

Evaluation of Methods used by the South Pacific Commission for Identification of Skipjack Population Structure

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The use of data from blood genetics, tagging, growth, maturity, juvenile occurrence, and parasite studies for examining skipjack population structure is discussed in light of experience by the Skipjack Survey and Assessment Programme of the South Pacific Commission. Results from analyses of these data support several different hypotheses of skipjack population structure in the Pacific Ocean. This confusion reflects, in part, the limited information content of these data for inferring population structure. Therefore unconditional support for any one hypothesis is misleading, particularly as the potential for fishery interactions differs markedly amongst the hypotheses.

Before choosing a most likely hypothesis of skipjack population structure, gaps in the basic biological data, specifically geographical distribution of spawning and movement of pre-recruits, should be filled. Obtaining comprehensive new data will be costly and time-consuming and will not overcome inherent weaknesses of the traditional methods. There is a need to weigh the benefits to be gained from improved knowledge of population structure against the benefits to be gained from a better understanding of interaction amongst components of the rapidly expanding fishery for skipjack.

L'utilisation de données provenant d'études sur le sang, la génétique, le marquage, la croissance, la maturité, la présence de juvéniles et les parasites est traitée à la lumière de l'expérience acquise dans le cadre du Programme de Recherche et d'Évaluation du Listao de la Commission du Pacifique sud. Les résultats obtenus par l'analyse de ces données viennent appuyer diverses hypothèses concernant la structure de la population de listao dans l'océan Pacifique. Cette confusion reflète en partie l'intérêt limité de ces données en ce qui concerne une information permettant de formuler des hypothèses quant à la structure de la population. Une adhésion sans réserves à l'une quelconque des hypothèses peut donc induire en erreur, surtout du fait que le potentiel d'interaction des pêcheries diffère de façon sensible selon les hypothèses.

Avant de procéder au choix de la structure la plus probable de la population de listao, il convient de combler des lacunes dans l'information de base sur la biologie, en particulier pour ce qui est de la distribution géographique de la ponte et des déplacements des pré-recrues. L'obtention d'une information exhaustive est coûteuse, demande beaucoup de temps, et n'éliminera pas les faiblesses inhérentes aux méthodes traditionnelles. Il est nécessaire de jauger les avantages qui découleront de connaissances plus amples sur la population, par rapport à ceux que représenterait une meilleure compréhension des phénomènes d'interaction entre les divers éléments de la pêcherie de listao, laquelle se développe rapidement.

Se debate el empleo de datos de genética de la sangre, marcado, crecimiento, madurez, aparición de juveniles y estudios de parásitos para examinar la estructura de la población de listado, a la luz de la experiencia del Programa de Evaluación y Encuesta sobre el Listado, de la Comisión del Pacífico Sur. Los resultados de los análisis de estos datos apoyan varias y diferentes hipótesis sobre la estructura de la población del listado en el Pacífico. Esta confusión refleja, en parte, la escasez de la información contenida en estos datos, lo que no permite sacar una conclusión sobre la estructura de la población. Por lo tanto, un apoyo incondicional de cualquiera de estas hipótesis conduciría al error, especialmente debido a que el potencial de interacciones en la pesquería difiere mucho entre dichas hipótesis.

Antes de escoger la hipótesis más plausible sobre estructura de la población del listado, se deben rellenar los vacíos existentes en los datos biológicos básicos, y específicamente en lo que se refiere a la distribución geográfica del desove y movimiento de los pre-reclutas. El obtener datos nuevos y suficientemente amplios será costoso y largo y no compensará la inherente deficiencia de los métodos tradicionales. Es necesario comparar los beneficios que se podrían obtener de un mejor conocimiento de la estructura de la población con los beneficios que resultarían de un mejor entendimiento de la interacción entre los componentes de la pesquería de listado, en rápida expansión.

1. Introduction

Before the South Pacific Commission's Skipjack Survey and Assessment Programme (Kearney 1983) commenced, Fujino (1970b, 1972, 1976) had concluded from an analysis of blood electrophoretic data that there were two genetically isolated subpopulations of skipjack, one in the central/eastern Pacific and one in the western Pacific. Later, Sharp (1978) proposed five skipjack subpopulations in the Pacific Ocean using similar data. The degree to which fisher-

ies exploit skipjack of the same genetic origin could differ greatly depending on which, if either, of these hypotheses was true. Skipjack differing in genetic origin might also be expected to differ in productivity. If so, fishing strategies designed to optimize yield might need to be varied amongst fisheries; clearly a first step is to describe skipjack population structure.

Assessments of skipjack population structure by the Skipjack Programme, based on electrophoretic

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analysis of skipjack blood samples and analysis of tag and recovery data, were published soon after fieldwork finished (SPC 1980, 1981d). Since then, further analysis of skipjack migrations (SPC 1981a), growth (Sibert et al. 1983), distribution of spawners and juveniles (Argue et al. 1983), and occurrence of parasites (Lester 1981; Lester et al. MS) has provided a wider data base from which to evaluate methods for identifying of skipjack population structure.

2. Definitions

There is often ambiguity and confusion associated with use of the terms "stock" and "subpopulation". In a fishery context, a stock is a subdivision of a population that is vulnerable to a fishery. In a biological context, the term subpopulation is usually substituted for stock, with subpopulation implying a subdivision based on a degree of genetic isolation (SPC 1976). These terms are not compatible, because only in special circumstances would they describe the same subdivisions of a population.

By defining a stock as those fish vulnerable to a fishery, their spatial distribution could be considered simply as the area of the fishery where individuals from one or more subpopulations might be present. A subpopulation would normally cover a larger area due to movement of individuals beyond the operating range of the fishery. In the case of several subpopulations, it is likely that their spawners would be separated geographically, or temporally, and would not be exploited by the same fishery.

