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Assessment of Pacific Skipjack Tuna (*Katsuwonus pelamis*) Resources by Estimating Standing Stock and Components of Population Turnover from Tagging Data

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More than 140 000 tagged skipjack tuna (*Katsuwonus pelamis*) were released during 3 yr over a large portion of the central and western Pacific. Tag returns exceeded 6000. We developed a set of tag attrition models to analyze tag release and return data and catch and effort statistics for the study area. We used these models to assess the status of the skipjack resource in the whole study area and within subdivisions thereof. Total standing stock was estimated at 3 million metric tons (Mt), (95% confidence range 2.5–3.7 Mt). Overall attrition rate (including losses to natural mortality, fishing mortality and emigration) was $0.17 \cdot mo^{-1}$ ($0.15-0.20 \cdot mo^{-1}$). Total throughput was estimated at $6.2\ Mt \cdot yr^{-1}$ ($5.5-7.1\ Mt \cdot yr^{-1}$) compared with catch of $<0.3\ Mt \cdot yr^{-1}$. Overall harvest ratio was 0.04. Harvest ratios for seven subareas for which detailed catch and effort statistics were available ranged from 0.02 to 0.46; only one exceeded 0.17. Low harvest ratios over most of the study area during the period tags were at large imply a potential for increased skipjack catches in many subareas and in the whole study area.

Plus de 140 000 bonites à ventre rayé (*Katsuwonus pelamis*) marquées ont été relâchées dans une zone couvrant une grande partie du centre et de l'ouest du Pacifique au cours d'une période de 3 ans. On a pu récupérer plus de 6 000 étiquettes. Les auteurs ont élaboré une série de modèles d'attrition des étiquettes pour l'analyse des données sur l'étiquetage et le retour des étiquettes et des statistiques de prises et d'effort de pêche dans la zone étudiée. Les modèles ont servi à évaluer l'état de la ressource en bonites dans l'ensemble et les subdivisions de la zone d'étude. Le stock présent a été estimé à 3 millions de tonnes métriques (Mt) (niveau de confiance à 95 % de 2,5–3,7 Mt). Le taux d'attrition total (comprenant les pertes par mortalité naturelle, pêche et émigration) a été estimé à $0,17 \cdot mo^{-1}$ ($0,15-0,20 \cdot mo^{-1}$). La productivité totale a été estimée à $6,2\ Mt \cdot an^{-1}$ ($5,5-7,1\ Mt \cdot an^{-1}$) pour des prises inférieures à $0,3\ Mt \cdot an^{-1}$. Le rapport de récolte total était de 0,04. Les rapports de récolte de sept sous-zones pour lesquelles on disposait de statistiques détaillées sur les prises et l'effort de pêche se situaient entre 0,02 et 0,46 et un seul était supérieur à 0,17. Les faibles rapports de récolte pour la plus grande partie de la zone étudiée au cours de la période pendant laquelle les poissons marqués étaient en haute mer supposent une possibilité d'accroître les prises de bonites dans bon nombre de sous-zones de même que dans l'ensemble de la zone d'étude.

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Annual skipjack tuna (*Katsuwonus pelamis*) catches from the area of the South Pacific Commission increased rapidly from less than 5000 metric tons (t) in the early 1960's to approximately 220 000 t in the early 1980's. Skipjack are a short-lived, fast growing, highly fecund species distributed throughout all tropical and subtropical ocean waters. Their lifestyle is apparently quite suitable for supporting a high harvest rate. Nevertheless, with increased catches, many countries in the region became concerned that interactions among surface fisheries might be sizeable and that increased yields might not be sustainable. The Skipjack Survey and Assessment Programme was undertaken by the Commission to assess the status of the skipjack resource and its ability to support this increased fishing pressure. Tagging was adopted as the principal stock assessment technique (Anonymous 1975). Between October 1977 and August 1980 the Skipjack Programme tagged and released approximately 140 000 skipjack throughout and beyond the area of the South Pacific Commission (Fig. 1). Over 6000 of these tagged fish were recaptured and reported to the Commission.

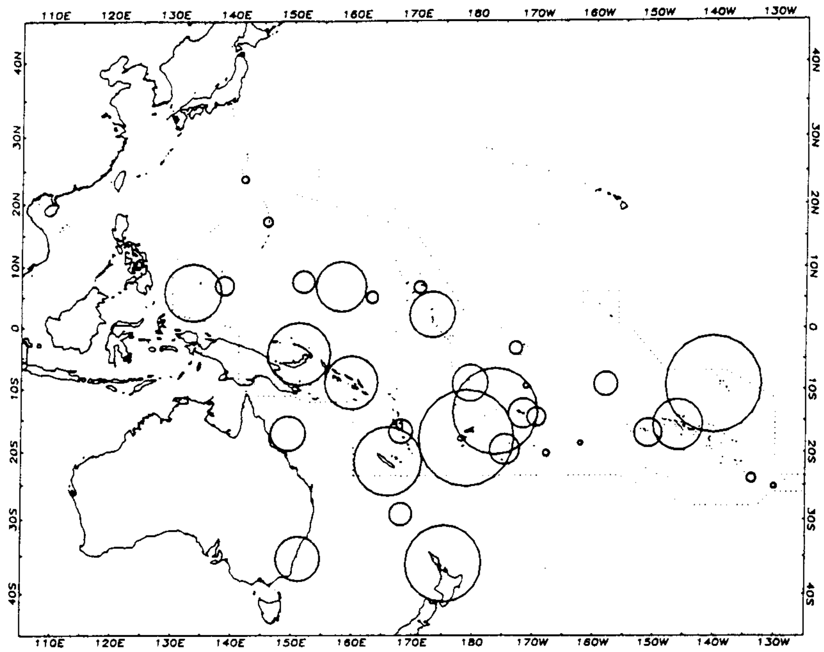

FIG. 1. Distribution of tag releases (circles) and boundaries of the South Pacific Commission Region (dotted line). The circles are centered on each subarea in which tags were released. The areas of the circles are proportional to the number of tagged skipjack released.

We present an analysis of tag release and recovery data for the purposes of assessing the standing stock of skipjack, rate of renewal (turnover) of the skipjack resource, and current levels of fishing pressure on the skipjack resource in the region as a whole and in the waters of individual countries and territories for which detailed catch and fishing effort data were available. For this purpose we developed a set of closely related analytical models which, using tagging data and catch and effort statistics, gives estimates and confidence limits for various parameters useful in defining the status of a population that is supporting a fishery. Some of these parameters are familiar: standing stock, natural mortality, and fishing mortality. Others are not so familiar but are useful in the context of this widely distributed and mobile species. We define these as follows.

Attrition: rate of loss of standing stock expressed as proportion of standing stock. It encompasses all loss factors including natural mortality, fishing mortality, emigration, and growth out of vulnerability to the fishery.

Throughput: product of attrition and standing stock; a measure of the passage of biomass through the stock. It encompasses death, emigration, and growth out of the vulnerable size class. Under steady-state conditions, it is also the in situ productivity plus immigration of vulnerable-sized individuals.

Harvest ratio: ratio of catch rate to throughput (equivalent to the ratio of fishing mortality to attrition). If fishing mortality is small relative to the population turnover, i.e. the harvest ratio is low, it is likely that fishing is having little impact on the population.

Tagging and Tag Recovery Methods

Tagging was carried out over a period of 3 yr in three 10-mo cruises each using one chartered Japanese pole-and-line vessel. The itinerary of the tagging cruises covered the whole study area, which includes the area of the South Pacific Commission and some adjacent waters where skipjack were known to be abundant (Kearney 1982b). The number of tags released in each area was not uniform (Fig. 1) because tagging success depended on fishing conditions, which were quite variable in space and time.

