ANALYSIS OF MIGRATIONS AND MORTALITY OF BLUEFIN TUNA, *THUNNUS THYNNUS*, TAGGED IN THE NORTHWESTERN ATLANTIC OCEAN[1,2]

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ABSTRACT

An analysis is presented on the release and return data from bluefin tuna, *Thunnus thynnus*, tagged in the northwest Atlantic Ocean from 1954 to 1970. There was an apparent northward movement of fish from the New Jersey area as the fishing seasons progressed. Tag returns from bluefin released in the Long Island and southern New England areas tended to be to the north at first and then to the south. Mean distances between release and return tended to be greater for fish released in the New Jersey area than for the other two areas. Estimates of mortality rates for tagged bluefin were made using the Chapman-Robson method and then adjusted for Type-I and Type-II tag shedding and Type-I tagging mortality. The average estimate of instantaneous fishing mortality is 0.57 and other losses (natural, tagging, and emigration) is 0.68 on an annual basis. The estimate of other losses is considerably higher than the natural mortality that would be expected for bluefin. Evidence is presented suggesting that the rate of emigration may be quite high. The average single season exploitation rate of tagged bluefin was estimated to be 0.33. It was noted that since bluefin may be both immigrating to and emigrating from the fishery the estimate of exploitation may not be representative of the entire population. Even though validity of available effort data is questionable, regression estimates of mortality and survival rates were made using catch per effort data. These estimates of survival are lower than those obtained using the Chapman-Robson method.

The data which form the basis for this report were assembled by the first author. This study is based upon releases of tagged bluefin tuna, *Thunnus thynnus*, that were made by a variety of organizations and individuals under the coordination of the Woods Hole Oceanographic Institution Cooperative Game Fish Tagging Program at various locations along the middle Atlantic bight of North America from July 1954 to August 1970 and returns of these tags to the end of 1970. Additional returns are expected in the future from more recent releases.

MIGRATIONS

Because of the variety of methods, locations, and dates of release, we needed to assemble the data by relatively homogeneous release groups. The criterion for constructing a release group for analysis of migrations was to develop homogeneous time-location strata of releases from which a minimum of 20 tags were recovered. This procedure allowed us to work with homogeneous groups, but eliminated roughly 10% of the recovered tags from our analysis. Table 1 summarizes these release groups and Figure 1 shows their localities. We can see from Table 1 that during the study period the tagging operations tended to shift from the New Jersey coast, to the New York coast, to the southern New England coast, and that releases in July tended to be south of those made in August or September.

Tagging data have been used to show some of the longer migrations of the bluefin tuna (Food and Agriculture Organization, 1972). We examined the shorter term recoveries from an analytic point of view. In order to do this, we made use of a method developed by Rothschild (Bayliff and Rothschild, in press). Using this method each release group was stratified into intervals of time at liberty. Release vectors (latitude and longitude) for each release group were used to compute an average or common release vector. Each recapture vector for the group was then standardized to the common release vector. The standardized vectors were then used to find 1) the average recapture vector and 2) the determinant of the recapture

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[1] This paper is dedicated to the memory of Gerald J. Paulik. He was a good friend and colleague and made important contributions to the theory of tagging.

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TABLE 1.—Release groups used for analysis of migrations of tagged bluefin tuna.

	General location of release					
	New Jersey Coast		Long Island Coast		Southern New England	
Release date	Group No.	No. of returns	Group No.	No. of returns	Group No.	No. of returns
July 1964	2A	33				
	2B	32				
	2C	27				
Aug. 1964			3	33		
July 1965	4A	36				
	4B	86				
	4C	38				
Aug. 1965	5A	22	5B	47	5C	24
July 1966	6A	114				
	6B	127				
	6C	45				
	6D	85	6E	62		
Aug. 1966			7A	20	7C	85
			7B	81	7D	36
					7E	55
					7F	203
					7G	177
Sept.-Oct. 1966			8	23		
July 1967	9A	23				
	9B	94				
Sept. 1967			10	27		
July 1968	11A	21	11B	39		
July 1969			12	24		
Aug. 1969					13	40
Sept. 1969					14	22
July 1970					15	17
Aug. 1970					16	25
1954-63					17	24

variance-covariance matrix. The determinant of the recapture variance-covariance matrix is proposed by Bayliff and Rothschild as an index of the dispersal of the fish. When the distance of the recoveries from one another is large, the determinant is large.

It should be noted that the vectors computed by this method are not on a per-unit-effort basis so that "migration patterns" reflect not only the apparent movement of the fish, but also the distribution of fishing effort. In order to more fully understand the nature of short-term movements, it will be necessary to study in some detail the complex problem of the distribution of bluefin tuna in the northwest Atlantic. Preliminary to more detailed analysis of these statistics, we surveyed some of the main features of the data, of which some are tabulated in Table 2.

First we considered the direction of movement. Figure 2 contains a synthesis of these data and shows the direction of movement by tagging location and time at liberty. It is implicit that we treated each symbol as reflecting the behavior of a sample of fish from the same statistical population. The main features of Figure 2 are that fish tagged off New Jersey in July tended to move in an eastward direction and both north and south during the first 2 wk at liberty, but then movement became strongly directed to the northeast. Fish released in the Long Island area initially tended to move toward the north, but after the first 30 days, their movement appeared to have been concentrated to the west and south. The same conclusion may be obtained from the southern New England releases.

