Doc. No. 2

ASSESSMENT OF SKIPJACK AND YELLOWFIN TUNA STOCKS IN THE WESTERN TROPICAL PACIFIC, USING DATA FROM LARGE-SCALE TAGGING EXPERIMENTS

by

John Hampton

Tuna and Billfish Assessment Programme
South Pacific Commission
B.P. D5
Noumea Cedex, New Caledonia

Working paper for
Western Pacific Yellowfin Tuna Research Group Workshop
Honolulu, Hawaii
June 17-24, 1992

DRAFT: NOT TO BE CITED

ASSESSMENT OF SKIPJACK AND YELLOWFIN TUNA STOCKS IN THE WESTERN TROPICAL PACIFIC, USING DATA FROM LARGE-SCALE TAGGING EXPERIMENTS

John Hampton

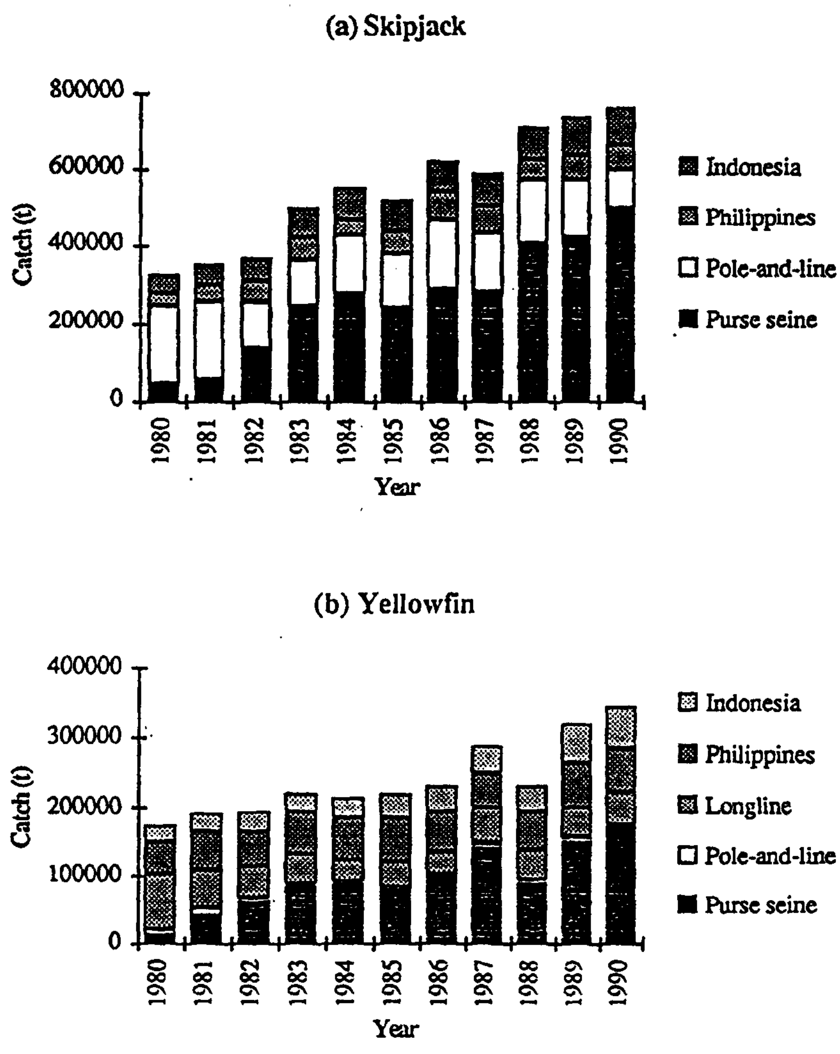
Tuna and Billfish Assessment Programme
South Pacific Commission
B.P. D5, Noumea Cedex, New Caledonia

Abstract

Data from three large-scale tagging experiments were analysed, using tag attrition models and simulation techniques, to estimate population sizes, natural mortality, fishing mortality and recruitment rates of skipjack (*Katsuwonus pelamis*) and yellowfin (*Thunnus albacares*) stocks in the major surface fishing area of the western tropical Pacific (10°N-10°S, 120°E-170°W). The results were used to assess the current status of the stocks and to estimate their exploitation potential. Two of the experiments were on skipjack, the first during 1977-1982 and the second during 1989-1991. The third experiment, on yellowfin, also occurred during 1989-1991. The results of the recent experiments show that skipjack have a high rate of natural mortality (0.16-0.19 month^{-1}), an equilibrium population size vulnerable to the fishery of 1.8-2.8 million t and a recruitment rate of 380,000-560,000 t month^{-1}. Slightly lower natural mortality rate, recruitment and population size were estimated from the earlier data. The fishing mortality rate for the earlier period was low (0.008-0.025 month^{-1}), and is currently estimated to be 0.024-0.038 month^{-1}. Yellowfin have a lower rate of natural mortality (0.08-0.10 month^{-1}), smaller population size (1.4-2.1 million t), lower recruitment rate (150,000-220,000 t month $^{-1}$) and lower fishing mortality rate (0.013-0.022 month^{-1}) than skipjack. For both species, the rates of fishing mortality are only 15-16% of the total mortality rates, indicating that, in spite of current annual catches in excess of 750,000 t for skipjack and 350,000 t for yellowfin, the stocks are lightly exploited. Projections based on the estimated parameters suggest that a doubling of the skipjack catch would reduce its equilibrium population sizes by only 11-20%. Similarly, doubling the yellowfin catch would result in a 5-24% decrease in equilibrium population size. A conservative management policy with respect to biological conservation would be to allow catches to gradually increase over several years by 50% of their current levels, i.e. to 1.2 million t for skipjack and 500,000 t for yellowfin. Careful and timely monitoring of various fishery indicators, such as catch per effort and size composition of the catch, *must* accompany any such increases. Although not investigated specifically in this study, there is currently little evidence of significant effects of the surface fisheries on the longline fishery, or of local depletion of stocks because of high local exploitation.

The western Pacific tuna fishery, with an estimated catch in 1990 of 1.2 million t (Lawson 1991), is the largest of its type in the world. Skipjack (*Katsuwonus pelamis*) and yellowfin tuna (*Thunnus albacares*) dominate the catch, comprising 65% and 29%, respectively, of 1990 landings. Large purse seine vessels from the United States, Japan, Korea, Taiwan and others are the most important component of the fishery in terms of catch. Skipjack and, to a lesser extent, yellowfin are also caught by long-range pole-and-line vessels from Japan and in domestic fisheries using various gears in Indonesia, Philippines, Solomon Islands, Kiribati and Fiji. Yellowfin are also caught, generally at larger size, by longliners. Over the past decade, steady increases in the catches of both species, due mainly to increased purse seine effort, have occurred (Figure 1).

Figure 1. Total catches of skipjack and yellowfin in the western Pacific Ocean.



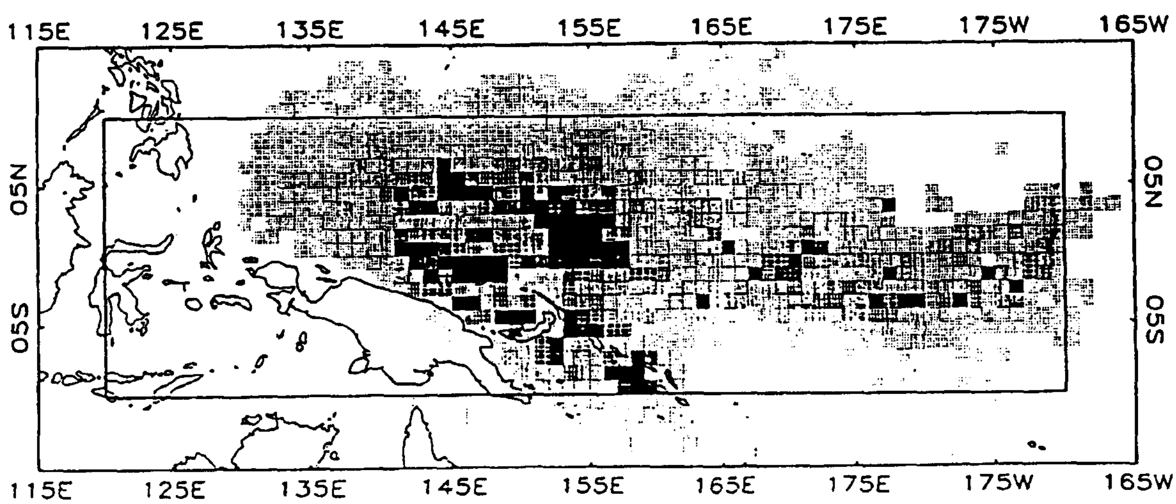
Research on skipjack was undertaken during 1977-1981 by the South Pacific Commission's Skipjack Survey and Assessment Programme (SSAP), mainly through a large-scale tagging experiment. This work showed that the skipjack stock in the western and central Pacific was large (2.5-3.7 million t) and subject to a rapid turnover rate (14-18% per month), of which less than 1% was due to fishing (Kleiber *et al.* 1987). This implied that there was potential for much greater skipjack catches from throughout the region.

Based partly on this advice, the fisheries indeed expanded throughout the 1980's, as noted above. Two important factors in the expansion are relevant to the present study. First, the increases in catch, largely by purse seiners, have been concentrated in the region 10°N-10°S and 130°E-170°W, a much smaller area than that to which the SSAP referred. Second, the increased skipjack catches have been accompanied by greatly increased catches of yellowfin, a species not investigated in detail by the SSAP. Towards the end of the 1980's, there was a clear need to re-assess the now larger and more concentrated skipjack fishery, and to provide a first assessment of the yellowfin stock in the western tropical Pacific. It was with these and other needs in mind that the South Pacific Commission embarked on a second, large-scale tagging project, the Regional Tuna Tagging Project (RTTP), in mid-1989.

In this paper, I analyse three tag-return data sets, two for skipjack and one for yellowfin, using tag attrition models with some novel features. The area to which the study refers is the current area of most intense exploitation: 10°N-10°S, 120°E-170°W. This area includes the Philippines and eastern Indonesian domestic fisheries, as well as encompassing most of the catch by the international purse seine fleet and Pacific Island domestic fisheries (Figure 2). The first skipjack data set (referred to as experiment 1) is a subset of the total SSAP data, defined by releases and associated recoveries within the study area. Releases occurred between October 1977 and August 1980, and recaptures were recorded until August 1982. The second skipjack data set (experiment 2) and the yellowfin data set (experiment 3) consist of RTTP releases and recoveries within the study area, with releases spanning July 1989 to September 1991 and recaptures until December 1991. Time series of catch data are analysed in conjunction with the tagging data.

The objectives of this study are to estimate skipjack and yellowfin population sizes, recruitment, natural mortality/emigration rates and fishing mortality rates for stocks available to surface fisheries in the study area. For skipjack, the analysis of the two data sets allows the temporal stability of parameter estimates and their robustness to very different exploitation patterns to be examined. On the basis of the parameter estimates, conclusions regarding the long-term exploitation potential of the stocks are drawn.

Figure 2. Distribution of skipjack and yellowfin catch from 1 July 1989 to 31 December 1991. Darker squares indicate areas of greater catch. Philippines and Indonesian domestic catches were unavailable. The study area is indicated by the box.



TAGGING EXPERIMENTS

Characteristics of the Experiments

All experiment 1 releases were made from chartered, commercial pole-and-line vessels (Japanese style, 200-250 GRT) suitably modified to carry out tuna tagging (Kearney 1982). Most experiment 2 and 3 releases were also made from such a vessel, supplemented with opportunistic tagging from smaller commercial pole-and-line vessels. Details of the tagging experiments are given in Table 1.

Table 1. Details of the three tagging experiments analysed in this study.

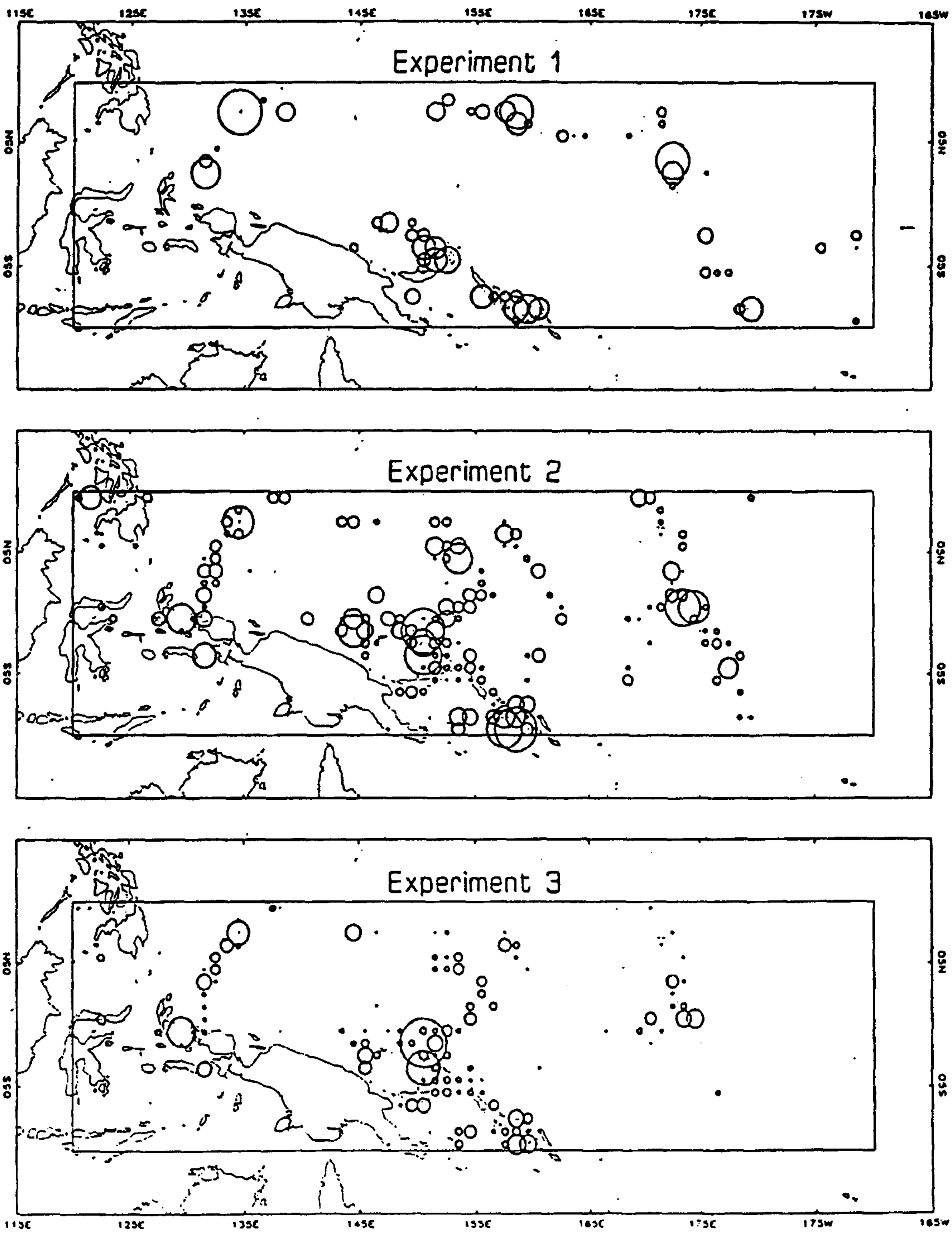
	Experiment 1	Experiment 2	Experiment 3
Project	SSAP	RTTP	RTTP
Species	Skipjack	Skipjack	Yellowfin
Release period	Oct 1977 - Aug 1980	Jul 1989 - Sep 1991	Jul 1989 - Sep 1991
Recapture period	Oct 1977 - Aug 1982	Jul 1989 - Dec 1991	Jul 1989 - Dec 1991
Total releases	37,143	77,465	29,089
Total returns	2,612	7,348	2,591
Return rate (%)	7.0	9.5	8.9

The tagging methods used in the SSAP were described by Kearney and Gillett (1982). The same methods were used during the RTTP, but the tags differed in their construction, size and material. Most tags used in the SSAP consisted of a hollow, temperature-resistant, vinyl streamer (3.0 mm external diameter, 11 cm long) glued to a nylon, single-barb, dart head. These tags were inserted into the fish as described by Kearney and Gillett (1982), using applicators made from 16-17 cm lengths of stainless steel hypodermic tubing (external diameter 4.58 cm), tapered and sharpened at one end. The tags used in the RTTP consisted of a solid polyurethane tube covered with clear plastic (13 cm long, 2.0 mm external diameter) that had been heat-fused to the tag head. A scaled-down version of this tag (10.5 cm long, 1.2 mm external diameter) was used for tuna less than 35 cm fork length. Similar applicators to those described above, but with slightly smaller external diameters (4.15 mm for the full-sized tags and 2.95 mm for the smaller tags) were used.

Skipjack was the principal target species in the SSAP, and fishing and tagging strategies were designed to maximize the release numbers of this species. Smaller numbers of yellowfin were also tagged when encountered, but the numbers were not sufficient to warrant analysis in this study. During the RTTP, strategies were adopted to maximize releases of tagged yellowfin, while still releasing substantial numbers of tagged skipjack. In particular, we tended to concentrate efforts on mixed schools of skipjack and yellowfin and pure yellowfin schools, rather than pure skipjack schools.

The geographical distribution of releases differs slightly among the three experiments (Figure 3). Experiment 1 releases were concentrated in the vicinity of islands, mainly for operational reasons (easy access to baitgrounds). For similar reasons, the greatest numbers of releases in experiments 2 and 3 were also in island areas, although there was a deliberate attempt to tag in oceanic areas as well, using innovative tuna and bait fishing techniques.

