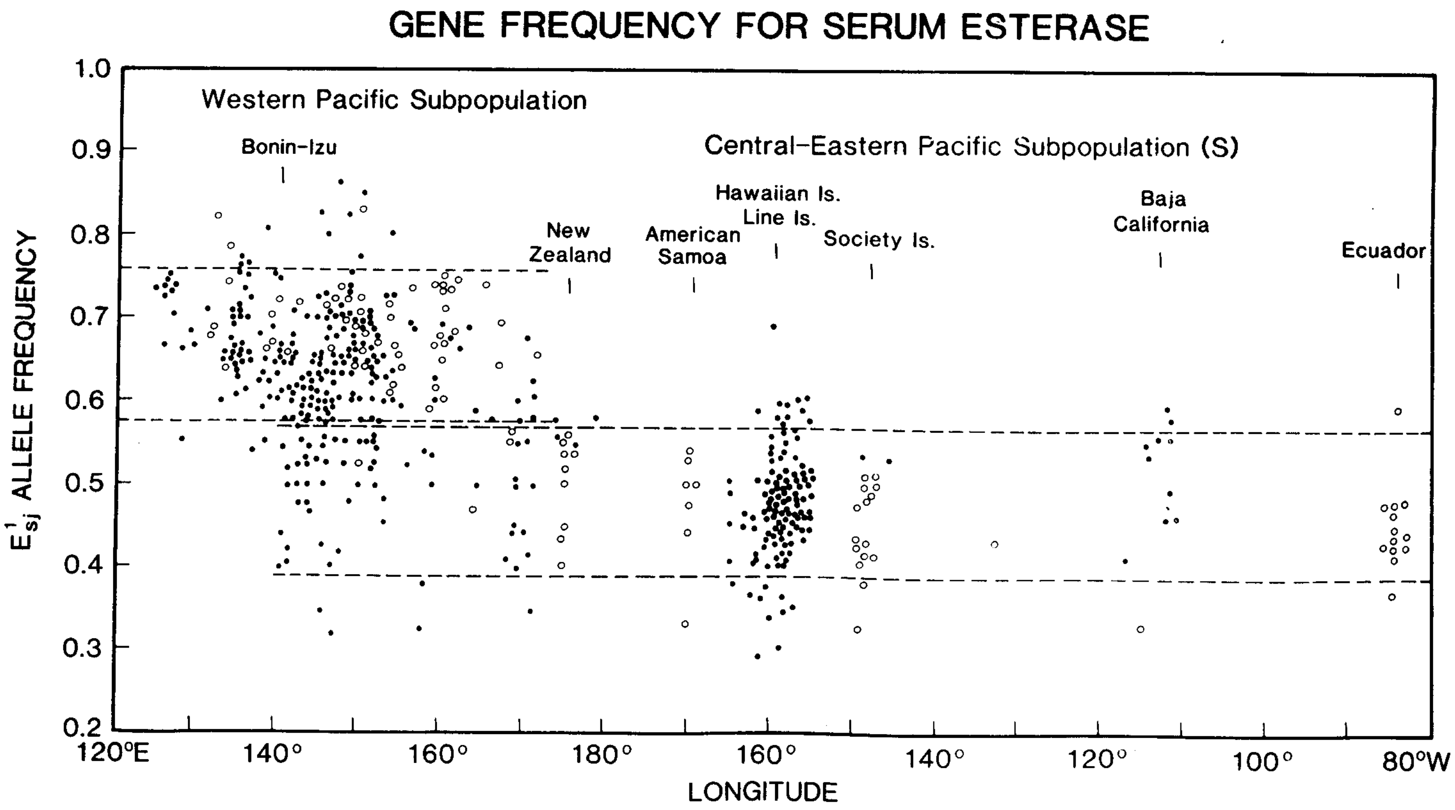


Figure 15. Gene frequency for serum esterase allele E^1_{sj} vs longitude of the sample location in the Pacific Ocean (from Fujino et al. 1981). Small dots and open circles represent individual lots of samples taken from the northern and southern hemispheres respectively. The dashed lines represent the 95% confidence limits of the "Western Pacific Subpopulation" (upper) and the "Central-eastern Pacific Subpopulation" (lower).

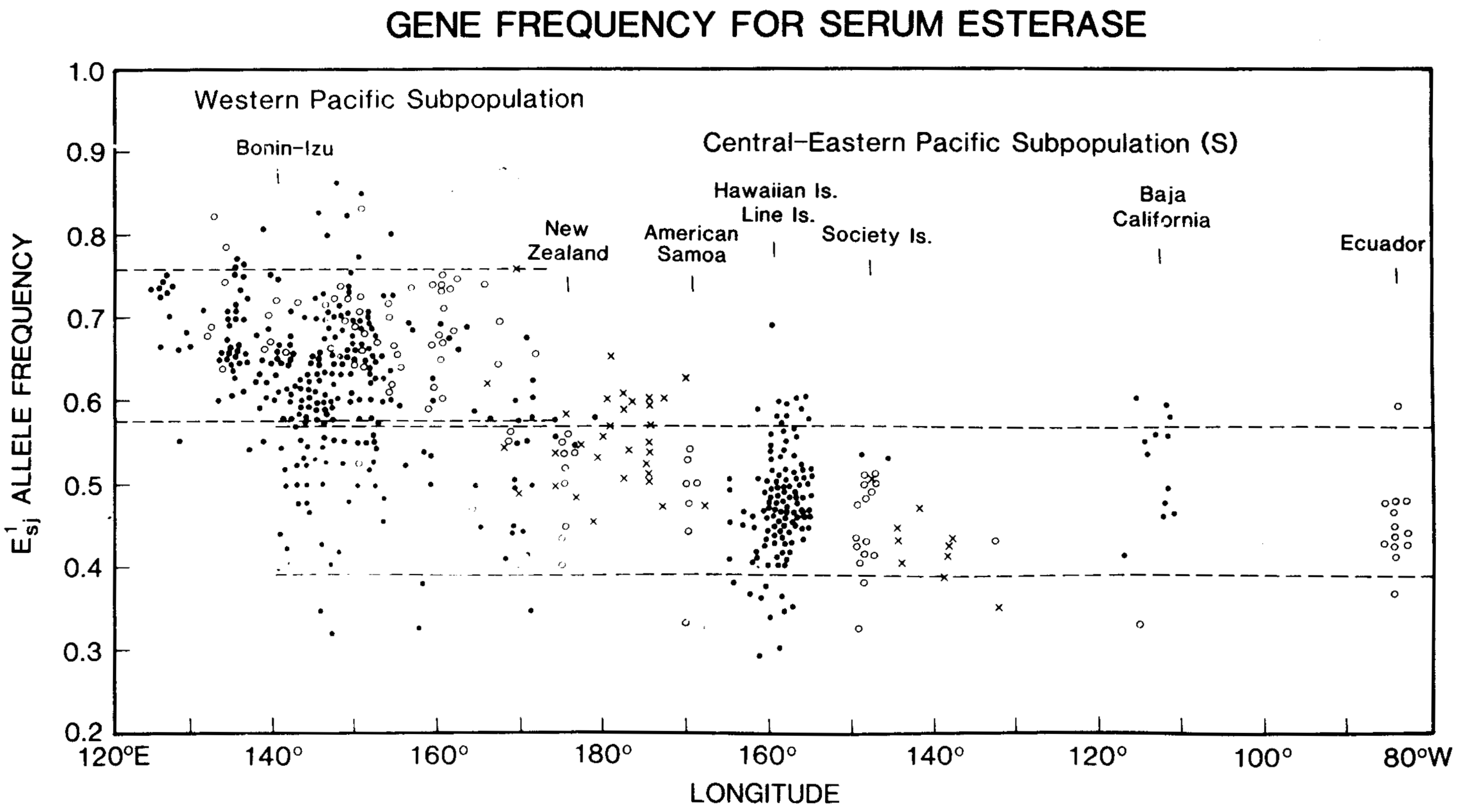


Figure 16. Gene frequency for serum esterase allele E^1_{sj} vs longitude of the sample location in the Ocean (from Fujino et al. 1981). Small dots and open circles represent individual lots of samples taken from the northern and southern hemispheres respectively. The crosses are South Pacific Commission samples (SPC 1981). The dashed lines represent the 95% confidence limits of the "Western Pacific Subpopulation" (upper) and the "Central-eastern Pacific Subpopulation" (lower).

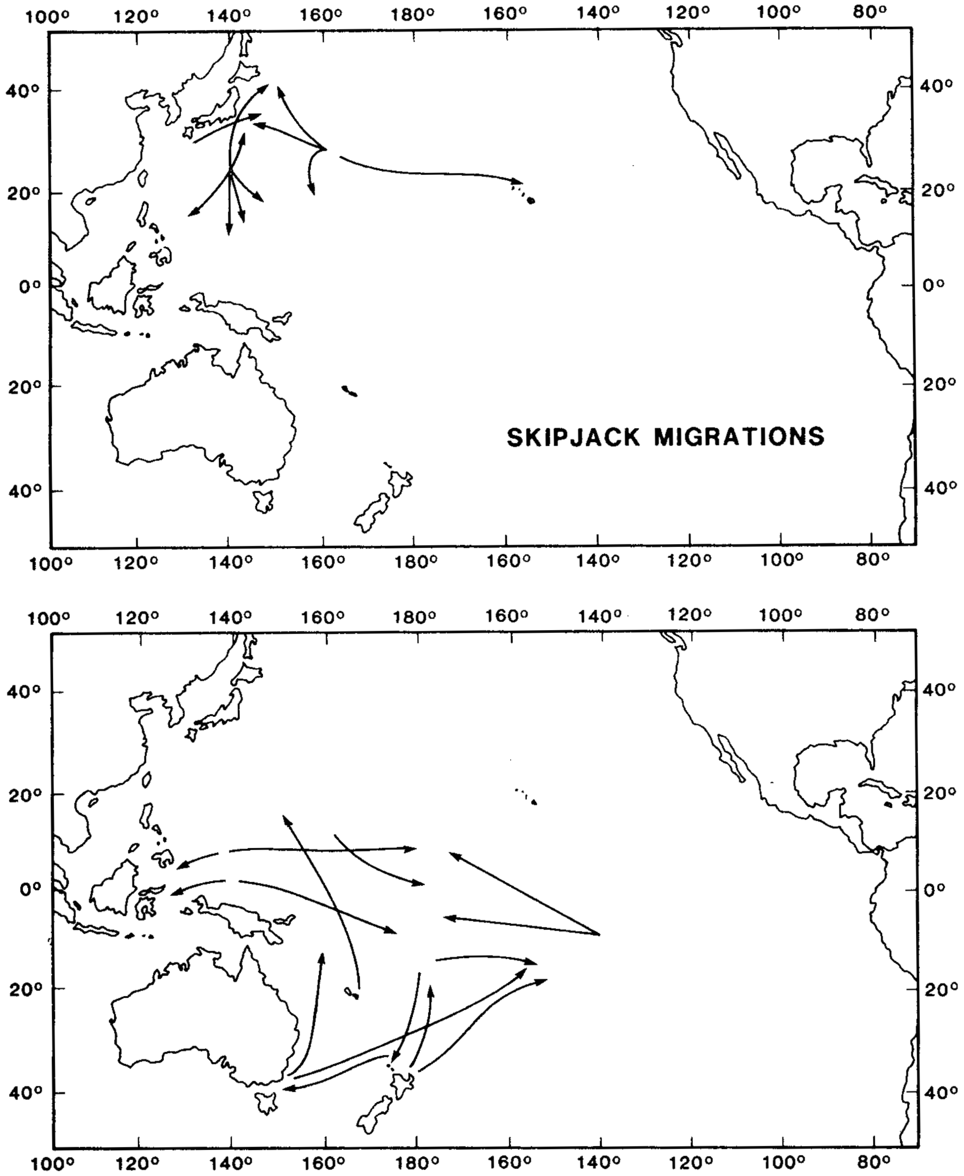


Figure 17. Upper; some long-distance migrations which have been recorded for tagged skipjack released by Japan in the Pacific Ocean (after IATTC 1984). Lower; some long-distance migrations which have been recorded for tagged skipjack released by the South Pacific Commission in the Pacific Ocean (after IATTC 1984; SPC 1984).