Skipjack were captured by pole-and-line fishing. The fish were poled onto tagging cradles where they were measured and tagged with plastic dart tags according to the technique described by Kearney and Gillett (1982). Fishermen on local and foreign-based vessels and workers at processing facilities were the primary sources of returned tags. Locally based fisheries within the study area were the pole-and-line operations in Papua New Guinea, Solomon Islands, Fiji and Palau, the *alia* fishery in Western Samoa, the *bonitier* fishery in the Society Islands of French Polynesia, and the purse-seine fishery in New Zealand. Information on local fisheries is contained in the final reports to the individual countries by the Skipjack Programme (e.g. Kearney 1982a; Argue and Kearney 1982, 1983; Gillett and Kearney 1983; Kleiber and Kearney 1983). Foreign fleets taking significant quantities of skipjack at the time most tags were at large were the long-range Japanese pole-and-line fleet and steadily increasing Japanese and United States purse-seine fleets.

Rewards were given and lotteries conducted to encourage return of tags (Kearney 1982b). It was possible to check efficiency of part of the tag return system with a tag-plant experiment in which 131 fish from the holds of purse-seiners were tagged and replaced in the holds by New Zealand Ministry of Agriculture and Fisheries personnel during the 1980−81 New

Zealand fishing season.

To investigate tag shedding and mortality due to tagging, a double tagging experiment was carried out in the waters of Fiji in 1980, during which 5399 double tagged skipjack were released, interspersed with 5626 single tagged fish (Skipjack Programme 1981). A further experiment was conducted with skipjack held at a research facility of the United States National Marine Fisheries Service at Kewalo Basin, Honolulu. Sixteen captive skipjack were tagged with Skipjack Programme tags and were observed for 7 wk along with 14 untagged controls (R. E. Kearney, unpubl.).

Analytical Methods

We assessed population parameters by analyzing plots of tag return rate (number of tags returned per unit time) against time at large. The tag return rate is expected to decrease with time because tag density in the fished populations should decline due to a variety of factors (e.g. mortality, emigration, tag shedding). The analyses described in this report were performed with a set of models in which tag return rates are predicted as a function of time from release and in which variations in exploitation are taken into account. The choice of model depends on which parameters are to be estimated and on whether catch data or effort data are used.

Derivation of Models

Immediate mortality and shedding have been defined as type 1 losses (Beverton and Holt 1957, p. 201; Bayliff and Mobrand 1972). These losses reduce the effective number of tagged fish at large at time zero. Thus if N_0 fish are tagged and if α is type 1 survival, then the effective number of tagged fish at the start is αN_0.

Following type 1 losses, a number of other factors reduce the population of tagged fish. Factors that affect all fish include natural mortality, emigration, fishing mortality, and growth out of vulnerability to the fishery. In addition, the population of tagged fish can undergo what is called type 2 or long-term loss by tag shedding and extra mortality due to carrying a tag. If, following type 1 losses, all attrition factors operate such that the tagged population decreases exponentially, then the number of tagged fish at large as a function of time, t, following tagging is

$$(1) \quad N = \alpha N_0 e^{-(Z+\psi)t}$$

where Z = total attrition rate for a group of untagged fish (time^{-1}) and ψ = additional attrition for tagged fish (time^{-1}). The rate at which usable tags are returned is given by

$$(2) \quad \frac{\partial r}{\partial t} = \beta F N = \alpha N_0 e^{-(Z+\psi)t}$$

where r = cumulative number of usable tag returns, F = fishing mortality (time^{-1}), and β = proportion of recaptured tags that are actually returned with usable recapture information. (Not all tag returns could be used in the analysis because some had unknown or imprecisely known times of recapture.)

We assume that ψ and β are constant during the time that tags are recovered. We also assume that Z is constant even though F, which is a component of Z, is likely to vary considerably with changes in effort expended by the fishery. For $Z \gg F$, this assumption in not bad, and later we will relax this assumption.

Defining F_i to be the average fishing mortality during the ith time unit following tagging and integrating Equation 2 under the assumption of constant attrition gives

$$(3) \quad r_i = \frac{\alpha\beta N_0 F_i}{(Z+\psi)} e^{-i(Z+\psi)}\left[e^{(Z+\psi)} - 1\right]$$

where r_i is the number of usable tag returns in time unit i. Equation 3 is a general model from which particular models were derived based on the following considerations.

The unknown fishing mortalities, F_i, can be approximated by

$$(4) \quad F_i \simeq qf_i \simeq \frac{c_i}{P}$$

where c_i = catch in biomass units in time unit i, P = standing stock in biomass units (assumed constant in time), q = catchability coefficient, or fraction of the standing stock harvested by one unit of fishing effort, and measured in inverse units of fishing effort (assumed constant in time), and f_i = units of fishing effort in time unit i.

Thus, either catch data or effort data can be used depending on which term in Equation 4 is substituted for F_i in Equation 3. Whether catch data or effort data are used influences the parameter estimates. Therefore, parameters that were estimated both ways are differentiated by a subscript, c, for parameters in models using catch data and a subscript, f, for parameters in models using effort data.

To complete the derivation of particular models, the following equations were substituted into the general model. The throughput (biomass per unit time) is given by

$$(5) \quad T = Z_c P.$$

Fishing mortality is not treated as constant over all time intervals, but a measure of the average fishing mortality can be obtained. If we have an average catch rate, $\bar{c}$, or an average effort rate, $\bar{f}$, then the average fishing mortality is given by

$$(6) \quad F_c = \frac{\bar{c}}{P};\ F_f = q\bar{f}.$$

The harvest ratio (unitless) is then given by

$$(7) \quad H_c = \frac{F_c}{Z_c};\ H_f = \frac{F_f}{Z_f}.$$

The resulting set of models is detailed in Table 1 wherein each equation, except for the last, has two parameters relevant to stock assessment which are confounded with α, β, and ψ, which we will call nuisance parameters.

The last model in Table 1 is an exception. All others allow the fishing mortality to vary with time, but contain the paradoxical assumption that the attrition rate is constant. When catch is used, this inconsistency is difficult to correct because standing stock should vary if the attrition varies. The model would therefore need to incorporate input and output of untagged fish with an attendant list of further assumptions.

However, when effort is used, it is logically consistent to allow to varying attrition rate and still assume a constant catchability. Defining M = attrition rate of untagged fish exclusive of fishing mortality (time^{-1}), we can substitute $M + F + \psi$ for Z in Equation 2. Then substituting qf_i for F and integrating leads to the last equation in Table 1. In this model the quantity $\alpha\beta$ is no longer confounded with other parameters. Therefore in theory this model could be used to estimate $\alpha\beta$. Note that the effort must vary for this to work because if f_i is constant, this

TABLE 1. Set of models used for estimating population parameters.

Parameters	Model
Z_c, P	$r_i = \frac{\alpha\beta N_0 c_i}{P(Z_c+\psi)} e^{-i(Z_c+\psi)} \left[e^{(Z_c+\psi)} - 1\right]$
Z_f, q	$r_i = \frac{\alpha\beta N_0 q f_i}{(Z_f+\psi)} e^{-i(Z_f+\psi)} \left[e^{(Z_f+\psi)} - 1\right]$
Z_c, T	$r_i = \frac{\alpha\beta N_0 Z_c c_i}{T(Z_c+\psi)} e^{-i(Z_c+\psi)} \left[e^{(Z_c+\psi)} - 1\right]$
Z_c, F_c	$r_i = \frac{\alpha\beta N_0 F_c c_i}{\bar{c}(Z_c+\psi)} e^{-i(Z_c+\psi)} \left[e^{(Z_c+\psi)} - 1\right]$
Z_f, F_f	$r_i = \frac{\alpha\beta N_0 F_f f_i}{\bar{f}(Z_f+\psi)} e^{-i(Z_f+\psi)} \left[e^{(Z_f+\psi)} - 1\right]$
Z_c, H_c	$r_i = \frac{\alpha\beta N_0 Z_c H_c c_i}{\bar{c}(Z_c+\psi)} e^{-i(Z_c+\psi)} \left[e^{(Z_c+\psi)} - 1\right]$
Z_f, H_f	$r_i = \frac{\alpha\beta N_0 Z_f H_f f_i}{\bar{f}(Z_f+\psi)} e^{-i(Z_f+\psi)} \left[e^{(Z_f+\psi)} - 1\right]$
$\alpha\beta$, M, q	$r_i = \frac{\alpha\beta N_0 q f_i}{(M+qf_i+\psi)} e^{-\left[iM + q\sum_{j=1}^{i} f_j + i\psi\right]} \left[e^{(M+qf_i+\psi)} - 1\right]$

Desired parameters	
P	standing stock
T	throughput
q	catchability
Z_c, Z_f	total attrition
F_c, F_f	fishing mortality
M	natural attrition
H_c, H_f	harvest ratio
Nuisance parameters	
α	type 1 tag retention and survivorship
β	proportion of recaptured tags that are reported and useful
ψ	type 2 tag slippage and mortality
Input data	
r_i	tag returns in time period i
c_i	catch in time period i
f_i	effort in time period i
$\bar{c}$	average catch per time period
$\bar{f}$	average effort per time period
N_0	number of tags released

model reverts to a two-parameter form.