Figure 3. **Distribution of tag releases for experiment 1 (skipjack, SSAP), experiment 2 (skipjack, RTTP) and experiment 3 (yellowfin, RTTP). Circle areas are proportional to numbers of tagged tuna released in one-degree squares. The largest circle size represents 5,000 releases.**



The size composition of releases in each of the experiments is shown in Figure 4. The sizes of tagged skipjack in experiments 1 and 2 are similar, with most being within the range 30-70 cm. Although no size composition data are available for the skipjack fishery contemporaneous to experiment 1, it is reasonable to assume that the sizes of tagged and commercially-caught skipjack were similar, as pole-and-line gear predominated in the fishery at that time. The size composition of skipjack caught by US purse seiners in the study area during the RTTP is similar to that of experiment 2 releases, although few skipjack less than 40 cm, and significant numbers of 70-80 cm skipjack, have been sampled in the commercial catches. These differences may result from the common practice of purse seiners of discarding tuna less than 40 cm, and possibly a higher vulnerability of large skipjack to purse seine gear compared to pole-and-line gear. The differences in size composition between tagged and purse seine caught yellowfin are greater. Very few yellowfin greater than 70 cm could be caught and tagged using pole-and-line gear, whereas yellowfin in the size range 70-150 cm comprise a large component of the US purse seine catch.

Comparisons of tagged tuna length frequencies with US purse seine catch length frequencies were dictated by the latter data being the only purse seine length-frequency data available. There are reasons to believe that the other major purse seine fleets (Japan, Korea and Taiwan) do not catch as much larger skipjack and yellowfin as the US fleet. These fleet-specific differences in fish size relate to differences in targeting log-associated tuna versus tuna in free-swimming schools. Therefore, the differences between the size compositions of the tagged tuna and the purse seine catch as a whole are likely to be substantially less than those depicted in Figure 4.

Tagging and Catch Data

The three sets of tagging data used in the analyses consist of tag release numbers classified by month of release, and recapture numbers classified by months of release and recapture. The associated catch data consist of monthly estimates of total catch in the study area corresponding to each recapture month. These data are set out in Table 2.

At the time of writing, experiments 2 and 3 were still in progress. Further releases and recaptures are expected during 1992, and these data will ultimately be included in this study. It is not expected that the addition of further tagging data will substantially alter parameter estimates, although their precision may be improved.

The catch data used in the current version of the analyses are approximate and are based on the estimated monthly skipjack catch during the SSAP (Kleiber *et al.* 1987) for experiment 1 and the estimated annual catches of skipjack and yellowfin for 1989-1990 (Lawson 1991) for experiments 2 and 3. The quality of these catch estimates will be upgraded substantially by mid-1992, at which time the analyses will be re-run. However, unless major changes to the catch data occur, it is not expected that the conclusions of this paper will be substantially changed.

Figure 4. **Sizes compositions of releases for the tagging experiments, and size compositions of skipjack and yellowfin caught by US purse seiners in the study area from 1 July 1989 to 30 September 1991.**

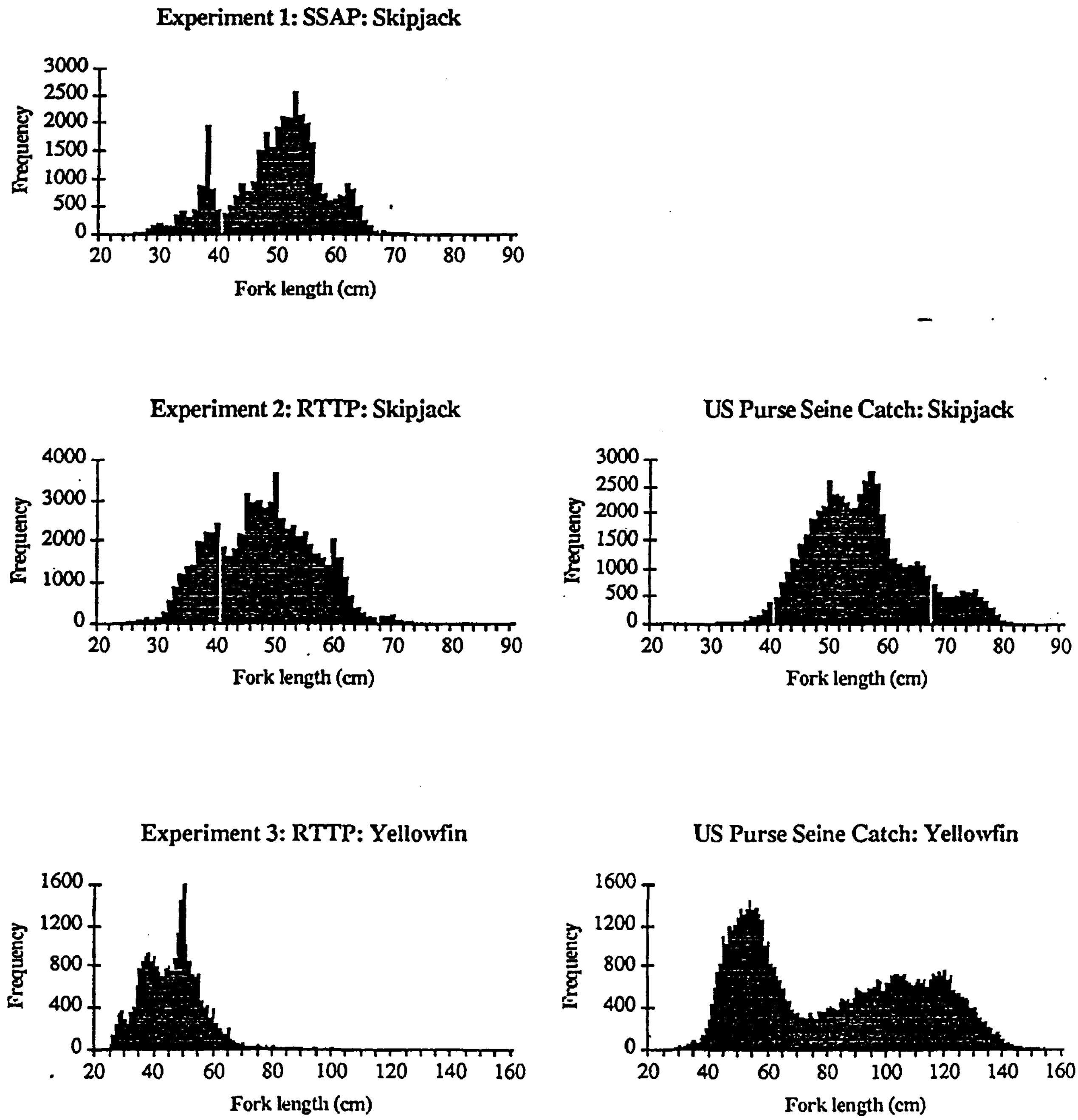


Table 2. Tag releases, recaptures and catch data (t) used in the study. For experiment 1, release and recapture period 1 refers to October 1977. For experiments 2 and 3, release and recapture period 1 refers to July 1989.

Experiment 1

		Release Period													
		1	2	9	10	11	13	14	20	21	26	27	33	34	35
Recapture period	Releases → / Catch	1205	1773	785	5501	1180	1896	553	3306	4533	1729	373	3624	4085	6600
1	19000	4													
2	19000	0	21												
3	19000	0	10												
4	19000	0	0												
5	19000	0	0												
6	19000	0	3												
7	19000	0	6												
8	19000	1	4												
9	19000	1	2	0											
10	19000	0	3	1	36										
11	19000	0	4	0	162	7									
12	19000	2	7	0	97	1									
13	19000	0	5	1	86	3	33								
14	19000	0	5	0	10	3	2	1							
15	19000	4	1	0	9	21	10	5							
16	19000	0	0	0	6	4	9	1							
17	19000	0	0	0	2	6	14	0							
18	19000	0	2	0	1	3	15	0							
19	19000	0	0	0	3	2	3	3							
20	19000	0	0	0	0	0	3	0	22						
21	19000	0	0	0	0	1	0	0	225	173					
22	19000	0	0	0	0	0	0	1	83	131					
23	19000	0	0	0	9	0	3	0	49	56					
24	19000	0	0	0	14	0	0	1	30	33					
25	19000	0	0	1	3	1	1	0	15	18					
26	19000	0	0	1	4	1	0	0	6	5	1				
27	19000	0	0	0	0	2	0	0	2	5	1	0			
28	19000	0	0	0	6	0	0	2	2	4	0	0			
29	19000	0	0	0	4	0	1	0	3	3	4	0			
30	19000	0	0	0	3	0	1	0	1	6	4	0			
31	19000	0	0	0	1	0	1	0	7	7	4	0			
32	19000	0	0	0	0	0	0	0	0	5	0	0			
33	19000	0	0	0	3	0	0	0	2	8	0	0	68		
34	19000	0	0	1	3	0	0	0	4	8	2	1	65	56	
35	19000	0	0	0	1	0	0	0	6	4	0	0	51	6	8
36	19000	0	0	0	2	0	0	0	3	4	0	0	24	7	12
37	19000	0	0	0	0	0	0	0	1	0	3	0	24	18	66
38	19000	0	0	0	0	0	0	0	2	3	0	0	32	17	46
39	19000	0	0	0	0	0	0	0	3	3	0	0	36	4	32
40	19000	0	0	0	0	0	0	0	0	0	0	0	46	9	14
41	19000	0	0	0	1	0	0	0	0	0	0	0	5	13	15
42	19000	0	0	0	0	0	0	0	0	0	0	0	4	6	15
43	19000	0	0	0	0	0	0	0	1	0	0	0	10	6	19
44	19000	0	0	0	0	0	0	0	0	1	0	0	8	4	16
45	19000	0	0	0	0	0	0	0	0	0	1	0	25	4	10
46	19000	0	0	0	0	0	0	0	0	0	0	0	20	2	23
47	19000	0	0	0	0	0	0	0	2	0	0	0	14	0	6
48	19000	0	0	0	0	0	0	0	0	0	0	0	10	4	5
49	19000	0	0	0	0	0	0	0	0	0	0	0	1	1	2
50	19000	0	0	0	0	0	0	0	1	0	0	0	0	1	2
51	19000	0	0	0	0	0	0	0	0	0	0	0	2	0	5
52	19000	0	0	0	0	0	0	0	0	0	0	0	0	0	3
53	19000	0	0	0	0	0	0	0	0	0	0	0	0	5	2
54	19000	0	0	0	0	0	0	0	0	0	0	0	0	0	4
55	19000	0	0	0	0	0	0	0	0	0	0	0	0	0	2
56	19000	0	0	0	0	0	0	0	0	0	0	0	0	0	2
57	19000	0	0	0	0	0	0	0	0	0	0	0	0	0	0
58	19000	0	0	0	0	0	0	0	0	0	0	0	2	0	2
59	19000	0	0	0	0	0	0	0	0	0	0	0	2	0	0
60	19000	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 2. (Continued)

Experiment 2

Recapture period	Releases → / Catch	Release Period 1	2	5	6	7	8	9	10	11	12	13	14	15	16
	Releases →	876	3159	111	485	3761	1487	1835	3537	1099	5533	3665	1759	2244	811
1	64000	1													
2	64000	69	128												
3	64000	23	149												
4	64000	14	97												
5	64000	18	31	0											
6	64000	9	5	1	0										
7	64000	0	2	0	16	2									
8	64000	4	12	0	5	7	3								
9	64000	0	6	0	3	23	4	141							
10	64000	1	4	0	1	38	16	30	3						
11	64000	0	5	0	3	29	18	7	12	3					
12	64000	3	2	1	2	37	10	10	46	19	43				
13	64000	1	4	0	3	38	14	11	79	17	170	108			
14	64000	4	6	0	3	28	12	22	46	13	56	102	1		
15	64000	1	2	0	1	13	8	4	28	5	46	58	1	12	
16	64000	1	4	0	0	10	10	7	28	5	71	22	15	53	2
17	64000	0	1	0	0	4	11	3	34	4	32	42	32	25	4
18	64000	0	1	0	1	0	6	0	11	0	9	69	24	19	0
19	64000	0	1	0	0	3	1	1	7	6	9	15	10	10	1
20	64000	0	0	0	0	4	2	1	7	3	11	14	10	15	3
21	64000	0	1	0	0	6	7	1	10	1	18	14	12	7	3
22	64000	0	0	0	0	2	2	0	4	0	19	15	17	13	2
23	64000	0	0	0	0	5	1	0	20	2	18	19	9	7	2
24	64000	0	0	0	0	3	1	2	5	0	4	7	5	5	2
25	64000	0	0	0	0	2	0	1	8	0	6	10	4	2	7
26	64000	0	0	0	1	1	0	0	0	1	4	9	2	2	2
27	64000	0	1	0	0	0	0	0	4	1	1	3	1	1	3
28	64000	0	0	0	0	3	0	0	0	1	5	1	0	1	1
29	64000	0	0	0	0	1	1	0	0	1	5	0	1	0	0
30	64000	0	0	0	0	0	0	0	1	0	2	1	0	0	0

Recapture period	Release Period 20	21	22	23	24	25	26	27
Releases →	8489	4848	4546	5325	2061	4804	6483	5128
20	634							
21	223	490						
22	213	106	103					
23	171	47	82	41				
24	112	21	41	85	0			
25	61	18	29	72	4	345		
26	46	19	18	124	10	16	18	
27	26	12	12	56	10	7	95	1
28	73	22	17	41	5	12	65	229
29	29	23	3	33	7	14	40	86
30	12	16	3	15	4	13	16	26

Table 2. (Continued)

Experiment 3

		Release Period													
		1	2	6	7	8	9	10	11	12	13	14	15	16	20
Recapture period	Releases → Catch	99	77	400	4511	1357	1581	2016	896	2683	897	865	1191	192	2608
1	28600	0													
2	28600	1	5												
3	28600	0	4												
4	28600	1	2												
5	28600	0	3												
6	28600	0	2	0											
7	28600	0	0	9	2										
8	28600	0	0	15	3	2									
9	28600	0	1	4	4	1	24								
10	28600	1	0	2	10	19	25	23							
11	28600	0	0	1	17	1	9	13	1						
12	28600	0	0	0	25	3	8	29	9	3					
13	28600	0	0	0	32	4	5	65	6	16	6				
14	28600	0	0	0	31	10	7	26	4	10	8	1			
15	28600	0	0	0	15	4	3	27	4	15	10	0	1		
16	28600	0	0	0	37	3	8	13	2	27	5	4	11	0	
17	28600	0	0	0	18	4	3	14	2	31	7	13	9	1	
18	28600	0	0	0	12	6	6	6	6	14	11	9	1	0	
19	28600	0	0	0	11	5	1	6	1	13	5	10	7	0	
20	28600	0	0	1	13	4	3	4	1	16	5	10	8	0	233
21	28600	0	0	0	16	8	2	7	0	17	2	10	7	0	41
22	28600	0	0	1	16	5	1	25	2	27	0	4	2	0	30
23	28600	0	0	0	11	2	1	15	2	20	5	4	3	0	14
24	28600	0	0	0	11	4	0	9	1	5	2	2	7	0	10
25	28600	0	0	1	7	1	0	2	2	10	3	2	4	0	4
26	28600	0	0	0	4	0	0	7	1	2	1	2	1	1	4
27	28600	0	0	0	1	3	2	2	2	4	1	0	0	0	10
28	28600	0	0	0	2	1	1	1	2	1	0	0	1	0	14
29	28600	0	0	0	4	1	0	3	1	9	3	0	0	0	3
30	28600	0	0	0	1	0	2	2	0	3	0	0	1	0	4

	Release Period						
	21	22	23	24	25	26	27
Recapture period / Releases →	2743	1759	163	118	977	1264	974
21	193						
22	187	27					
23	20	84	0				
24	10	55	3	0			
25	19	20	5	3	82		
26	15	16	3	0	2	0	
27	7	7	2	1	1	2	0
28	14	4	1	0	2	1	5
29	7	3	0	0	1	11	18
30	1	1	0	1	2	0	2

MODEL FORMULATION

Two population dynamics models are described and applied to the data. The first model is essentially an equilibrium model, in which losses from the population through natural mortality, fishing mortality and emigration are exactly balanced by recruitment. The population vulnerable to the fishery is therefore assumed to be constant for the duration of the experiment. In the second model, the equilibrium assumption is relaxed by allowing the population size to vary through a parameterization comprising an initial (pre-experiment) population size and a constant recruitment rate. Both models are fundamentally similar to tagging models described elsewhere (e.g. Wetherall 1982; Kleiber *et al.* 1987), with the exceptions that a number of tagged cohorts are analysed simultaneously, and the Baranov (1918) catch equation is used to link the dynamics of tagged fish to the overall population.

The following notation is used to describe the models:

i	Subscript indexing the time interval during which tagged fish were released.
j	Subscript indexing the time interval during which tagged fish were recaptured.
k	Subscript indexing fishing mortality prior to time interval j.
n	Subscript indexing recruitment prior to time interval j.
t	Total number of time intervals over which the tagging experiment occurs (from the first tag release interval to the last tag recapture interval, inclusive).
u	Number of time intervals during which tagged fish were released.
m	Number of time intervals after release before tagged fish are assumed to be randomly mixed with the untagged population.
N_{0i}	Number of tag releases during time interval i.
N_{ij}	Number of fish tagged during time interval i alive at the beginning of time interval j.
r_{ij}	Observed number of tag recoveries in time interval j from fish released in time interval i.
r'_{ij}	Number of tag recoveries in time interval j from fish released in time interval i, as predicted by the model.
M	Instantaneous rate of natural mortality.
E	Instantaneous rate of emigration from the area of the fishery.
S	Instantaneous rate of tag shedding.
G	Instantaneous rate of mortality due to tagging.
X	Instantaneous rate of tag attrition from all sources other than fishing ($X=M+E+S+G$).
Y	Instantaneous rate of total mortality of untagged fish from all sources other than fishing ($Y=M+E$).
F_j	Instantaneous rate of fishing mortality during time interval j.
F	Average instantaneous rate of fishing mortality across the t time intervals of the experiment.
α	Rate of immediate tag shedding.
β	Proportion of recaptured tags that are reported.
δ	Rate of immediate tagging mortality.
C_j	Total catch by the fishery in time interval j.
C_{av}	Average catch by the fishery across the t time intervals of the experiment.
P	Total equilibrium population size vulnerable to the fishery for the duration of the tagging

experiment.