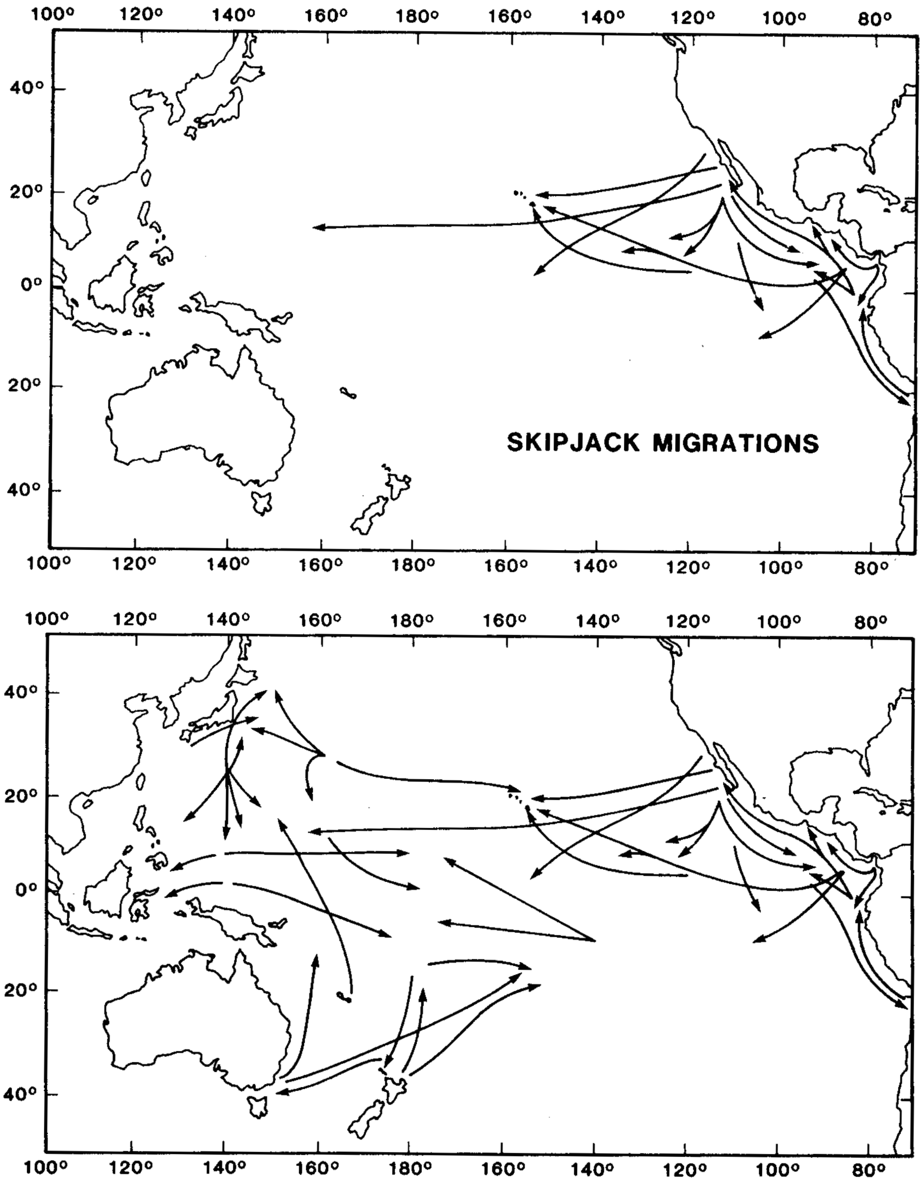


Figure 18. Upper; some long-distance migrations which have been recorded for tagged skipjack released by the Inter-American Tropical Tuna Commission in the Pacific Ocean (after IATTC 1984). Lower; some long-distance migrations which have been recorded for tagged skipjack in the Pacific Ocean (from IATTC 1984; SPC 1984).

While the fish is followed, data are collected that identify the horizontal path of the fish. If the transmitter is temperature- or depth-sensitive, data may also be collected on vertical excursions, temperature and depth distributions, swimming speed and associated oceanographic and biological correlates. Data on vertical position or water temperature have been collected at less than one-minute intervals, providing a highly detailed picture of the vertical excursions of free-ranging tuna. The only comparable data are some early observations using cine films of surface-feeding tunas taken from observation chambers of research vessels (Strasburg and Yuen 1960; Yuen 1966) or using sonar (Nishimura 1963; Yuen 1971).

In the following sections we outline typical tracking techniques, summarize the existing tracking data, identify some uncertainties, suggest a few management uses of ultrasonic tracking and draw three major conclusions from the existing tuna tracking information.

3.5.1 **Tracking Techniques**

(1) **The Transmitter**

Typically, the basic tracking system consists of a temperature- or depth-sensitive transmitter secured to the fish which is detected by directional hydrophone and receiver system located on the ship. The bearing of the fish, relative to the vessel, is determined by signal amplitude. The swimming depth or water temperature around the fish is telemetered by alterations in the pulsed repetition rate of the carrier frequency. The more rapid the pulse rate, the shallower the depth or the warmer the temperature.

Three major design criteria exist for a telemetry tag: size, life, and range. They are mutually exclusive because small size means small batteries and high resonant frequencies, which in turn limit life and range. If battery size is held constant, life is sacrificed for range or vice versa. Range, size and life are, in turn, determined by the source level or power of the transmitter, the carrier frequency, the pulse rate and length of the temperature- or depth-telemetering functions, and the size of the battery (Priede 1986).

To gain the maximum range from the minimum power input, the lowest possible carrier frequency should be employed. However, the resonant frequency of the signal generating element, the piezo-ceramic transducer, is inversely related to its size. Since the transducers are usually hollow cylinders, the largest tag diameter allowable for a particular application determines the minimum frequency. For tuna 40-80 cm long, 35 or 50 khz is usually employed in a tag of about 1.6 cm in diameter. For these frequencies a range of about 1 km under average tracking conditions is considered normal.

(2) **Attachment of the Transmitter**

In earlier tracking studies, the tag was forced into the stomach of tuna; when water temperature was monitored, a lead was run from the tag, through the opercular slit, to a thermistor exposed to the surrounding water. While having the advantage of rapid application and minimum trauma, two disadvantages readily became apparent. First, if the tag was large relative to the stomach volume, the tag was regurgitated, usually within hours. Second, the signal seemed significantly weakened by the fish's body (Laurs et al. 1977). As a result, in most recent studies tags are attached externallly using sutures or nylon "tie-wraps". The tag is placed either distal to the second dorsal or the anal fin or, in the case of bluefin (Carey and Lawson 1973), harpooned to the dorsal surface adjacent to the first dorsal fin. Wobbling of the tag, which causes erosion of the skin and underlying muscle, is eliminated by suturing at the front and midline of the tag (Holland et al. in press).

(3) Tracking Procedures

Tracking procedures are described by Holland et al. (in press), and will not be discussed in detail here. For successful tracking it is essential that the hydrophone be shielded from the water stream and securely mounted. It is important that the signal can be received while the boat is underway at a fairly brisk speed (approximately 6 knots). Holland et al. (in press) also emphasized the importance of crew comfort; successful tracking demands an alert crew since tuna can swim faster than the boat for short periods of time. If a fish is lost the crew must be aware of its escape direction to relocate it.

Since the boat is usually within about 1 km of the fish, horizontal position of the boat and the tracked fish is considered the same; positions are usually taken every 30 to 60 min. The pulse interval of the tag is converted to depth or water temperature by applying conversion factors determined by calibration. Generally these measurements are made at 1-3 minute intervals either by laborious counting by ear and timing with a stop watch, or automatically by pulse interval or frequency counters. Holland et al. (in press) employed a tape record to make a permanent record of the track for later analysis with a pulse interval meter connected to a microcomputer. From these measurements and temperature-depth profiles taken by expendable bathythermograph, temperature and depth distributions are constructed for each fish. Total path swum is considered to be a sum of movements between depth position to depth position along the hypotenuse of a triangle projected on a vertical plane whose horizontal leg was determined from 30-60 minute position information. Swimming speed estimates are thus an improvement over those obtained from just horizontal movement, but are still underestimates of true swimming speeds especially when the fish make frequent brief changes in heading. Estimates of swimming speed are, of course, most accurate during periods of relatively fast movement on a steady course.

3.5.2 Tuna Tracks to Date

Fifty-three successful tracks of tunas have been reported as of August 1985 (Table 5). The tracks averaged 26.75 hrs, ranging from 1 hr to 10 days, although the two longest tracks reported (168 hrs, Yuen 1970 and 144 hrs, Holland et al. [in press]) were intermittent tracks where the fish was either lost or abandoned and relocated later. Only reported tracks are considered here, although other unreported, and presumably unsuccessful (i.e. very short), tracks exist. Carey and Lawson (1973) mention five bluefin tracks that were of adequate duration (presumably), but they presented no data because the fish remained in water of constant temperature and they were interested primarily in thermoregulatory behavior.

The first successful tracks of tuna were by Yuen (1970); he tracked two skipjack in the waters off the island of Oahu, Hawaii. A notable feature of these tracks was the striking ability of the fish to move away from and return to a precise location each day. The skipjack spent the day on a shallow bank; within a couple of hours of sunset, they swam away from the bank on a fairly straight course until about 2 AM (local standard time), and then a more erratic swimming pattern was observed. Although the fish swam away from the bank by different courses each night, it was usually back at the same location on the bank by sunrise. Yuen (1970) believed that the fish swam faster at night.