Fitting the Models

Parameters were estimated by fitting the models given in Table 1 to the tag return results, with input of catch or effort data and input of independent estimates of $\alpha\beta N_0$ and ψ. Fitting was conducted iteratively with either the generalized Marquardt algorithm (Conway et al. 1970) or the simplex algorithm of Nelder and Mead (1965). The varying attrition model could be fitted with all three parameters being adjusted or with one or two of the parameters fixed.

Because finding a tagged fish among many untagged fish is a rare event, we presumed that the statistical distribution of tag counts is approximately the Poisson distribution. We therefore used a square root transformation (Sokal and Rohlf 1969, p. 384).

Goodness-of-fit, G, was measured by the proportion of the total variance in the observed data accounted for by the model, i.e.

$$(8)\quad G = 1 - \frac{S_{\min}}{(n-k)\sigma_T^2}$$

where $S_{\min}$ is the minimum residual sum of squares, n is the number of data points used in the analysis, k is the number of parameters estimated, and σ_T^2 is the variance of the transformed input data.

Confidence Limits

When fitting two-parameter models, the boundary of the joint confidence region of the two parameters corresponds to a contour line on the sum-of-squares surface at which the residual sum of squares is equal to a critical value defined by

$$(9)\quad S_{\text{crit}} = S_{\min}\left[1 + \frac{k}{(n-k)} F_{0.05(k,n-k)}\right]$$

where $F_{0.05(k,n-k)}$ is the critical value of the F-distribution at probability level 0.05 with k and $n - k$ degrees of freedom and where k is the number of data points used in the analysis (Conway et al. 1970). A numerical searching algorithm was devised to trace the contour on the sum-of-squares surface. With the varying attrition model, when three parameters were fitted, it was necessary to trace a critical sum-of-squares shell in three dimensions with the critical sum-of-squares given by Equation 9 with $k = 3$. Confidence intervals for individual parameters were obtained from the extremes of the joint 95% confidence region.

Note that except for the actual observed tag return data, uncertainties in input data are ignored in this method of calculating confidence intervals.

Determining Values for β

Estimating β is complicated by the fact that tagged fish can be found in a variety of ways. For the purpose of this analysis we assumed two discovery modes: by fishermen and by personnel of shore-based processing facilities. Recaptured tags can be broken into usable returns from fishermen, unusable returns from fishermen, tags found by fishermen but not returned, and tags missed by fishermen. The latter category can be further broken into usable returns from shore, unusable returns from shore, tags found ashore but not returned, and tags not found at all. An expression β can be derived as follows. Let u_f, u_s = number of usable returns from fishermen and from shore, v_f, v_s = number of unusable returns from fishermen and from shore, ζ_f = tags returned as a proportion of tags found by fishermen, and ζ_s = tags returned as a proportion of tags missed by fishermen (i.e. as proportion of all tags that came ashore, whether found or not). The β factor is the ratio of the number of usable returns to the total number of recaptures and is given by

$$(10)\quad \beta = \frac{u_f + u_s}{\frac{u_f + v_f}{\zeta_f} + \frac{u_s + v_s}{\zeta_s}}.$$

Assumptions of the Models

In addition to the usual assumptions that tagged and untagged fish are equally vulnerable to fishing gear, a series of assumptions was made in deriving the set of analytical models. Simulations were conducted to investigate the consequences to the parameter estimates of violating some of these assumptions (P. Kleiber, A. W. Argue, J. R. Sibert, and R. Farman, unpubl.).

Temporal distribution of tag releases

One assumption is that all tags are released at time zero rather than throughout the first time interval. This is correct for the aggregate data set but not so for most subarea data. The simulation results showed that the models are insensitive to this problem as long as tag returns are available for more than a few time intervals.

Constant parameter values

A principal assumption is that there is little variation in parameter values during the tagging experiment. To use the catch-based models, the population and the attrition rate should be constant; to use the effort-based models, the catchability and the attrition rate should be constant. A subsidiary assumption, for all but the variable attrition model, is that variations in fishing mortality are small relative to the total attrition rate. Simulation showed that the models are robust to large cyclical variations from steady state. In this case the estimates are close to the average values of the varying parameters. If there are large one-way trends, the models are less robust, and the standing stock and catchability estimates tend to reflect the starting values more than the averages.

A result detrimental to effective fishery management would occur if the harvest ratio was so underestimated that the fishery appeared capable of sustaining increased fishing pressure when in fact it could not. In the simulation exercise, the scenarios under which this could happen involved a drastic downward trend in the population, particularly when this was in response to a sharp decrease in recruitment or a sharp increase in mortality. A sharp decrease in recruitment or increase in mortality by a factor of 2 caused underestimation of the harvest ratio by less than a factor of 1.4. Thus, large departures from steady state cause smaller underestimates of the harvest ratio.

Parameters that apply to individual fish, such as attrition rate, are also assumed to be the same for all fish, though we might expect that such parameters would vary as a function of size or age. In a preliminary analysis we found little evidence for an effect of fish size on total attrition rate (see below).

Territory covered by tagging experiment

An implicit assumption in the derivation of the models is that the stock, of which P is a measure, is a clearly defined entity. However, the effective boundary of the stock which the tagged fish represent is not so clearly defined when the area of operation of a fishery is surrounded by unfished areas and when the fish in the fished area can exchange with fish in the unfished area. In such a case, the territory occupied by a cohort of tagged fish can be expected to expand with time. However, the number of tagged fish simultaneously diminishes due to attrition, which thereby limits the duration of the experiment. The effective size of the territory covered by the tagging experiment therefore depends on the relative rates of migratory expansion and attrition. A simulation of this situation resulted in an estimated stock size corresponding to the population occupying a zone approximately twice the area of the fished zone.

Data Used in Analyses

Table 2 gives the tag return data and other input data used in the analyses. Two data sets were organized differently from the others. These are the data for the whole study area, i.e. aggregate data, and for the Trust Territory and Guam subarea. For these we combined the returns from many tag release episodes according to time at large (elapsed time between release and recapture) without regard to the actual dates of release and recapture. Thus the returns in any months-at-large category were not necessarily all contemporaneous. We did this because detailed catch and effort statistics were not available for all of the release episodes which occurrred at many times throughout the 3 yr of the release phase of the tagging experiment and at many places throughout these large areas. This lack of fishery statistics precluded analyzing the release episodes separately. No fundamental change to the models was necessary except that a constant average catch rate had to be assumed because of lack of better data and because the tags, being noncontemporaneous, could not all be associated with the same historical series of catch rates.

The tag data for all subareas other than the Trust Territory and Guam refer to releases and recaptures during specific date spans, 10-d periods for New Zealand and months for other areas.

In Table 2, the t columns identify either the months-at-large category or the specific date span of recapture. The r_i columns give the number of usable recaptures in the territory in question. The few recaptures by the tagging vessel were excluded for all data sets because the fishing effort of this vessel was, for the most part, identical to the places and times of tag release. Returns with unknown dates of recapture were also excluded. If an imperfectly known recapture date could be ascertained to fall within a range of dates such that the extent of the range was less than half the time from release to the midpoint of the recapture range, then the return was accepted and the recapture date taken to be the midpoint of the range. Otherwise the return was rejected. For some individual subareas, the returns were additionally filtered (see below).