P_0	Total population size vulnerable to the fishery at the end of the time interval prior to the first tag releases.
P_j	Total population size vulnerable to the fishery at the beginning of time interval j.
R	Rate of recruitment to the population, assumed constant across time intervals.

Tag releases during the i-th time interval are assumed, for computational convenience, to be released instantaneously at the beginning of the period. Assume, for the moment, that tagged fish mix instantaneously upon release throughout the population at large (m=0). The predicted number of tag recoveries from i-th period releases during time interval j is:

$$r'_{ij} = N_{0i}\, e^{-\sum_{k=i}^{j-1} F_k + (j-i)X} (1-\alpha)(1-\delta)\,\beta \frac{F_j}{F_j + X}\left[1 - e^{-(F_j + X)}\right] \quad (1)$$

where X=Y+S+G. In model 1, F_j is parameterized using its relationship with the fishery catch C_j, as expressed by the Baranov (1918) catch equation:

$$C_j = P \frac{F_j}{F_j + Y}\left[1 - e^{-(F_j + Y)}\right]. \quad (2)$$

In model 2, the equilibrium assumption inherent in equation 2 is relaxed by assuming that the population at the end of the time period before the first tag releases, P_0, is supplemented by a constant recruitment, R, at the beginning of each subsequent time period for the duration of the tagging experiment. The population dynamics and exploitation of the untagged fish are now expressed as:

$$C_j = P_j \frac{F_j}{F_j + Y}\left[1 - e^{-(F_j + Y)}\right] \quad (3)$$

where

$$P_j = P_0\, e^{-\sum_{k=1}^{j-1} F_k + (j-1)Y} + R\left[\sum_{n=1}^{j-1} e^{-\sum_{k=n}^{j-1} F_k + (j-n)Y} + 1\right]. \quad (4)$$

Parameter Estimation

The parameters to be estimated are P and Y (equations 1 and 2) in the case of model 1 and P_0, R and Y (equations 1, 3 and 4) in the case of model 2. The steps involved in parameter estimation are:

Step 1 For each time interval j (j=i,...,t), compute F_j from equation (2) (model 1) or equations (3) and (4) (model 2) as a function of the model parameters P and Y (model 1) or P_0, R and Y (model 2) and the data C_j (using a technique such as Newton-Raphson).

Step 2 Compute r'_{ij} from equation (1) as a function of the data N_{0i}, known parameters α, β, δ, S and G, and the model parameters P and Y, or P_0, R and Y.

Step 3 Compute the likelihood of the data r_{ij}, given the model defined by the parameters, by the multinomial likelihood equation

$$\Theta_i = \frac{N_{0i}! \left(1 - \sum_{j=i}^{t} P(r_{ij})\right)^{N_{0i} - \sum_{j=i}^{t} r_{ij}} \prod_{j=i}^{t} P(r_{ij})^{r_{ij}}}{\left(\prod_{j=i}^{t} r_{ij}!\right)\left(N_{0i} - \sum_{j=i}^{t} r_{ij}\right)!}$$

where

$$P(r_{ij}) = \frac{r'_{ij}}{N_{0i}}.$$

Step 4 Repeat steps 1 to 3 for all u tag release periods, and minimize the joint negative log-likelihood function (using a suitable function minimization subroutine)

$$\Phi = -\log_e \left[\prod_{i=1}^{u} \Theta_i\right]$$

to derive maximum likelihood estimates of P and Y or P_0, R and Y.

As noted earlier, model 1 is an equilibrium model with losses from the population being balanced by recruitment. An approximate average recruitment rate can be determined by substituting the maximum likelihood estimates of P and Y into

$$R = P(F_{av} + Y)$$

where the average fishing mortality rate for the duration of the experiment, F, is found by solving

$$C_{av} = P\frac{F}{F+Y}\left[1 - e^{-(F+Y)}\right].$$

Decisions regarding the more appropriate model for each data set can be made by likelihood-ratio tests (Kendall and Stuart 1979). Simply put, the null hypothesis that model 1 is the correct model is rejected in favour of the alternative, model 2, if $2.(\Phi_{model\ 1} - \Phi_{model\ 2})$ is greater than a critical χ^2 value (χ^2_{crit}=3.86 for a rejection region of 0.05 with df 1).

The Mixing Assumption

For any tagging experiment, even those involving highly mobile tunas, it is unreasonable to assume that the tagged fish mix instantaneously with the untagged population across the area of the fishery. Let us now assume that m time intervals after tagging are required for complete mixing to occur. The number of tagged fish still present in the population at the beginning of time interval $i+m$ is now the effective tag release number for releases originally made in period i, and only tag recoveries in time intervals $i+m,..., t$ make up the data r_{ij}. This effective tag release number is unknown, but can be estimated as a function of the model parameters and tag returns prior to mixing, by solving (using the Newton-Raphson) equation (1) for F_j ($j=i,..., i+m-1$) with the actual tag returns, r_{ij}, replacing r'_{ij}, and substituting the F_j so obtained into

$$N_{i\,m+i} = N_{0i}\, e^{-\sum_{k=i}^{i+m-1} F_k + mX} (1-\alpha)(1-\delta).$$

Steps 1 to 4 then proceed as before, but substituting the new effective release numbers for N_{0i} and evaluating Φ using tag recoveries from only the post-mixing time intervals.

ESTIMATION OF "NUISANCE" PARAMETERS

Several parameters of the model are completely or partially confounded with the parameters of interest, and therefore must be estimated independently or be assigned assumed values. These "nuisance" parameters are the tag-shedding parameters α and S, the tagging mortality parameters δ and G, the reporting rate β, and the instantaneous rate of emigration E. The number of periods required for mixing of tagged and untagged populations, m, might also be regarded as a "nuisance" parameter. These parameters were treated in the following ways:

Tag Shedding

Tag shedding rates were estimated from double-tagging experiments carried out during the course of the SSAP and the RTTP. The models and fitting procedure described by Hampton and Kirkwood (1989) were used for this purpose. Of the four models described by Hampton and Kirkwood (1989), their model 2 was found to be optimal for each of the double-tagging data sets. This model has the form

$$Q_t = (1-\alpha)\, e^{-St}$$

where Q_t is the probability of a tag being retained at time t after release. The results of fitting this model to the double-tagging data are given in Table 3 and the tag retention probabilities for these models displayed graphically in Figure 5.

Table 2. (Continued)

Experiment 2

		Release Period													
		1	2	5	6	7	8	9	10	11	12	13	14	15	16
Recapture period	Releases → / Catch	876	3159	111	485	3761	1487	1835	3537	1099	5533	3665	1759	2244	811
1	64000	1													
2	64000	69	128												
3	64000	23	149												
4	64000	14	97												
5	64000	18	31	0											
6	64000	9	5	1	0										
7	64000	0	2	0	16	2									
8	64000	4	12	0	5	7	3								
9	64000	0	6	0	3	23	4	141							
10	64000	1	4	0	1	38	16	30	3						
11	64000	0	5	0	3	29	18	7	12	3					
12	64000	3	2	1	2	37	10	10	46	19	43				
13	64000	1	4	0	3	38	14	11	79	17	170	108			
14	64000	4	6	0	3	28	12	22	46	13	56	102	1		
15	64000	1	2	0	1	13	8	4	28	5	46	58	1	12	
16	64000	1	4	0	0	10	10	7	28	5	71	22	15	53	2
17	64000	0	1	0	0	4	11	3	34	4	32	42	32	25	4
18	64000	0	1	0	1	0	6	0	11	0	9	69	24	19	0
19	64000	0	1	0	0	3	1	1	7	6	9	15	10	10	1
20	64000	0	0	0	0	4	2	1	7	3	11	14	10	15	3
21	64000	0	1	0	0	6	7	1	10	1	18	14	12	7	3
22	64000	0	0	0	0	2	2	0	4	0	19	15	17	13	2
23	64000	0	0	0	0	5	1	0	20	2	18	19	9	7	2
24	64000	0	0	0	0	3	1	2	5	0	4	7	5	5	2
25	64000	0	0	0	0	2	0	1	8	0	6	10	4	2	7
26	64000	0	0	0	1	1	0	0	0	1	4	9	2	2	2
27	64000	0	1	0	0	0	0	0	4	1	1	3	1	1	3
28	64000	0	0	0	0	3	0	0	0	1	5	1	0	1	1
29	64000	0	0	0	0	1	1	0	0	1	5	0	1	0	0
30	64000	0	0	0	0	0	0	0	1	0	2	1	0	0	0

	Release Period							
	20	21	22	23	24	25	26	27
Recapture period / Releases →	8489	4848	4546	5325	2061	4804	6483	5128
20	634							
21	223	490						
22	213	106	103					
23	171	47	82	41				
24	112	21	41	85	0			
25	61	18	29	72	4	345		
26	46	19	18	124	10	16	18	
27	26	12	12	56	10	7	95	1
28	73	22	17	41	5	12	65	229
29	29	23	3	33	7	14	40	86
30	12	16	3	15	4	13	16	26

10

Table 2. (Continued)

Experiment 3

Recapture period	Releases → / Catch	1	2	6	7	8	9	10	11	12	13	14	15	16	20
	Releases →	99	77	400	4511	1357	1581	2016	896	2683	897	865	1191	192	2608
1	28600	0													
2	28600	1	5												
3	28600	0	4												
4	28600	1	2												
5	28600	0	3												
6	28600	0	2	0											
7	28600	0	0	9	2										
8	28600	0	0	15	3	2									
9	28600	0	1	4	4	1	24								
10	28600	1	0	2	10	19	25	23							
11	28600	0	0	1	17	1	9	13	1						
12	28600	0	0	0	25	3	8	29	9	3					
13	28600	0	0	0	32	4	5	65	6	16	6				
14	28600	0	0	0	31	10	7	26	4	10	8	1			
15	28600	0	0	0	15	4	3	27	4	15	10	0	1		
16	28600	0	0	0	37	3	8	13	2	27	5	4	11	0	
17	28600	0	0	0	18	4	3	14	2	31	7	13	9	1	
18	28600	0	0	0	12	6	6	6	6	14	11	9	1	0	
19	28600	0	0	0	11	5	1	6	1	13	5	10	7	0	
20	28600	0	0	1	13	4	3	4	1	16	5	10	8	0	233
21	28600	0	0	0	16	8	2	7	0	17	2	10	7	0	41
22	28600	0	0	1	16	5	1	25	2	27	0	4	2	0	30
23	28600	0	0	0	11	2	1	15	2	20	5	4	3	0	14
24	28600	0	0	0	11	4	0	9	1	5	2	2	7	0	10
25	28600	0	0	1	7	1	0	2	2	10	3	2	4	0	4
26	28600	0	0	0	4	0	0	7	1	2	1	2	1	1	4
27	28600	0	0	0	1	3	2	2	2	4	1	0	0	0	10
28	28600	0	0	0	2	1	1	1	2	1	0	0	1	0	14
29	28600	0	0	0	4	1	0	3	1	9	3	0	0	0	3
30	28600	0	0	0	1	0	2	2	0	3	0	0	1	0	4

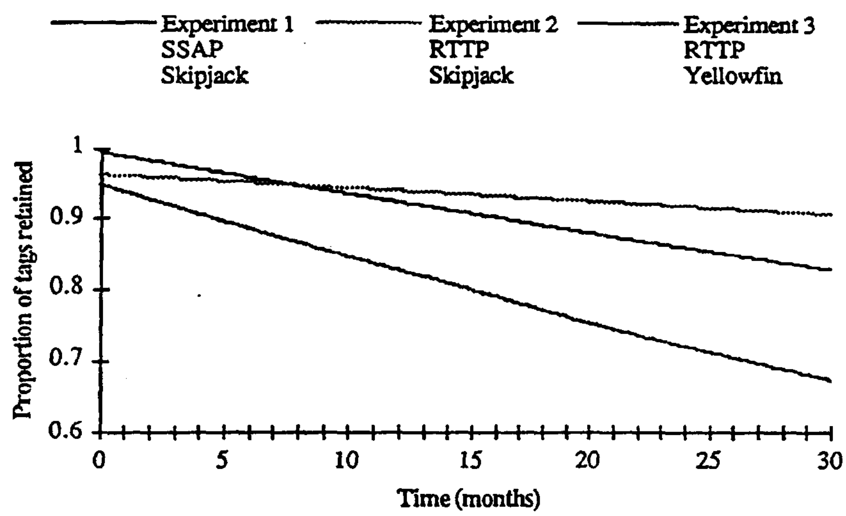
Release Period

Recapture period	Releases →	21	22	23	24	25	26	27
	Releases →	2743	1759	163	118	977	1264	974
21		193						
22		187	27					
23		20	84	0				
24		10	55	3	0			
25		19	20	5	3	82		
26		15	16	3	0	2	0	
27		7	7	2	1	1	2	0
28		14	4	1	0	2	1	5
29		7	3	0	0	1	11	18
30		1	1	0	1	2	0	2

Table 3. Estimates of tag-shedding parameters.

Experiment	Project	Species	Number double tagged	Number recaptured with 2 tags	Number recaptured with 1 tag	Parameter estimates α	S
1	SSAP	Skipjack	5,521	512	20	0.0100	0.0061
2	RTTP	Skipjack	2,518	166	16	0.0395	0.0020
3	RTTP	Yellowfin	1,385	110	19	0.0527	0.0115

Figure 5. Estimated tag retention probabilities based on models fitted to double-tagging data.



Tag retention rates for skipjack are similar for experiments 1 and 2, but yellowfin appear more likely to shed their tags than skipjack. This possibly relates to the greater difficulty, on average, of tagging yellowfin, which have tougher skin and behave more erratically on the tagging cradle than skipjack.

Tagging Mortality

High quality-control standards during the tagging operations of all experiments were applied so as to minimize stress, and resulting mortality, on the fish. Observations of tagged fish behaviour immediately after release suggest that stress is minimal. There have been numerous instances of newly tagged tuna immediately rejoining the feeding school and being recaptured within seconds of release. The resumption of normal feeding behaviour strongly suggests that tuna are not unduly affected by capture and tagging when procedures as described earlier are employed. Observations of very high recapture rates for some schools tagged in close proximity to fishing activity support this assertion. For example, 447 recaptures from 681 skipjack releases and 59 recaptures from 103 yellowfin releases were recorded from school # 429, which was tagged in the Solomon Sea, Papua New Guinea, in February 1990. Several purse seiners were fishing in this vicinity during and after tagging. It is unlikely that such high recapture rates would be possible if significant immediate tagging mortality had occurred. It therefore seems reasonable to assume that immediate tagging mortality is rare. In these analyses, I have assumed it to be zero, however a significant violation of this assumption would cause the F_j to be under-estimated.

There is less evidence regarding the absence of a long-term mortality associated with tagging. However, tag insertion wounds appear to heal quickly and cleanly, and have not been observed to be infected. Increased predation mortality associated with bearing tags is unlikely in rapidly-swimming tunas. In the absence of any evidence to the contrary, I have assumed G to be zero. If G were in fact significant, it would be incorporated into the Y estimates, but other parameters would be unaffected.

Tag Reporting

Non-reporting of tags is likely to affect every tagging experiment where tag recoveries are generated by a commercial or recreational fishery. During these experiments, various incentives, such as tag rewards and lotteries, were used to promote the return of tags. Nevertheless, some non-reporting will have occurred and must be accounted for in the parameter estimation.

One method used to estimate the reporting rate is tag seeding. This involves the tagging of a sample of dead fish in the catch before tag detection processes begin. If seeding is carefully and discreetly carried out, the proportion of seeded tags returned is an estimate of the reporting rate. For the SSAP, only one tag-seeding experiment was carried out (on a purse seiner in New Zealand), with 25% of the seeded tags recovered. However, because most of the SSAP tag recoveries were made by pole-and-line vessels, other analyses, based on sequential detection mode data (Kleiber *et al.* 1987), were used to characterize tag reporting rates. These analyses produced a worst-case β estimate of 0.47 and a best-case estimate of 0.87. The value used in the parameter estimations for experiment 1 is the mid-point of this range, 0.67.

During the RTTP, a thorough tag-seeding programme was carried out, with selected observers on US and Japanese purse seiners tagging up to five fish caught during the course of a voyage. Seeding was generally carried out discreetly on the main deck while sampling, or on the well deck immediately before fish stowage. As almost all purse-seine-caught tagged fish are detected during vessel unloading or processing in canneries, the seeded tags were thus available to all detection processes and were indistinguishable from genuine tags. Forty-one such individual experiments had been carried out on vessels that had unloaded their catch at the time of writing. Overall, the recovery rate of seeded tags to date has been 0.70. This value has been used for experiment 2 and 3 parameter estimations in the present study. The treatment of reporting rate in the simulations is outlined in a later section.

Emigration From the Area of the Fishery

Permanent emigration from the fishery, or any other behaviour that tends to reduce the average vulnerability of the population to the fishery over time, is totally confounded with M in these models. In this study, E is thought to be minimal as the study area chosen encompasses much of the high-abundance area of the stocks. Also, recaptures of tagged fish outside the study area were relatively rare. However, in interpreting the results, I make no attempt to separate Y into its components (M+E).