An examination of the mean distance (Figure 2) shows fish released off New Jersey tended to be recovered at a slightly greater distance to the north than the south. The fish moved approximately 7 or 8 miles per day. By the second 15-day period, the fish moved about 60-100 miles to the northeast. The pattern for Long Island releases, based on only a few observations, shows that movement distance of these fish during 1-15 days was approximately the same as that for the New Jersey releases. The short-term recoveries of southern New England tagged fish reflect even less average distances than New Jersey short-term releases suggesting that either the fish off southern New England moved less than off New

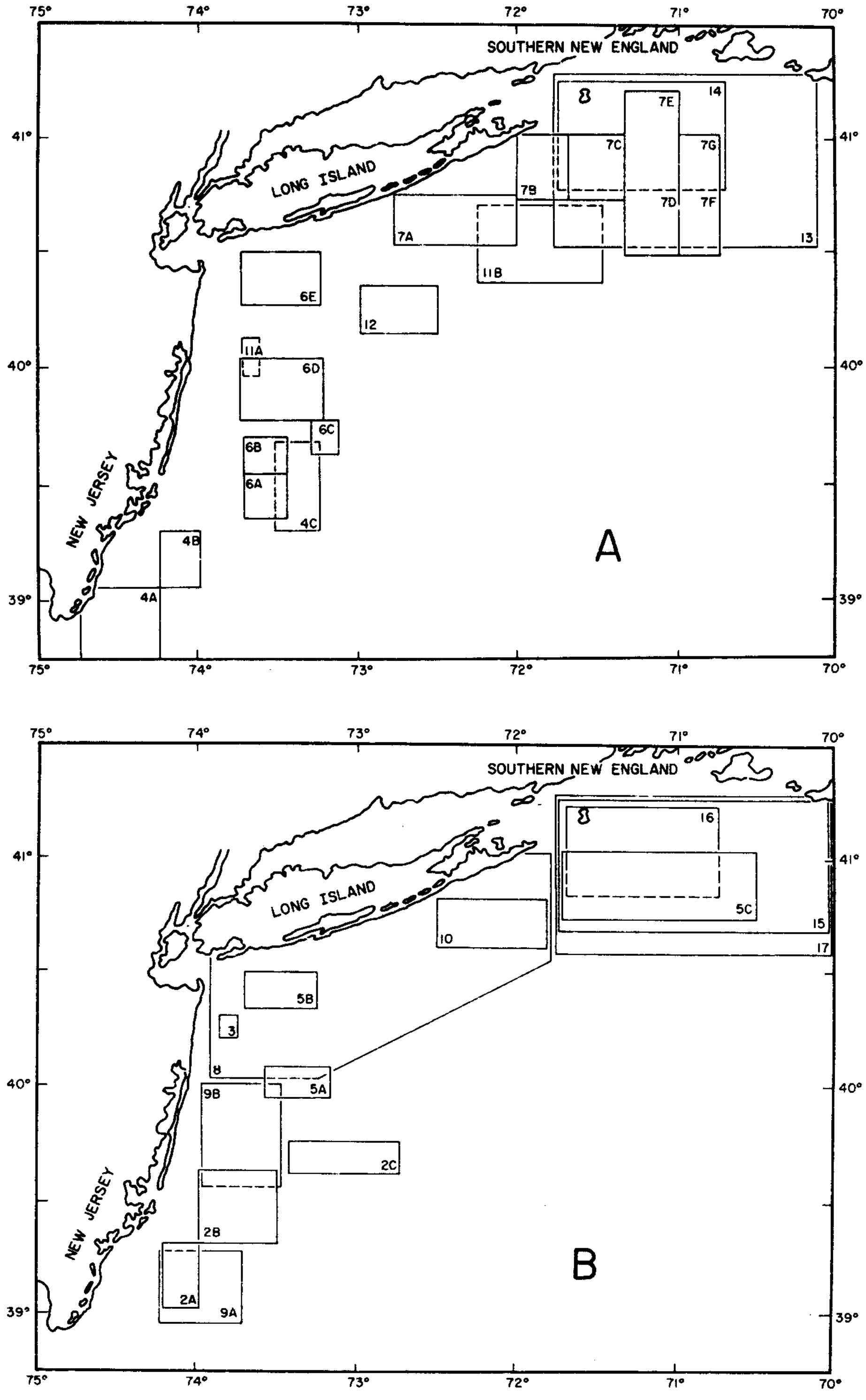

FIGURE 1.—Part A and Part B: Map of middle Atlantic bight showing release group locations of tagged bluefin tuna.

TABLE 2.—*Summary of statistics on movements of tagged bluefin tuna. All distance measures are nautical miles.*

Release group	Time at liberty (days)	Mean miles N-S[1]	Mean miles E-W[2]	Deter-minant $(\times 10^4)$	Mean distance	No. of fish	Release month	General release location
2A	1-15	26.5	34.1	2.3	50.5	13	July	N.J.[3]
	16-30	74.2	74.9	26.0	114.0	9	1964	
	31-60					1		
	61-180					0		
2B	1-15	−9.2	11.4	2.9	31.8	18	July	N.J.
	16-30	25.1	58.5	1.4	89.7	7	1964	
	31-60					2		
	61-180					0		
2C	1-15	−7.2	−15.0	1.3	29.6	14	July	N.J.
	16-30					1	1964	
	31-60					1		
	61-180					0		
3	1-15	8.0	12.2	0.3	32.6	12	Aug.	L.I.[4]
	16-30					1	1965	
	31-60					0		
	61-180					0		
4A	1-15	12.0	18.3	3.8	33.6	18	July	N.J.
	16-30	83.6	52.8	11.7	102.0	8	1965	
	31-60					1		
	61-180					1		
4B	1-15	20.9	7.4	8.7	46.4	39		N.J.
	16-30	70.8	21.2	0.2	74.6	28		
	31-60					3		
	61-180					0		
4C	1-15	25.3	−16.6	13.4	47.9	17	July	N.J.
	16-30	62.3	3.1	1.1	64.8	13	1965	
	31-60					0		
	61-180					0		
5A	1-15	25.8	−15.4	19.4	48.5	9	Aug.	N.J.
	16-30	53.5	5.4	17.2	60.4	12	1965	
	31-60					0		
	61-180					0		
5B	1-15	24.8	−17.9	9.5	47.2	8	Aug.	L.I.
	16-30	44.8	−1.8	36.0	54.9	5	1965	
	31-60					0		
	61-180					0		
5C	1-15					0	Aug.	S.N.E.[5]
	16-30					0	1965	
	31-60					0		
	61-180					0		
6A	1-15					2	July	N.J.
	16-30					3	1966	
	31-60	59.1	25.9	18.7	86.4	11		
	61-180	57.0	−11.1	0.01	58.6	23		
6B	1-15					4	July	N.J.
	16-30	52.8	39.6	0.2	76.7	5	1966	
	31-60	62.2	70.0	90.9	112.0	20		
	61-180					4		
6C	1-15					0	July	N.J.
	16-30					2	1966	
	31-60					1		
	61-180	39.9	−23.7	0.002	46.7	9		
6D	1-15	−5.5	5.6	62.3	41.1	10	July	N.J.
	16-30	4.0	3.3	1.7	20.7	6	1966	
	31-60	30.6	15.6	51.9	64.7	9		
	61-180	30.0	−13.2	0.006	33.1	14		

See footnotes at end of table.