Table 5

Successful ultrasonic tracking of tunas.

Species	Size	Month/Year	Area	Duration (hr)
Yuen (1970)				
Skipjack	44 cm	8/1969	Kaula Bank, HI	168
Skipjack	40 cm	8/1969	Penguin Bank, HI	12
Carey and Lawson (1973)				
Bluefin	230 kg	8/1969	St. Margaret Bay,	6
Bluefin	270 kg	7/1970	Nova Scotia	22
Bluefin	270 kg	7/1970	"	13
Bluefin	230 kg	7/1970	"	24
Bluefin	270 kg	7/1970	"	32
Bluefin	230 kg	7/1970	"	56
Bluefin	230 kg	5/1970	38°N, 71°W	23
Bigeye	70 kg	10/1970	39°N, 70°W	17
Laurs, Yuen and Johnson (1977)				
Albacore	84 cm	8/1972	36°N, 122°W	28
Albacore	87 cm	8/1972	36°N, 122°W	41
Albacore	85 cm	8/1972	36°N, 122°W	50
Dizon, Brill and Yuen (1978)				
Skipjack	70 cm	5/1977	Penguin Bank, HI	24
Skipjack	70 cm	5/1977	"	11
Skipjack	70 cm	5/1977	"	10
Carey and Olson (1982)				
Yellowfin	87 cm	4/1981	8°N, 79°W	9
Yellowfin	89 cm	4/1981	8°N, 79°W	46
Yellowfin	98 cm	5/1981	10°N, 109°W	18
Yellowfin	96 cm	5/1981	10°N, 109°W	48
Yonemori (1982)				
Yellowfin	63 cm	11/1981	1°S, 158°E	9
Yellowfin	68 cm	11/1981	1°S, 158°E	8
Yellowfin	70 cm	11/1981	1°S, 158°E	15
Yellowfin	64 cm	11/1981	1°S, 158°E	32
Bard and Pincock (1982)				
Skipjack	44 cm	7/1981	5°N, 0°E	3
Skipjack	45 cm	7/1981	2°N, 4°E	7
Levenez (1982)				
Skipjack	55 cm	11/1981	9°N, 21°W	44
Skipjack	53 cm	11/1981	9°N, 21°W	19

Table 5. (continued)

Dotson (personal communication)				
Albacore	73 cm	7/1979	31°N, 119°W	31
Albacore	86 cm	7/1979	31°N, 121°W	29
Albacore	76 cm	9/1979	32°N, 121°W	8
Albacore	88 cm	7/1980	32°N, 121°W	12
Albacore	86 cm	8/1980	32°N, 121°W	7
Albacore	82 cm	8/1980	32°N, 121°W	1
Albacore	87 cm	8/1980	33°N, 120°W	3
Albacore	80 cm	8/1981	33°N, 124°W	11
Albacore	79 cm	8/1981	33°N, 124°W	23
Albacore	68 cm	8/1981	33°N, 124°W	15
Albacore	83 cm	8/1981	33°N, 124°W	22
Albacore	80 cm	2/1982	31°N, 139°W	14
Albacore	85 cm	2/1982	31°N, 139°W	25
Holland (personal communication)				
Bigeye			Leeward Oahu, HI	24
Bigeye			"	28
Yellowfin			"	5
Yellowfin			"	24
Yellowfin			"	48
Yellowfin			"	9
Yellowfin			"	12
Yellowfin			"	14
Yellowfin			"	40
Yellowfin			"	144
Yellowfin			"	36
Yellowfin			"	38
			AVERAGE TRACKING DURATION	26.75

Carey and Lawson (1973) were interested primarily in demonstrating that bluefin were capable of physiological thermoregulation. They used temperature-sensitive sonic tags and published only the tracks in which bluefin showed an inverse thermal response to water temperature changes, i.e. water temperature decreasing, fish temperature constant or increasing. Some of the published tracks did show what was later found to be a common tuna behavior, namely, dramatic and frequent vertical excursions. The fish made abrupt dives periodically from surface water of 18°C to the thermocline at 4-5°C.

In 1972 Laurs et al. (1977) tracked albacore and, for the first time, complete oceanographic measurements were taken by a second vessel to correlate fish movement with habitat. They observed that albacore concentrated in the vicinity of upwelling fronts (for feeding?) and moved away from an area when upwelling ceased and the front disappeared. The albacore also seemed to avoid water where the surface temperature was below 15°C.

Dizon et al. (1978) employed depth-sensitive, rather than temperature-sensitive, tags for tunas. They tracked three large skipjack and described the characteristic vertical diving and ascending behavior and modal depth, temperature and swimming speed values. Dives were noted from the surface to as deep as 273 m; during the day, their modal depth was in the lower part of the mixed layer, but at night the fish spent more time near the surface, and extreme vertical excursions were much less common.

Carey and Olson (1982) observed that yellowfin in the eastern tropical Pacific swam in the region between the surface and the bottom of the thermocline, but spent most of their time in the upper part of the thermocline, and occasionally made very deep dives--one fish dove to 464 m (Figure 19). They noted that the tracked yellowfin spent little time at the surface, and suggested that feeding yellowfin might spend more time in the mixed layer but migrating or non-feeding fish would be found in the thermocline. This concept of a characteristic depth used when migrating would be observed by later investigators.

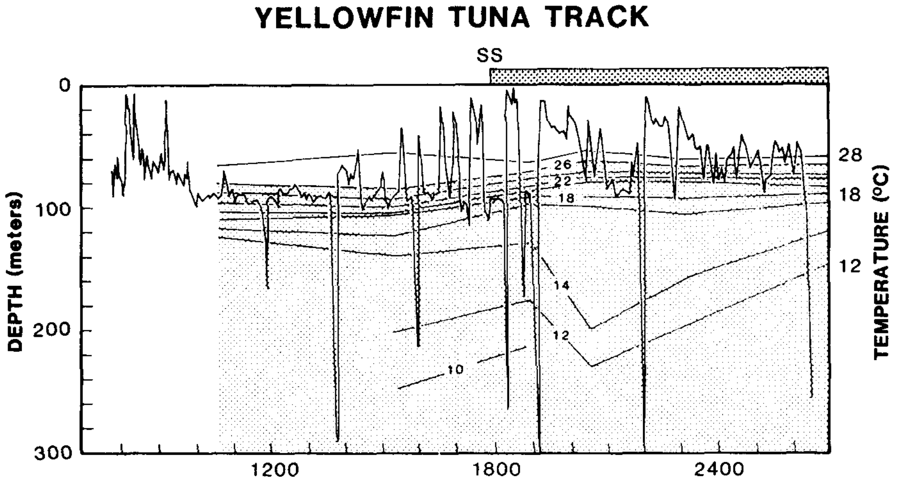


Figure 19. Vertical projection of a track of a 98-cm yellowfin tuna (#4, 12-13 May 1981; redrawn from Carey and Olson 1982). This fish was tracked for 18 hours near Clipperton Island (10°N, 109°W). At 0225 hours this fish dove to 464 m. SS is sunset. The stippling denotes water below the top of the thermocline.

Yonemori (1982) successfully tracked four yellowfin somewhat smaller than those of Carey and Olson (1982) in the western Pacific around "payaos," a Philippine fish aggregation device. He observed similar, very active, vertical excursions. The deepest dive was to 200 m. At about an hour before sunrise, the fish made an abrupt transition from a modal depth (50 m) in the mixed layer (29°C) to a modal depth (175 m) in the middle of the thermocline (22°C) (Figure 20).

Bard and Pincock (1982), tracking two skipjack in the Gulf of Guinea, noted that the thermocline or some associated property limited vertical movements to the upper 50 m (17°C). In contrast, Levenez (1982) observed spectacular diving behavior in two somewhat larger skipjack tracked west of the Gulf of Guinea. One fish preferred a modal temperature of 28°C, but periodically dove to below 14°C. The other fish also spent the majority of its time in the upper mixed layer where the water was quite warm (24-28°C), but deep dives were persistently made--to more than 400 m where the temperature was 9.5°C and the oxygen was less than 1.5 ml/l.

The 6 albacore tracks from the North Pacific demonstrated that their behavior, like that of other tracked tunas, is characterized by dramatic and frequent vertical excursions (Laurs et al. 1980; Dotson pers. comm.). They noted that albacore, like skipjack, swam deeper during the day, but in