Mixing Periods

The selection of an appropriate value for *m* can be based on the observed rate of dispersion of tagged tuna, if sufficient information on recapture locations is available. Specific analyses could be carried out using diffusion-advection models (Fournier and Sibert 1991); however, such models are complex and are not yet readily available. For experiments 2 and 3, I used tag recapture data for RTTP cruises RT4-90 and RT5-90 to make qualitative judgements on appropriate values for *m*. During these cruises, 3,217 skipjack and 4,211 yellowfin were released during the period 7-24 January 1990 at Tench Island, Papua New Guinea, a location very close to the center of the study area. Plots of tag recaptures over the 12 months following tagging indicate that tagged skipjack (Figure 6) and yellowfin (Figure 7) dispersed rapidly throughout the area of the fishery. Skipjack were recaptured in most locations where purse seine effort took place during the second two-month period after tagging. Yellowfin recaptures were well dispersed by the third two-month period. Therefore, I have assumed in the analyses of experiments 2 and 3 that 4 months are required for complete mixing to occur. This is also consistent with the findings of Bayliff (1988), who concluded that tagged skipjack in the eastern Pacific Ocean were randomly mixed with untagged skipjack after 3-5 months at liberty. Using experiment 3 as an example, the effects of different assumed *m*'s on parameter estimates and their precision were investigated.

A similar analysis for experiment 1 was not feasible, because the distribution of fishing effort (mainly pole-and-line) at the time of the SSAP is currently unavailable. However, it is probably reasonable to assume that mixing might have been slower than for the recent experiments, because of the tendency of the SSAP to release most fish close to islands, where longer residence times might occur. Therefore, I have assumed *m* to be 5 months in experiment 1.

An investigation of spatial effects on tagging experiments, using a simulation model, is presented later in the paper.

Figure 6. Dispersal patterns of skipjack tagged in the vicinity of Tench Island on 7-24 January 1990, in relation to the distribution of purse seine fishing effort.

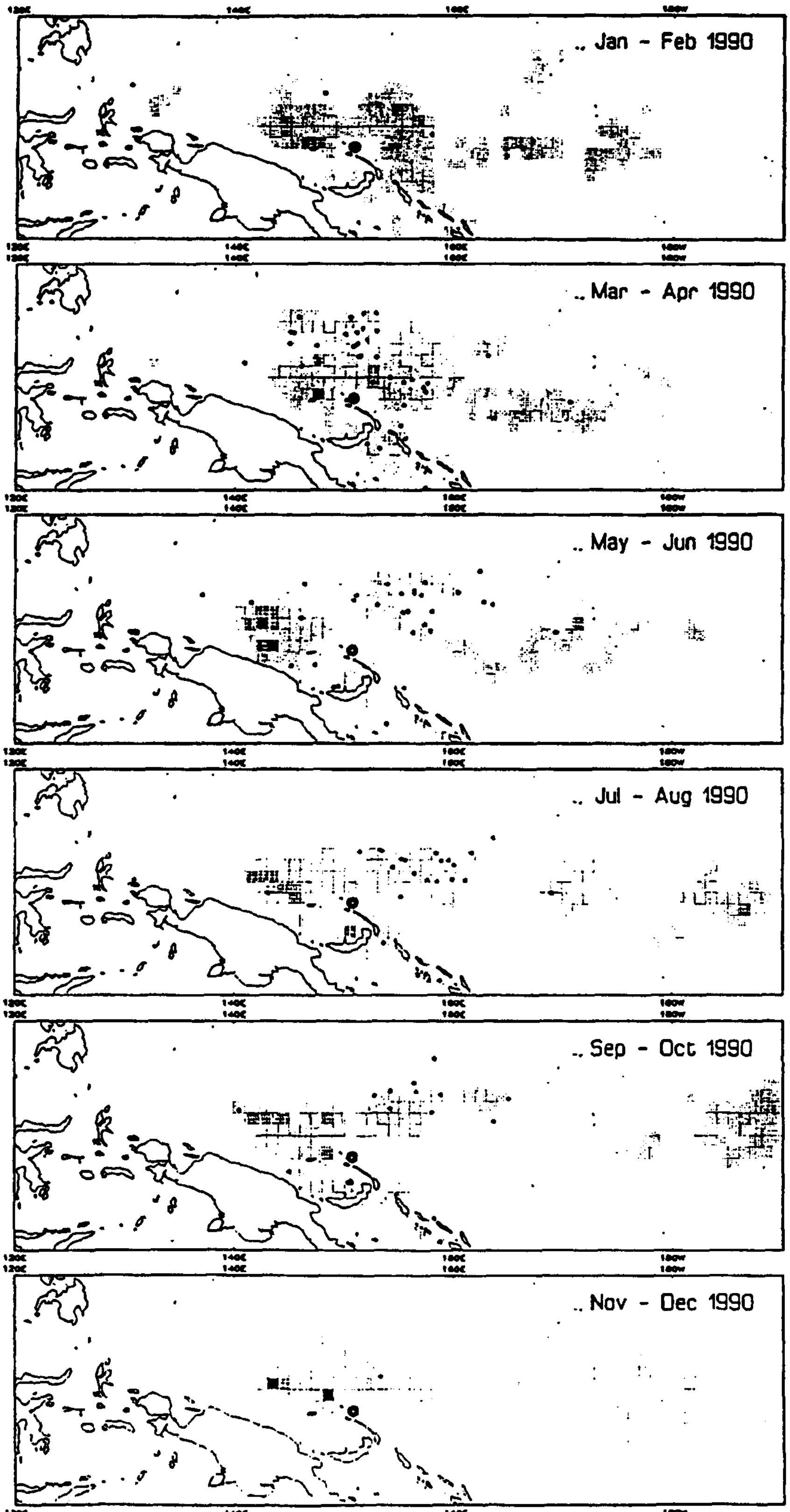
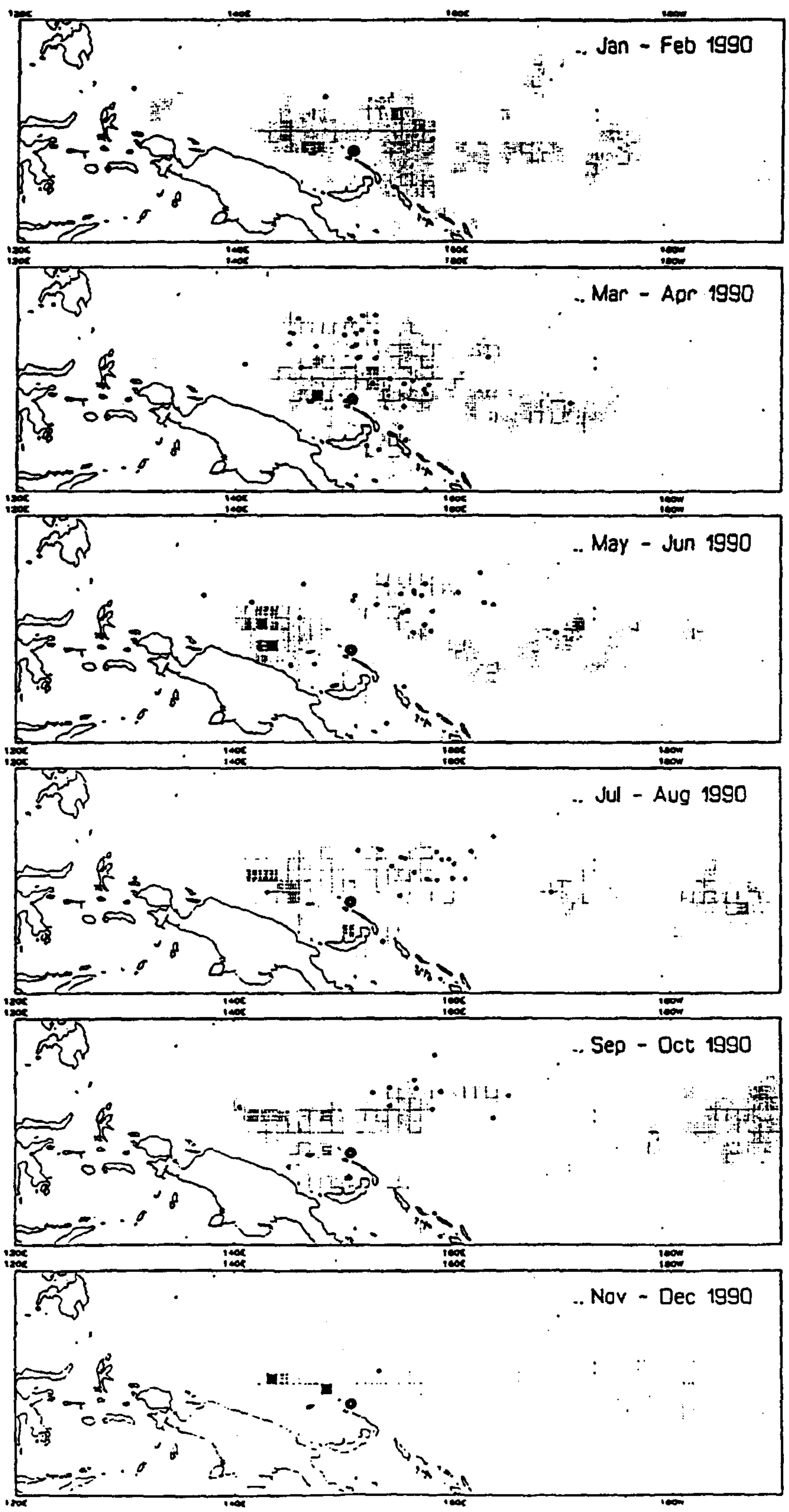


Figure 7. **Dispersal patterns of yellowfin tagged in the vicinity of Tench Island on 7-24 January 1990, in relation to the distribution of purse seine fishing effort.**



ESTIMATION OF CONFIDENCE INTERVALS

It is necessary to derive confidence intervals about the estimated parameters for any useful interpretation of the results. A possible method is to calculate the asymptotic covariance matrix using the inverse-Hessian method (Bard 1974). However, a more flexible method is that using Monte-Carlo simulations (see Press *et al.* 1986 for a full discussion). The main advantage of this method is that a range of errors in measured data and assumed parameters can be incorporated into the confidence intervals of the estimated parameters, if reasonable assumptions regarding the error structures can be made.

In the present study, a Monte-Carlo procedure was devised to incorporate the effects of (i) errors in the estimated catches, C_j and (ii) error in the reporting rate, β, assumed in the estimation procedure, into the estimates of parameter confidence intervals. The procedure was as follows:

Step 1 Obtain maximum-likelihood estimates of parameters by the methods described above, and assume these estimates to be the true parameter values.

Step 2 Determine realistic error structures for C_j and β.

Step 3 Generate 100 sets of simulated tag return and catch data using a simulation model in which the true values of C_j are randomly sampled from appropriate distributions, and the fate of each tagged fish is determined by a stochastic decision-making process. Actual tag release numbers and the maximum likelihood parameter estimates derived in step 1 are used in each simulation.

Step 4 Obtain 100 sets of "pseudo"-maximum-likelihood parameter estimates from the simulated data sets, each assuming different values of β, sampled from an appropriate distribution.

Step 5 Calculate the mean parameter estimates, their covariance matrix, confidence intervals and correlation coefficients.

These simulations (for the estimation of approximate confidence intervals) are termed the primary simulations. Additional simulations were carried out to test the effects of different error structure assumptions on the parameter estimates and their confidence intervals.

Error Structure of C_j

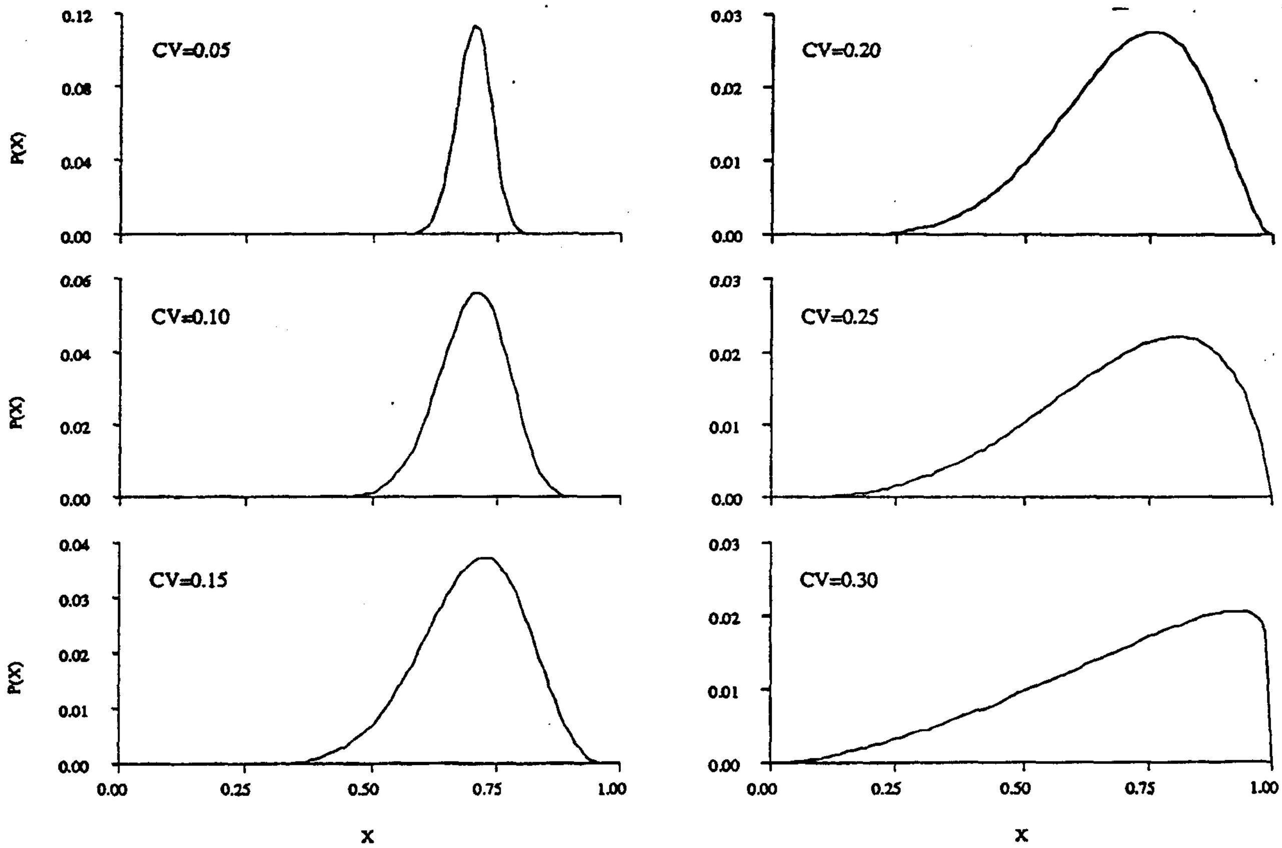
I assumed for the primary simulations that the error structure of the catch estimates was described by a normal distribution of mean C_j and a coefficient of variation (cv) of 0.10. This was based on a subjective assessment of possible sources and magnitudes of error in the catch data available for this study. The effects of different cv's on the precision of estimated parameters were examined in separate simulations. Note that this error structure assumes that the mean catch for the period of the experiment and any trend in monthly catch is accurately reflected by the C_j means

Error Structure of β

For experiment 1 estimations, it was assumed that β =0.67, however the range of possible values of β was 0.47-0.87, with no information to suggest that any one value within this range was more likely than any other. Therefore, the error structure of β for experiment 1 was modeled as a uniform distribution with limits of 0.47 and 0.87.

For experiments 2 and 3, some information on β was obtained from tag-seeding experiments, which suggested a mean value of 0.70. It was therefore appropriate that the error structure for β be modeled as (coincidently) a beta distribution with a mean of 0.70. The beta distribution has useful properties that influenced this choice, the most important being that the distribution has limits of zero and one. I assumed that the distribution had a cv of 0.10 in the primary simulations. This was somewhat arbitrary, although much higher values would have resulted in significant probabilities of very low reporting rates (Figure 8). Apart from the tag seeding experiments, we know that the absolute lower limit of β is the tag recovery rate (currently approaching 10%). Also, recovery rates in excess of 50% for some schools would suggest that $\beta<0.5$ is very unlikely. Therefore, a cv of 0.10 appears reasonable. The effects of different cv's (as displayed in Figure 8) were investigated in separate simulations.

Figure 8. Hypothetical error distributions for β. Each distribution has a mean of 0.70 and a different coefficient of variation.



RESULTS AND DISCUSSION

Model Fit

Likelihood-ratio tests suggest that model 2 provides a significantly better fit than model 1 to experiment 1 data ($P<0.05$), but the extra complexity of model 2 does not significantly improve on the fit of model 1 to the data from experiments 2 and 3 ($P>0.05$). On these statistical criteria, we would reject model 1 in favour of model 2 for experiment 1, but accept model 1 for experiments 2 and 3. In reality, the choice of models, for these data, makes little difference to the estimated parameters or to the conclusions regarding status of the stocks.

The models appear to describe the aggregate rate of tag return, by month of recapture and by period at liberty, with reasonable accuracy (Figure 9). Some of the minor anomalies in the fits may be rectified when more accurate monthly catch data are available. Some impression of the variation in model fit among the different release sets (months) can be gained from Figure 10. For some release sets, the observed numbers of tag returns differ substantially from those predicted by the fitted model (e.g. experiment 1 month 33, experiment 2 month 2 and experiment 3 month 9). This variation is most likely the result of spatial effects not incorporated into these models. However, for most release sets, the fitted models provide reasonable approximations to the observed data.