The c_i columns in Table 2 give the tons of skipjack caught, and the f_i columns, if present, give the effort in boat days, or purse-seine sets in the case of New Zealand. Except for the Trust Territory and Guam, catch and effort for the first recapture period in each subarea data set were prorated to adjust for timing of tag release during the initial period.

Average monthly catch, $\bar{c}$, and effort, $\bar{f}$, were used in some models. The averages were calculated over the period of time included in the data set. Months with zero catch and effort were included in the average. Catch and effort in individual months could be considerably different from the average, particularly for the highly seasonal New Zealand fishery. Catch and effort were averaged for December–March in New Zealand.

In several cases, the first one or two recapture periods in a

TABLE 2. Tag return and other data used to estimate population parameters. Includes aggregate and subarea data sets.

Aggregate data ($\alpha\beta = 0.60$, $\bar{c} = 19000$)

t	r_t	c_t
$N_a = 140000$		
a1	2820	19000
2	506	19000
3	379	19000
4	261	19000
5	198	19000
6	120	19000
7	115	19000
8	93	19000
9	94	19000
10	114	19000
11	142	19000
12	106	19000
13	72	19000
14	62	19000
15	75	19000
16	42	19000
17	17	19000
18	24	19000
19	16	19000
20	23	19000
21	13	19000
22	8	19000
23	10	19000
24	11	19000
25	3	19000
26	6	19000
27	8	19000
28	7	19000
29	2	19000
30	0	19000
31	1	19000
32	1	19000
33	1	19000
34	1	19000
35	0	19000
36	1	19000
37	0	19000
38	0	19000
39	0	19000
40	0	19000
41	0	19000

Trust Territory and Guam ($\alpha\beta = 0.68$, $\bar{c} = 4900$)

t	r_t	c_t
$N_a = 8887$		
1	45	4900
2	14	4900
3	10	4900
4	43	4900
5	35	4900
6	16	4900
7	14	4900
8	16	4900
9	5	4900
10	2	4900
11	0	4900
12	4	4900
13	0	4900
14	0	4900
15	3	4900
16	3	4900
17	1	4900
18	1	4900
19	2	4900
20	2	4900
21	0	4900
22	0	4900
23	0	4900
24	0	4900

New Zealand ($\alpha\beta = 0.37$, $\bar{c} = 2300$, $\bar{f} = 150$)

t	r_t	c_t	f_t
$N_a = 2678$			
790221	2	336	37
790301	223	2396	120
790311	7	148	18
790321	30	215	24
790401	1	3	1
791121	0	25	7
791201	0	15	7
791221	0	35	6
800101	5	1319	94
800111	0	2100	87
800121	1	1186	86
800201	3	1986	135
800211	1	142	18
800221	0	219	33
$N_a = 6298$			
790301	280	1917	96
790311	8	148	18
790321	48	215	24
790401	0	3	1
791121	0	25	7
791201	0	15	7
791221	0	35	6
800101	5	1319	94
800111	3	2100	87
800121	6	1186	86
800201	6	1986	135
800211	1	142	18
800221	0	219	33
800301	1	1191	76
800311	0	493	36
800321	1	113	19
800501	0	18	5
800521	0	49	5
800601	2	35	9
800611	0	12	2

Papua New Guinea ($\alpha\beta = 0.68$, $\bar{c} = 2000$, $\bar{f} = 670$)

t	r_t	c_t	f_t
$N_a = 6009$			
a7905	20	379	114
a7906	391	2153	598
7907	208	2972	1035
7908	100	2492	913
7909	58	1840	899
7910	27	654	614
7911	5	811	706
7912	3	286	212
8003	1	609	440
8004	5	1956	802
8005	1	2243	985
8006	2	2860	1005
8007	3	2878	1068
8008	7	5514	1100
8009	5	3982	988
8010	0	3697	850
8011	0	3055	831
8012	0	1800	553
8101	0	222	99
8103	0	1814	447
8104	0	4675	918
8105	0	3085	977
8106	0	3340	962
8107	1	3421	1077
8108	1	2100	964
8109	0	1660	805
8110	0	1435	626
8111	0	426	185
8112	0	77	42

Solomon Islands (1977) ($\alpha\beta = 0.64$, $\bar{c} = 1200$, $\bar{f} = 340$)

t	r_t	c_t	f_t
$N_a = 1709$			
7711	17	754	317
7712	10	365	397
7801	0	15	73
7803	0	15	34
7804	3	941	460
7805	5	888	465
7806	1	1526	515
7807	5	1973	551
7808	3	1587	512
7809	4	2304	517
7810	7	2317	497
7811	5	2915	514
7812	5	2723	518
7901	1	1106	223
7904	2	1438	305
7905	0	1788	485

Solomon Islands (1980) ($\alpha\beta = 0.54$, $\bar{c} = 2200$, $\bar{f} = 490$)

t	r_t	c_t	f_t
$N_a = 2012$			
8006	9	354	179
8007	28	2550	558
8008	25	2778	554
8009	9	2770	574
8010	8	3244	566
8011	20	3313	566
8012	16	2774	594
8101	18	1531	463
8104	5	1210	258
8105	5	1881	560
8106	11	2934	614
8107	4	2796	628
8108	6	3474	640
8109	2	2631	639
8110	0	2087	630
8111	0	2131	632
8112	1	1231	415

Fiji ($\alpha\beta = 0.80$, $\bar{c} = 350$, $\bar{f} = 120$)

t	r_t	c_t	f_t
$N_a = 11646$			
a8004	594	185	76
a8005	183	65	86
8006	6	76	42
8007	11	116	33
8008	19	90	49
8009	2	99	20
8010	2	79	21
8011	2	106	45
8012	11	229	41
8101	27	737	198
8102	42	862	161
8103	35	953	193
8104	8	605	150
8105	12	536	138
8106	10	418	132
8107	5	387	140
8108	1	76	23
8110	3	77	33
8111	1	143	82
8112	2	298	147
8201	0	600	224
8202	1	686	226
8203	1	696	241
8204	0	485	231
8205	0	589	275
8206	0	285	168
8207	0	118	81
8208	0	42	31

Society Islands French Polynesia ($\alpha\beta = 0.82$, $\bar{c} = 100$)

t	r_t	c_t
$N_a = 823$		
7812	0	60
7901	1	56
7902	4	64
7903	4	91
7904	1	110
7905	3	170
7906	2	130
7907	0	94
7908	0	89
7909	0	48
7910	0	62
7911	0	100
$N_a = 896$		
a7901	0	7
7902	2	64
7903	1	91
7904	0	110
7905	0	170
7906	0	130
7907	0	94
7908	0	89
7909	0	48
7910	0	62
7911	0	100
7912	1	54
8001	0	190
8002	0	130
8003	0	83
8004	0	82
8005	0	160
8006	0	97
8007	1	78
8008	0	32
8009	0	55
8010	0	150
8011	0	130
8012	0	180

Gilbert Group Kiribati ($\alpha\beta = 0.82$, $\bar{c} = 20$)

t	r_t	c_t
$N_a = 4403$		
7807	26	22.6
7808	159	49.5
7809	82	63.5
7810	78	76.3
7902	0	0.8
7903	0	3.8
7904	1	9.4
7905	0	8.3
7906	0	26.8
7907	0	8.8
7908	0	12.1
7909	0	6.8

data set were disregarded in the analysis. In Table 2 the rows corresponding to these are preceded by an "a." The early returns in any tagging experiment can easily be anomalous because of inadequate mixing of tagged fish in the tagged population. In the present analysis, early returns were disregarded if there was good reason to assume a problem with mixing in the first recapture period(s), and if doing so significantly improved the ability of the model to fit the data.

For each subarea other than the Trust Territory and Guam, releases and recoveries were selected to make the analysis relevant to a local fishery. Releases made outside the area of the local fishery were eliminated as was one release of fish of a substantially different size range than were caught in the local fishery. Tags recovered outside the subarea of release were not considered. Details of tag selection are presented in individual reports prepared for each subarea (Kearney 1982a; Argue and Kearney 1982, 1983; Gillett and Kearney 1983; Kleiber and Kearney 1983; Tuna Programme 1984a, 1984b).