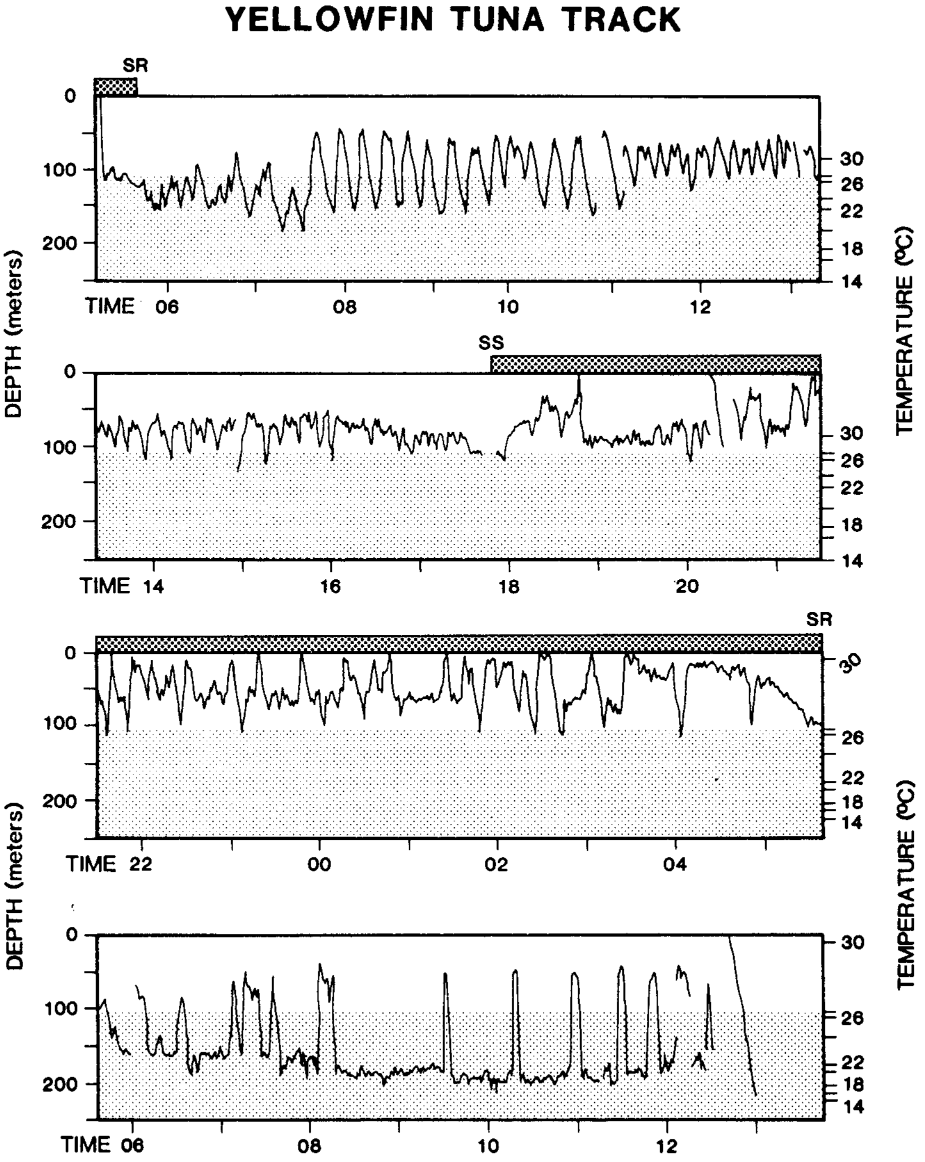


Figure 20. Vertical projection of a track of a 64-cm yellowfin tuna caught around a payao (redrawn from Yonemori 1982). This fish was tracked for 32 hours in the vicinity of 0°55'S, 157°53'E. Toward the end of the track, the fish spent the majority of the time well below the thermocline. SS is sunset and SR is sunrise. The stippling denotes waters below the top of the thermocline.

contrast to skipjack, spent most of the time in the upper thermocline. Albacore apparently oriented to a seamount in a manner similar to that described by Yuen (1970) for small skipjack orienting to banks.

Holland and co-workers (NMFS, Southwest Fisheries Center, P.O. Box 3830, Honolulu, HI, 96812) have tracked tunas over the past 2 years usually on the leeward (southwestern) side of Oahu, Hawaii, using a small (10-m) vessel. The combination of protected waters, a highly-efficient tracking vessel, refined tracking techniques (Holland et al. in press), and a system of fish aggregation devices (FADs) have yielded excellent results (Holland pers. comm.). To date, 10 yellowfin and 2 bigeye have been followed, and their behavior is essentially the same as that reported in previous studies: abrupt vertical migrations, modal depth in the upper thermocline or lower mixed layer for the yellowfin and the lower thermocline for the bigeye, and precise orientation to specific features (payaos, banks, or seamounts). The bigeye also demonstrated highly periodic, similar ascents from depth. Supported also is the concept of migrations occurring at depth and the fish shoaling at night.

3.5.3 **Uncertainties**

Some uncertainties exist in the interpretation of tracking records. A key issue is whether the behaviors noted are normal or the result of trauma caused by the attachment of the tag or disturbances produced by the tracking vessel. Holland (pers. comm.) was told that a fisherman had recovered, by trolling, a transmitter-tagged fish which had been at liberty 3 weeks. The fish obviously was healthy enough to feed and appeared normal (except for the tag) to the fisherman. Also, many of the investigators reported that their transmitter-tagged fish had joined a fish school.

Another caveat to any generalizations drawn from the data is that the tracked fish represent a relatively narrow size range of the representative species. There is no way of knowing if the behaviors observed, particularly the dramatic vertical excursions and the modal or preferred temperature, are typical of the large size classes of the various species, since data exist (except those of Carey and Lawson 1973) only for the smaller individuals.

Swimming speeds estimated from the horizontal and vertical components of a tuna movement vector are minimums. Small horizontal excursions not observable from the tracking vessel might be a significant portion of the total energy expenditure. In fact, the estimated swimming speeds from ultrasonic tracking work generally are below Magnuson's (1973) theoretical minimum for maintaining hydrostatic equilibrium during horizontal swimming.

3.5.4 **Management Implications**

Holland and co-workers (pers. comm.) and Yonemori (1982) attached transmitters to tunas to examine behaviors in association with FADs. Holland suggested that a knowledge of horizontal movements between and around various aggregation devices would enable managers to be more effective in FAD placement, and density, depth of placement, and fishing strategies could be evaluated.

Tracking data also seem useful for directing fishing effort, since information on habitat preferences could be used to determine fishing depths and temperatures. Tracking information could also be used to describe escape responses when tuna are encircled by a purse seine. Drawing on observations that purse seining is less effective in the western as opposed to the eastern Pacific, Green (1967) suggested that vulnerability to a purse seine is markedly reduced when the thermocline is deep because tuna avoid swimming into or through the thermocline, but tracking information contradicts Green's (1967) explanation. Yellowfin tracked in the eastern and western Pacific (Carey and Olson 1982; Yonemori 1982) show no reluctance to penetrate and inhabit the thermocline (Figures 19 and 20).

Ultrasonic tracking also provides critical data for the construction of energy budgets and growth models. Transmitter-equipped fish provide the only source of information on distribution of swimming speeds, and hence estimates of daily energy requirements. Perhaps most important, tracking provides accurate information on the vertical movements and distribution, a key information need for virtually all work on movement dynamics of tunas.

3.5.5 **Conclusions**

Four concepts concerning small-scale movements of tunas of the size range and species tracked have emerged from the tracking efforts to date:

(1) Tracking records of tuna demonstrate persistent, frequent, rapid and extensive vertical excursions. Owing to the rapid rate of descent or ascent, (records have a characteristic spiky appearance) the fish is submitted to rapid and large temperature and pressure changes. This must affect its ability to sense and respond to subtle horizontal temperature differences. Speculations on the use of these horizontal temperature gradients for orientation must be tempered by this observation.

(2) At night the modal depth of tuna shoals usually shifts from deeper layers to layers near the surface, and sometimes this is characterized by heightened vertical excursion activity at dawn and dusk.

(3) Several investigators (Carey and Olson 1982; supported by Holland pers. comm. and Dotson pers. comm., NMFS, Southwest Fisheries Center, La Jolla, California, USA) suggest that migrating tunas make fewer vertical excursions and maintain a lower modal depth than fish believed to be feeding. When tuna are maintaining a steady compass heading, fewer vertical excursions are noted. Identification of a species-specific traveling or migrating depth range or temperature range would be extremely useful, and present reports indicate that they may exist for certain habitats. Work by Laurs and Dotson and by Holland et al. may clarify this point when published.

(4) Cursory inspection of the illustrations of the tracking records indicates that the modal temperatures experienced by the various tagged fish appear to be very different. Striking differences in temperatures experienced by the fish appear to exist between day and night. Also abrupt shifts in modal depth or temperature were sometimes seen in fish in the same area and even in the same fish. It would have been instructive to summarize these modal depths and temperatures, but most of the authors do not provide such data.

Holland et al. (pers. comm.) speculated that the persistent vertical excursions have a thermoregulatory function, and serve to provide a more consistent internal temperature since internal temperature lags the water temperature, especially in large fish, (Neill and Stevens 1974; Stevens and Neill 1978). For example, many excursions into cool, deep water could compensate for high levels of feeding activity in the warm water of the mixed layer. Or frequent ascents into the mixed layer could, in contrast, compensate for relatively lower activities as the fish migrates in the thermocline. We suggest that the relationships developed by Neill and co-workers (Neill and Stevens 1974; Neill et al. 1976; Dizon et al. 1978; Stevens and Neill 1978; Dizon and Brill 1979, a) for estimating internal body temperature based on size, activity, and water temperature could be applied to time series of swimming speeds and water temperatures obtained from the tracks to examine changes in the theoretical internal temperature.

It might explain the seemingly chaotic ambient temperature changes apparent in the tracking record and show that the persistent vertical excursions are indeed behavioral thermoregulation.

4. POTENTIAL TECHNOLOGY

In the following three sections we discuss techniques which might be applied or are beginning to be applied to the study of tuna movement dynamics. These technologies include development of new tagging systems, measurement of physiological state, and reconstruction of movement histories from microconstituents of mineralized tissue.

4.1 Future Tagging Systems for Tuna

Of considerable importance to the study of the movements of tunas are tagging systems that might be used to: 1) increase the recovery rates over those of conventional tags; 2) assure that complete and correct data are secured for each tagged fish recovered; 3) provide a fishery-independent system that identifies fish position; and 4) extend our knowledge of the paths followed by tunas beyond the time and space limits of tracking individual fish using acoustic tags (about 3 to 5 days, 300-1000 km).

Six tagging systems or approaches are discussed here in varying degrees of detail. This is not an exhaustive list, but merely the systems which emerged from our discussion. The systems we describe differ in the degree of practicality, costs, and applicability to specific fisheries or fishery problems. We occasionally give approximate costs in U.S. dollars (1985) of tagging equipment or of research and development. These are merely the best guess of the panel and experts. The subject of telemetry systems is also reviewed by Mitson (MS).

4.1.1 Fishery-dependent, Auto-detectable Systems

An ideal fishery-dependent tag recovery system is one in which the identity code of a marked fish and possibly other data (position of vessel and time of capture) are automatically recorded when a fish is caught. No such tagging system presently exists, nor it is likely that one will be developed in the near future. On the other hand, automatic tag detection systems exist and an automatic reading tag is under development for salmon. Each is discussed below.

(1) **Coded Ferromagnetic Implanted Tags**

Tuna tags are recovered by fishermen, unloaders and cannery workers, who are requested to return them to fishery agencies along with data on date of capture, fish size and other details. Tags are often recovered but are not returned or returned with incomplete or incorrect data. This problem could be eliminated with the use of hidden tags which are detected automatically. Existing systems in salmon and herring fisheries, developed by Northwest Marine Technology (Shaw Island, Washington, USA; Jefferts et al. 1963) allow the injection of coded, magnetically-detectable tags into juvenile or possibly larval fish. These inert tags remain in the tissue and are recovered upon capture; recovery involves either an automatic system which, when triggered by a magnetometer scanning the conveyor belt in the processing plant, diverts a portion of the catch for examination, or a hand-held magnetometer used to examine the catch for tagged specimens.

Depending on the size of the tag (< 1 mm and up), binary codes are permanently etched or notched into the inert tag material. After the tagged fish is identified, the tag is dissected from the fish and read under a microscope. Alternatively the fish head can be x-rayed and the code (notches) read in the radiograph.

Costs of the tags (about $0.15 each for individually coded tags) and a hand-held tagging gun (0.5-1.0 K$) are modest, but the cost of an automatic tag detection system that could be installed in a tuna cannery would be expensive (75-100 K$), require research and development, and be practical only for some canneries. A hand-held magnetometer (3 K$), with which the port sampler scans the fish while they are being unloaded, would be more practical for tuna.