Skipjack Parameter Estimates

The estimates of model parameters for skipjack tagging experiments confirm that skipjack have a large natural mortality rate, of the order of 0.13-0.19 month^{-1} (Table 4), which is consistent with the estimate of 0.14-0.19 month^{-1} of Kleiber *et al.* (1987) for the western Pacific and several estimates for the eastern Pacific (e.g. 0.14-0.20 month^{-1} [Bayliff 1977]; 0.20 month^{-1} [Forsbergh 1987]). In the case of the western Pacific, migration of skipjack from the study area probably contributes a small amount to these estimates. Estimates of Y are relatively unaffected by whether or not equilibrium conditions are assumed. Slightly higher rates are observed for experiment 2 (0.16-0.19 month^{-1} [model 1]) compared to experiment 1 (0.14-0.16 month^{-1} [model 2]). As a consequence, higher recruitment rates are obtained for experiment 2 (380,000-560,000 t month^{-1}) compared with experiment 1 (120,000-280,000 t month^{-1})

The estimates of P (model 1) for experiments 1 and 2 are similar, and their 95% confidence intervals overlap considerably. Model 2 estimates of P_0 show wide variation among the different analyses and wide confidence intervals. However, in all cases P_j tends, with time, to move rapidly towards, and stabilize near, the P estimates of model 1.

Fishing mortality rates for skipjack remain low in comparison to total mortality rate, although they are higher now (0.024-0.038 month^{-1} [model 1]) than at the time of the SSAP (0.008-0.025 month^{-1} [model 2]). In spite of the increases in skipjack catch over the past ten years, fishing still only accounts for about 15% of skipjack total mortality (the "harvest ratio" of Kleiber *et al.* 1987).

Figure 9. Plots of observed data, aggregated by recovery month and months at liberty, against the fitted models. Estimated tag recoveries were determined by model 2 for experiment 1 and model 1 for experiments 2 and 3. Month 1 for experiment 1 is October 1977; month 1 for experiments 2 and 3 is July 1989.

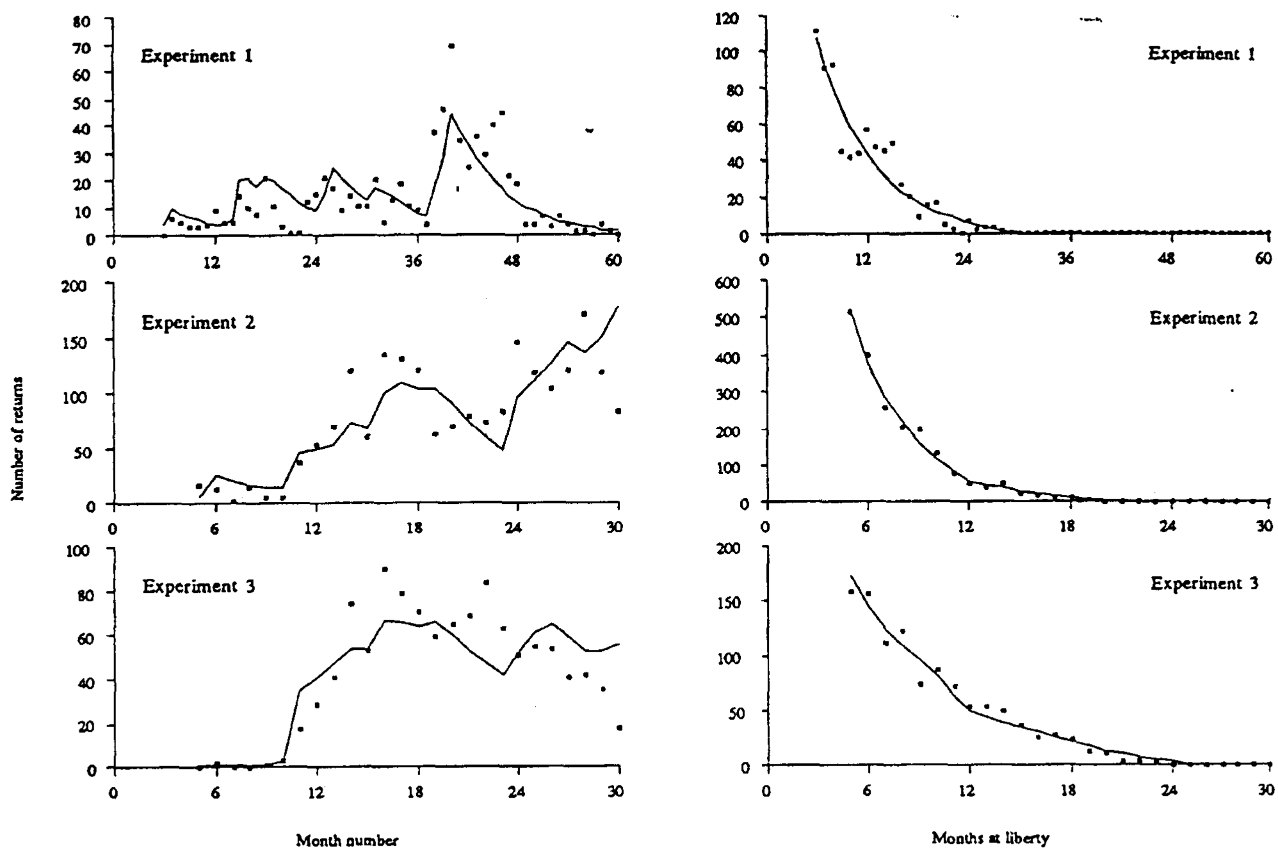


Figure 10. Observed data plotted against the fitted model for selected individual release months.

Experiment 1

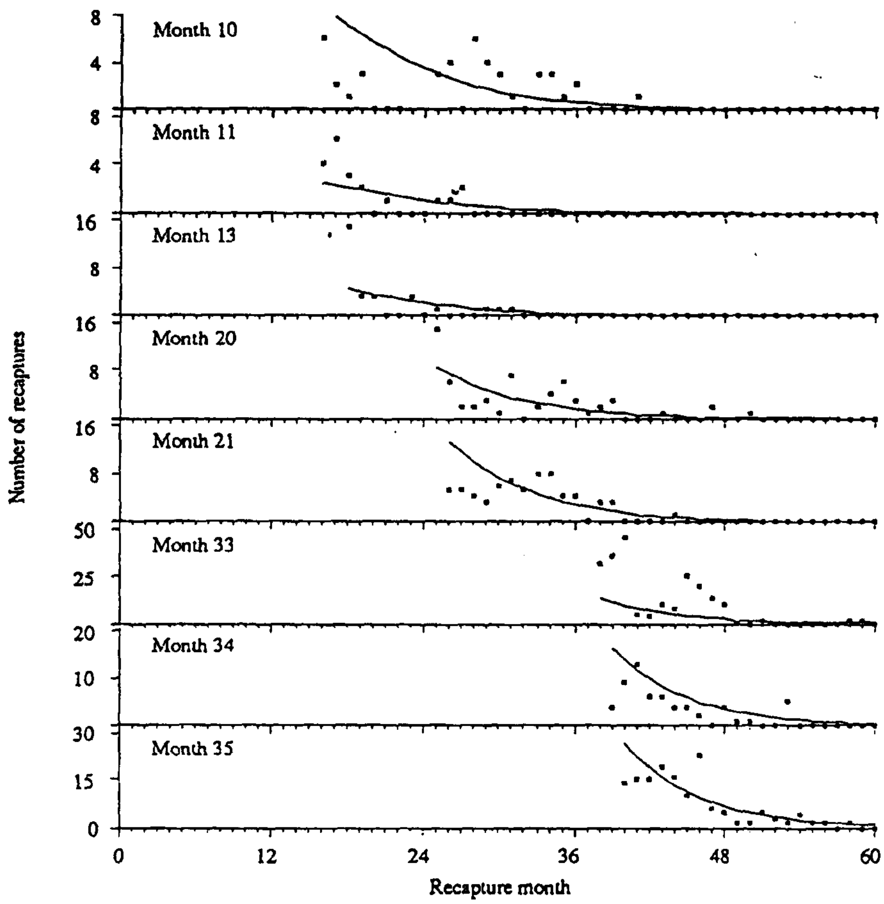
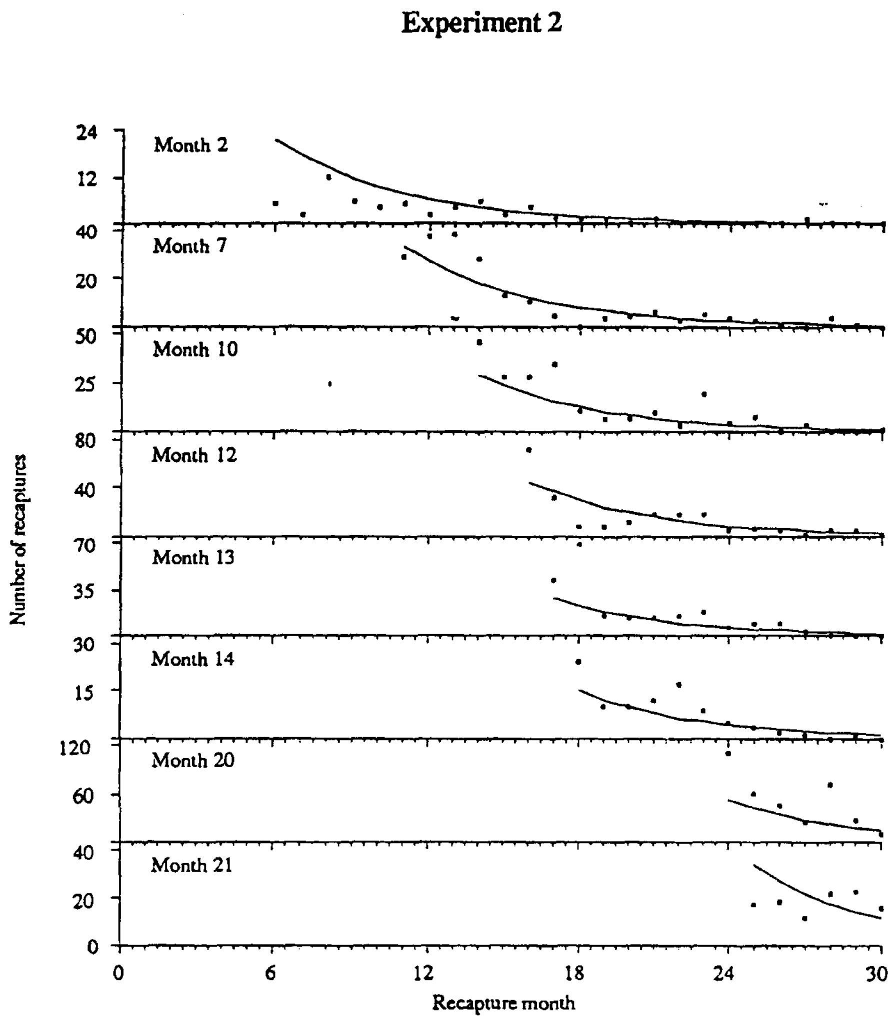


Figure 10. (Continued)



26

Figure 10. (Continued)

Experiment 3

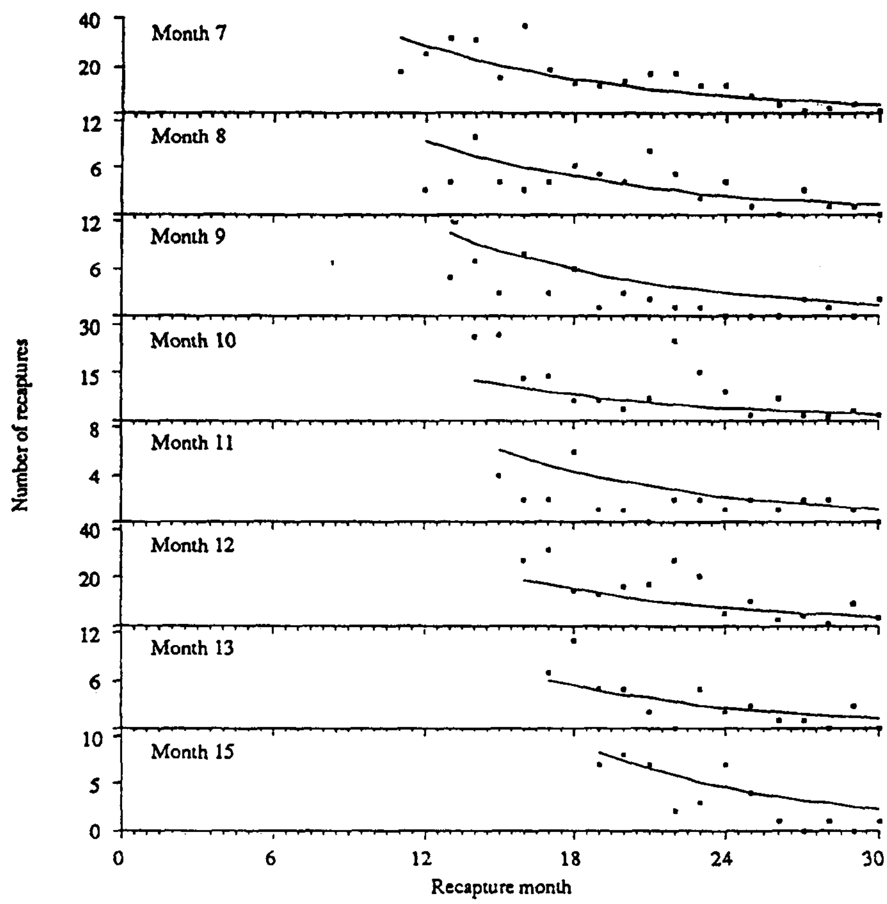


Table 4. Summary of parameter estimates and simulation results for the three experiments. All instantaneous rates are monthly. All population quantities are in millions of tonnes.

Experiment	Species	Model	Known parameters							Estimated parameters				
			S	α	G	δ	β	m		Y	P_0	P	R	F[1]
1	Skipjack	1	0.0061	0.01	0.0	0.0	0.67	5	Estimate	0.145	-	1.73	0.272	0.012
									Mean[2]	0.144	-	1.74	0.272	0.012
									sd[2]	0.0059	-	0.32	0.047	0.0024
									Lower[2]	0.133	-	1.11	0.180	0.007
									Upper[2]	0.156	-	2.37	0.364	0.017
		2	0.0061	0.01	0.0	0.0	0.67	5	Estimate	0.152	14.02	-	.202	0.016
									Mean	0.152	14.75	-	0.201	0.024
									sd	0.0062	4.01	-	0.042	0.0027
									Lower	0.140	6.88	-	0.119	0.008
									Upper	0.164	22.61	-	0.283	0.025
2	Skipjack	1	0.0020	0.04	0.0	0.0	0.70	4	Estimate	0.174	-	2.32	0.474	0.031
									Mean	0.174	-	2.30	0.470	0.031
									se	0.0061	-	0.25	0.048	0.0035
									Lower	0.162	-	1.81	0.377	0.024
									Upper	0.186	-	2.79	0.564	0.038
		2	0.0020	0.04	0.0	0.0	0.70	4	Estimate	0.175	2.09	-	0.425	0.031
									Mean	0.175	2.16	-	0.419	0.032
									se	0.0067	0.76	-	0.046	0.0037
									Lower	0.162	0.67	-	0.330	0.025
									Upper	0.189	3.64	-	0.508	0.039
3	Yellowfin	1	0.0115	0.05	0.0	0.0	0.70	4	Estimate	0.089	-	1.76	0.187	0.017
									Mean	0.089	-	1.75	0.186	0.017
									se	0.0066	-	0.20	0.019	0.0022
									Lower	0.077	-	1.36	0.148	0.013
									Upper	0.102	-	2.15	0.224	0.022
		2	0.0115	0.05	0.0	0.0	0.70	4	Estimate	0.084	1.05	-	0.191	0.015
									Mean	0.084	0.99	-	0.190	0.016
									se	0.0072	0.50	-	0.024	0.0022
									Lower	0.069	0.01	-	0.143	0.011
									Upper	0.098	1.98	-	0.237	0.020

1 F for model 2 refers to the arithmetic mean of F_j for the last five time periods.

2 The means, standard errors (se), lower and upper 95% confidence bounds of the estimates, are based on 100 simulations in which (i) C_j varied with a coefficient of variation (cv) of 0.10; (ii) assumed β for experiment 1 was sampled from a uniform distribution with bounds of 0.47 and 0.87; and (iii) assumed β for experiments 2 and 3 was sampled from a beta distribution with a mean of 0.70 and a cv of 0.10.

Yellowfin Parameter Estimates

Yellowfin exhibit a lower rate of natural mortality/emigration (0.08-0.10 month^{-1}), smaller equilibrium population size (1.4-2.1 million t), lower recruitment rate (150,000-220,000 t month^{-1}) and lower fishing mortality rate (0.013-0.022 month^{-1}) than skipjack (Table 4). These estimates imply a harvest ratio similar to that of skipjack, 16%.

The estimate of Y (about 1.0 year^{-1}) is similar to estimates of annual M derived for yellowfin in the eastern Pacific (0.64-0.90 [Hennemuth 1961]; <2.0 [Bayliff 1971]; 0.80 [Murphy and Sakagawa 1977]). The lower fishing mortality rate compared to skipjack suggests that yellowfin catchability by purse seine and the other surface gears is lower than that of skipjack. This is consistent with the lower yellowfin catch per effort that the purse seine fleets typically record, and suggests that this is primarily due to lower vulnerability than to a smaller population size.