Both stocks and subpopulations may be considered in terms of short or long time periods. For example, a stock could be simply the fish vulnerable to one unit of gear on a time scale of part of one day. At the other extreme, on a time scale of many generations, a stock could include all fish that were vulnerable to the fishery and whose descendants become vulnerable to the fishery. So defined, a stock could encompass vulnerable adults from one or more subpopulations. For a subpopulation, the time scale could span many thousands of generations and involve a degree of genetic isolation bordering on that required for speciation. Alternatively, a subpopulation might simply refer to a breeding group, that is a portion of the population that tends to breed predominantly amongst its own members, and whose integrity might change with, for example, annual fluctuations in the environment.

The choice of an appropriate definition depends on the objectives of the investigation. For most fishery investigations, pragmatism dictates this choice, and investigators attempt to identify the biological unit(s) which are responsible for the bulk of production that a

fishery harvests, and which are reproductively isolated to the extent that their production is self-sustaining. Such units, which have at least some properties of a subpopulation, are commonly called stocks.

3. Genetic Analysis of Skipjack Blood Samples in Conjunction with Tagging Data

The Skipjack Programme used combined data from blood sampling and tagging to test hypotheses relating to skipjack movement and population structure. The Programme obtained fifty-eight blood samples consisting of 100 individual skipjack from each of fifty-eight schools, and tagged a total of 32,427 skipjack from these schools. None of the female skipjack from which blood specimens were taken were running ripe; only a few had ripe gonads. Forty two loci were analysed for electrophoretically detectable polymorphisms (Richardson 1983). Three loci showed polymorphisms that were suitable for a traditional population analysis: of these, only serum naphthyl esterase exhibited sufficient geographic variability to be suitable for detailed consideration.

The Skipjack Programme hosted two workshops at which specialists in the fields of population genetics and fishery population biology met with the Programme's scientists to jointly consider the statistical analyses and resulting interpretations of the combination of blood genetics and tagging data. Both workshops dealt with additional published and unpublished blood genetics data for the eastern, central and western Pacific Ocean that were provided by participants. The results and interpretations from these workshops (SPC 1980, 1981d) were summarized in (SPC 1981b), and are expanded here as follows.

3.1 RESULTS AND INTERPRETATIONS

Esterase gene frequencies in skipjack showed a pronounced longitudinal gradient across the study area, with flattening of this gradient occurring to the east of 120°W longitude (Figure 1). This gradient is consistent with the concept of a cline. Underlying the clinal hypothesis is the assumption that "... the probability of two fish mating is a decreasing function of the distance between their birth places ..." (SPC 1981d). In other words, there is an isolation-by-distance component to the population structure. Acceptance of this model implies that there are no genetically isolated skipjack subpopulations in the study area, which is contrary to hypotheses advanced by both Fujino and Sharp using different sets of blood genetics data. This conclusion is supported by Graves and Dizon (this volume) who found no evidence of genetic isolation between skipjack from the Atlantic and Pacific oceans, using the powerful technique of restriction enzyme analysis of mitochondrial DNA.

Existence of the esterase gradient was considered to be strong evidence that the Pacific skipjack do not comprise a single panmictic population, in which all adults of one generation have an equal chance of mating.

The gradient in esterase gene frequency is consistent with two possible distributions of skipjack spawning, one being a relatively even distribution of spawning in tropical waters across the study area. One could also view the gradient as the zone of contact between skipjack from two or more centres of high spawner density (breeding groups) perhaps at the approximate extremes of the study area or beyond. Thus the gradient could represent a mingling primarily of migrants from the centres of spawning, or a zone of weak hybridization where there may be lowered breeding success. The similarity between eastern Pacific esterase gene frequencies (east of 120°W in Figure 1) and those from French Polynesia (155°W) suggests that most skipjack from the eastern Pacific, where reproduction is thought to be much less successful (Klawe 1963), could have the same genetic origin as those in French Polynesia. Observations on the occurrence of skipjack juveniles in stomachs of adults and on gonad development (Section 6.) support the view

that there are several centres of skipjack spawning. An isolation-by-distance model of skipjack reproduction is consistent with either an even distribution of spawning or several geographical centres of spawning.

The tagging data implied that there is some mixing of adult skipjack over a wide area (Section 4.). If such mixing involved reproducing skipjack and hence genetic exchange, it would have to be offset by some degree of selection in order to maintain a cline.

No obvious relationship was evident between esterase gene frequency for particular skipjack schools and subsequent movement of tagged skipjack from these schools, nor was there a significant relationship between net movement of tagged skipjack from each school and the difference between actual gene frequency and gene frequency estimated from the regression line in Figure 1 (SPC 1981d). It was concluded that gene frequency for a school was not a predictor of skipjack movement.

The workshop participants concluded that a clinal population structure was a reasonable alternative hypothesis to the isolated subpopulation hypotheses advanced by Sharp and Fujino.