TABLE 2.—Continued.

Release group	Time at liberty (days)	Mean miles N-S[1]	Mean miles E-W[2]	Determinant (x10^4)	Mean distance	No. of fish	Release month	General release location
6E	1-15	−28.2	3.0	1.8	35.9	14	July 1966	L.I.
	16-30	5.0	58.1	36.0	82.4	6		
	31-60					3		
	61-180	−3.8	−3.6	1.2	16.8	10		
7A	1-15					1	Aug. 1966	L.I.
	16-30					2		
	31-60					1		
	61-180					0		
7B	1-15	0.6	22.1	0.8	26.8	11	Aug. 1966	L.I.
	16-30	−11.4	−15.5	8.8	52.4	7		
	31-60					1		
	61-180					0		
7C	1-15	−2.0	6.0	1.3	17.9	9	Aug. 1966	S.N.E.
	16-30	−3.6	6.0	1.0	28.9	8		
	31-60					1		
	61-180					0		
7D	1-15	13.2	2.5	6.2	28.2	10	Aug. 1966	S.N.E.
	16-30	7.2	−14.9	12.0	46.5	8		
	31-60					1		
	61-180					0		
7E	1-15	−17.3	2.6	8.8	29.3	15	Aug. 1966	S.N.E.
	16-30	−8.8	−21.7	30.3	50.3	5		
	31-60					1		
	61-180					0		
7F	1-15	7.5	−20.0	4.5	36.0	39	Aug. 1966	S.N.E.
	16-30	7.5	−17.4	3.3	28.9	65		
	31-60	1.3	−26.2	15.6	48.0	14		
	61-180					1		
7G	1-15	−3.8	−19.1	3.0	32.2	37	Aug. 1966	S.N.E.
	16-30	−0.7	−15.9	3.1	29.9	50		
	31-60	−4.6	−24.6	12.8	48.0	14		
	61-180					1		
8	1-15					1	Sept.-Oct. 1966	L.I.
	16-30					0		
	31-60					0		
	61-180					0		
9A	1-15					2	July 1967	N.J.
	16-30	87.7	12.7	0.003	69.1	9		
	31-60	86.8	26.8	9.4	76.6	8		
	61-180					0		
9B	1-15	−18.4	−7.1	1.0	27.4	14	July 1967	N.J.
	16-30	13.1	−3.6	1.7	24.0	12		
	31-60	27.0	7.1	13.5	39.3	47		
	61-180					2		
10	1-15					0	Sept. 1967	L.I.
	16-30					0		
	31-60					2		
	61-180					0		
11A	1-15					0	July 1968	N.J.
	16-30					2		
	31-60					0		
	61-180		−4.0	0.008	22.8	9		
11B	1-15	5.8	22.4	4.2	32.8	13	July 1968	L.I.
	16-30	10.4	35.8	0.3	39.9	11		
	31-60					1		
	61-180					4		
12	1-15					4	July 1969	L.I.
	16-30					0		
	31-60					4		
	61-180					0		

See footnotes at end of table.

TABLE 2.—Continued

Release group	Time at liberty (days)	Mean miles N-S[1]	Mean miles E-W[2]	Determinant (x 10^4)	Mean distance	No. of fish	Release month	General release location
13	1-15					1	Aug.	S.N.E.
	16-30					1	1969	
	31-60					1		
	61-180					0		
14	1-15					0	Sept.	S.N.E.
	16-30					0	1969	
	31-60					0		
	61-180					0		
15	1-15					3	July	S.N.E.
	16-30	−1.7	−20.6	3.5	28.1	9	1970	
	31-60	−24.4	−6.8	0.5	28.2	5		
	61-180					0		
16	1-15	−13.1	−14.7	2.0	28.3	9	Aug.	S.N.E.
	16-30	−33.0	−11.6	69.6	67.7	7	1970	
	31-60					3		
	61-180					1		
17	1-15					0	1954-63	S.N.E.
	16-30					3		
	31-60	−.2	−10.4	222.9	57.1	5		
	61-180					0		

[1] Positive values signify northward movement. Negative values signify southward movement.
[2] Positive values signify eastward movement. Negative values signify westward movement.
[3] New Jersey.
[4] Long Island.
[5] Southern New England.

Jersey or that the intensity of the southern New England fishery was greater than that off New Jersey. While the latter may be true, there may be alternative interpretations and additional analysis is required. It is also suggested that analysis be undertaken for tags returned after the season of release.

MORTALITY ESTIMATION

The number of recoveries per year from releases by year, months within years, and various groupings of years, months, and release locations were employed to estimate the survival rates for young bluefin in the middle Atlantic bight of North America. The first analyses were run using only the data employed to form the basic groups as defined in the migration analysis, thus eliminating some releases which were substantially different with respect to their location and/or time of release than for most of the fish tagged. Although this reduced the numbers of returns used, it probably did not greatly affect the estimates of mortality rates.

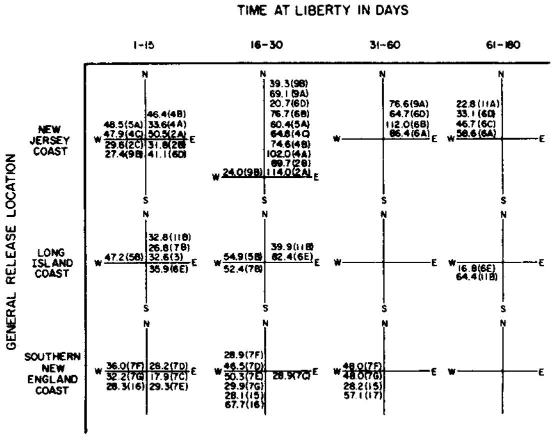

FIGURE 2.—Summary of mean distance and direction of migration of tagged bluefin tuna stratified by time at liberty and by general area of release. Distances are in nautical miles. Release group numbers are given in parentheses.