Statistical Properties of the Estimates

The standard errors of the parameter estimates and associated 95% confidence intervals (Table 4), conditional on the assumed errors in C_j and β, suggest that most of the parameters are determined with reasonable precision. For experiments 2 and 3, the cv's of P, R and F are around 0.1, while the cv of Y is <0.1. For experiment 1, the cv's of all parameters except Y are higher (~0.2).

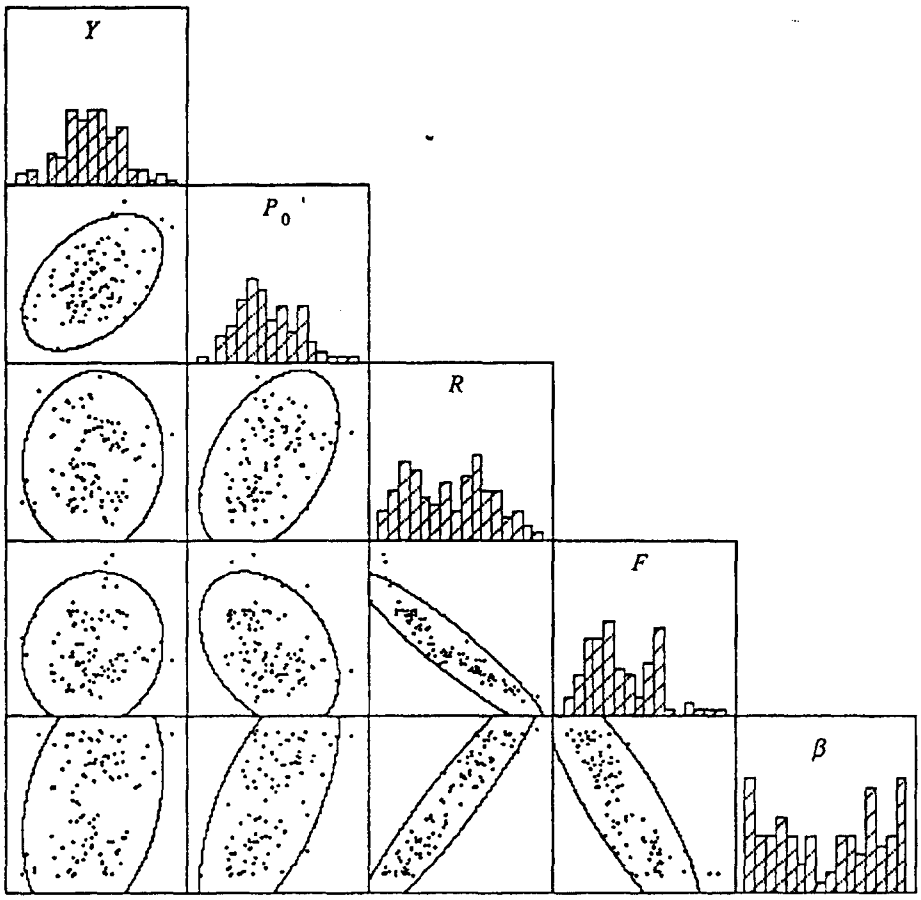
The cv's for P_0 (0.25-0.50) are higher than for the other parameters. However, this has little effect on other model parameters, as the influence of P_0 on P_j and F_j declines rapidly with time, particularly when Y is high.

The simulation results indicate that Y is not significantly correlated with other model parameters. (Figure 11). For experiment 1, where model 2 was preferred, low to moderate correlation between P_0 and other model parameters was apparent. For experiments 2 and 3, where model 1 was preferred, P is strongly correlated with R, F and β. Similarly, R is strongly correlated with F and β, and F is strongly correlated with β. However, recall that F and R are not parameters of model 1 in the statistical sense (i.e. they are not estimated directly from the data), but are analytical functions of P, Y and C_j. Their high correlation with P and each other therefore comes as no surprise.

The effects of the random errors in β require special comment. β is strongly correlated with one true model parameter in applications of both model 1 and model 2. For model 1 (experiments 2 and 3), β is positively correlated with P, and, as a consequence, positively correlated with R and negatively correlated with F. For model 2 (experiment 1), β is positively correlated with R (and to a lesser extent with P_0) and again as a consequence, negatively correlated with F. These strong correlations stress the need for good estimates of β if the tagging experiment is to be useful for estimating F, and hence useful for stock assessment. We might also note that the standard errors of the estimates of all parameters except Y are substantially higher for experiment 1 than for experiments 2 and 3. This results largely because of the greater uncertainty of β, expressed as a uniform distribution between wide limits, in experiment 1.

Figure 11. Distributions, scatter plots and correlation coefficients among parameters estimated from simulated data. The 95% confidence region for each parameter combination is indicated in the scatter plots. For experiment 1, the results were derived using model 2; for experiments 2 and 3, model 1 was used.

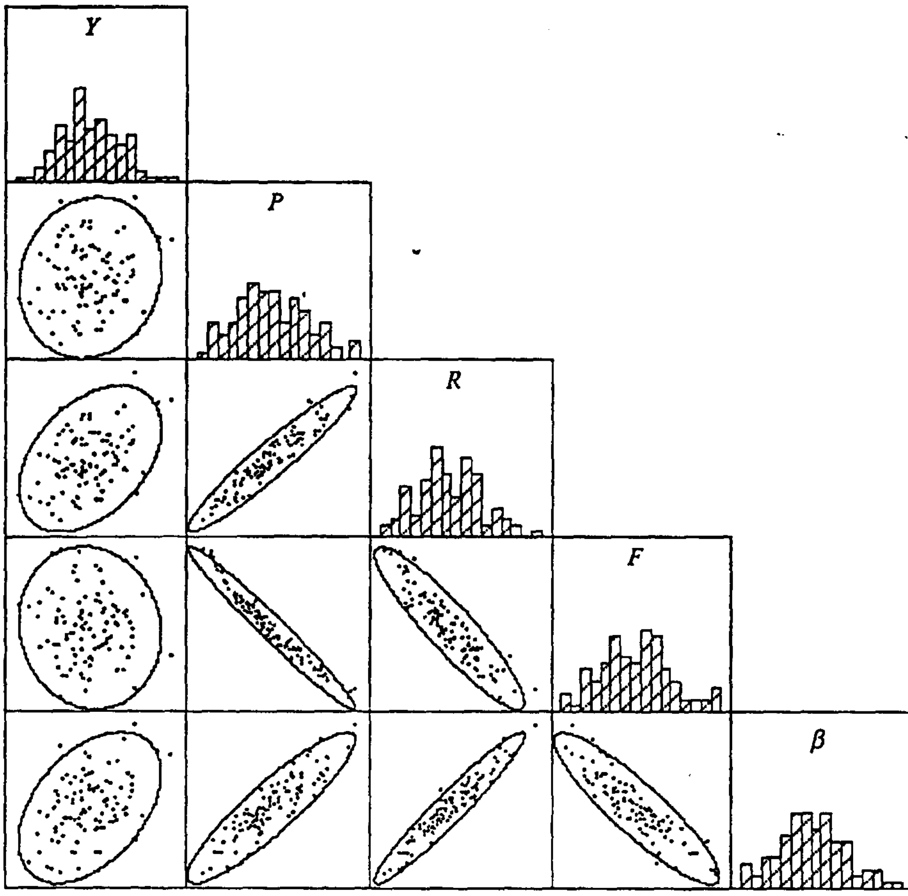
Experiment 1



Y				
0.48	P_0			
0.06	0.45	R		
0.10	-0.36	-0.94	F	
0.28	0.63	0.95	-0.86	β

Figure 11. (Continued)

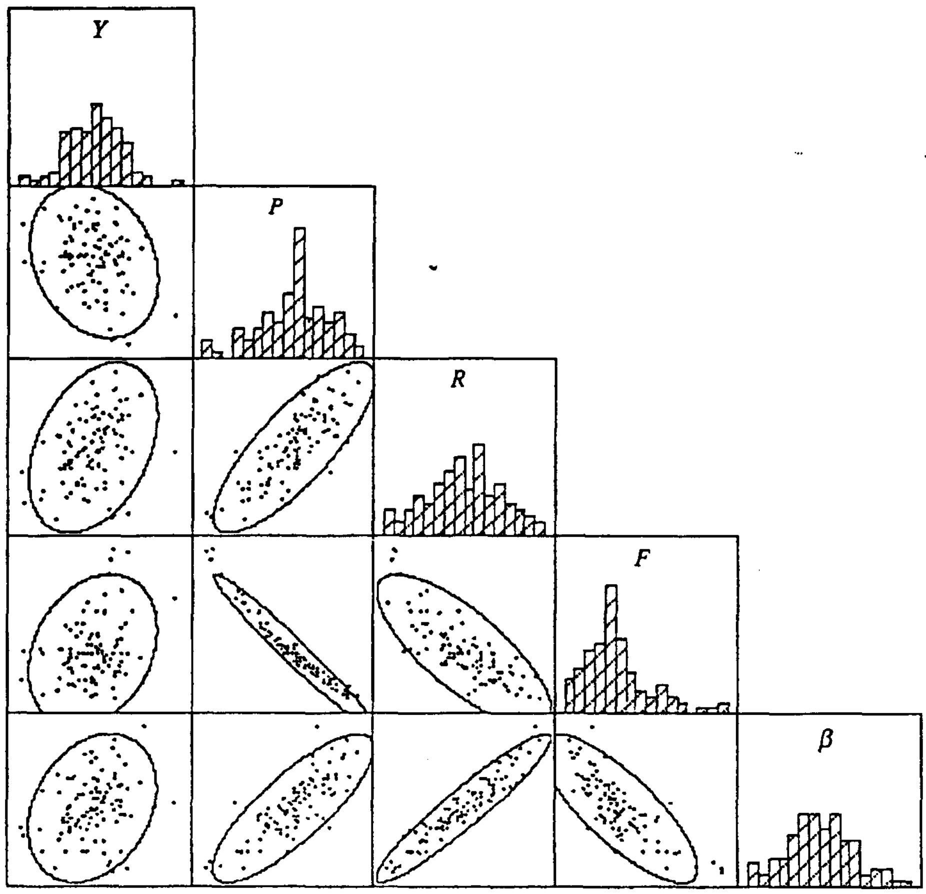
Experiment 2



Y				
0.12	P			
0.41	0.95	R		
-0.08	-0.98	-0.92	F	
0.45	0.91	0.96	-0.90	β

Figure 11. **(Continued)**

Experiment 3

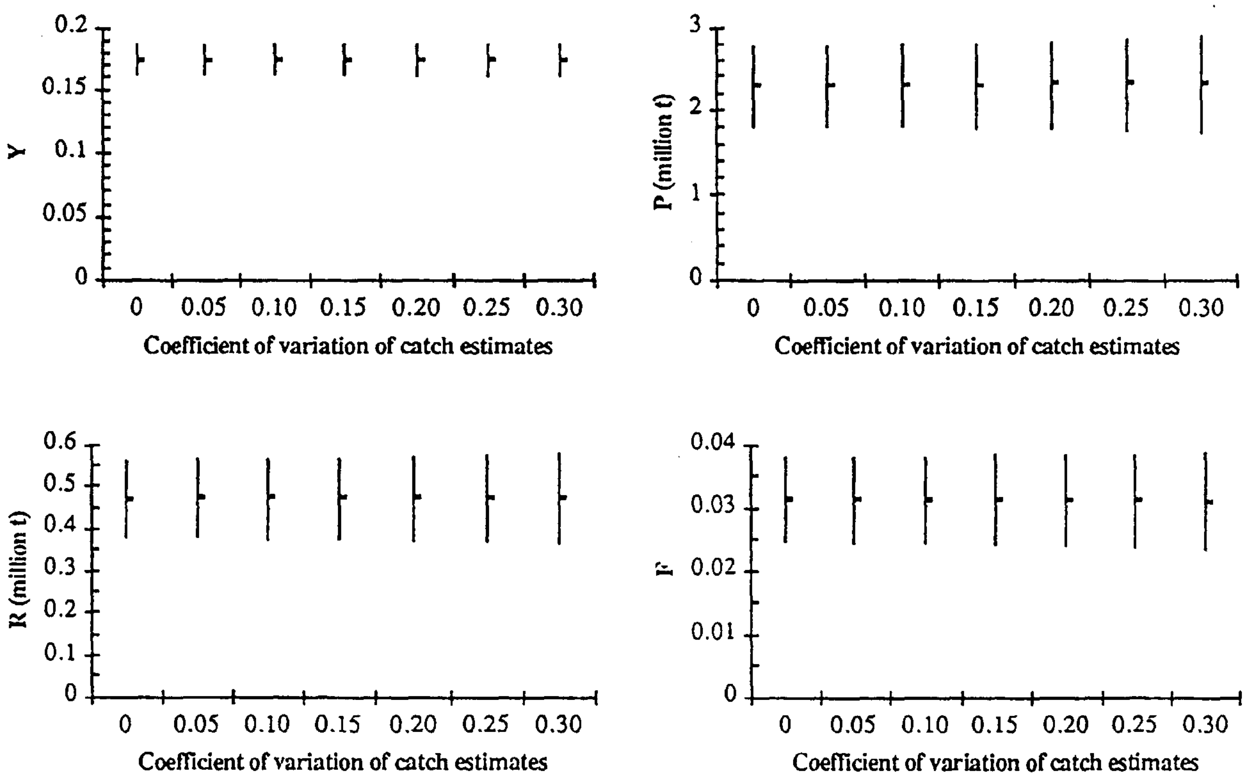


Y				
-0.24	*P*			
0.37	0.81	*R*		
0.27	-0.98	-0.77	*F*	
0.27	0.82	0.94	-0.80	*β*

Effect of Catch Uncertainty

The effects of different levels of catch uncertainty on model 1 parameter estimates were investigated by running several sets of simulations analogous to experiment 2. These simulations were identical to the primary simulations, except that the catch cv was set to different levels. The mean parameter estimates and their confidence intervals are not affected by random errors in the catch data (Figure 12). We can conclude from this that as long as the catch estimates accurately represent the true mean catch (averaged over the period of the experiment) and capture any real trend that exists, the models applied in this study are robust to random errors in the estimates.

Figure 12. Effects of errors in catch data on parameter estimates. The bars represent 95% confidence intervals based on 100 simulations analogous to experiment 2. Simulated data were analysed using model 1.

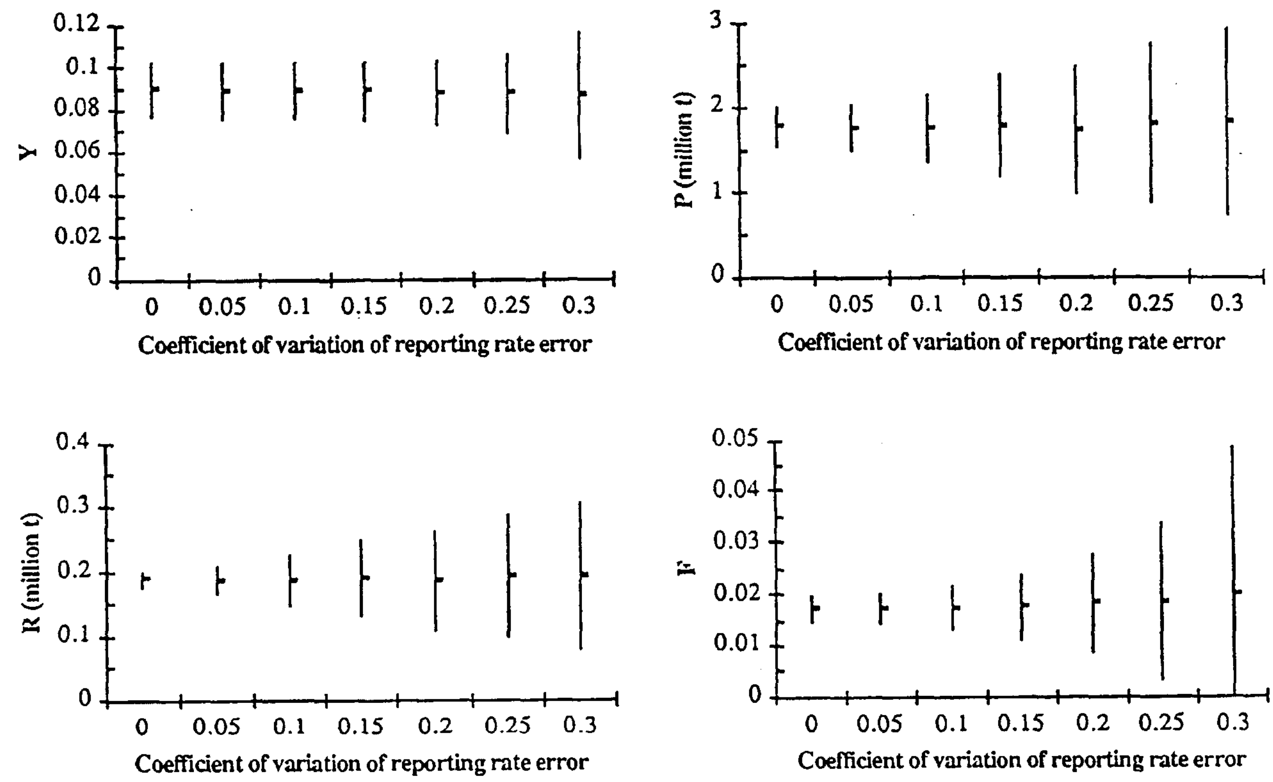


Effect of Reporting Rate Uncertainty

The parameter correlations discussed earlier suggested that model results are sensitive to errors in the assumed value of β. In the primary simulations, it was argued that a beta distribution with a mean of 0.70 and a cv of 0.10 is a reasonable error structure for β for the purpose of calculating standard errors and confidence intervals of estimated parameters. Additional simulations were carried out to determine the effects of different cv's in the β error distribution.