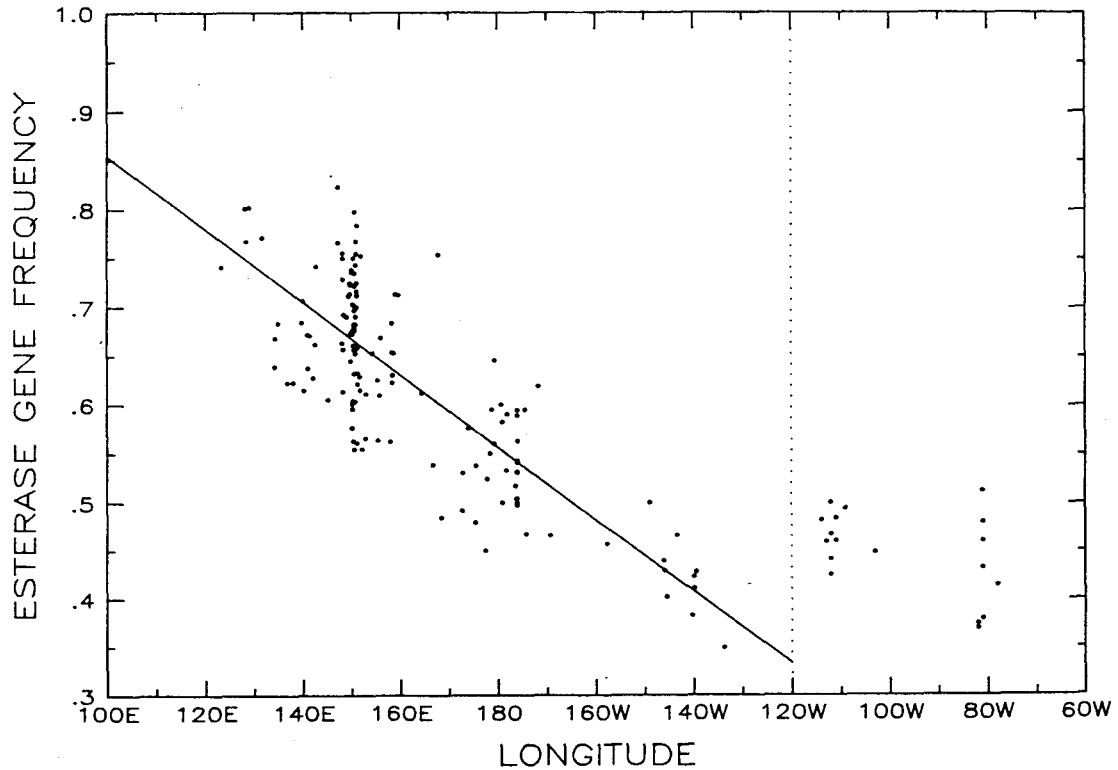


Figure 1. Skipjack serum esterase gene frequency versus longitude of the sample location. The regression line was fitted to the data for 145 samples to the left of 120°W (dotted line); the correlation coefficient was -0.81 ($p < 0.01$). Eighteen samples from eastern Pacific waters are to the right of the dotted line. Figure redrawn from (SPC 1981d).

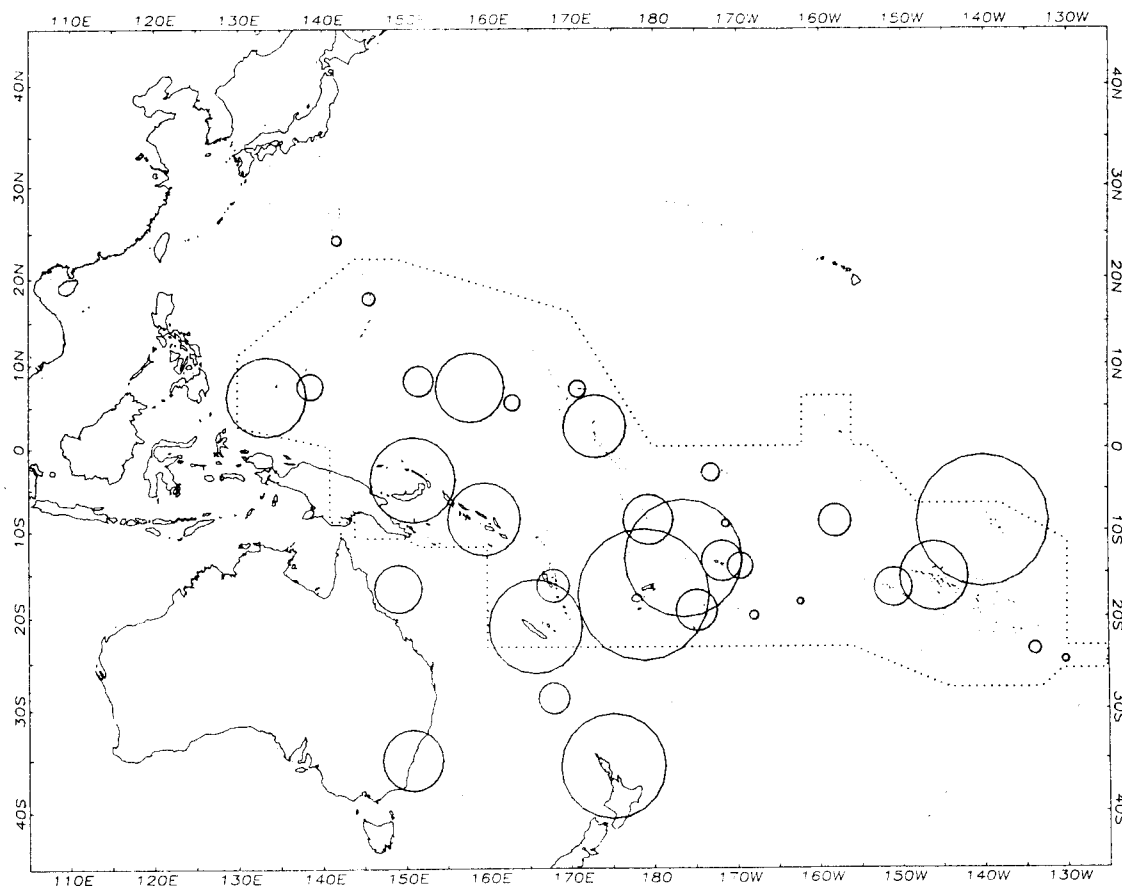


Figure 2. Distribution of tag releases (circles) and boundaries of the South Pacific Commission Region (dotted line). The circles are centred on each country, territory or subdivision thereof, and are proportional to the number of tagged skipjack released in each location. Figure from Kleiber et al (1983b).

4. Tagging

Between October 1977 and August 1980, 140,433 skipjack were tagged and released. The itinerary of the tagging vessel was planned so that releases of tags in the area of the South Pacific Commission and adjacent areas where skipjack were known to be abundant would be as widespread as possible (Figure 2). Migration patterns that became evident from recoveries of these releases were expected to clarify skipjack population structure.