Results and Discussion

Estimation of Nuisance Parameters

Considerable effort was expended to maintain high standards in the tagging procedure (Kearney and Gillett 1982) to maximize α, in the tag return system (Kearney 1982b) to maximize β, and in the quality of the tags themselves to minimize ψ. To analyze the results, however, it was necessary to estimate values for these nuisance parameters.

Estimates of $\alpha\beta$ with the variable attrition model

The variable attrition model (last equation in Table 1) was fitted to the five data sets containing effort in Table 2. N_0 was set to the values given in Table 2, and the parameters M, q, and $\alpha\beta$ were adjusted by the fitting procedure. In three cases the process converged to impossible values (negative M or $\alpha\beta$ greater than 1), and in two cases possible values resulted. Investigation of the three-dimensional confidence regions for the latter two cases (Fig. 2 and 3) revealed that $\alpha\beta$ was very ill-defined by the analysis. The 95% confidence range (approximately 0.05−1.0) covers most of the possible range (0−1).

Estimation of β

Estimation of β using Equation 10 requires the factors ζ_f and ζ_s. A range of values for ζ_f can be obtained from the double tagging results in Fiji. Using the approach of Bayliff and Mobrand (1972), an estimate of 0.997 (95% confidence range 0.82−1.0) was obtained for the quantity $\rho d_f \zeta_f$, where ρ is the short-term (type 1) tag retention (1 minus tag shedding rate) and where d_f is the proportion of recaptured tags that are discovered by fishermen (Tuna Programme, unpubl. analyses). This range also applies to ρ, d_f, and ζ_f individually because all three quantities can only be in the range (0−1).

In a tag-plant experiment designed to measure ζ_s, 25% of the planted tags were returned, all from shore-based processing facilities, principally in Pago Pago. This experiment was conducted more than 1 yr after most of the recoveries from the regular tagging program were obtained from shore facilities. Thus, it is possible that the low recovery of planted tags reflects a more recent problem in the tag recovery system, or a problem specific to seine-caught fish from New Zealand processed in Pago Pago. Unfortunately, tag-plant experiments were not done on pole-and-line caught fish or on fish destined for other processing facilities. It is also possible that tags placed in dead

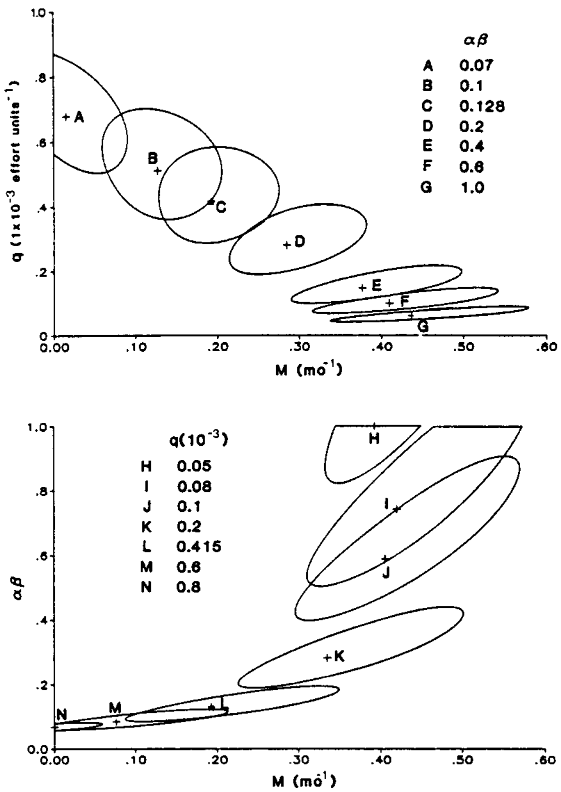

FIG. 2. Confidence regions for estimates of the three parameters of the variable attrition model using the Papua New Guinea data set. In the upper plot, slices through the confidence region at various levels of $\alpha\beta$ are shown. The $\alpha\beta$ axis extends downward from the plane of the page. In the lower plot the figure is rotated forward about the M-axis so that the q-axis rises upward from the plane of the page. Slices at various levels of q are shown. In the upper plot, the crosses give the best-fitting q and M values with $\alpha\beta$ fixed at each level, and in the lower plot the crosses give the best-fitting $\alpha\beta$ and M values with q fixed at each level. The star in each plot gives the best-fitting point for the three-parameter fit.

fish are more easily lost than tags placed in live fish. Taking the tag-plant results at face value, ζ_s could have been as low as 0.25. However, ζ_s might very well have been higher for Pago Pago and other processing facilities during the time that tagged fish from live releases were passing through these facilities. Worst and best case values of 0.25 and 1.0 were assumed for ζ_s.

Assuming the ranges given above for ζ_f and ζ_s, worst and best case values of β were calculated by Equation 10 and are given in Table 3.

Estimation of α

The parameter α depends on type 1 mortality and type 1 tag shedding. As shown above, the type 1 tag shedding rate, $1 - \rho$, must be low. Type 1 tagging mortality is more difficult to determine. However, high tag return rates (>50%) have been observed in the eastern Pacific (Anonymous 1978). This strongly suggests that the combination of type 1 tagging mortality and tag shedding was low. This conclusion is further

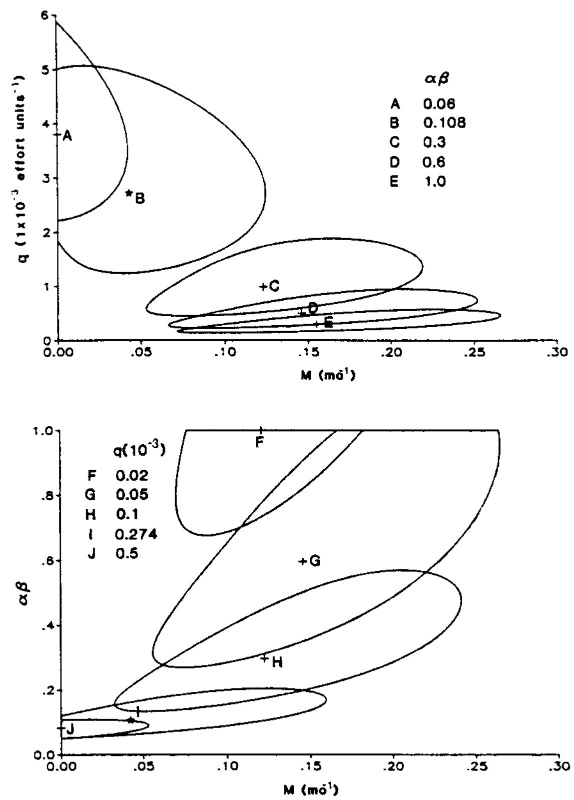

FIG. 3. Confidence regions for estimates of the three parameters of the variable attrition model using the 1980 Solomon Islands data set. In other respects, this figure is similar to Fig. 2.

supported by an experiment with captive skipjack in which no significant difference in mortality between tagged and untagged fish was observed (R. E. Kearney unpubl.).

In the absence of further quantitative information, a figure of 10% has been assumed here for the type 1 losses, i.e. a value of 0.9 for α.

Values of $\alpha\beta$ *used in subsequent analyses*

The values of $\alpha\beta$ used as input to the analytical model are given at the head of each data set in Table 2. These were derived from an assumed value of 0.9 for α and a value for β midway between the worst and best case values given in Table 3.

Type 2 tag loss, ψ

The parameter ψ can include type 2 shedding and also type 2 mortality. Type 2 shedding estimated from double tagging was $0.0073 \cdot mo^{-1}$ (Skipjack Programme 1981). Type 2 mortality is not so readily estimated, but the double tagging results suggest that it is a minor factor. Except for fish smaller than 45 cm, the proportion returned of the double-tagged skipjack was not significantly less than that of single-tagged skipjack released at the same time (Skipjack Programme 1981). The difference noted for small fish could have resulted from type 1 (affecting α) or type 2 (affecting ψ) losses. We looked for and did not find any influence of size on total attrition, $Z + \psi$ (see next section), as would be expected if there was significant, size-dependent, type 2 mortality. This suggests that the reduction in returns for the small double-tagged fish was predominantly a type 1 phenomenon. In any case, these small fish accounted for less than 15% of the returns considered in this report. Type 2 mortality was therefore assumed to be zero, and the value of ψ for all data sets was taken to be the estimate of type 2 tag shedding.