Estimates of Y are quite robust to increases in reporting rate error (Figure 13), as long as the mean of the error distribution is constant throughout the experiment. The effect on the other parameters is much more marked -- while no bias in the parameter estimates is introduced, their confidence intervals increase as the cv of the β distribution is increased. Estimates of F appear to be particularly sensitive in this regard. This again stresses the need for precise estimates of β for tagging-based stock assessments.

Figure 13. Effects of error in β on parameter estimates. The bars represent 95% confidence intervals based on 100 simulations analogous to experiment 3. Simulated data were analysed using model 1.

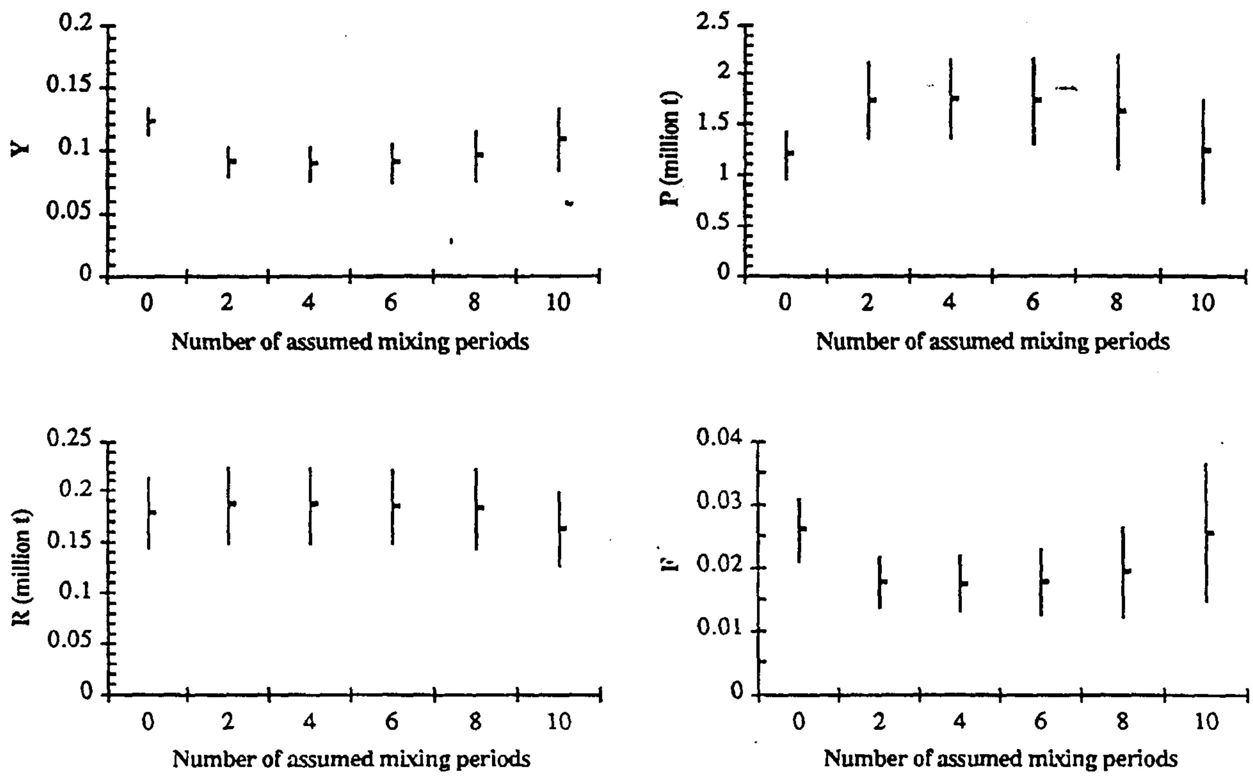


Effect of Assumed Mixing Period

A series of simulations was carried out to test the effects of different assumed mixing periods. First, parameter estimates from real data (experiment 3, model 1) were obtained for m=0,2,4,6,8 and 10 months. These estimates were then used as input to the simulation model in an identical fashion to the primary simulations, and their standard errors and confidence intervals obtained.

As long as at least two months are allowed for mixing, the results of experiment 3 appeared fairly robust to different assumed mixing periods. However, it is apparent that the parameter confidence intervals increase slightly as more time is allowed for mixing and fewer recapture data are available for analysis.

Figure 14. Effects of different assumed mixing periods on parameter estimates. The bars represent 95% confidence intervals based on 100 simulations analogous to experiment 3.



Spatial Effects -- Can They Be Ignored?

As noted in earlier sections, the models developed for these analyses are spatially aggregated -- all parameters have the implicit interpretation of being average quantities representative of the study area as a whole. In reality, most fisheries have a large degree of spatial structure -- the fish will tend to be more abundant in some places than in others, and the spatial distribution of catch and effort will be similarly heterogeneous. Tagging experiments will also have spatial structure. Typically, more releases are made in areas where fishing effort tends to concentrate, either because fish are more abundant in these areas or because such areas are simply more accessible to both the fishing fleet and the tagging vessel. This was the case for the experiments analysed in this study, although, as noted earlier, attempts were made in experiments 2 and 3 to distribute releases as widely as possible throughout the study area.

In the analyses presented here, I attempted to reduce the possible bias in parameter estimates that might result from ignored spatial structure by defining a period during which the tagged fish would randomly mix with the untagged fish throughout the study area. In order to examine the effectiveness of this technique, a simple simulation, incorporating spatial structure in fishing mortality and tag releases, was devised. The strategy was to then ignore the spatial effects by aggregating tag recaptures across the simulated area (as is done with real data), estimate population parameters using model 1 with a range of assumed mixing periods, and to compare these parameters with the real values used in the simulation.

Simulated Tagging Experiment with Spatial Structure

The simulated population and fishery was designed to have characteristics similar to those of yellowfin (but much simplified, of course):

1. A study area identical to that of the real experiments, with the exception that no land masses were included, was defined. The area measures 20° of latitude by 70° of longitude and is referenced in the same manner as the real study area (120°E-170°W, 10°N-10°S).
2. The untagged fish population is at equilibrium and has uniform density. The total biomass is 2.1 million t (1,500 t per one degree square).
3. Fishing mortality occurs throughout the area. In all but two areas, F=0.015 month^{-1} and is time invariant. At 2°N-3°S, 134°-139°E and 2°N-3°S, 170°-175°E, F=0.075 month^{-1} (relative to the populations in those individual areas) and is time invariant. This results (by way of equation 3) in aggregate monthly catches of 33,854 t (28,694 t in the low-F area and 5,160 t in the high-F areas).
4. At the beginning of month 1, 2,000 tagged fish are released at the mid-points of each high-F area. At the same time, 1,000 tagged fish are released at 6°30'N,155°30'E and at 6°30'S, 154°30'E. Recaptures are generated over the next 36 months.
5. Tagged (and untagged) fish diffuse at a rate of 2°x 2° per month (14,400 nmi^2 month^{-1}) and reflect off the boundaries of the study area. This rate of diffusion appears to be typical of western Pacific skipjack and yellowfin.
6. All fish are subject to a natural mortality rate of 0.1 month^{-1}. All other sources of tag loss are assumed to be zero.

The distributions of recaptures during the first and sixth months after release are represented in Figure 15. In month 1, the recaptures are highly clustered around the release points, particularly in the high-F areas. By month 6, tagged fish have dispersed over a wider area, but most of the recaptures are still generated within the high-F areas. The simulation, by intent, represents a fairly extreme case of spatially heterogeneous fishing effort and tag release.

The partial time series of recaptures (Figure 16) shows the effects of different tag release strategies. If releases only occur in the high-F areas, there is a distinct upwards bending of the left end of the tag attrition curve due to the concentration of fishing effort in the vicinity of tag releases. This effect quickly diminishes as tagged fish disperse from the high-F area. If releases occur only in the low-F areas, the tag attrition curve appears linear. If releases occur in both high- and low-F areas, as described above, the tag attrition curve is still bent upwards at its left end, but not as severely as for high-F area releases only.

For the total simulated recapture series (releases in both high- and low-F areas), it appears that the bias in parameter estimates (high Y and F, low P and R) caused by the high numbers of recaptures in the initial periods can be effectively eliminated by allowing a sufficient mixing period in the analysis (Figure 17). For the population parameters used in this simulation (the dispersion coefficient is the most critical), 4-6 months would appear to be a sufficient mixing period.

By contrast, if tagged fish are released only in the low-F areas, the opposite parameter bias is observed, and this bias appears to persist even when relatively long periods of mixing are allowed (Figure 18). This may result because of the long time required for dispersal of tagged fish from their points of release into high-F areas compared to the reverse situation; thus a much greater portion of the tag attrition curve is affected.

It is possible that this result may be generally applicable, at least for tuna tagging experiments, although further simulations would be necessary to verify this. But if so, it suggests that experimental designs should avoid a situation where releases only occur in low-F areas. Where tagging experiments are to be used as the basis for stock assessment, as in this study, it is worth noting that any residual bias in parameter estimates, after allowances for mixing, will have the effect of producing slight over-estimates of F, if the majority of releases were made in high-F areas. Advice based on these results would therefore err on the side of caution.

Figure 15. Spatial distribution of simulated tag recaptures during month 1 and month 6 (darker shades indicate larger recapture numbers). The simulated experiment consisted of 2,000 releases at each of the mid-points of the two dark squares (high-F areas) and 1,000 releases at each of the two points marked by + (low-F area).

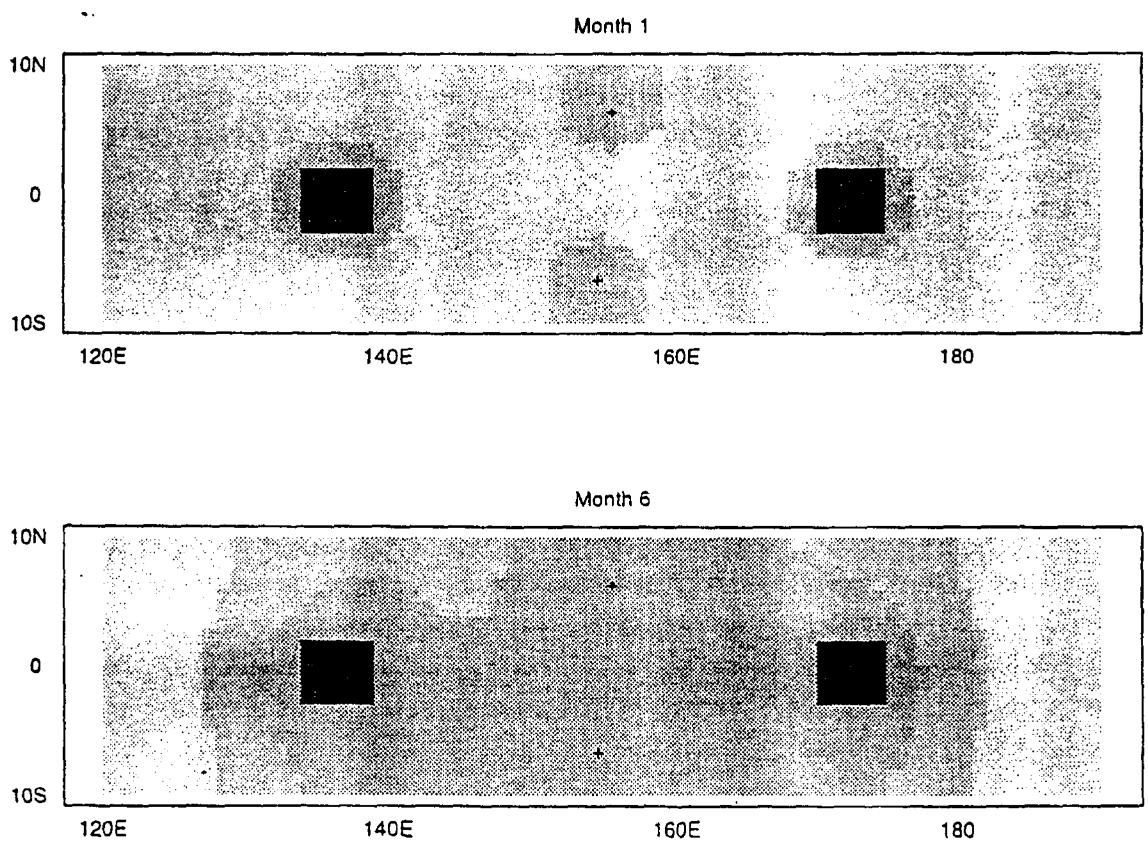


Figure 16. Tag recaptures by month (to month 20) for the simulated experiment.

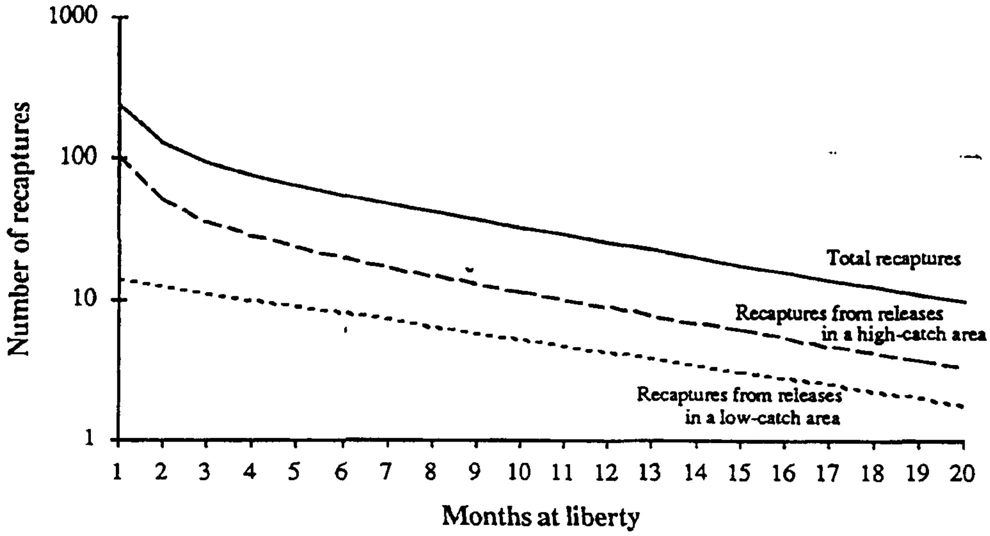


Figure 17. Model 1 parameter estimates for the simulated experiment for a range of assumed mixing periods. The true simulated population parameters are indicated by the horizontal lines.