(2) Passive Integrated Transponder (PIT) Tag

The PIT system, developed by Identification Devices, Inc., Westminister, Colorado, USA, is currently being evaluated as an automatically-read tag for salmon (Prentice and Park 1984). The tag automatically transmits the identity codes of salmon as they move at 3 m/s through a 30-cm dia. tube; 94% readability has been recently obtained (E. Prentice, pers. comm., National Marine Fisheries Service, Manchester Fisheries Research Laboratory, Manchester, Washington, USA). The PIT tag is small (10 x 2.1 mm) and has no power source, but responds to a strong radio frequency (RF) pulse with a serial message. The RF pulse provides power to the circuitry for the message transmission. The fish identification, of course, is encrypted in the message. The tag is presently injected intraperitoneally with a hypodermic syringe; laboratory work indicates tag implantation produces no noticeable effects on growth or incidence of disease in salmon (Prentice and Park 1984).

The PIT system would be impractical for tunas at present because of its short detection range (7.5 cm) and high cost of development, but technological developments might make the system practical in the future. Development of the PIT system for salmon is proceeding under the supervision of Earl Prentice (address given above), and it is anticipated that a pilot installation for salmon will be functional by the summer of 1985.

4.1.2 Tags That Indicate Geographic Position

A major information gap exists between the short (1-3 day) highly-detailed paths of acoustically-tracked tunas and the two position points recorded for marked and eventually recaptured fish. Many (Joseph and Wild 1984) have recognized the need for combining the advantages of the two approaches. The major barriers to expanding the time scale and coverage of acoustic tracking of tuna are: crew endurance (3-5 consecutive days is the maximum that can be expected of a single crew) and vessel costs (at present the limit is one fish tracked per vessel). The life of the present commercially-available acoustic tags (20 or more days) is far beyond the endurance of a single crew. As endurance is increased by using bigger vessels and larger crews, cost mounts precipitously. We discuss below the advantages and disadvantages of three potential systems that could increase the number of fish tracked and the duration of the track. A more detailed technical discussion of the limitations of acoustic and satellite tracking systems is provided by Priede (1986).

(1) Sonobouy-Transponder Systems

A system composed of a number of small floating receivers in fixed positions and transmitters attached to many fish would be practical under certain conditions. When a transmitter-equipped fish swam within the range, the receiver would record or rebroadcast the identity code of the fish. Conventional pulsed ultrasonic tags would be impractical for this application because their range would be too short, since the system would probably be based on an omnidirectional hydrophone. A scanning hydrophone would greatly increase costs. Detection range could be increased to some extent by using transponding tags on the fish. Transponders have the advantage of longer life (the transmitter transmits only when queried) and larger range, since signal-to-noise ratios are improved because of the relatively precise relationship between the query signal and the return from the tag.

Inexpensive ($200) anti-submarine warfare (ASW) sonobouys could be used as receivers; ASW sonobouys are wide-band ultrasonic receivers which rebroadcast the received acoustic signals on very high frequencies (VHF) to stations located within line-of-sight of the buoys. However, extensive modifications would be required for their use in a transponder system: a transmitter would have to be installed to query the area periodically for the presence of tagged fish; the receiver section would have to be modified from wide-band to a narrow frequency band centered on the tag's frequency; and the buoy transmitter would have to be altered to retransmit on frequencies other than the ASW ones, or if the system needs recording capabilities, those would have to be installed. These modifications of the ASW sonobouys would probably cost $1000-$3000 per buoy.

The transponding fish transmitters were estimated to cost from $100 to $500 each and have a query range of about 0.5 to 1.0 km from the omnidirectional hydrophone. Receiver costs severely limit the number that could be deployed, and thus restrict the system's use to situations where the expected fish path is circumscribed or the presence of fish in a particular area needs to be ascertained. The system could be used profitably in situations where fish remain near fish aggregation devices.

(2) **"Pop-up" Tags**

A tagging system in which the tag surfaced after a specified condition was met (elapsed time, mortality, etc.) and "reported" its position could be a powerful tool. Such a fishery-independent tag recovery system would solve many problems related to tuna movement, including incomplete and erroneous data furnished by fishermen or others, and tag loss through emigration out of the fishery, or mortality. While such a system is easily conceived, realization is technically difficult. In addition, because the system described here would provide only two geographic positions, tag unit cost must be relatively low.

Electronically-controlled fusible links that could release the tag are available now (Nelson and McKibben 1981; J.M. McKibben pers. com., Ultrasonic Telemetry Systems, 8315 Millikin Ave., Whittier, CA, USA). The cost of such release systems (about $100), size (about 2 x 5 cm including battery) and precision of release and transport to the surface (0.5-1h) would allow a design of a practical system.

Position reporting could be done most cheaply by relying on aircraft. From the air, a VHF signal transmitted by the tag when it reached the surface could be detected along a track 300 nm wide. Knowledge of the precise time of release would limit aircraft costs. We believe that $200 per tag (including release mechanism) could be realized. Although no technical barriers exist to the development of such a tag, they are not in commercial production and we believe that research and development costs would be substantial.

Ideally, position could be reported via ARGOS satellite. The advantages of satellite recovery of information are obvious and, if a "mortality" pop-up could be incorporated, the data would be of great value in resolving issues related to natural mortality and emigration of tunas.

On the other hand, present size (100 mm dia., 250g) and costs of ARGOS transmitters ($2000 each) exclusive of the timed-release component (see above) make satellite reading of pop-up tags impractical at present. It also seems unlikely that cost will substantially decline in the near future because of the high cost of the precision oscillator used to transmit the signal to the satellite (less than 2 Hz drift out of a mega Hz causes rejection by ARGOS). Nor are great reductions in size likely because of the high (2 watt) power requirement for transmission (the battery makes up about two-thirds of the tag weight). Thus, because of their cost and size, satellite tags seem an impractical system for tracing tuna movements at present. On the other hand, satellite tags are an area of intensive experimentation (Mitson MS), and substantial reductions in size and costs have already been accomplished. In the unlikely event that substantial reductions occur in the future the pop-up satellite tag for tuna should be reconsidered.

(3) **Archival Position-Recording Tags**

Northwest Marine Technology, Inc., has completed a feasibility design for a miniature (1 cm x 6 cm) tag which allows storage of 8k bytes as a function of elapsed time. The tagged fish could remain at large for 5 years, the useful life of a lithium battery, but data collection can extend over only one year because sufficient battery power (about 1 microwatt) must be reserved to maintain data in the memory. The tag would collect data from three environmental sensors (ports) and record them and elapsed time for eventual reading when the tag is recovered by the fishery. The tag is, essentially, a highly-compact, low-power consuming microprocessor. Its greatest advantage lies in the ability of the user to configure its software and its sensors to meet a variety of experimental situations. Although the development cost of such a tagging system is substantial, Northwest Marine Technology has indicated it would develop the tag if a $100K commitment to purchase tags were made (satisfactory tag performance guaranteed before payment). The number of tags included in the initial contract would be 100 or more, depending on tag size, software and other specifications.

While collection of environmental data, such as temperature and depth, over extended periods would be extremely useful in answering specific behavioral and physiological questions, the most important application of the tag is that it could record a series of geographic positions and still collect temperature and depth information. Longitude can be accurately determined by including a photoresistor and measuring the Greenwich time of sunrise, and latitude can be determined from depth-specific seawater temperatures. As 8k bytes can be stored by the ultra-miniature tag, it could record 3 data items 7 times per day for a year or equivalently 50 times per day, one day per week for a year.

Recognizing that recoveries decrease geometrically with time, data acquisition rate could be easily programmed to be non-linear (programming of sampling intervals can be done after the tag is constructed). For example, initially data could be collected and stored at hour or half-hour intervals until the memory was filled, and then the acquisition rate could be reduced to intervals of a week or fortnight and the new data would be stored over the old (retaining sufficient amounts of the old data so that the time series remained complete). In this manner highly detailed daily records of depth, temperature, and position could be recorded during the period that returns from the fishery are the most likely (the first 100 days at large) without losing valuable position data inherent in long-term recoveries.

A simulation study of the precision of latitude estimates was completed by Smith and Goodman (1986). Each fish position was considered independently and the precision was a function of the variance in the long-term mean depth-temperature relationship for a particular time of year. The simulation indicated that the minimum precision that could be expected using temperature and depth data recorded by the tag was within 5 degrees of latitude. The precision of the longitude estimate is a function of the interval of time used to measure sunset and sunrise and therefore is under the control of the experimenter. Resolution on the order of one degree could be readily achieved. Five degrees of latitude is the minimum precision that could be expected, as the model is very conservative. Taking into account the previous position of the fish, and having real-time oceanographic measures of surface temperature from satellites and other sources could increase the precision 2 or 3 fold.

(4) Archival Pop-up Tags

The ideal tag would be a data recording tag as described in the previous section that surfaced and reported the data to a satellite at a specified time. This tag is essentially a marriage of the two systems previously discussed (pop-up and archival position-recording tags). The high unit cost of such a satellite tag might be acceptable in this case because many fish positions as well as a wealth of environmental data would be acquired rather than a single fish position determined from satellite. In addition such a system would be truly fishery independent, and the rate of recovery of information would be high.

The chief problem with such a tagging system is that the message length permitted by ARGOS is far too short to utilize the unique features of the archival tag because ARGOS would permit only a few data points to be transmitted. The short message length is a necessary feature of ARGOS, which is a low-altitude satellite that moves rapidly across the horizon. The low altitude reduces the power transmission requirements and the short message length enables many users to share the same satellite. The high-quality oscillator, an important cost factor in an ARGOS compatible tag, is not strictly necessary if location of the tag by the satellite is not required as would be the case for an archival tag. However, ARGOS will not permit such a degradation since the fine frequency separation is used to monitor several transmitters simultaneously.

An important step in development of such a tag would be to develop a new set of satellite specifications and determine if they could be accommodated within the NOAA satellite program. Data archiving requires a much larger data capacity than is normal and a satellite channel might have to be specially dedicated to monitoring such tags. Some oceanographers in the NOAA program are advocating longer message lengths for ARGOS, so development of such a tag may be possible in the future.

Thus a pop-up, data recording tag for tunas is technically feasible if an accommodation can be reached with satellite specifications. In fact, the Lowestoft Laboratory (Directorate of Fisheries Research, Ministry of Agriculture, Fisheries and Food , United Kingdom) has taken up the challenge to significantly reduce the size of a satellite transmitter to meet the requirements for a pop-up satellite tag for tuna. A study is underway for the design of a data storage tag which can be incorporated into the pop-up satellite tag. This also includes an investigation of methods for position finding and recording. Final designs and specifications should be achieved in 1986 (R. Mitson, Lowestoft, U.K., pers. comm.).