TABLE 3. Worst and best case values of β are calculated from Equation 10 using worst and best case assumptions about ζ (0.82 and 1.0 for ζ_f; 0.25 and 1.0 for ζ_s).

Data set	Where found	Tag returns: Useable u	Tag returns: Reject v	β: Worst case	β: Best case
Aggregate	Fishermen	4641	125	0.47	0.87
	Shore	711	706		
Trust Territory and Guam	Fishermen	190	9	0.58	0.94
	Shore	26	6		
New Zealand	Fishermen	231	12	0.19	0.64
	Shore	403	352		
Papua New Guinea	Fishermen	838	7	0.62	0.90
	Shore	0	82		
Solomon Islands (1977)	Fishermen	65	1	0.55	0.88
	Shore	3	8		
Solomon Islands (1980)	Fishermen	167	6	0.43	0.77
	Shore	0	45		
Fiji	Fishermen	977	23	0.80	0.98
	Shore	1	0		
Society Islands	Fishermen	20	0	0.82	1.0
	Shore	0	0		
Gilbert Group	Fishermen	346	0	0.82	1.0
	Shore	0	0		

TABLE 4. Distribution of tag returns among subareas for three classes of size at release. The total returns are not necessarily the same as the totals of returns in Table 2 because in this case, tags were selected with regard to the existence of accurate length measurement at release and accurate time of recapture, but without regard to other selection criteria involved in assembling the data sets in Table 2.

Data set	Fork length: <45 cm	Fork length: 45–55 cm	Fork length: >55 cm	Total tag returns
Aggregate	634	3536	630	4800
Fiji	139	1380	114	1633
Solomon Islands	157	290	55	502
Papua New Guinea	14	573	311	898
Palau	204	52	51	307
Ponape	1	95	44	140
New Zealand	100	536	8	644
Wallis and Futuna	3	67	6	76
Tuvalu	1	21	6	28
Gilbert Group	3	354	8	365

Effect of Size at Release on Attrition

To test for the effect of size at release on attrition rates, the

TABLE 5. Estimates of tag attrition (mo^{-1}) with 95% confidence intervals for three classes of size at release. Results are given for the aggregate data set and for subareas with 20 or more returns in more than one size class. One data set, WTG, is the sum of returns for Wallis and Futuna, Tuvalu, and the Gilbert Group.

Data set	Fork length		
	<45 cm	45–55 cm	>55 cm
Aggregate	0.17 (0.15–0.20)	0.17 (0.14–0.20)	0.27 (0.22–0.33)
Fiji	0.18 (0.10–0.32)	0.57 (0.09–0.24)	0.12 (0–0.33)
Solomon Islands	0.17 (0.11–0.26)	0.18 (0.12–0.25)	0.27 (0.17–0.42)
Papua New Guinea		0.34 (0.21–0.58)	0.63 (0.42–0.92)
Palau	0.21 (0.17–0.27)	0.15 (0.08–0.25)	0.37 (0.19–0.69)
Ponape		0.20 (0.13–0.29)	0.22 (0.06–0.48)
New Zealand	1.1 (0.9–10.4)	1.2 (0.9–10.5)	
WTG		0.24 (0.14–0.46)	0.30 (0.07–0.69)

aggregate tagging data and seven subsets of the data were broken into three categories of size at release, <45, 45–55, and >55 cm (Table 4). Six subsets consisted of subarea data with 20 or more returns in at least two of the size categories. One additional subset was made up of returns from three subareas which in combination gave 20 or more returns in two size classes.

The aggregate and six of the subsets were put into months-at-large classes in the same way as the aggregate data in Table 2. The New Zealand subset was broken into 10-d periods. Total attrition was estimated by fitting the first model in Table 1 to the data, using a constant catch rate for subarea as well as aggregate data under the assumption that the effects of changing catch rate on attrition estimates would be roughly equivalent for the different size classes.

The resulting attrition estimates (Table 5) can be used to compare size classes within a subarea or the aggregate data set, but they should not be used to compare attrition rates between countries. The only significant result is a higher attrition rate for large fish in the aggregate case. However, a large portion of the large fish were released in Papua New Guinea (Table 4) where, as we shall see (Table 6), the attrition rate was particularly high. Therefore the result for aggregate data could be a Papua New Guinea effect instead of a size effect, a conclusion that is supported by the lack of significant effect of size for individual subarea data.

Tag Attrition Curves

The decline in tag return rate with time is shown for the aggregate data set in Fig. 4. As indicated in Table 2, the value for the first month was not included in the fitting. The bump in the observed data at approximately 1 yr could be the result of seasonality in the fisheries. Most fisheries in the region have a period of higher fishing effort each year lasting from a little over 1 mo (New Zealand) to several months (Papua New Guinea). Because tags tended to be released in each subarea during these periods, it is to be expected that a surge of tag returns would coincide with increased fishing, approximately 1 yr following tagging.

The predicted values decline smoothly in Fig. 4 because we could not account for variations fishing activity in the aggregate case. When we were able to account for such variations, the predicted values decline jerkily (Fig. 5) because they reflect variations in catch, as well as the steady decline due to all the components of attrition.

Parameter Estimates from the Analytical Model

Table 6 gives goodness-of-fit and parameter estimates obtained from all but the variable attrition model. Table 7 gives the goodness-of-fit and parameter estimates obtained by fitting the variable attrition model to the data sets for which effort data were available.

The results from the variable attrition model are close in most cases to the corresponding results from the fixed attrition models. The goodness-of-fit was not improved, and the catchability estimates are likewise much the same. The last two columns in Table 7 match well except for the New Zealand results. In this case the discrepancy between variable attrition and fixed attrition models may be due to the large degree of seasonality in the New Zealand fishery, the resulting large variation in attrition being more easily accounted for by the possibility of variable attrition in the model.

The parameter estimates in Tables 6 and 7 form the basis of Skipjack Programme reports for individual subareas wherein the implications of these results to fisheries in the subareas are discussed in detail.

Reliability of the parameter estimates

The confidence limits reported in Tables 6 and 7 do not include uncertainty in the values of the nuisance parameters, and therefore, the confidence ranges in the tables are minimum estimates.

Accounting for uncertainty in ψ (the type 2 shedding rate) would directly affect the confidence ranges of attrition, and thus to a similar extent the estimates of throughput and harvest ratio. The 95% confidence range of ψ is $0.0031-0.0116 \cdot mo^{-1}$. However, given its small magnitude relative to the attrition rate, its variance is unlikely to significantly affect the confidence ranges of any of the above parameters.

Accounting for the uncertainty in the value of $\alpha\beta$ would affect the confidence ranges of all parameters except Z_c and Z_f. The range between the best and worst case estimates of β can be large (Table 3), and the assumed value of α is a guess based on little quantitative information. The confidence ranges given in Tables 6 and 7 would be larger if the uncertainty in $\alpha\beta$ had been included, which can be seen in the three-parameter confidence regions for Papua New Guinea and Solomon Islands, 1980 (Fig. 2 and 3). It is interesting to note, however, that the effect of uncertainty in $\alpha\beta$ is dependent on whether this quantity is in the upper or lower part of its possible range (0–1). Thus the confidence range of M is considerably reduced if $\alpha\beta$

TABLE 6. Results from the analytical models in Table 1 using data in Table 2. The upper figure in each cell is the best parameter estimate, and if given, the lower two figures are the 95% confidence limits. Effort data was not available for all data sets; therefore, there are some blank cells for quantities that depend on the effort value. For the New Zealand and Society Islands, data from releases in consecutive periods were used in one fitting of the model. G_c = % of variance explained by model with catch data, G_f = % of variance explained by model with effort data, P = standing stock (Mt), T = throughput (Mt·mo^{-1}), q = catchability (sets^{-1} in New Zealand, vessel-days^{-1} elsewhere), Z_c = attrition (mo^{-1}) with catch data, Z_f = attrition (mo^{-1}) with effort data, F_c = fishing mortality (mo^{-1}) with catch data, F_f = fishing mortality (mo^{-1}) with effort data, H_c = harvest ratio (dimensionless) with catch data, H_f = harvest ratio (dimensionless) with effort data.