Method of Release

In all years since 1961, with the exception of 1963, tuna were captured for tagging by both sport and commercial gear (purse seine). In Table 3 the proportions of tagged fish returned were compared for the two methods of original capture. Five of the nine chi-square tests of the hypotheses of homogeneity indicate highly significant differences in the return percentages between the types of gear used to capture the tuna for tagging. When only the 5 yr with significantly different return rates for the types of gear, i.e., 1965, 1966, 1968, 1969, and 1970 are considered, higher return percentages were obtained for sport tagged fish in 4 of

TABLE 3.—Chi-square tests of equality of return probabilities between sport and commercial gear releases of tagged bluefin tuna in the northwestern Atlantic Ocean. Each test has 1 degree of freedom.

	Sport			Commercial			
Year	Release	Return	Return rate (%)	Release	Return	Return rate (%)	Chi-square value
1961	129	7	5.4	21	0	0	1.20
1962	52	4	7.7	25	0	0	2.03
1964	10	3	30.0	455	128	28.1	0.02
1965	43	17	39.5	1,629	244	15.0	19.18**
1966	187	84	44.9	3,772	1,094	29.0	21.60**
1967	14	3	21.4	614	183	29.8	0.46
1968	41	11	26.8	219	104	47.5	5.98*
1969	244	91	37.3	92	15	16.3	13.63**
1970	425	162	38.1	32	6	18.8	4.80*

**Significant at the 0.01 level.
*Significant at the 0.05 level.

the 5 yr. The data cannot be pooled over years to increase the numbers in individual cells in the chi-square tables since the recovery percentages and numbers tagged vary so greatly from year-to-year.

However, the Mantel-Haenszel test can be used to examine the data in toto (Snedecor and Cochran, 1967:255-256). The calculations resulted in a value of 8.89, which is highly significant. As is discussed in a later section, we think that most of the difference between return rates of sport and commercial tagged fish is caused by immediate tagging mortality. Immediate tagging mortality does not affect estimates of instantaneous total mortality. Therefore, we decided to use as much of the available data as possible and combined the data for estimates of mortality rates. Immediate tagging mortality does affect estimates of rates of exploitation and the components of mortality. Adjustments were made in an attempt to remove the effects of immediate tagging mortality and tag shedding.

Total Mortality Estimates - Chapman and Robson Method

Following the notation of Bayliff and Mobrand (1972), the number of tags remaining on bluefin at time t (years) is given by

$$N_t = N_0 \pi \rho e^{-Zt} \tag{1}$$

where N_t = Number of tags remaining on bluefin at time t
N_0 = number of released tags
π = portion of bluefin which remain alive after Type-I, immediate, tagging mortality takes place
ρ = portion of tags which are retained after Type-I shedding takes place
Z = instantaneous total losses on an annual basis.

$$Z = F + X$$

where F = instantaneous fishing mortality on an annual basis
X = instantaneous other losses on an annual basis.

$$X = M + G + L + E$$

where M = instantaneous natural mortality on an annual basis
G = instantaneous Type-II tagging mortality on an annual basis
L = instantaneous Type-II tag shedding on an annual basis
E = instantaneous emigration from fishing grounds on an annual basis.

The number of tags returned during a year is given by

$$n_t = \frac{FcN_t}{Z} (1 - e^{-Z}) \tag{2}$$

where n_t = number of tags returned between t and $t + 1$
c = portion of recovered tags that are returned.

Many assumptions are implicit in the above model. An exponential model is assumed to be correct. It is assumed that all instantaneous shedding, mortality, and emigration rates are constant—within years and among years. Since fishing was concentrated during the summer season, the assumption of constant fishing mortality is not valid. Also fishing effort probably varied over the years of the study. Available measures of fishing effort are thought to be inaccurate but were used in the last part of the analysis. The validity of the assumption of constant rate of emigration is not known, but tag returns suggest that transatlantic migrations are sporadic. This suggests that the assumption of constant emigration is not valid. While we recognize that some of our assumptions probably are invalid, it is our judgment that the effect of the violations on our results is not serious.

For the first part of the analysis we assumed that c, π, and ρ equal one. In the first analysis minimum variance unbiased estimates of the total annual survival rates were computed by the method developed by Chapman and Robson (1960) for the recovery data by year pooled in a variety of different ways over release categories. Confidence intervals were computed for s, the fraction surviving per year, and Z, the associated instantaneous mortality rate. A chi-square test was used to determine if the number of recaptures in the first recovery period is compatible with the survival pattern exhibited by the rest of the data, i.e., if the hypothesis of constant F and X is true. This test was applied sequentially, i.e., the second year was defined as the first recapture category and the test repeated until either all recapture years were eliminated or a survival rate was obtained from some subset of the data. For all releases the tagging year was taken as the first recapture category at the start of the analysis. The results of the survival rate computations are shown in Table 4 for the following data groupings:

1) Over all years
2) Over three adjacent release years
3) Individual years
4) July releases for three adjacent release years
5) Individual months within years
6) Release groups as defined in Table 1.

An obvious feature of this analysis is that in many of the recapture series, the numbers recovered the first year or two were higher than expected from the entire recapture series. This result is somewhat surprising because it might be expected that the number recaptured the first year would be underrepresented because of less exposure to the fishery. Three possible factors that could have caused the higher than expected recaptures in the first year or two after release are:

1) Tagged fish were released into an area where fishing activity was concentrated.
2) The proportion of the population migrating into the fishing area decreased as the fish became older; thus the availability of the tagged fish in the fishing area may have fallen off rapidly enough in later years to have caused a disproportionate number of recaptures in the first and second years after release.
3) The method of estimation assumes constant fishing mortality rates and other loss rates; variability in recovery effort could have caused the number of recaptures per year to deviate from a simple exponential decline with time.