4.1 MIGRATION

Figure 3 presents a selection of tag returns plotted as straight line arrows between tagging and recovery location. The impression from Figure 3 is one of considerable mixing of skipjack. It should be noted, however, that the overall impression of many wide-ranging migrations in Figure 3 does not reflect the average case for all tag recoveries. This figure overemphasizes long distance, relatively rare migrations, due to the procedure used to select recoveries for the figure (see caption Figure 3). The lack of apparent

movement beyond the area surveyed may reflect poor chances of recovery as a result of low fishing effort, and environmental barriers to migration at high latitudes (skipjack are seldom encountered polewards of 40° latitude or in waters cooler than 16°C).

Figure 4 shows that tag recoveries in a particular area (Solomon Islands) decrease as the distance between the recovery area and tag release site increases. For the total study area, the majority (86%) of tag recoveries were made less than 250 nautical miles from their release site and within 180 days of tagging (Figure 5). It was only within the smaller group of skipjack that were at large for more than 180 days (bottom graph in Figure 5) that long-distance migrations were common. This suggests that few skipjack of the size that were tagged were available to fisheries for long enough to be recovered at great distances from their release site.

There are several limitations to the use of tag migration data for examination of skipjack population structure. Curved pathways, if present, are not readily

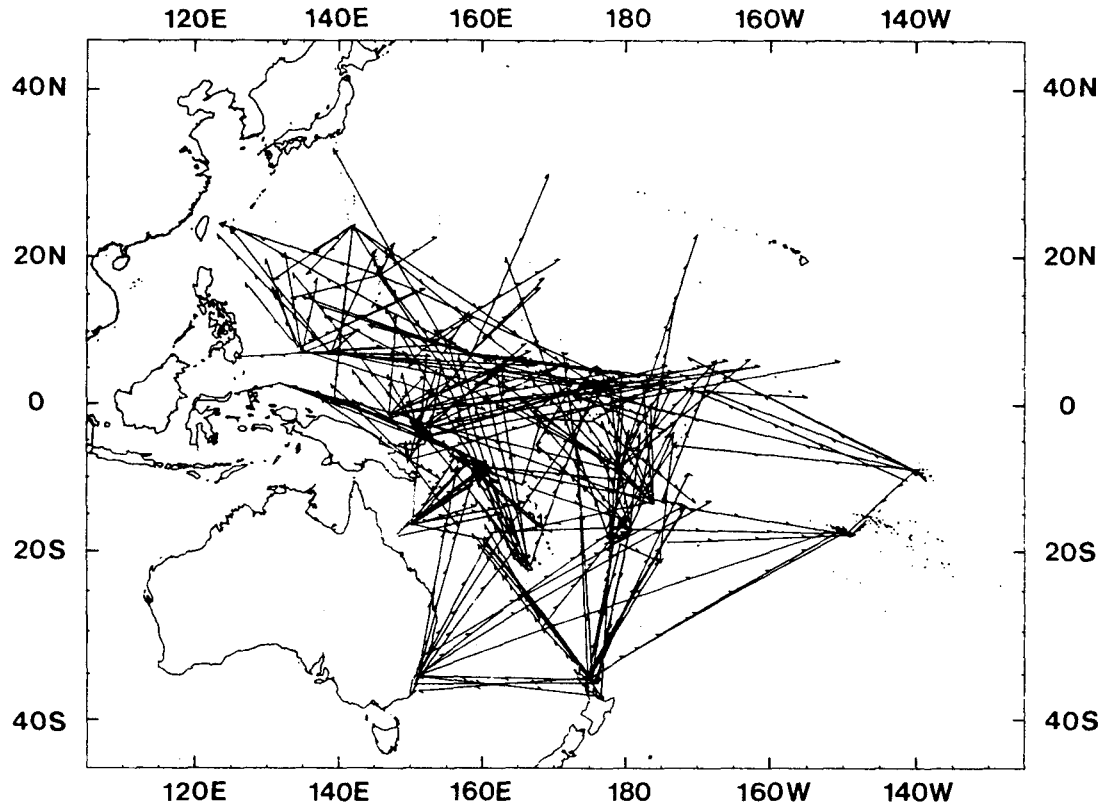


Figure 3. Straight line representations of movements of skipjack tagged by the Skipjack Programme and subsequently recovered. Movements plotted have been selected to show no more than two examples between any pair of ten degree squares, one in each direction, and no more than one example of movement wholly within any ten degree square. Tick marks on the arrows represent 90-day periods between release and recapture. Figure redrawn from (SPC 1981a).

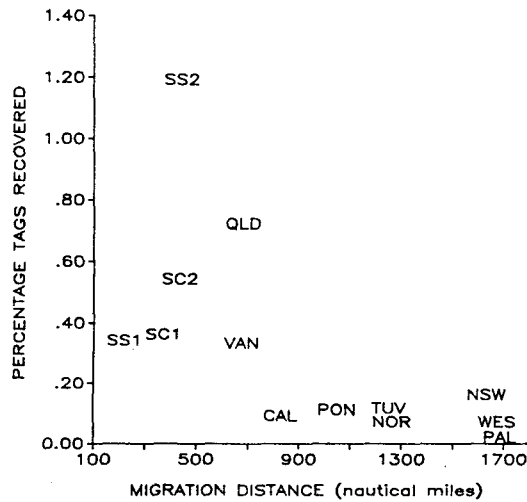


Figure 4. Relationship between tag recovery rate by Solomon Islands pole-and-line vessels and average distance travelled by tagged skipjack released in countries (areas) external to the Solomon Islands fishing area. Abbreviations are explained in the Appendix. Figure redrawn from Argue and Kearney (1982).