Data set	G_c	G_f	P (10^3)	T (10^3)	q (10^{-3})	Z_c	Z_f	F_c	F_f	H_c	H_f
Aggregate	0.95		3000 2500–3700	520 460–590		0.17 0.15–0.20		0.0063 0.0051–0.0077		0.037 0.032–0.042	
Trust Territory and Guam	0.71		660 370–1310	150 100–250		0.23 0.14–0.36		0.0074 0.0038–0.0131		0.032 0.020–0.048	
New Zealand	0.91	0.85	13 10–17	5.0 3.8–7.0	1.2 0.8–1.7	0.38 0.30–0.52	0.39 0.29–0.62	0.17 0.13–0.22	0.18 0.12–0.25	0.46 0.33–0.60	0.46 0.29–0.65
Papua New Guinea	0.96	0.95	35 27–45	13 11–16	0.090 0.060–0.144	0.38 0.32–0.46	0.47 0.35–0.65	0.058 0.045–0.075	0.061 0.040–0.097	0.15 0.13–0.18	0.13 0.10–0.16
Solomon Islands (1977)	0.69	0.52	49 25–124	11 7–19	0.027 0.008–0.065	0.23 0.13–0.34	0.14 0.01–0.29	0.024 0.010–0.049	0.0092 0.0027–0.0223	0.11 0.06–0.17	0.067 0.034–0.270
Solomon Islands (1980)	0.63	0.68	89 49–185	13 9–22	0.056 0.029–0.096	0.15 0.07–0.26	0.16 0.09–0.26	0.025 0.012–0.046	0.027 0.014–0.047	0.16 0.10–0.25	0.17 0.11–0.24
Fiji	0.80	0.68	39 20–79	7.3 4.8–11.4	0.081 0.036–0.164	0.19 0.13–0.26	0.19 0.12–0.26	0.0091 0.0044–0.0174	0.0097 0.0043–0.0197	0.048 0.031–0.072	0.056 0.030–0.084
Society Islands	0.36		9.7 1.8–67.1	5.7 2.1–20.1		0.59 0.20–1.30		0.010 0.001–0.055		0.017 0.005–0.048	
Gilbert Group	0.91		1.0 0.5–2.1	0.38 0.24–0.64		0.37 0.16–0.69		0.019 0.009–0.038		0.052 0.031–0.083	

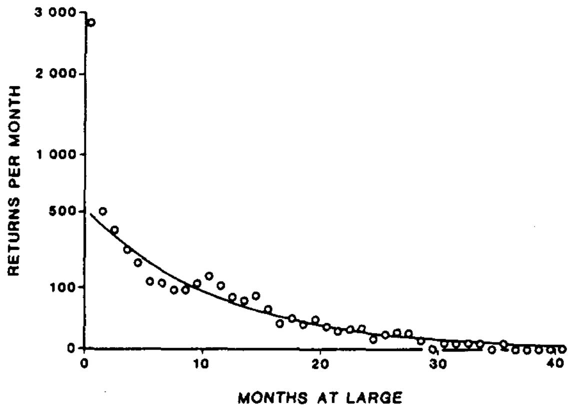

FIG. 4. Aggregate tag attrition curve. Points are the aggregate tag return rates (Table 2). The solid line gives the expected values based on the best fit of first model form in Table 1. The y-axis is a square root scale.

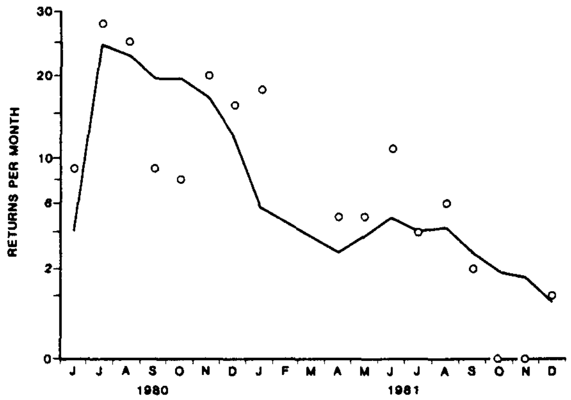

FIG. 5. Example tag attrition curve for a subarea (Solomon Islands, 1980). In other respects, this figure is similar to Fig. 4.

is known to be greater than 0.4, but more precise definition of $\alpha\beta$ within the range 0.4−1 would not narrow the confidence range of M much further (Fig. 2 and 3).

It must be stressed that the parameter values for individual subareas, and overall, apply to the time of the tagging experiment. Since that time, significant changes have occurred in several fisheries in the region. In addition, periodic major environmental events occur that presumably could affect skipjack populations in the tropical central and western Pacific waters (Wyrtki 1975; Donguy and Henin 1978).

Standing stock and throughput

The standing stock in different areas, under conditions of uniform stock density, would be proportional to the size of the area. Therefore, differences among individual country results would reflect the size of the areas covered by the different tagging experiments, which by design roughly covered the area of the locally based fisheries. Such is evident in Table 6 by comparison of P for the Gilbert Group with P for the other individual subareas. The Gilbert Group estimate is smaller than all others, and the "fishery" was a single vessel survey concentrated near a single atoll, a much smaller area than the other individual country fisheries. The aggregate estimate of P is much larger than the sum of estimates for individual subareas in Table 6 because these are only a portion of the area included in the aggregate. Between these extremes, differences among subareas are difficult to interpret, firstly because of the large overlapping confidence intervals and secondly because of the difficulty in evaluating the effective area covered by the fisheries during the tag recovery period.

Throughput, T, should be only approximately proportional to the size of the fished area, since throughput is the product of attrition and standing stock and attrition has a component due to emigration which is expected to vary inversely with the size of the fished area.

TABLE 7. Results from varying attrition model with data sets containing effort values in Table 2. The parameter $\alpha\beta$ was fixed to the values given in Table 2. The format of the entries in each cell is the same as in Table 6. For comparing M with results from fixed attrition models, values of attrition minus fishing mortality (Z_f-F_f) from Table 6 are included in the last column of this table.

Data set	G	q (10^{-4})	M	Z_f-F_f
New Zealand	0.85	13 9−18	0.35 0.25−0.58	0.21
Papua New Guinea	0.95	0.88 0.60−1.30	0.41 0.31−0.55	0.41
Solomon Islands (1977)	0.51	0.26 0.08−0.64	0.13 <0.01−0.27	0.13
Solomon Islands (1980)	0.68	0.55 0.39−0.96	0.14 0.07−0.22	0.13
Fiji	0.68	0.79 0.35−1.56	0.18 0.12−0.24	0.18

Attrition

Attrition and its components are not expected to be proportional to the area covered by the experiment. However, attrition is not necessarily independent of area because it includes a component due to dispersive movement of fish. This component tends to increase in importance with decreasing size of the area under consideration. Therefore the attrition is expected to vary inversely with area and, for large areas, approach a dispersion-free attrition rate. It is probably for this reason that the aggregate attrition estimate was lower than all but one of the individual country estimates (though only three have non-overlapping confidence intervals).

Under the assumption of steady state, the attrition rate is also the population turnover rate. Simulation modelling showed that in a non-steady-state situation the attrition estimate would tend to reflect the average attrition over the time of the experiment. Thus if the lack of steady state is attributable to seasonal fluctuations, and tags are returned over a period of at least 1 yr, then the attrition estimate would reflect the yearly average population turnover. Furthermore, simulation showed that in nonequilibrium conditions (i.e. when the sum of inputs is different from the sum of outputs), the estimate of Z_c tends to be closer to the sum of inputs and Z_f closer to the sum of outputs. The implication is that if Z_c is larger than Z_f, then the population is increasing whereas if Z_c is less than Z_f, then the population is decreasing. The only cases in which there were appreciable differences between Z_c and Z_f were the results from the 1977 Solomon Islands data set ($Z_c > Z_f$) and from the Papua New Guinea data set ($Z_c < Z_f$). (The confidence regions given in Table 6 are not relevant in judging the significance of a difference between estimates of Z_c and Z_f when these parameters are obtained from the same data sets because there is likely to be a high positive covariance between the two estimates, which would tend to minimize the variance of the difference between them.) It may only be fortuitous that the increasing trend in P in Solomon Islands (October 1977 versus June 1980) was consistent with that predicted by the 1977 estimates of Z_c and Z_f, since the confidence intervals for the two estimates of P are large and overlapping. (In this case, where the results from two independent sets are compared, the confidence regions in Table 6 are relevant.) The trend predicted for Papua New Guinea could not be checked because there was no further tagging experiment in these waters.