Several aspects of the data emerge from Table 4. The estimates of survival rates are low but highly erratic; restricting the releases to finer time-location grids did not improve the stability of the estimates as might be expected. Since no time trend in survival is evident, pooling over years is a useful device to average out some of the fluctuations in the data. In one sense this is a substitute for use of recapture effort statistics and working with the number of recoveries per unit of recovery effort. The recaptures per year were combined over years using various weighting factors to develop adjusted numbers recaptured per year. None of these weighting schemes offered an improvement in the use of the simple unweighted average percent recapture per year at liberty for the years 1964-68. The proportion surviving per year as estimated from the simple average of the percentages was 0.188. This value is well within the confidence interval of the s-value of 0.231 estimated from the actual numbers pooled over all years. For the latter estimate, however, we did not use the recoveries made during the first 2 yr at liberty.

Inclusion of the first two recapture periods in the Chapman-Robson analysis, particularly for the last set of release groups which are fairly homogeneous, had the general effect of reducing the survival estimates. The numbers of recaptures

TABLE 4.—Survival rate estimates for various release group categories of tagged bluefin tuna.

Type of group[1]	Group	Recapture years used in s and Z computation	s(95% confidence interval)	Z(95% confidence interval)
1	All	[2](1, 2), 3, 4, 5	0.231 (.16, .30)	1.44 (1.14, 1.75)
[1]2	1963-65	-	Not constant (NC)	
	1964-66	[2](1, 2), 3, 4, 5	.174 (.09, .26)	1.70 (1.23, 2.16)
	1965-67	(1)[1], 2, 3, 4, 5	.118 (.10, .14)	2.13 (1.93, 2.32)
	1966-68	[2](1, 2), 3, 4, 5	.254 (.14, .37)	1.32 (0.88, 1.77)
	1967-69	[2](1), 2, 3, 4	.103 (.04, .17)	2.19 (1.60, 2.79)
	1968-70	-	NC	
3	1964	-	NC	
	1965	1, 2, 3, 4	.343 (.29, .39)	1.07 (.93, 1.21)
	1966	[2](1, 2), 3, 4, 5	.233 (.14, .32)	1.42 (1.03, 1.81)
	1967	(1)[1], 2, 3, 4	.323 (.24, .41)	1.11 (0.86, 1.37)
	1968	1, 2, 3	.243 (.17, .31)	1.39 (1.11, 1.68)
	1969		NC	
4	July 1963-65	1, 2, 3	.146 (.10, .19)	1.90 (1.61, 2.19)
	July 1964-66	[2](1, 2), 3, 4, 5	.400 (.20, .60)	0.87 (0.39, 1.34)
	July 1965-67	[2](1, 2), 3, 4, 5	.355 (.18, .53)	0.99 (0.51, 1.46)
	July 1966-68	[2](1, 2), 3, 4, 5	.367 (.19, .55)	0.96 (0.49, 1.42)
	July 1967-69	1, 2, 3, 4	.246 (.19, .30)	1.39 (1.17, 1.61)
	July 1968-70	-	NC	
[3]5	July 1964	1, 2	.128 (.06, .19)	2.00 (1.50, 2.49)
	Aug. 1964	-	NC	
	July 1965	1, 2, 3	.160 (.11, .21)	1.81 (1.48, 2.13)
	Aug. 1965	-	NC	
	July 1966	[2](1, 2), 3, 4, 5	.407 (.21, .60)	0.85 (0.40, 1.30)
	Aug. 1966	[2](1, 2), 3, 4, 5	.085 (.05, .12)	2.43 (2.08, 2.79)
	July 1967	1, 2, 3, 4	.244 (.18, .31)	1.39 (1.13, 1.66)
	Aug. 1967	-	NC	
	July 1968	1, 2, 3	.201 (.13, .27)	1.57 (1.23, 1.92)
	July 1969	-	NC	
	Aug. 1969	-	NC	
6	G1	1, 2, 3, 4	.582 (.45, .72)	0.53 (0.31, 0.75)
	G2A	1, 2	.189 (.06, .32)	1.57 (0.90, 2.24)
	G2B	1, 2	.065 (.00, .15)	2.45 (1.10, 3.79)
	G2C	1, 2	.160 (.01, .31)	1.68 (0.78, 2.58)
	3	-	NC	
	4A	1, 2, 3	.190 (.07, .31)	1.57 (0.95, 2.20)
	4B	1, 2, 3	.165 (.09, .24)	1.75 (1.30, 2.21)
	4C	1, 2	.083 (.00, .18)	2.27 (1.18, 3.36)
	5A	-	NC	
	5B	-	NC	
	5C	-	NC	
	6A	-	NC	
	6B	-	NC	
	6C	-	NC	
	6D	-	NC	
	6E	-	NC	
	7A	-	NC	
	7B	[2](1, 2), 3, 4, 5	.375 (.01, .74)	0.88 (0.04, 1.71)
	7C	[2](1), 2, 3, 4	.083 (.01, .16)	2.34 (1.49, 3.19)
	7D	-	NC	
	7E	-	NC	
	7F	-	NC	
	7G	-	NC	
	8	[2](1), 2, 3, 4	.125 (.00, .26)	1.88 (0.83, 2.94)
	9A	1, 2	.154 (.01, .30)	1.72 (0.82, 2.62)
	9B	1, 2, 3, 4	.205 (.13, .28)	1.55 (1.19, 1.92)
	10	-	NC	
	11A	1, 2, 3	.357 (.17, .54)	0.98 (0.48, 1.47)
	11B	1, 2, 3	.240 (.12, .36)	1.37 (0.87, 1.87)
	12	-	NC	
	13	-	NC	
	14	-	NC	

[1] Includes tags assigned by cruise number.

[2] Recapture years eliminated by chi-square test of full recruitment to tagged population are shown in parentheses.

[3] July results include tags assigned by cruise number.

dropped off so rapidly, however, after the first two recapture periods that little reliability can actually be placed on estimates using only data from the tail end of the time series.

This first examination of the recaptures by time at liberty was followed by a revised analysis of the July releases each year and all releases each year for 1964 through 1968. An attempt to include all tags in the analysis was made by assigning tags without recorded release dates to most likely release dates by means of the accompanying information, e.g., by cruise number. For the most part this revision produced minor changes in the estimates of total survival rates. Raw exploitation rates were estimated from the total number of recaptures per release using all data whether or not any information was available on date of recapture.