discerned from straight line arrows between tagging and recovery location. Additional confusion can result if the pathways themselves are shifting either seasonally or on other time scales. This situation is further complicated because tags were not released simultaneously over the whole of the study area. Care must be taken not to give undue weight to long migrations, which are the ones that stand out in Figure 3, but are hardly the most common (Figure 5). Random movement adds to the difficulty of identifying underlying directed movements, if such exist. Another difficulty results from the non-uniformity of fishing intensity in time and space. For example, many tagged skipjack were released within commercial fisheries, hence, to some degree, the distributions of tag recoveries in Figure 5 reflect the nearby location of fishing effort. Without taking this factor into account, any conclusions about migration patterns and distances moved could be partly or totally an artifact of the distribution of fishing effort. There is little hope of solving this problem without catch and effort statistics for all fisheries responsible for recapturing and returning tags. Unfortunately, adequate fishery statistics are not yet available to the South

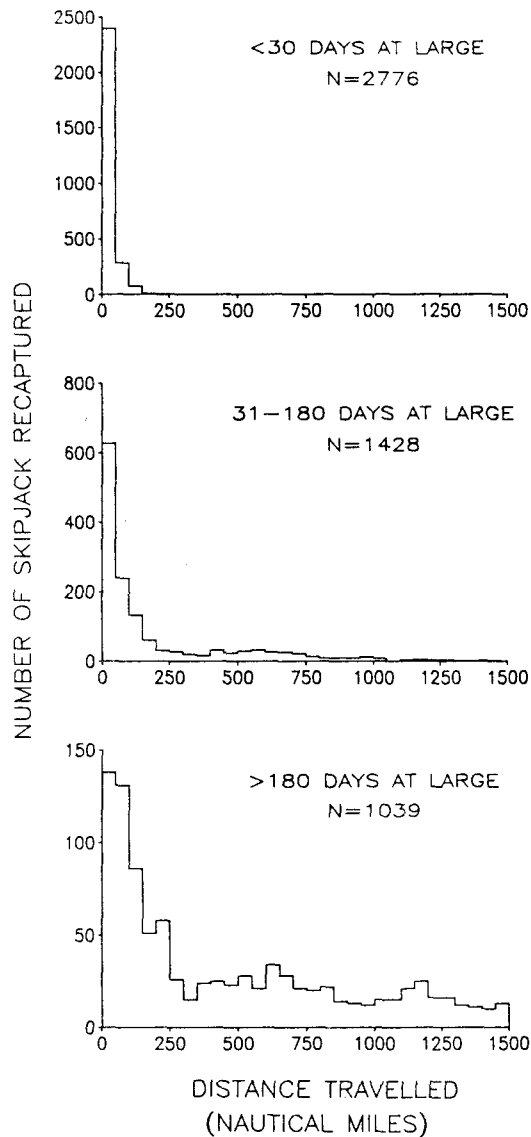


Figure 5. Numbers of skipjack tag recoveries by distance travelled and time-at-large. Data are for tag returns received by 4 November 1982. Recaptures for 96 fish, which travelled more than 1500 miles, are included in the sample sizes of the middle and lower graphs, but are not shown.

Pacific Commission for the whole of the period of tag releases and recoveries. Finally, without knowing the reproductive stage of each skipjack at the time it was tagged and at the time it was recovered, it is impossible to say whether movements of tagged fish represent adults homing to spawning areas, or simply the movement of dispersing fish to any number of spawning or feeding areas.

4.2 LEVEL OF IMMIGRATION

Results in Section 4.1 did not take fishing intensity

into account. Kleiber et al. (1983a) describe an immigration statistic that does this and expresses immigration as the percentage of recruitment in a "destination" country that arose from immigrants from a "donor" country. Table 1 presents these percentages for countries in the study area for which tags were recovered and catch statistics were available. Although levels of immigration were generally low (<15%) between fisheries in these countries, they were not insignificant and confirm that there is mixing of adult skipjack and potential for significant genetic exchange over large distances.

Table 1. Interaction between stocks fished by donor and destination countries expressed as the percentage of recruitment in the destination country estimated to arise from immigrants from the donor country. Table from Kleiber et al. (1983a) and SPC (1984).

Donor Country	Destination Country	Interaction	Approximate Nautical Miles Between Countries
Solomon Islands	Papua New Guinea	1-5%	550
Papua New Guinea	Solomon Islands	8-12%	550
New Zealand	Fiji	14%	1200
New Zealand	French Polynesia (Society Islands)	9%	2340
Fiji	New Zealand	<1%	1200
Federated States of Micronesia	Solomon Islands	1%	1100
Federated States of Micronesia	Papua New Guinea	1%	1100
Papua New Guinea	Marshall Islands	<1%	1400
Northern Mariana Islands	Federated States of Micronesia	17%	700
Palau	Marshall Islands	2%	2300
Federated States of Micronesia	Marshall Islands	37%	1200
Federated States of Micronesia	Northern Mariana Islands	11%	700

5. Growth

Geographical variation in skipjack growth might also suggest biological subpopulations. Analysis of covariance was used to compare growth increments (length at recovery minus length at tagging) among countries and time periods. A Taylor series was used to express growth increments as a sum of derivatives of the von Bertalanffy growth model, thus accounting for different size at tagging and days at liberty. Results demonstrated that skipjack growth increments varied significantly among countries and time periods (Sibert et al. 1983). In Figure 6 these results are illustrated by point estimates and joint confidence intervals for L_{∞} and K of the von Bertalanffy model, for some of the country data sets used in the analysis of covariance, as well as for eastern and western Pacific data sets that were matched to have times at liberty and sizes at release as similar as possible. Overlap-

ping confidence intervals are a feature of these results. For the few cases in which confidence intervals do not overlap, it is hard to discern a geographical pattern that could be interpreted as due to different subpopulations. Sibert et al. (1983) ascribed these differences in growth parameters to differences in environmental conditions (e.g. temperature, salinity, food supply) conducive to growth.