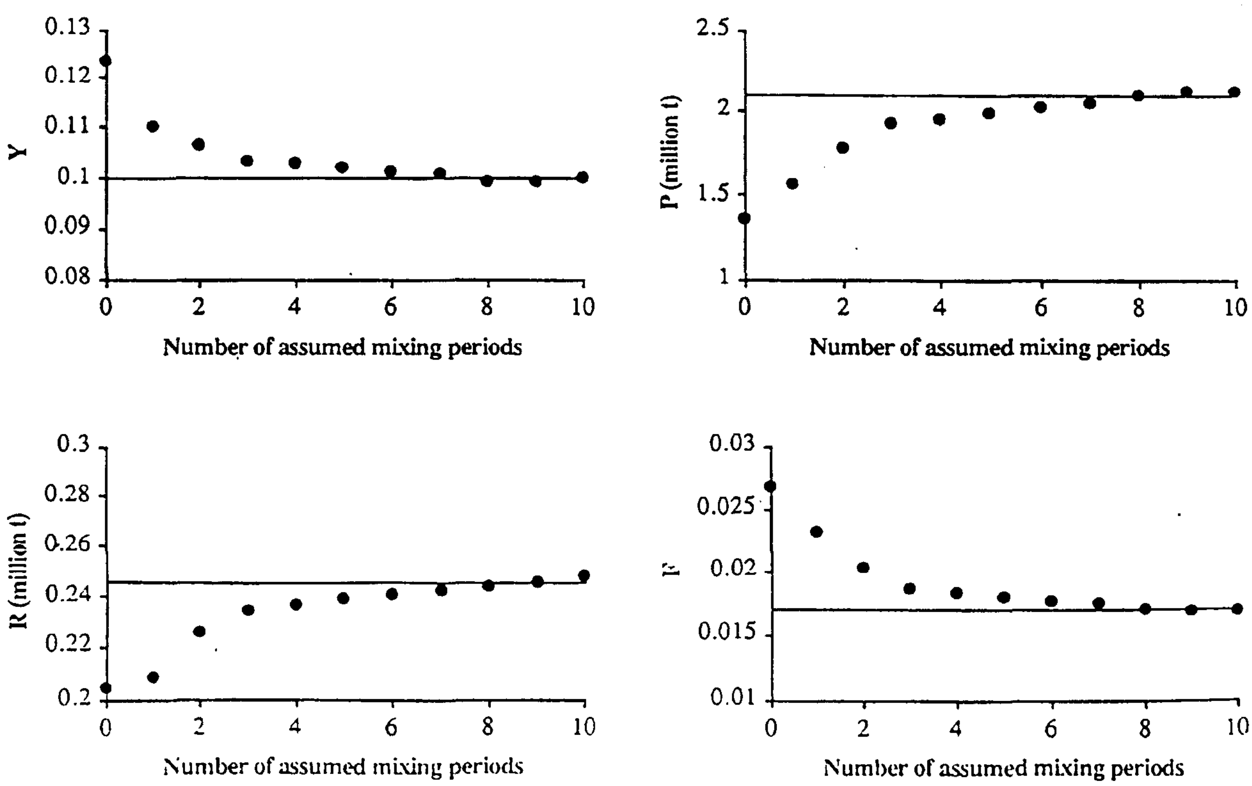
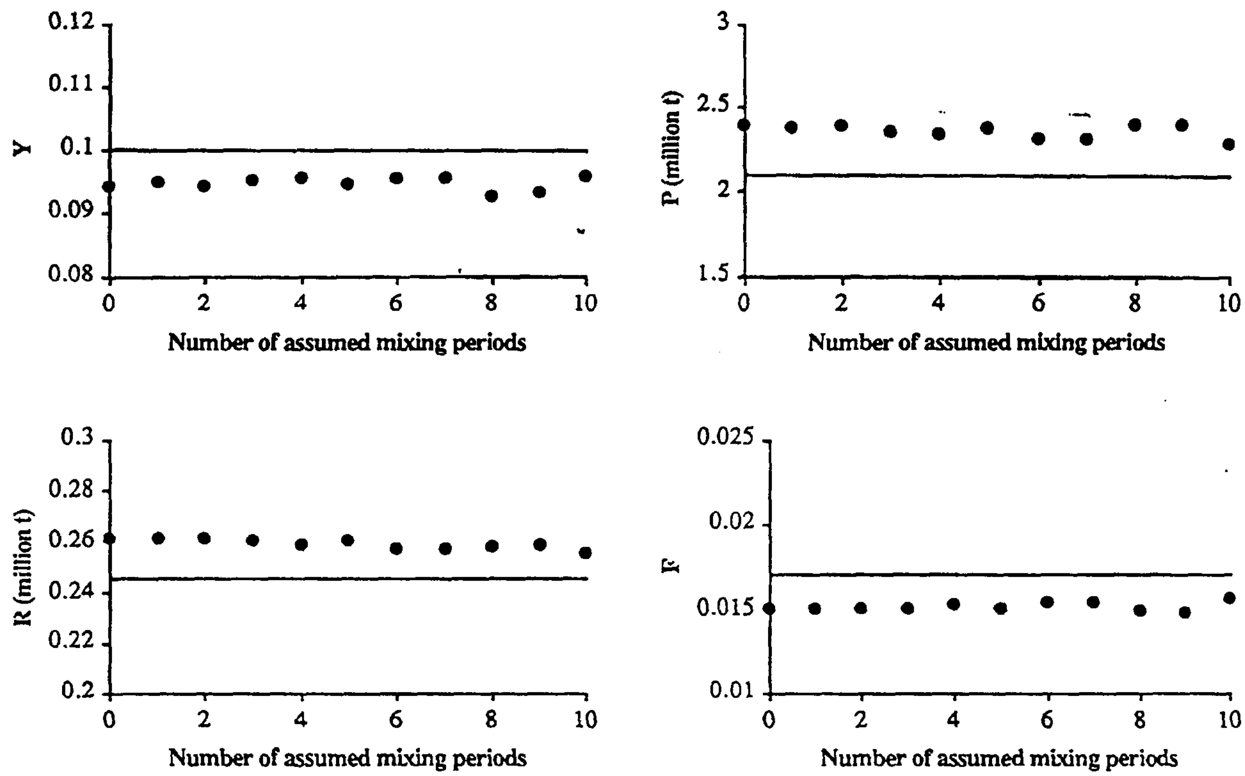


Figure 18. Model 1 parameter estimates for the simulated experiment with tag releases only in low-*F* areas, for a range of assumed mixing periods. The true simulated population parameters are indicated by the horizontal lines.



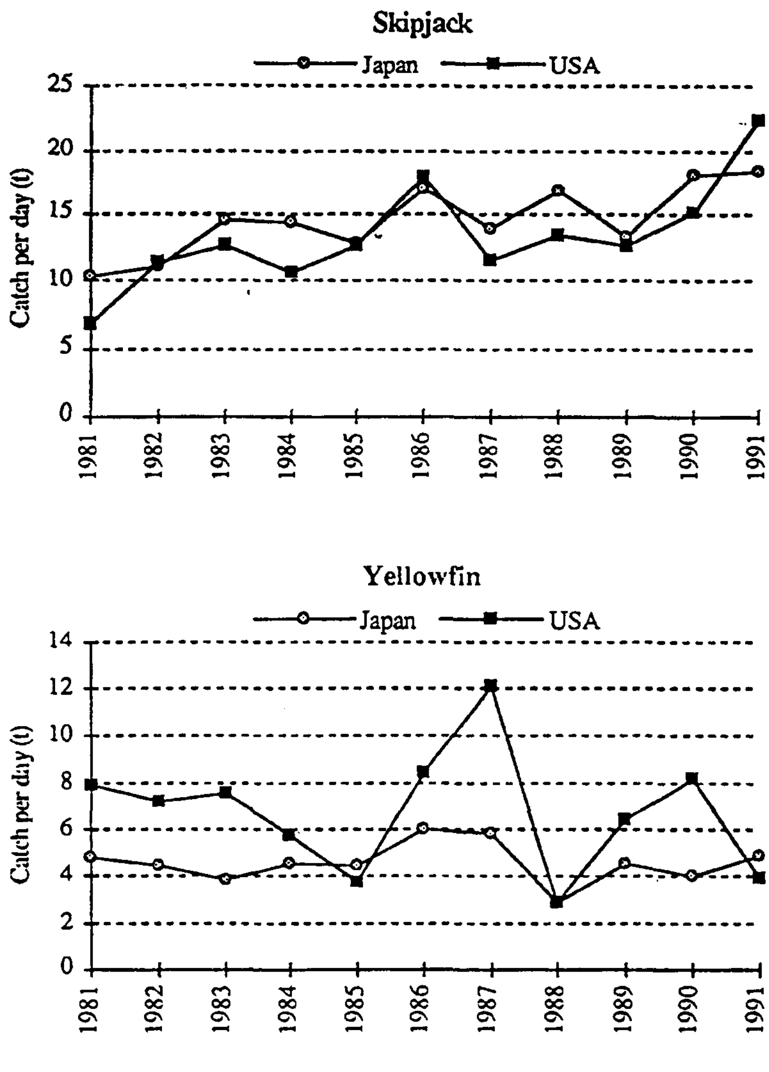
CONCLUSIONS

Status of the Stocks and Exploitation Potential

The currently modest fishing mortality rates and harvest ratios for both skipjack and yellowfin imply that, to date, the stocks have not been significantly affected by fishing. This is supported by observations of purse seine catch per effort time series for the Japanese and United States fleets[1], which, while variable, show no significant negative trend (Figure 19). Moreover, the results of the analyses indicate that the stocks are currently under-exploited; this implies that there is a potential for further increased catches. It is of course of interest to fisheries management agencies to what *extent* catches may be safely increased. While precise answers to this question are rarely possible for developing fisheries, some indications can be given on the basis of the model 2 parameter estimates for experiments 2 and 3.

1 Purse seine catch and effort data are most reliable for the Japanese and United States fleets.

Figure 19. Catch per effort of skipjack and yellowfin by Japanese and United States purse seiners in the western tropical Pacific.



One means of assessing exploitation potential is to predict the response of the population to various increased catch levels. This can be done by calculating future population sizes under the expanded catch regimes using equations (3) and (4), substituting P_t for P_0 and using the model 2 estimates of Y and R. As these equations are fundamentally stable, P_j will decrease in response to the increased catch before reaching a new equilibrium level, P_{new}. The percentage change from P_t to P_{new} can be regarded as an estimate of the impact of the increased catch level on the population.

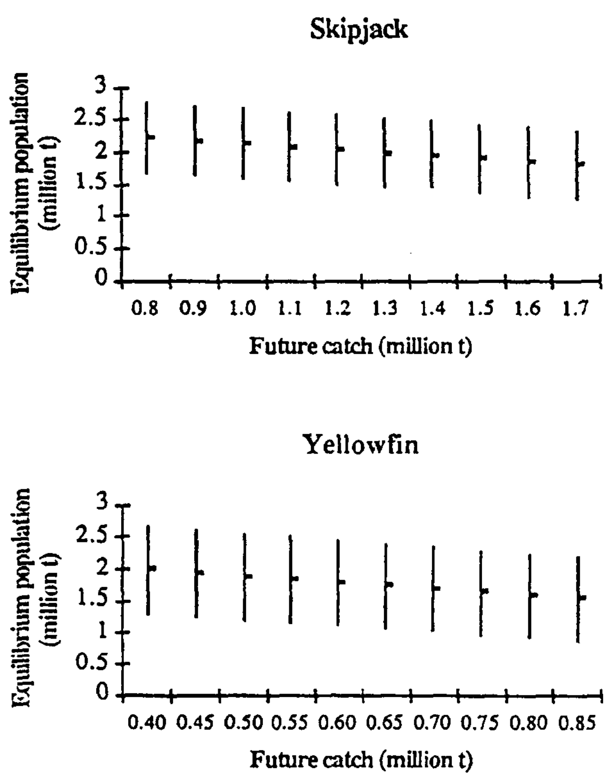
P_{new} for a range of increased catches of skipjack and yellowfin were determined (Figure 20). For skipjack, it is estimated that a doubling of the current annual catch (to about 1.5 million t) would reduce its equilibrium population biomass by only 11-20%[2]. Similarly for yellowfin, a doubling of the current annual catch (to 750,000 t) would result in an estimated 5-24%[2] reduction in equilibrium biomass. Such reductions would be unlikely to impact recruitment and would probably be undetectable in catch per effort

[2] 95% confidence intervals

time series.

Projections of this nature require various assumptions to be made. Temporal stability of parameters *Y* and *R* is one such assumption. With tagging experiments, we are taking "snapshots" of the population at specific times, and population parameters can vary to some extent among "snapshots" as we have seen with experiments 1 and 2. The maintenance of the current spatial distribution of the stocks, their vulnerability to the gears, and various other biological characteristics must also be assumed. For these reasons, it would be inadvisable to attempt to extrapolate the current catch levels too far or to place undue reliance on the numerical results of such extrapolations. Rather, this method is best used to decide whether current catches should be maintained, reduced or increased, and, in case of the latter, to indicate very approximately the magnitude of catch increases that might be considered.

Figure 20. Predicted equilibrium population levels (with 95% confidence intervals) associated with different equilibrium catches.



Management Implications

On the basis of these analyses, it is considered that a gradual increase over several years in skipjack and yellowfin catches by 50% of their 1991 levels, i.e. to approximately 1.2 million t for skipjack and 500,000 t for yellowfin, would represent a conservative management policy with respect to biological conservation. In the short term, economic factors, rather than the ability of the stocks to sustain increased catches, may limit the growth of the fishery. Careful and timely monitoring of various fishery indicators, such as catch per effort and catch size composition, must accompany any increase in catches. Also, further stock assessments based on fisheries data should be periodically carried out; some of the parameters estimated in this study should be useful for such assessments.

There are two other important management considerations that require comment. First, although the stocks as a whole may be able to accommodate increased exploitation, there is the possibility that increased exploitation might cause interaction effects among some components of the fishery. Of uppermost concern to Pacific Island Governments is that increased catches of yellowfin by purse seiners may have an adverse effect on catch rates of yellowfin by longliners, from which substantial revenue is derived from access fees. To date, there have been no consistent trends in longline catch per effort to suggest that purse seine and other fisheries have had a negative impact on the longline fishery (Hampton 1991). This observation is consistent with the low fishing mortality rates estimated for yellowfin in this study. Also, at the time of writing, no tagged yellowfin had been recaptured by longliners, despite 110 recoveries (as at 15 April 1992) by other gear types, mostly purse seine, of a size (>90 cm fork length) vulnerable to longlining. Although some tagged yellowfin may ultimately be recaptured by longliners, this observation is also consistent with there being little interaction between surface and longline gears at present. Further studies are required on vulnerability cycles of yellowfin to these gears, so that some predictions can be made regarding the likely impacts of increased purse seine catches on longline catch rates.

The second additional management issue of concern is that of local depletion of stocks. If very large catches are taken in a small area relative to the overall distribution of the stock, local abundance could be significantly reduced, affecting catch per effort and profitability of the local fishery. Local effects such as these have not been considered in this study. The extent to which these effects may occur will be strongly influenced by the degree of movement of fish into and out of the local area. If such movement is rapid, the effects of high local exploitation will be quickly diluted across the range of the stock. If this is not the case, then local depletion of the stock may indeed occur. Some qualitative analyses of movement data, such as those shown in Figures 7 and 8, would suggest that mixing is quite rapid and that local exploitation effects will be quickly diluted over a large area. However, these results are not conclusive, and a more thorough quantitative treatment of the movement data is required. Such a study is currently in progress and will be reported at a later time.

ACKNOWLEDGEMENTS

The RTTP was conducted by the South Pacific Commission Tuna and Billfish Assessment Programme, with funding assistance from the European Community Fifth European Development Fund. All staff of the Programme, led by Tony Lewis, contributed in some way to the success of the RTTP. Special acknowledgements are due to those who labored long and hard at sea in the quest for more tagged tuna, particularly Kevin Bailey, David Itano, Joel Opnai, Eti Palu, Filipe Viala, Eroni Dolodai and Captain Iefata Paeniu and the crew of the M.V.*Te Tautai.* Veronica Logez coordinated tag recovery procedures and received invaluable assistance from many individuals and agencies. Special thanks are due to Gordon Yamasaki, Dennis Therry, Masahiro Asano, Zainal Abidin, Edwin Orchaka and Sammy Resma for their efforts in collecting thousands of tags with good recapture data. Peter Williams assisted with the compilation of figures and data for this paper. I am also grateful to Pierre Kleiber who constructed the movement simulation model. Earlier drafts of this paper were considerably improved by the comments of ....

LITERATURE CITED

Baranov, T.I.

1918 On the question of the biological basis of fisheries. Nauchn. Issled. Ikhtiol. Inst. Izv. 1:81-128 [in Russ.].

Bard, Y.

1974 Nonlinear parameter estimation. Academic Press, NY, 341 p.

Bayliff, W.H.

1971 Estimates of the rates of mortality of yellowfin tuna in the eastern Pacific Ocean derived from tagging experiments. Inter-Amer. Trop. Tuna Comm., Bull., 15:379-436.

Bayliff, W.H.

1977 Estimates of the rates of mortality of skipjack tuna in the eastern Pacific Ocean derived from tagging experiments. Inter-Amer. Trop. Tuna Comm., Internal Rep. 10:59 p.

Bayliff, W.H.

1988 Integrity of schools of skipjack tuna, *Katsuwonus pelamis*, in the eastern Pacific Ocean, as determined from tagging data. Fish. Bull., U.S. 86:631-643.

Forsbergh, E.D.

1987 Rates of attrition, cohort analysis and stock production models for skipjack tuna, *Katsuwonus pelamis*, in the eastern Pacific Ocean. Inter-Amer. Trop. Tuna Comm., Internal Rep. 20:37 p.

Fournier, D., and J. Sibert

1991 Evaluation of diffusion-advection equations for the estimation of movement patterns from tag recapture data. FAO Expert Consultation on Interactions of Pacific Tuna Fisheries, Noumea, New Caledonia, 3-11 December 1991. TIC/91/R#4.

Hampton, J.

1991 A review of tuna fishery interaction in the western and central Pacific Ocean. FAO Expert Consultation on Interactions of Pacific Tuna Fisheries, Noumea, New Caledonia, 3-11 December 1991. TIC/91/R#24.

Hampton, J. and G.P. Kirkwood

1990 Tag shedding by southern bluefin tuna *Thunnus maccoyii*. Fish. Bull., U.S. 88:313-321.

Hennemuth, R.C.

1961 Year class abundance, mortality and yield-per-recruit of yellowfin in the eastern Pacific Ocean, 1954-1959. Inter-Amer. Trop. Tuna Comm., Bull., 6:1-51.

Kearney, R.E.

1982 Development and implementation of the Skipjack Survey and Assessment Programme. *In* Kearney, R.E. (ed.), Methods used by the South Pacific Commission for the survey and assessment of skipjack and baitfish resources, p. 3-18. South Pac. Comm., Tuna and Billfish Assess. Prog. Tech. Rep. No. 7, Noumea, New Caledonia.

Kearney, R.E. and R.D. Gillett

1982 Methods used by the Skipjack Survey and Assessment Programme for tagging skipjack and other tuna. *In* Kearney, R.E. (ed.), Methods used by the South Pacific Commission for the survey and assessment of skipjack and baitfish resources, p. 19-43. South Pac. Comm., Tuna and Billfish Assess. Prog. Tech. Rep. No. 7, Noumea, New Caledonia.

Kendall, M.G., and A. Stuart

1979 The advanced theory of statistics. Vol. 2. Inference and relationship. Charles Griffin, London, 748 p.

Kleiber, P., A.W. Argue, and R.E. Kearney

1987 Assessment of Pacific skipjack tuna (*Katsuwonus pelamis*) resources by estimating standing stock and components of population turnover from tagging data. Can. J. Fish. Aquat. Sci. 44:1122-1134.

Lawson, T.

1991 Status of tuna fisheries in the SPC area during 1990, with annual catches since 1952. South Pac. Comm., Tuna and Billfish Assess. Prog. Tech. Rep. No. 27, Noumea, New Caledonia, 73 p.

Murphy, T.C., and G.T. Sakagawa

1977 A review and evaluation of estimates of natural mortality rates of tunas. Inter. Comm. Conser. Atlan. Tunas, Coll. Vol. Sci. Pap., 6:117-123.

Press, W.H., B.P. Flannery, S.A. Teukolsky, and W.T. Vetterling

1986 Numerical recipes: the art of scientific computing.Cambridge University Press, Cambridge, NY, 818 p.

Wetherall, J.A.

1982 Analysis of double tagging experiments. Fish. Bull., U.S. 80:687-701.