Estimates of Fishing and Other Losses

We used the following equations to estimate rates of exploitation, fishing, and other losses:

$$\hat{u}_T = R/N_0$$

where $\hat{u}_T$ = estimate of total exploitation of tagged bluefin tuna over n years
R = number of tag returns.

$$\hat{u}_1 = \hat{u}_T / \sum_{i=0}^{n} \hat{s}^i$$

where $\hat{s}$ = survival rate estimated from revised data by the Chapman-Robson method
$\hat{u}_1$ = estimate of single season exploitation of tagged bluefin tuna.

$$\hat{F} = \hat{u}\ (-\ln \hat{s})/(1 - \hat{s})$$

$$\hat{X} = \ln(\hat{s}) - \hat{F}$$

These estimates for July releases are shown in Part A of Table 5, and in Part B of the same table, estimates of the same set of parameters for all releases are given with the exception of the single season exploitation rates. We believe that distributing the releases during the entire fishing season, rather than restricting them to the first part of the season, July, makes it impossible to estimate a single season exploitation rate. It will be noted that the actual observed exploitation rates are high, especially in view of the fact that no corrections were made for either immediate tagging mortality, tag shedding, or nonreporting. The total recapture percentages range from 16% to 48%.

Lenarz et al. (1973) estimated that the rate of immediate tag shedding $(1 - \rho)$ for Atlantic bluefin tuna is 0.027 and that the instantaneous rate of tag shedding (L) is 0.310. Their estimates were used to correct our estimates of exploitation and mortality rates for shedding as follows:

TABLE 5.—Estimates of total survival, rate of exploitation, fishing mortality rate and total other loss rate of tagged bluefin tuna for July releases and for all releases by year of release.

Item	1964	1965	1966	1967	1968
Part A. July releases only:					
(N) Numbers released	397	951	2,047	448	226
(R) Numbers recovered	96	169	461	131	108
$\hat{s}$	0.128	0.160	0.407	0.244	0.201
$\hat{u}_1$	0.211	0.150	0.143	0.224	0.385
$\hat{u}_T$	0.242	0.178	0.225	0.292	0.478
$\hat{F}$	0.497	0.327	0.217	0.418	0.773
$\hat{X}$	1.558	1.506	0.697	0.999	0.838
$(\hat{F} + \hat{X})$	2.056	1.833	0.899	1.411	1.604
Part B. All releases by year:					
(N) Numbers released	465	1,672	3,959	628	260
(R) Numbers recovered	132	262	1,177	187	116
$\hat{s}$	0.196	0.343	0.233	0.323	0.243
$\hat{u}_T$	0.284	0.157	0.297	0.298	0.446
$\hat{F}$	0.463	0.168	0.433	0.337	0.631
$\hat{X}$	1.167	0.902	1.024	0.793	0.784
$(\hat{F} + \hat{X})$	1.630	1.070	1.457	1.130	1.415

$$(\hat{F} + \hat{X})^* = \hat{F} + \hat{X} - L$$

where $(\hat{F} + \hat{X})^*$ = estimate of total instantaneous apparent mortality corrected for tag shedding rate,

$$\hat{s}^* = e^{-(\hat{F} + \hat{X})^*}$$

where $\hat{s}^*$ = estimate of annual survival corrected for shedding rate,

$$\hat{u}_T^* = \hat{u}_T/\hat{\rho}$$

where $\hat{u}_T^*$ = estimate of total exploitation of tagged bluefin tuna corrected for immediate tag shedding,

$$\hat{u}_1^* = \hat{u}_1/\hat{\rho}$$

where $\hat{u}_1^*$ = estimate of seasonal exploitation corrected for immediate tag shedding,

$$\hat{F}^* = \hat{u}_1^* \; (-\ln s)/(1 - \hat{s})$$

where $\hat{F}^*$ = estimate of F corrected for immediate tag shedding,

$$\hat{X}^* = -\ln(\hat{s}^*) - \hat{F}^*$$

where $\hat{X}^*$ = estimate of X corrected for immediate tag shedding,

$$\hat{u}_1^{**} = \frac{\hat{F}^*}{\hat{F}^* + \hat{X}^*} \; (1 - \hat{s}^*)$$

where $\hat{u}_1^{**}$ = estimate of single season exploitation of tagged and untagged bluefin corrected for all tag shedding, and

$$\hat{u}_T^{**} = \hat{u}_1^{**} \sum_{i=0}^{n} (\hat{s}^*)^i$$

where $\hat{u}_T^{**}$ = estimate of total exploitation of tagged and untagged bluefin corrected for all tag shedding.

The estimates are shown in Table 6. Estimates of $\hat{X}^*$ (other losses) range from 0.366 to 1.234 (average = 0.792). The estimates of $\hat{X}^*$ are considerably higher than expected values of M (natural mortality) for bluefin. Bluefin are very long-lived fish and values of M of 0.1 to 0.2, if M is constant, would seem reasonable. Thus, there may be significant amounts of Type-I (immediate) and Type-II (long-term) tagging mortality, nonreporting, and/or apparent mortality caused by emigration.

TABLE 6.—Estimates of rates of exploitation and mortality of bluefin tuna corrected for tag shedding.