4.1.3 Conclusions

The ideal tag recovery system in which the identity code and position and environmental history are automatically recorded is presently impractical. No system presently exists that will automatically read fish identity codes when fish are captured or processed, but the PIT tag is a first step. On the other hand, a tag that stores data on fish position and the environment which is recovered when the fish is recaptured (archival tag) is practical. Sonobouy-transponder systems and pop-up tags (detected by aircraft) might also be practical, but are of more limited use. The sonobouy-transponder system would probably be most useful in studying the behavior of tuna associated with fish attraction devices and the VHF pop-up tag might be used in areas where movements are greatly constrained by the coastline or when short-term recoveries are of interest. The costs of development might not justify the limited use of the VHF pop-up tag for tunas.

Of the systems considered in this report, we believe that the archival tag has the greatest potential. We believe that widespread use of the archival tag in conjunction with conventional mark and recapture studies would result in a quantum advance in knowledge of tuna movement dynamics. The ideal tagging system of this genre is an archival tag that surfaced and reported the data to a satellite (archival pop-up tag). The chief barrier to development of such a system appears to be a lack of compatibility with existing satellites, a problem that could be overcome in the future. For the present, we recommend development and testing of an archival tag in which the tags are recovered through the fishery. Tuna stocks for which tag recovery rate is high are the preferred stocks for the initial application of the tag. We also encourage a feasibility study of satellite recovery systems for an archival tuna tag.

4.2 Measurements of Physiological State

Interpretation of tag recovery data for estimation of movements, growth, and mortality would be aided by collecting information on the physiological condition of the fish at the time of tagging. Such measurements would help identify the factors motivating movement and regional and seasonal differences in life history characteristics. To date, fishery work has relied primarily on crude indices of condition, such as length-weight relationships and gonadosomatic indices, but the potential exists to infer much of a fish's present and past history from biochemical analyses and examination of tissue structure. Modern techniques, developed or being developed, allow or will allow determination of whether the physiological condition of a tuna is improving or deteriorating, its growth, swimming and feeding history, and its exact position in sexual maturity and many other characteristics (Love 1980). Such information would be invaluable for interpreting patterns and rates of movements of tunas and identifying the extent of heterogeneity in vital rate parameters (reproduction, growth, and mortality). Love (1980) lucidly summarizes this point of view and the existing literature on fishes. We briefly summarize below a few of the many possible approaches and provide some representative references.

4.2.1 Reproductive State

The gonadosomatic index is a useful measure of seasonality in reproduction in tunas (Orange 1961), although more informative techniques exist. A precise assessment of the female reproductive condition is possible by histological examination of formalin-preserved ovarian tissue from freshly-caught fish. When properly calibrated, identification and ageing of postovulatory follicles in active ovaries indicate time of last spawning (Hunter and Goldberg 1980). Alternatively, the incidence of females with hydrated oocytes can be used to estimate spawning frequency. In inactive ovaries, classification of atretic oocytes indicates time elapsed since the ovary was active (Hunter and Macewicz 1985). Frequency of spawning in tuna populations has recently been estimated for south Pacific skipjack (Hunter et al. MS) and black skipjack (Schaefer 1986).

Results indicated that south Pacific skipjack probably spawn nearly every day during peak spawning months and black skipjack every 2.5-4.0 days.

4.2.2 Growth

Measurement of recent growth (days to weeks) could be useful in interpreting differences in the pattern of movements among tagged fish or between areas. Several biochemical techniques are potentially useful as indices of recent growth; RNA/DNA ratios (Buckley 1984), polyribosome to monoribosome ratio (Lied et al. 1982); [14-C]-glycine uptake by scales (Smagula and Adelman 1983); and possibly messenger RNA (Somero and Lowery pers. comm., U. of California San Diego, La Jolla, CA, USA).

A number of publications describe the use of RNA/DNA as an index of recent growth in fish, and the technique has been successfully applied in the assessment of habitat quality for marine fish larvae (Buckley 1984).

Use of polyribosome to monoribosome ratios as an index of growth or nutritional condition (Lied et al. 1982) seems promising because the ratio would be much more sensitive to short-term changes than RNA/DNA. This technique is still in the developmental stage, however.

Uptake of [14-C]-glycine by the osteoblasts that remain attached to scales is another method that has been used to assess growth in fishes (Smagula and Adelman 1983), but the technique probably would require incubation on board ship and is less practical for tuna research than the other methods which require only that samples from live fish be frozen until returned to the laboratory for analysis. Calibration of any index with fish growth using captive fish is preferable, although an index of growth might be useful even without direct calibration.

4.2.3 Caloric Density

Analysis of fat concentration in tissues is one of a few biochemical techniques that have had widespread use in fisheries (Shul'man 1974), but rarely has it been applied to tunas or used for interpretation of movements. North Pacific albacore reduce their supply of fat during their transoceanic migration, and fat stores are replenished by active feeding prior to reaching the north American coast (Dotson 1978). Clearly, knowledge of caloric density would be quite helpful in interpreting movements of albacore.

Because the techniques are simple, the traditional approach to measuring caloric density in fishes has been to measure total lipid or water content. Boggs (1984) showed that the total lipid content in tunas is closely correlated with their water content. However, thin layer chromatography and flame ionization detection techniques make possible estimates of lipid classes (such as trigylcerides, cholesterol, free fatty lipids and polar lipids) in tissue samples as small as 25 g dry weight (Hakanson 1984). Fat profiles permit identification of changes in structural as well as storage lipids, and therefore are a more precise and informative measure of nutritional state. Also only small amounts of tissue need be collected, so the technique could be used to provide a precise measure of nutritional condition without damaging the fish at the time of tagging. It would be important to calibrate such work by determining a representative sampling location in the body as Boggs (1984) did for yellowfin.

4.2.4 Starvation and Energy Consumption

Many possibilities exist for assessing the degree of starvation and recent food assimilation rates. The time course of starvation-induced histopathology in larval fishes has been calibrated in the laboratory and used to measure the fraction of larvae dying of starvation per day in the sea (O'Connell 1980; O'Connell and Paloma 1981; Theilacker 1986). Some of these characteristics might be useful in adult tuna. For example, one might examine appearance of hepatocytes, glycogen concentration in the liver or the arrangement of cells in the pancreas (O'Connell 1980; O'Connell and Paloma 1981). Other potentially fruitful measures include activity of proteolytic enzymes in white muscle, fat content of the intestine (which might integrate ingestion events over 1-2 days), and the buffering capacity of muscle. In skipjack, histidine declines dramatically after less than a week of starvation (R. Brill pers. comm., NMFS, Southwest Fisheries Center, Honolulu, HI, USA). Since histidine is an important intracellular buffer in fish muscle, starved tuna with low histidine levels may be less able to cope with the proton load (from lactic acid) generated during burst swimming, and thus be more at risk.

4.2.5 Duration and Intensity of Activity

It seems likely that biochemical characterization of the musculature of tunas could be used to estimate the duration and intensity of previous activity. There is evidence in the literature of pervasive (weeks to months) biochemical changes in the locomotory musculature of mammals in response to exercise (reviewed in Holloszy and Booth 1976), and some evidence exists that similar changes occur in fish (Johnston and Moon 1980, 1980a).In addition, a correlation has been noted between glycolytic enzyme activities (lactate and malate dehydrogenase) of epaxial white muscle and routine metabolic rate in a variety of fishes (Childress and Somero 1979). Work in progress indicates that biochemical profiles (lactate dehydrogenase, citrate synthase, cytochrome-c oxidase activities, myoglobin concentration, and nucleic acid ratio) will provide indices of activity levels and growth and permit the calculation of feeding ration (S. Kaupp pers. comm., U. of California San Diego, La Jolla, CA, USA). Clearly, indices of past activity levels would be helpful in interpreting movements, estimating energy requirements and assessing fitness.

4.2.6 Mortality Risk

Natural mortality is a critical component in population models. Its estimation is useful in interpreting data on movements of tunas. For example, the expectation that fish released in area A will be recaptured in area B is dependent on natural mortality, as well as the movement from area A to B and fishing effort along the path between the areas and in area B. Natural mortality has been or might be estimated from results of large-scale tagging experiments (Bayliff 1971; Cayré, Diouf, Fonteneau, and Santa Rita Viera 1986), observed declines in year-class abundance, and various indirect mathematical manipulations (Beverton and Holt 1959; Hennemuth 1961; Pauly 1980). Such methods only approximate the actual natural mortality, and implicitly or explicitly assume that natural mortality is constant for all age classes recruited into the fishery despite the fact that it must be, by definition, age-specific. Clearly, measurements of the physiological state that collectively provide a profile of size-specific mortality risk would be a valuable addition to large-scale tagging experiments. It would be important in such an assessment of mortality risk to consider not only mean levels of such indices in sea-caught tuna, but the form of the distribution. For example, the distribution of RNA/DNA appears to be truncated in wild larval fish, with slow-growing individuals less abundant in the sea than one would predict from laboratory work (Buckley 1984).

Many of the indices described in the above sections would be appropriate elements in a mortality risk assessment. Also, some biochemical index of the ageing process would be a useful addition to other measurements. Such an index might be currently available by measuring the concentration of lipofuscin. Lipofuscin accumulates in tissues of a number of organisms in proportion to metabolic rate and, in some insects, a linear relationship exists between chronological age and lipofuscin concentration (Ettershank et al. 1983). Although not used to assess physiological or chronological age in fishes, it has been used to identify different cohorts of krill (Ettershank 1983). In addition to assessment of mortality risk, lipofuscin concentration might also find application in tuna movement studies as an index of chronological age of tagged individuals (via a small biopsy) or for identifying differences in metabolic processes between groups of tunas.

4.2.7 Summary

A few of many possible measurements of physiological state are summarized above. All appear valuable for interpreting tuna movements. Some, such as caloric density, RNA/DNA ratios and histological analysis of female reproductive condition, involve applying techniques used on other fishes to questions of interest to tuna biologists. The accuracy of most measurements would be improved by calibration experiments on live captive tuna. We believe that application of the existing techniques and development of new ones should be encouraged as part of a broad program on the dynamics of tuna movements.