The aggregate estimate of attrition is $0.17 \cdot mo^{-1}$ (0.15–0.20). When fishing mortality is subtracted the remaining attrition is $0.16 \cdot mo^{-1}$. Joseph and Calkins (1969) reported a comparable estimate of skipjack attrition, excluding F, of $0.14 \cdot mo^{-1}$ from a tagging experiment in the northern zone of the eastern Pacific fishery. Ssentongo and Larkin (1973) gave a method for calculating attrition in exploited fish populations given the length of fish at recruitment, the mean length in the catch, and values for the parameters L_∞ and K of the von Bertalanffy growth model. For skipjack, assuming a length at recruitment of 38 cm and a mean length in the catch of 50.4 cm (the mean length of skipjack tagged by Skipjack Programme), and using values of $L_\infty = 62.5$ cm and $K = 0.17 \cdot mo^{-1}$ (Sibert et al. 1983), the predicted value of attrition is $0.24 \cdot mo^{-1}$, which drops to $0.23 \cdot mo^{-1}$ when our estimate of F is subtracted. Pauly (1979) reported a regression equation for predicting natural mortality of a fish species given its von Bertalanffy parameter values and its mean environmental temperature. The regression equation was based on reported natural mortality estimates from a wide variety of fish families (including skipjack among several examples of scombrids). It is unclear to what extent attrition mechanisms other than natural mortality and fishing mortality are included the estimates used to derive the regression equation. Assuming the values given above for L_∞ and K and a mean water temperature of 25°C, the Pauly estimate of natural mortality for skipjack is $0.18 \cdot mo^{-1}$, which is similar to our overall estimate of attrition.

Catchability

Catchability coefficients, q, for pole-and-line gear (Table 6) range from $2.7 \times 10^{-5} \cdot$ fishing day^{-1} for November 1977 tagging in Solomon Islands to $9.0 \times 10^{-5} \cdot$ fishing day^{-1} for May–June 1979 tagging in Papua New Guinea; however, all estimates have overlapping confidence intervals and little can be made of the differences among subareas. For purse-seiners in New Zealand, q is $1.2 \times 10^{-3} \cdot set^{-1}$ or $1.8 \times 10^{-3} \cdot$ fishing day^{-1} using the average of 1.5 sets $\cdot$ fishing day^{-1} for the 1979–80 and 1980–81 New Zealand fishing seasons (Argue and Kearney 1983). This catchability for purse-seiners is 28 times higher than the average for pole-and-line gear in Table 6, which probably reflects greater fishing power for purse-seiners and greater skipjack vulnerability in the coastal waters of New Zealand.

Harvest ratio

Having defined the harvest ratio and having obtained estimates thereof, it is useful to have a bench mark to show whether a given estimate is high, indicating heavy fishing pressure, or low, indicating the possibility for increased yield. The harvest ratio is analogous to the X-factor of Gulland (1971), defined such that

$$(11) \quad Y = XT_v$$

where Y is the potential yield and T_v is the virgin turnover. On the basis of two arguments, Gulland suggested that the maximum yield from a fishery is obtained with a value of approximately 0.5 for X. One argument is based on the Schaefer model and has been shown by Francis (1974) to be unreliable. The other argument is based on the Beverton–Holt yield per recruit model wherein for a broad range of conditions, the maximum yield per recruit is obtained with a value close to 0.5 for X. Beddington and Cooke (1983) argued that for most realistic sets of parameter values, a value of X somewhat smaller than 0.5 gives maximum yield. However, if the Beverton–Holt yield is calculated for a skipjack-like fish with the values of L_∞ and K assumed above and a natural mortality of $0.16 \cdot mo^{-1}$, the harvest ratio (or X) producing maximum yield is seen to be in the neighborhood of 0.5–0.7 with a size at recruitment between 36 and 40 cm (Fig. 6). It should be noted that the sustainability of yields under Gulland's second argument depends on an assumption of constant recruitment, regardless of standing stock level (Beddington and Cooke 1983). Nevertheless, a harvest ratio close to 0.5 would seem to be a good signpost for a skipjack fishery approaching full exploitation.

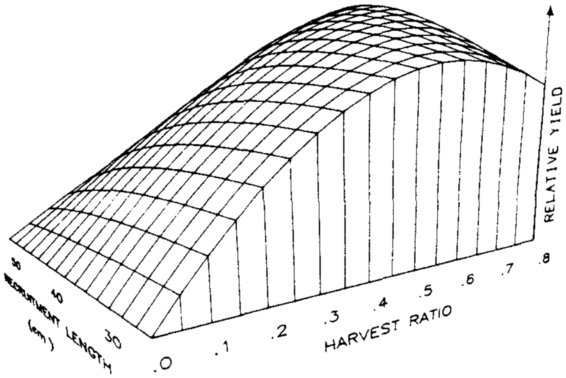

FIG. 6. Beverton-Holt yield surface. Relative yield is plotted as a function of harvest ratio and length at recruitment. Natural mortality is assumed to be $0.16 \cdot mo^{-1}$. L_∞ and K of the von Bertalanffy growth model are assumed to be 62.5 cm and $0.17 \cdot mo^{-1}$, respectively (Sibert et al. 1983).

The estimates of harvest ratio (Table 6) tend to be lower than 0.5. For the aggregate case, the harvest ratio is low, 0.04, implying that fishing is having little impact on the skipjack resource in the study area as a whole. For subareas with well-established commercial fisheries (New Zealand, Papua New Guinea, and Solomon Islands), harvest ratios are higher, 0.15–0.46, while the other subareas, which have small or fledgling fisheries, have low harvest ratios, <0.1. Low harvest ratios for a large part of the study area imply that there is a potential for greatly increased skipjack yield, both within individual subareas and in the study area as a whole. However, recently expanded purse-seine fisheries in the vicinity of the Trust Territory, Papua New Guinea, and Solomon Islands have undoubtedly realized some of this potential.

Conclusion

The results of the analyses given in this paper provide evidence that the resource of skipjack in the study area of the Skipjack Programme is large, its rate of turnover is high, and the rate of mortality due to fishing during the study period was only a small fraction, <0.05, of the rate of turnover. This implies that skipjack catches over the whole study area could be substantially increased from those of the study period. The tag recapture and attrition models used to obtain aggregate estimates and confidence intervals for standing stock, turnover, and fishing mortality were applied to tagging data from subareas with skipjack fisheries for which catch statistics were available. Parameter estimates so derived suggest that the impact of fishing in the smaller areas is larger than the overall impact of fishing.

It should be emphasized that the results reported here apply to the time of the tagging experiment. Substantial development of purse-seining has occurred in the region since that time. This large increase in fishing effort, the large confidence intervals of parameter estimates, and the occurrence of high harvest ratios in some subareas all argue for a cautious approach in planning further development of skipjack fisheries in the central and western Pacific.

The analytical techniques used in this study are based on a set of models derived to address the situation of skipjack and of the tagging experiment conducted by the Skipjack Programme. With due attention to our discussion of assumptions, these techniques could be applied to other situations with similar salient features. The activity of the fishery can vary during the experiment, but large trends in conditions of fishery or environment during the experiment should be a warning signal. The behavior of the fish should be similar across all sizes (ages) that are tagged and should not have large trends during the experiment. These analyses should be used cautiously with long-lived fish that are exposed to the fishery for a long time, but fish like skipjack with a high turnover rate, and consequent short time in the fishery, would be good candidates.

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