6. Distribution of Spawners and Juveniles

Measures of timing and geographical distribution of spawning are important for understanding population structure. Gonad indices (see caption Figure 8) were calculated for female skipjack by month and by 12° latitude, 10° longitude cells (Argue et al. 1983). High index values (>50) are associated with skipjack whose gonads have a high percentage of eggs that are ready to be spawned (Raju 1964a). Similar temporal and spatial analyses of the numbers of juvenile skipjack per 100 adult skipjack predators were carried out. This is an index of apparent abundance of juveniles, previously used by Yoshida (1971) and Mori (1972b) to examine seasonal and geographical variation in relative abundance of juvenile skipjack.

Argue et al. (1983) discuss the results of these analyses in detail. They suggest that during the survey

period of the Skipjack Programme, skipjack spawning in tropical waters was most intense, south of the Equator, during the warmer months, October to March, and that skipjack juveniles and spawning adults were concentrated within the study area in two locations — one amongst the Marquesas and Tuamotu Islands, and the other in the waters of Papua New Guinea, Solomon Islands and Vanuatu (Figure 7). In these regions apparent abundance of skipjack juveniles increased with increasing maturity of female skipjack gonads (Figure 8). These results imply a similar distribution of spawning and juvenile skipjack in the study area. At first glance these results support the idea that there are separate subpopulations. However, as mentioned in Section 3, existence of areas of higher spawning intensity does not conflict with the concept of a cline. As well, there was evidence of some spawning throughout the year in all tropical waters surveyed by the Programme, which is consistent with the hypotheses of a clinal population structure and an even distribution of spawning. Finally, large-scale oceanographic events may alter the distribution of juveniles and spawning adults, and there are geographic gaps in the available data. These factors suggest caution when using the above results to support models of population structure.

7. Parasites

Internal and external parasites carried by skipjack in different parts of the Pacific may be used to clarify patterns of movement and population structure of skipjack. In December 1979, the Programme began collecting viscera and gills from five skipjack per school, for a maximum of three schools per day, for subsequent parasite analysis. Counts were made of the numbers of larval *Tentacularia coryphaenae* (a tapeworm common in skipjack) that were visible in the walls of the body cavity of skipjack sampled from each school.

Skipjack samples for parasite analysis were taken over a wide range of tropical waters, and also from subtropical waters of New Zealand and Norfolk Island. Preliminary results from a multivariate analysis presented by Lester (1981) showed that the

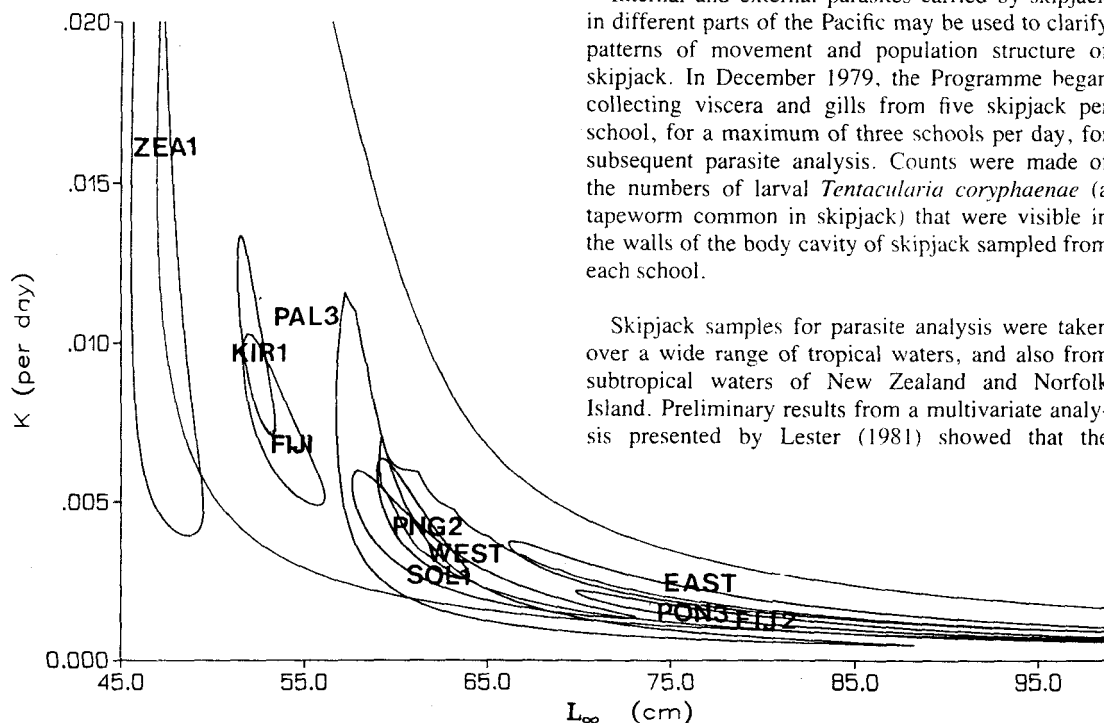


Figure 6. Approximately 95 percent joint confidence regions for K and L_{∞} for data sets based on Skipjack Programme tag releases and recoveries. Position of the abbreviations indicate point estimates of parameters for corresponding geographic regions and times. Abbreviations are explained in the Appendix. Figure from Sibert et al. (1983).