Item	1964	1965	1966	1967	1968
$(\hat{F} + \hat{X})^*$	1.746	1.523	0.589	1.101	1.294
$\hat{s}^*$	0.174	0.218	0.555	0.333	0.274
$\hat{u}_T^*$	0.249	0.183	0.231	0.300	0.491
$\hat{u}_1$	0.217	0.154	0.147	0.230	0.396
$\hat{F}^*$	0.512	0.336	0.223	0.429	0.795
$\hat{X}^*$	1.234	1.187	0.366	0.671	0.499
$\hat{u}_1^{**}$	0.242	0.172	0.168	0.260	0.446
$\hat{u}_T^{**}$	0.284	0.218	0.342	0.388	0.611

It seems plausible that some Type-I tagging mortality exists. In an earlier section it was noted that, more returns were obtained from sport gear releases than from commercial gear releases. Statistically significant, more returns were obtained from sport releases than commercial releases in 1965, 1966, 1969, and 1970. A possible cause of the difference in return rates could be that sport tagged bluefin are of different ages than commercially tagged bluefin. Bluefin of different ages could suffer different rates of tagging mortality and shedding, and could behave differently. Data have not been compiled in a fashion that allows examination of the age at release by the two gear types. We recommend that it be and assume for the present that age-dependent effects are negligible. The differences in return rates could also be caused by Type-I tagging mortality. Experienced taggers report that sport-gear-caught bluefin appear to be in better condition than those caught by commercial gear. Also, commercial gear tends to capture entire schools of bluefin while sport gear captures one bluefin at a time. Thus, bluefin released from sport gear tend to be released into the immediate area of a school of bluefin while bluefin released from commercial gear are not. There may be an advantage for bluefin to be in a school. Bayliff (1973) found that return rates of purse-seine-caught yellowfin tuna tagged immediately after a set is made can be more than two times higher than yellowfin tagged at a later time (Table 7). This evidence suggests that Type-I tagging mortality is very important

TABLE 7.—Releases, returns, and percentages of return of yellowfin tuna for IATTC[1] Cruise 1055, by time between commencement of tagging and release of fish (from Bayliff, 1973).

Time (min)	Number released	Number returned	% returned
0-10	1,920	277	14.4
10-20	1,972	195	9.9
20-30	1,563	86	5.5
30-40	1,145	47	4.1
40-50	934	44	4.7
>50	975	23	2.4
Total	8,509	672	7.9

[1] Inter-American Tropical Tuna Commission.

for purse-seine-caught yellowfin tuna. Bayliff[6] (pers. commun.) believes that bluefin tuna are more hardy than yellowfin tuna and thus expects that Type-I tagging mortality is lower for bluefin than for yellowfin.

Assuming that sport releases suffered insignificant amounts of Type-I tagging mortality and using the Mantel-Haenszel weighting procedure, the 1964-68 average Type-I tagging mortality for commercial tagged fish was 21%. During this period, 96% of the releases were commercial tagged fish. The average Type-I tagging mortality for all releases during 1964-68 was 20%.

The rates of exploitation and mortality were corrected for Type-I tagging mortality as follows:

$$\hat{u}_T^{***} = \hat{u}_T^{**}/\pi$$

where $\hat{u}_T^{***}$ = estimate of total exploitation corrected for shedding and Type-I tagging mortality,

$$\hat{u}_1^{***} = \hat{u}_1^{**}/\pi$$

where $\hat{u}_1^{***}$ = estimate of seasonal exploitation corrected for shedding and Type-I tagging mortality,

$$\hat{F}^{**} = \hat{u}_1^{***}(-\ln \hat{s}^*)/(1 - \hat{s}^*)$$

where $\hat{F}^{**}$ = estimate of F corrected for shedding and Type-I tagging mortality, and

$$\hat{X}^{**} = -\ln(\hat{s}^*) - \hat{F}^{**}$$

where $\hat{X}^{**}$ = estimate of X corrected for shedding and Type-I tagging mortality.

The estimates are shown in Table 8. The values of $\hat{X}^{**}$ range from 0.300 to 1.109 (average = 0.678) and are still higher than the expected rate of natural mortality for bluefin. The large difference between values for 1964-65 and the values for 1966-68 is worth noting. Food and Agriculture Organization (1972) reports that a relatively large number of bluefin tuna tagged in the northwest Atlantic in 1965 were recovered in the Bay of Biscay during the following year. This suggests that a large-scale transatlantic migration occurred between the 1965 and 1966 fishing seasons. Thus migration from the fishery is a plausible explanation for a portion of $\hat{X}^{**}$.

TABLE 8.—Estimates of rates of exploitation and mortality for northwest Atlantic bluefin tuna. The rates have been corrected for tag shedding and a hypothetical value of Type-I tagging mortality.

	1964	1965	1966	1967	1968	Average
u_T^{***}	0.355	0.272	0.428	0.465	0.764	[1]0.456
u_1^{***}	0.302	0.215	0.210	0.325	0.558	[1]0.327
F^{**}	0.639	0.419	0.278	0.536	0.995	0.573
X^{**}	1.110	1.104	0.311	0.564	0.300	0.678

[1] Calculated from averages of F^{**} and X^{**}.

Total Mortality Estimates – Regression Method

We next used available effort data for examining the effect of changes in effort on our estimates of mortality. The effort data were obtained from inquiries and logbooks of purse seiners that participated in the commercial fishery for bluefin in the northwestern Atlantic. The data have not been standardized by vessel class. We question the validity of the data as a measure of fishing effort, i.e., proportional to F, because a varying portion of the fleet relied heavily on airplane scouting. Conversion of the data to a standard unit of effort is worth a study in itself and we recommend that such a study be carried out.

In another attempt to estimate total mortality the natural logarithm of the number of returns per unit effort (Table 9), taking the number of boat-days recorded per season as a legitimate measure of effort, was regressed on time as measured to the center of each year following the release. An exact

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[6] Bayliff, W. H. Inter-Am. Trop. Tuna Comm., P. O. Box 271, La Jolla, CA 92037.

TABLE 9.—Returns of tagged bluefin tuna per boat-day by years at liberty.

Year	0	1	2	3	4
Part A. July releases only:					
1964	0.0902	0.0344			
1965	0.3538	0.0968	0.0374		
1966	0.9839	1.3957	0.1059	0.0526	0.0111
1967	0.5080	0.3647	0.0421	0.0037	
1968	1.0235	0.1579	0.0222		
Part B. All releases:					
1964	0.1100	0.0786			
1965	0.4029	0.3280	0.1925	0.0718	
1966	2.8495	3.1016	0.6235	0.0842	0.0222
1967	0.5241	0.7059	0.1684	0.0481	
1968	1.0353	0.2000	0.0333		

analytical formulation of this mortality model has two independent variates—cumulative time and cumulative effort. Not only are these two variables so highly correlated that it is virtually impossible to obtain useful estimates of the two regression coefficients, but also there are too few data points available for multiple regression analysis. The regression coefficient of the simple cumulative time regression is a crude measure of the total mortality rate. The fitted regression lines are shown in Figure 3 for July releases and in Figure 4 for all releases for each year. The values of the coefficients are given in Table 10.