4.3 Reconstruction of Movement Histories From Microconstituents of Mineralized Tissue

The tissues of fishes living in different environments are believed to acquire a unique chemical composition because of differences in local water chemistry, temperature, niche differences, and other characteristics of the environment. These differences in chemical composition are believed to be conserved in the skeletons of teleosts and constitute an ecological record because their bones are usually acellular (no osteocytes in the bone matrix), and the resorption of acellular bone is unlikely. New analytical techniques may make possible reconstruction of such histories. Work such as this could help identify the origins and size specific movements of tunas. Such work was not considered in our discussions because the formation of a separate working group has been proposed to evaluate the use of chemical constituents for age determination and estimation of stock heterogeneity and transfer rates of tunas (Joseph and Wild 1984). Although a thorough review was impractical, the panel believed that the potential of these methodologies was so great that some mention should be made of them here. For this short synopsis, we drew upon unpublished documents of T.J. Mulligan (University of Maryland, Chesapeake Biological Laboratory, Solomons, Maryland) and R. Radtke (Hawaii Institute of Marine Biology, University of Hawaii, USA) as well as the published literature

4.3.1 General Summary

To define movement patterns, otoliths or vertebrae may be preferable for microconstituent analysis because they may contain a record of the age of a fish as indicated by daily or annual growth increments, and perhaps more importantly, the constituents, once deposited, are likely to be stable and not resorbed as they are in scales (Mugiya and Watabe 1977). It is also preferable that the method be nondestructive and sensitive enough to determine the chemical composition within regions of estimated age on otoliths or vertebrae. Considering these criteria, the best method at this time appears to be X-ray fluorescence spectroscopy (Calaprice et al. 1975;

Mulligan et al. 1983). In this method the presence of elements is detected by measuring the energies of the X-rays produced when a section of an otolith or vertebrae is exposed to a high energy electron or proton beam. Because X-ray fluorescence is nondestructive, a sample can be run repeatedly and specific regions within the same skeletal part can be targeted for analysis. At the conclusion of the analysis, the data consist of an array of numbers, with each number corresponding to the total number of characteristic X-rays in a given energy range. From these X-ray energy spectra, the elemental composition is determined. The information can then be analyzed in various fashions, and the entire elemental profile or the relative concentrations of specific elements or their ratios can be used. Nonparametric or parametric pattern recognition techniques are applied to these data to identify groups or clusters of fish having similar chemical composition. The equipment, precision, analytical procedures, and statistical methods for microconstituent analysis in fishes have evolved considerably over the years, but some controversy still exists regarding the optimal approach to be used.

A number of recent studies have documented that chemical differences exist in mineralized tissues of fishes, and various pattern recognition techniques have been used to separate stocks of sockeye salmon (Calaprice 1971; Calaprice et al. 1971, 1975; Mulligan et al. 1983) and Atlantic bluefin (Calaprice 1986).

In addition to examination of such data for group similarities in elemental composition, it is theoretically possible to obtain a historic record of temperature changes experienced by the fish. The strontium-calcium ratio (Sr/Ca) in coral skeletons is negatively correlated with water temperature at the time of calcium deposition (Smith et al. 1979; Schneider and Smith 1982), and Sr may be substituted interstitially in the aragonite of fish otoliths in a temperature-dependent manner. Radtke and Targett (1984) found cyclic patterns in Sr/Ca in transects of the otoliths of an Antarctic fish; the cyclical patterns may be related to seasonal water temperatures. This apparent seasonality in the microconstituents of scallops and bluefin vertebrae was also noted by Calaprice et al (1971) and Calaprice (1986); his work is described in greater detail in subsequent sections. Recently, the Sr/Ca content in otoliths was determined for cod larvae reared in the laboratory at different temperatures. This laboratory calibration established that the Sr/Ca was a function of temperature, but that Sr was not deposited in equilibrium with inorganically precipitated aragonite (Radtke 1984). The slope of the relationship between temperature and Sr/Ca was the same as predicted with the equilibrium equation for inorganic aragonite, but the elevation of the line was much lower, indicating that metabolic processes probably controlled the amount of strontium incorporated into the otolith. Laboratory calibration on a species-by-species basis will probably be required to use Sr/Ca to reconstruct reliable thermal histories. It may be preferable to use a mix of more elements for more accurate temperature indicators, as shifts in the ratio of other elements with temperature, such as Cl/Br, can also be expected.

Stable isotopic concentrations of oxygen in fish vertebrae or otoliths may also provide a potentially useful historical record of the hydrographic environment experienced by the fish. For example, the isotope ratio of O^{18}/O^{16} seems to be an indicator of water temperature; oxygen is hypothesized to be deposited in otoliths in isotopic equilibrium with the surrounding seawater (Devereux 1967; Degens et al. 1969). Kolodny et al. (1983) found good agreement between temperatures deduced from O^{18} values in fish bones and water temperature and showed that isotopic concentrations were not affected by the concentrations in the food fed to the fish. If this is true for tunas, construction of a thermal history from isotopic analysis of the otolith may be possible.

The standard method of measuring the oxygen isotope ratio requires dissolving the sample and employing a mass-spectrometer, a destructive method complicated by the heterogeneous nature of the skeletal parts. Calaprice (1986) briefly describes an accelerator-based method he used to determine oxygen isotope ratios in bluefin vertebrae, which seems to eliminate these problems. In this preliminary study, vertebrae of juvenile bluefin from the western Atlantic had higher O^{18}/O^{16} ratios than did those from the eastern Atlantic, indicating that temperatures in their first winter were lower for fish in the eastern Atlantic. This result is reasonable since the temperature of the eastern bluefin nursery grounds in the Mediterranean can be 13°C or more cooler in winter than the western bluefin nursery grounds in the Gulf of Mexico. Similarly, Mulcahy et al. (1979) found that the O^{18} increased with age in a benthopelagic macrourid, indicating an ontogenetic movement into deeper, colder habitats, which agrees with field observations. However, the maximum depth predicted on the basis of the predicted temperatures exceeded the maximum depth (minimum temperature) of the species in the region studied. Thus, the equilibrium equation for O^{18} correctly identified the historical patterns of movement, but the estimated temperatures seemed inaccurate (R. Wilson, Scripps Institution of Oceanography, University of California at San Diego, pers. comm.). Temperature calibration of O^{18}/O^{16} ratios in larval cod otoliths in the laboratory has indicated that heavy isotope was not deposited in equilibrium with the surrounding environment, but that the deposition of the heavy isotope was temperature dependent (Radtke 1984). And similarly, oxygen isotope studies of otoliths of bluefin tuna held in captivity indicate that otolith carbonate was not derived directly from seawater bicarbonate (R. Radtke, pers. comm.). Clearly some biological processing of isotopes exists in cod, bluefin, and presumably other fishes; and species-specific O^{18} deposition rates must be calibrated before they can be used to reconstruct thermal histories.

4.3.2 Bluefin Stock Identification Using Microconstituents of Vertebrae

Recently, Calaprice (1986) analyzed juvenile (school fish) and adult (giant) bluefin tuna from fisheries in the western Atlantic, eastern Atlantic, and Mediterranean to estimate the degree of interchange of fish between eastern and western Atlantic fisheries. He used proton-induced rather than the more common electron-induced X-ray spectra to characterize the composition of inorganic elements of vertebrae. By analyzing 0.9-mm diameter sections of vertebrae, he produced linear transects of vertebral chemical composition from the center (area formed as juveniles) to the outer edge (area formed just prior to capture).

Ratios of elements such as calcium, strontium, phosphorus, sulphur, chlorine, bromine, and zinc varied cyclically as the vertebra was traversed from the center to the outer edge, indicating possible seasonality in deposition.

Comparisons of the chemical composition of vertebrae of bluefin from eastern and western Atlantic indicated that they probably intermix. The inferred degree of interchange was relatively low, with more fish immigrating from the eastern Atlantic to the west than the reverse. Of the 94 juveniles from the western Atlantic, 5.5% had patterns similar to the 131 fish from the eastern Atlantic, whereas none of the eastern Atlantic juveniles had patterns similar to those of the Western Atlantic. Similarly, the immigration of giant bluefin from the eastern Atlantic to the western Atlantic (inferred from chemical pattern similarity) ranged from 9.9 to 12.7% in two different years, and immigration from west to east was 2.6-9.9%.

4.3.3 Conclusions

The results for bluefin indicate that identification of chemical patterns in vertebrae has great potential for studying movement pattern. At present microconstituent analysis has been used primarily to identify the origins of the fish, rather than to provide a chronology of movements. Clearly, if chronologies of spatial movements can be resolved from chemical analysis, it would constitute a major breakthrough in tuna movement dynamics. Ideally, the chemical composition of specific habitats needs to be linked to specific chemical patterns in bones. This is not a straightforward problem as metabolic processes and biomagnification through food webs may substantially alter elemental composition of bones relative to their concentrations in seawater. Laboratory experimentation to identify such processes are needed, as are process-oriented field studies including microconstituent analysis of tagged fish recovered from the fishery. Further, chronologies are dependent upon the same assumptions and require the same validation as routine age estimations.

At this point the precision and power of the analytical techniques (chemical and statistical) have far outstripped physiological and environmental understanding of the processes. Laboratory studies are needed that confirm the conservation of induced chemical patterns in the vertebrae. Optimism is in order. Experimentally-induced hypercalcemia does not cause resorption of the bone of otoliths or vertebrae of fishes such as tunas which have acellular bone (Mugiya and Watabe 1977). Wendelaar Bonga et al. (1983) found that calcium and phosphate of opercular bones and fin rays were resorbed after treatment with a metabolite of vitamin D in a fish with acellular bone. Clearly, physiological processes do exist that could alter the microconstituent content of acellular bone. Although the physiological literature supports the hypothesis that microconstituents of acellular bone, under normal circumstances, are conserved, additional laboratory studies are needed to substantiate this assumption and to identify the extent metabolic processes are involved. Laboratory calibrations are also needed to verify that Sr/Ca, or O^{18}/O^{16} and other ratios of elements, are indices of temperatures experienced by the fish and to determine the correct temperature coefficients for tunas. Further, experiments are needed to determine the extent biomagnification affects elemental composition, for example by feeding fish food of known isotopic composition (Kolodny et al. 1983). These and other laboratory studies would strengthen the interpretations derived from chemical pattern analysis. Such laboratory work in conjunction with field studies could be done at relatively low cost, and even work on fishes other than tunas using key elements would help in this regard. It would also be important to include process-oriented work on chemical pattern chronology in any international program on tuna movement dynamics, as such a program could provide field validation for the method.

5. REQUISITES FOR RAPID ADVANCES IN KNOWLEDGE

For seven major tuna stocks we have documented the importance of increasing our understanding of the movements of tuna and we have identified the required information needs. Our review of existing fields of knowledge (mark and recapture, tuna oceanography, and ultrasonic telemetry) and potential, new technologies (tagging systems, physiological state assessment and microconstituent analysis) indicates that, although substantial progress has been made, major gaps remain in knowledge and technoclogy. A major theme of all of our deliberations was the optimal approach to increase the rate of knowledge acquisition. Knowledge and technology will continue to grow in the years to come, but the new demands on management of tuna resources make an acceleration of the present rate highly desirable. For rapid progress we believe increased effort in the following four areas is indispensable.

- Establish international arrangements to share tuna movement data, analyze movements on an oceanwide and worldwide basis and link the analyses to major international oceanographic programs.
- Increase the numbers and kinds of observations of the movements of tuna in the vertical plane.
- Develop and use technology for tracing the actual paths followed by tunas over extended periods and for measuring movements independent of the fishery.
- Conduct intensive studies on tuna movement dynamics which incorporate a wide range of disciplines and combine old with the new technologies that we have discussed.