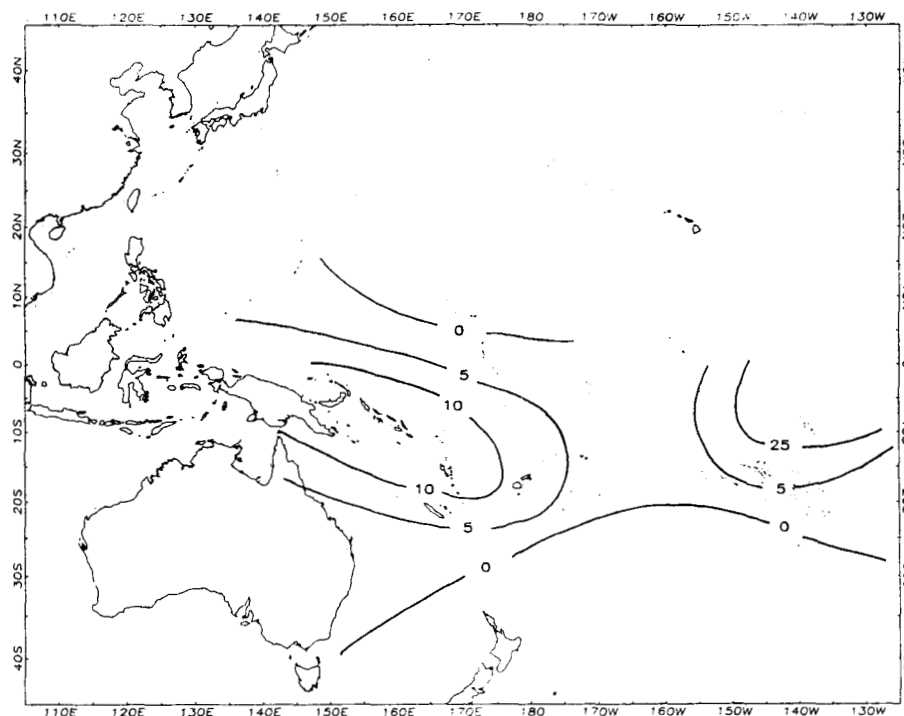


Figure 7. Isopleths of apparent abundance of juvenile skipjack (numbers of juveniles per 100 skipjack predator stomachs). Samples were collected between October 1977 and August 1980 and isopleths were estimated from average values for samples taken within 12° latitude by 10° longitude cells during October to March and April to August time periods. Figure redrawn from Argue et al. (1983).

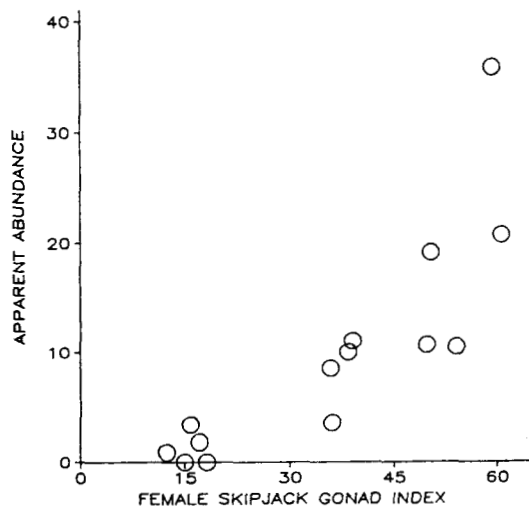


Figure 8. Relationship between skipjack juvenile apparent abundance and female skipjack gonad index, for samples of adult skipjack from 12° latitude by 10° longitude cells in the centres of high skipjack juvenile apparent abundance in Figure 7. The correlation coefficient was 0.84 ($p < 0.01$). Gonad Index = 10^3 (gonad weight gm/(fork length mm)³). Figure redrawn from Argue et al. (1983).

skipjack caught in widely separated tropical areas carried similar long-lived parasites, but that skipjack caught in New Zealand had different parasites from those caught in tropical waters to the north. New Zealand fish did carry tropical parasites at approximately the same level as skipjack caught in the tropics, which suggested that New Zealand fish were recent arrivals from the tropics (Lester et al. MS). These results provided no evidence of discrete skipjack sub-populations.

8. Evaluation

8.1 WHAT LIFE HISTORY STAGE WAS SAMPLED?

To infer population structure from biological or tagging data, it is important to know the life history stage of the sampled or tagged skipjack. Frequently, this information has been absent. For many samples taken for blood analyses, there were no measures of maturity, hence these samples could consist of mature pre-spawning skipjack, of post-spawning skipjack, of immature skipjack, or of some combination. Similarly, the tag releases could have been of non-migrant

skipjack, of skipjack that had concentrated in spawning areas, of skipjack traveling along possible dispersal or migration pathways, or of skipjack homing to spawning area.

Not knowing which life history stage was sampled or tagged limits the inferences one can make regarding genetic exchange between areas. Inability to estimate genetic exchange confuses the choice of an appropriate population model.

8.2 DISPERSAL, MIGRATION, SELECTION

In the case of the blood genetics data, the observed esterase gradient (cline) could be maintained by various combinations of movement and selection¹. If the esterase cline was maintained by high selection on each generation of very young skipjack, then dispersal of older fish could be extensive and the cline would still be maintained. To maintain the cline when selection is negligible requires that adults disperse little, although they could migrate extensively as long as they returned home to spawning areas.

Various combinations of movement and selection have different potentials for fishery interactions. Table 2 presents examples of these combinations and their potential fishery interactions. At this time, neither the electrophoretic data nor the analysis of tagging data allow one to choose with confidence from the different alternatives of how the cline may be maintained.

Table 2. The potential for fishery interactions under different levels of selection, dispersal and migration/homing. Table adapted from SPC (1981b).

Selection	Dispersal	Migra- tion/ Homing	Potential for Fishery Interactions
<i>Clinal Hypothesis — Even Distribution of Spawning</i>			
High	Extensive	Negligible	High
High	Negligible	Negligible	Low
Negligible	Negligible	Extensive	High
Negligible	Negligible	Negligible	Low
High	Negligible	Extensive	High
<i>Clinal Hypothesis — Two or More Breeding Units</i>			
High	Extensive (but little between units)	Negligible	High in mixing zone Low between breed- -ing areas
Negligible	Negligible	Extensive	High in mixing zone and between breeding areas

8.3 ENVIRONMENTAL VARIABILITY

Surface waters in the tropical Pacific are thought to undergo major physical changes, such as the strong El

¹ As used here, dispersal refers to movement of skipjack to different breeding locations at varying distances from where they were spawned; migration refers to movement (perhaps for feeding) of skipjack to areas at varying distances from where they were spawned, followed by homing to the area where they were spawned.

Niño warming that peaked in 1983 in the eastern and central Pacific (Rasmusson et al. 1983). These, in turn, may greatly alter the geographical distribution of productivity throughout the pelagic food chain. It follows, then, that mobile pelagic species such as skipjack may respond by altering spawning distribution and intensity, recruitment of juveniles, growth, and movement patterns. If so, measures of these variables over relatively short time periods would be of limited value for inferring population structure.

8.4 PRE-RECRUITS

A major shortcoming to date of blood genetics sampling, parasite sampling and tagging is that these techniques have focused entirely on post-recruitment skipjack. Larval and juvenile skipjack (less than 15 cm in length) could undergo extensive movement simply by passive association with ocean currents. Young skipjack of up to 45 cm may undergo feeding movements of great distance from areas in which they were spawned. For example, Kearney (1978) hypothesized that juvenile and young skipjack followed the 20°C isotherm in a poleward direction until they reached areas where surface waters approached 20°C. This hypothesis is supported by data in Argue et al. (1983). Such movement, if substantiated, would imply a potential for long and short term genetic exchange, and fishery interactions, over large distances.

9. Discussion and Conclusions

It is as important to understand the limitations of data collected by following a particular line of research, as it is to recognize alternative hypotheses arising from the data. To this extent we feel that results (summarized in Table 3) from our analysis of a suite of data (blood genetics, tagging, growth, maturity, juvenile occurrence, parasite infestations) pertaining to skipjack population structure has been most fruitful. The clinal population hypothesis was put forward (SPC 1980, 1981d) as an alternative to the isolated subpopulation hypotheses (Fujino 1970b, 1976; Sharp 1978). Distribution of juveniles and spawning offered conditional support to the isolated subpopulation hypotheses, although possible modification of these distributions through environmental change should be noted. Tagging, growth, and parasite data, as discussed, have weaknesses when used to investigate population structure, but on balance, they offered conditional support for the clinal hypothesis. In brief, none of the analyses considered by the Skipjack Programme provided sufficiently clear cut results to support a particular population structure hypothesis. Consequently, we conclude that unconditional support for any of the hypotheses, such as that proposed by Fujino et al. (1981) for the two isolated subpopulations hypotheses, is misleading and predic-

tions of skipjack movement based on either hypothesis (Fujino 1972; Richardson 1983) are at best premature.

Table 3. Summary of results from methods used by the South Pacific Commission (SPC) to investigate skipjack population structure

Method	Results Pertaining to Population Structure	Management Utility
Blood genetics samples	SPC analyses support a clinal hypothesis, but it is unclear how the cline is maintained. Other investigators using different blood genetics data have inferred genetically isolated subpopulations.	Subjective and conflicting evidence of potential for fishery interactions.
Tagging	No oceanic barriers to migration. Conditional support for clinal hypothesis.	Quantification of population parameters and fishery interactions.
Growth	Estimates of growth parameters vary in space and time suggesting a strong environmental rather than genetic effect.	Estimation of yield.
Juvenile distribution/maturity	Juvenile and spawning skipjack appear concentrated at longitudinal extremes of the study area. Conditional support for isolated subpopulation hypotheses.	Delineation of areas where spawning may be concentrated.
Parasites	No evidence of discrete subpopulations.	Evidence of movement between tropical and subtropical waters.

Our analyses have pointed out some shortcomings of traditional approaches to investigations of population structure. These include gaps in knowledge of the relative abundance, distribution and movement of skipjack at all life history stages, but particularly for spawners and for young skipjack prior to recruitment. These gaps weaken inferences of population structure made from the traditional data, particularly data arising from opportunistic sampling of adults. In the past, many questionable assumptions were necessary to get around these limitations. This reduced the scientific and management value of results from investigations on population structure of skipjack.

Obtaining sufficient new data to distinguish between hypotheses, using traditional methods in an area as large as the western and central Pacific, will be costly and time consuming. Before embarking on this work it is important to consider to what extent its successful completion would help to achieve overall research objectives. In the Pacific Ocean there is yet

no evidence that skipjack recruitment is being impaired by levels of catch. Nevertheless, dramatic changes have taken place in the fishery. Catch has apparently increased substantially in a small portion of the central and western Pacific (Kearney 1983), but little reliable statistical information is available. With increased catch the potential for within-generation interactions between fisheries and fishing gears has grown. Lack of statistics and the potential for fishery interactions are of great concern to countries deriving revenue from the skipjack resource. Thus there is a need to weigh benefits that improved knowledge of population structure would bring against those to be obtained from improved information on fishery interactions and fishing statistics, which are needed immediately if countries of this region are to maximize economic benefits from the large skipjack resource.

Appendix

ABBREVIATIONS FOR GEOGRAPHIC REGIONS AND TIME PERIODS. Years are the survey years for which data are included in Figures 4 and 6.

CAL	— New Caledonia 1977, 1978
EAST	— Eastern Pacific
FJI	— Fiji 1978
FJI2	— Fiji 1980
KIR1	— Kiribati 1978
NOR	— Norfolk Island 1980
NSW	— New South Wales (Australia) 1979
PAL	— Palau 1980
PAL3	— Palau 1980
PNG2	— Papua New Guinea 1979
PON	— Ponape (Federated States of Micronesia) 1979
PON3	— Ponape (Federated States of Micronesia) 1980
QLD	— Queensland (Australia) 1979
SC1	— Santa Cruz Islands (Solomon Islands) 1977
SC2	— Santa Cruz Islands (Solomon Islands) 1980
SS1	— Solomon Sea (Papua New Guinea) 1977
SS2	— Solomon Sea (Papua New Guinea) 1979
SOL1	— Solomon Islands 1977
TUV	— Tuvalu 1978
VAN	— Vanuatu 1978
WES	— Western Samoa 1978
WEST	— Western Pacific
ZEA1	— New Zealand 1979