Many research suggestions and information needs are mentioned throughout the text but we restrict our comments here to these four requisites. Each is discussed below.

5.1 Communications and Analysis of Historical Data

Creation of data files and wider distribution of existing files on tuna movement would foster broader understanding of tuna movements through inter-ocean analysis of movements; facilitate comparative studies of stocks; lead to more cooperation with less duplication of effort; and avoid the pitfalls of interpretation of movements from regional data. Three types of files--tag release and recapture, oceanography, and catch and effort--should be distributed to members of the tuna research community. Such communication is particularly important in the Indo-Pacific region. The establishment of a system for coordinated analysis of tuna movement data on an ocean-wide basis would be an important first step in developing an international research program on tuna movement dynamics.

The more obvious benefits of oceanwide sharing of movement data were discussed in detail in the section entitled "Reexamination of Tuna Movement Data" and require no additional comments. We consider here two of the less obvious benefits: use of the comparative method for understanding movements, and linking such data to new initiatives in oceanography.

5.1.1 Comparative Studies

An important opportunity exists for developing a better conceptual understanding of the movements of tunas by comparative studies of their movements using data from previous and current studies. For example, at present we cannot discern the extent differences in movement patterns among species and stocks is attributable to the environment or to species- and size-specific differences in movement patterns. Comparisons of estimates of various life history parameters among species and among stocks within species (including K of the von Bertalanffy growth equation and coefficient of natural mortality [Beverton and Holt 1959; Pauly 1980] and various physiological parameters [Sharp and Dizon 1978]) has been useful in developing conceptual understanding of stocks and species. Comparisons of parameters of movement estimated for as many stocks as possible have similar conceptual value. The simplest parameters are numbers of releases and returns and return rates--the latter divided by the former (Table 1). Tabulations of numbers of recaptures during various intervals, for example 0-30 days, 31-60 days, 61-180 days, 181-365 days, etc. at liberty and distributions of net distances travelled by fish at liberty for those periods (Kearney 1983) would also be useful. Other parameters which might be estimated and compared include A^2 and V (Table 2).

On a finer scale, standardizing the analysis of existing (and future) ultrasonic tracking data offers an important opportunity to advance fundamental understanding of tuna movement behavior by comparative study of behaviors with regard to depth and temperature among species, sizes, and areas. Most acoustic tracks of depth, temperature, or both are available only as pictorial graphs of swimming depth or temperature against time. Although these are valuable illustrations, they are not amenable to spectral analyses of the distributions of these parameters or to comparisons, except in a highly qualitative manner, between tracks, studies or species. We recommend that published reports provide distributions of temperatures or depths experienced by the fish and tabulated modal depths and temperatures. Some of this information could be recovered by digitizing the published graphs, and this would be a valuable exercise if reasonably accurate modal depths and temperatures could be extracted.

We recommend an effort to recover modal depth and temperature information whenever possible from previous data sets and strongly recommend that future investigators provide spectral analyses of the temperature and depth distributions of tracked fish stratified by day and night.

5.1.2 Integration with Oceanography Programs

Further analysis of historic catch and effort and tagging data using a broader concept of the features that affect vertical or horizontal distributions of tunas by affecting the aggregation or production of their forage seems warranted. For example, accurate models of the wind stress fields exist for some of the oceans and they could be easily developed for areas such as the southwest Pacific, where the models do not exist. Wind stress fields could be used to identify seasonal shifts in areas of convergence and divergence, as indicated by the zero wind stress curl. This analysis locates local areas of upwelling and increased productivity. The seasonal shift in forage or tuna movement might be examined profitably by plotting tuna distribution on moving coordinate systems based on an environmental parameter or an index of one, such as the zero curl line, an ocean front, or some other moving boundary. Such analyses would profit by consideration of vertical as well as horizontal dimensions. Regardless of the research approach, however, we believe establishment of linkages to existing and future broad-scale oceanographic programs, such as TOGA and WOCE, would be of great benefit.

5.2 Vertical Structure

For a major advance in the understanding or predicting of tuna movements, more data on the vertical structure of the habitat and the distribution of tunas within it are essential. The need for expanding our knowledge of vertical movements of tuna was a recurrent theme throughout our discussions. The present meager level of information needs to be expanded to include a greater size range of tuna and more habitat types. Sea-surface temperature and tuna distribution at the surface are only a crude index of events in subsurface layers, and better correlations would probably be obtained if vertical temperature structure and tuna distribution were better documented. At present we cannot measure vertical structure of the ocean from space, but recent advances in physical oceanography indicate that it may be possible in the future using satellite information and a historical understanding of the relationship between sea-surface temperature and deeper structure. Substantial progress will depend on tuna studies that examine the vertical distribution of tunas within the context of the vertical structure of the water column. Acoustic tracking of individual fish is the preferred approach. Although, using present technology, few fish can be studied, new technologies may increase the numbers and duration of tracks (see next section). Net displacement of groups is the most critical issue. Research gill nets and longline studies conducted with a knowledge of the structure of the water column also seem to be a promising approach that could be implemented using existing technology.

5.3 The Paths of Tunas Over Extended Periods

A key area for new technology is the development of devices that identify the paths of tunas in three dimensions over extended periods of weeks or months and provide a movement history independent of the fishery. Advances in very large-scale integrated circuit technology provide the potential of collecting detailed records of temperature, depth and geographical position in a tag to an accuracy of about 5 degrees of latitude and less than 1 degree of longitude in temperate waters (Smith and Goodman, 1986). Presently the most practical device of this type, the archival tag (see previous discussion), must be recovered to obtain the stored data, and thus is not totally fishery independent, although the position data is independent. Despite this limitation, we believe that the archival tag is an extremely important first step in development of tags to trace the movements of tunas independent of the fishery. We strongly recommend the development of this tag and initial testing in those stocks for which there are high rates of fishing mortalities and for which cooperation from fishermen, unloaders, and cannery workers can be expected.

5.4 Intensive Studies on Tuna Movement Dynamics

We believe that intensive studies on tuna movement dynamics which include, in addition to conventional mark and recovery of tunas, a wide range of disciplines and combine old with new technologies could lead to a fundamental advance in knowledge. Ideally, the experimental design of a major field study on mechanisms of tuna movement should contain mark and recapture, measurements of tuna in three dimensions, assessment of physiological state, microconstituent analysis of mineralized tissue, and measurement of the physical and possibly the biological characteristics of the habitat. Combining information from these five elements would provide the most powerful approach to defining movement and mixing of tunas among regions that modern technology can provide. Such a program would provide not only several independent measurements of movement in different time and space scales but a broad behavioral, physiological and environmental framework which could be used to interpret movement patterns and identify mechanisms.

A program of this kind would require development and testing of new methodologies (e.g. safe biopsies, storage of biological specimens and testing of new physiological state measurements) and new equipment (e.g. archival tags). Such work must be begun well in advance of the major investigation of tuna movement. For example, the definitive paper describing a test of the coded-wire tag for salmon was published in 1963 (Jefferts et al. 1963), but practical application to research and management problems took ten years. The techniques for tagging and recovery had to develop to a stage where managers were confident that large expenditures could be justified.

Each of the five major elements of this idealized program on tuna movement dynamics is briefly discussed below.

5.4.1 **Mark and Recapture**

Because of the large number of tuna movement trajectories that can be determined from the recoveries of the tags of a single cruise and the existence of extensive files of data, mark and recapture experiments must be central to any major study of tuna movements. The function of the measurements discussed in the following section is to enhance the ability to interpret the spatial and temporal patterns of recoveries of marked fish and possibly to reinterpret past data.

5.4.2 **Movements In Three Dimensions**

To correlate movements with habitat characteristics and to develop a fundamental understanding of the dynamics of tuna movements require an understanding of the pattern of movement in the vertical as well as the horizontal plane. Deployment of archival tags and conventional ultrasonic transmitters which collect depth distributions is needed. The latter are needed because, in many of the fisheries, insufficient numbers of recoveries of fish would make the archival tagging approach financially prohibitive. Archival tags, where practical, are far superior because long-term patterns of vertical movements would be provided, whereas acoustic tracking has been limited to less than a week and usually less than two days. Even a few recoveries of archival tags would provide extremely valuable information on the relation between migratory paths and habitat characteristics.

5.4.3 **Physiological State**

If more can be known about the physiological condition of tunas at the tagging and capture sites, then variation in movement patterns of individual fish, of groups of different sizes of fish, and variation in different regions, and during different seasons will be more accurately interpreted, as will the determination of vulnerability to various types of fishing gear. Even greater power of interpretation might be realized if the physiological state could be assessed from a non-damaging biopsy of the tagged and released individuals, rather than from sampling the school. A survey of the physiological state is essential because it is the only method for identifying likely motivating factors which form the basis of the observed movement patterns; this survey also might identify regional or seasonal heterogeneity in critical life history parameters, such as growth rate and mortality risk.

5.4.4 **Microconstituent Analysis**

A chronology of the microconstituents of vertebrae or otoliths of tuna captured in the course of the program would provide a method of assessing movement patterns and degree of mixing of tuna from different regions that would be independent of other methods (conventional tagging, tracking and/or records from archival tags). Thus, inclusion of microconstituent analysis in the program is strongly recommended. It would be particularly important to determine the chronology of microconstituents of the vertebrae of tagged tuna that were recovered in the course of the work; analysis of tuna that carried an archival tag for extended periods would be particularly valuable. Analyses of tagged fish might identify the very important links between habitat and chemical composition. An intensive program of this nature could provide the field validation needed for routine use of microconstituents in fishery work.

5.4.5 Habitat Characteristics

Measurement of the physical, and possibly the biological, characteristics of the habitat is essential for correlating habitat with observed movement patterns. In addition, real-time measurements of temperature structure of the water column, as well as surface temperature measurements by satellite centered on the tagging site and covering a broad area, would greatly increases the precision of the position estimates eventually obtained from the archival tag. Agencies involved in satellite image and data analysis need to be involved early in the planning stages to insure that adequate satellite coverage exists.

5.5 Need for Coordination

The idealized intensive program on movement dynamics we have discussed would have to draw from a broad scientific and institutional base. No single organization could marshal the resources to conduct such a program. Cooperative links would need to be established between government and institutional fishing agencies, the oceanographic community and academic researchers. Clearly the success of such a program would depend upon effective coordination among countries and organizations. Similarly coordination is essential for the sharing and distribution of existing data on tuna movements. Such cooperative activities would foster broader understanding of tuna movements through inter-ocean analysis of movements, facilitate comparative studies of stocks and help establish cooperative comparative studies on the same species of tuna in different oceans.

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