With the exception of 1966, when the returns per boat-day increased during the year following release (and the data were eliminated from the regression), the logarithms of the recaptures per unit effort decrease in a linear fashion and it is clear the regressions provide reasonable fits to the data points. Seven of the eight estimated survival rates shown in Table 10 are lower than their counterparts in Table 5. Both of these analyses provide at best only crude approximations of the true survival rates; however, they do show fair general agreement. The catch-per-effort estimates indicate the loss rates are tending to increase with time.

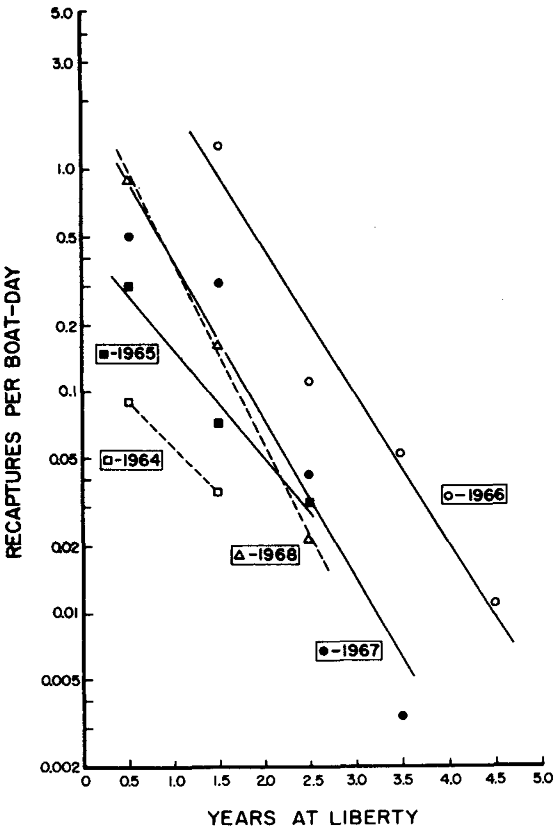

FIGURE 3.—Regression of recaptures per boat-day vs. time at liberty for July releases of tagged bluefin tuna.

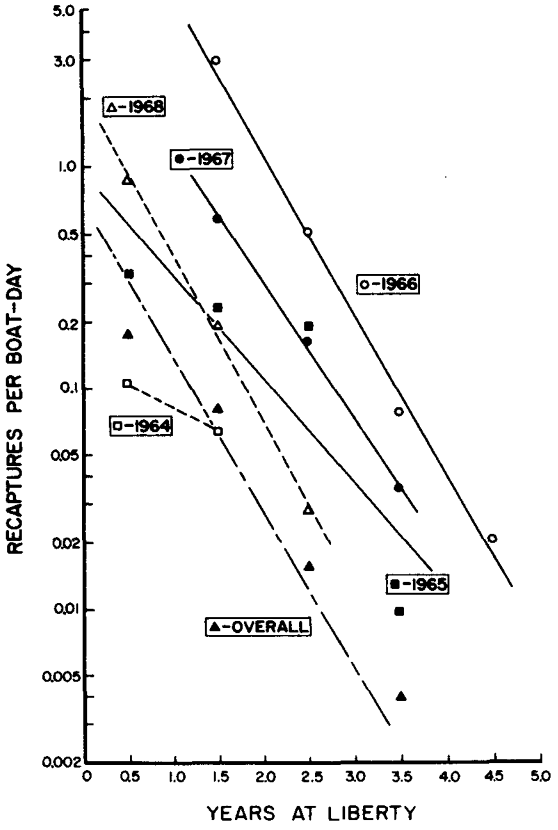

FIGURE 4.—Regression of recaptures per boat-day vs. time for all releases, by year, of tagged bluefin tuna.

TABLE 10.—Estimates of total survival rates of tagged bluefin tuna from regression analysis of return per unit-of-effort data.

	July releases only		All releases	
Year	Z	s	Z	s
1965	1.12	0.33	1.08	0.34
1966[1]	1.51	0.22	1.68	0.19
1967	1.70	0.18	1.41	0.24
1968	1.87	0.15	1.73	0.18
Average[2]	1.55	[3]0.21	1.48	[3]0.23

[1] Recaptures in release year not included in 1966 regression analysis.

[2] Regression estimates using average unweighted percentage returns for 1964-68 are: $Z = 1.67$ and $s = 0.19$. This estimate happens to be exactly the same as the estimate of $Z = 1.67 =$ (average time at liberty)^{1} where average time at liberty is 0.60 yr.

[3] Survival rate computed from average Z-value.

DISCUSSION

Exactly what these "survivals" are measuring is of prime interest. They are properly thought of as the results of disappearance rates which are composed of mortalities (F, M, and G), tag shedding, and changing migratory patterns with age. Apparently few of the older fish entered the surface fishery in the western north Atlantic during the period of the study and the decreasing proportion of the population that entered the fishery is a primary factor lowering the apparent survival. In 1966 when the fish tagged were significantly younger than in the other years—having an average age of 1.4 yr as opposed to average ages of at least a year older in other tagging years—the greatest return of tags occurred during the year after release. For these younger bluefin, a higher proportion returned to the fishing area the year after they were released than for the older tagged fish.

The exploitation rate on the tagged fish was exceedingly high when they were in the fishery. The high fishing mortality rates in Table 8 may underestimate the true rates for tagged bluefin; most of the various sources of error that may bias these estimates act to decrease the estimate of the fishing rate relative to its true value. However, it is known that bluefin available to the northwest Atlantic fisheries are not a closed population. Tagging studies have revealed transatlantic migrations to and from the fishery. Migration could also occur from the middle Atlantic. Thus it must still be determined whether the high exploitation rate applied to the population or just to the portion of the population that entered the fishery. Ricker (1958:35) describes the effects of tagging fish that are more vulnerable to fishing than other members of the population. "Again, if fish of certain sizes are more vulnerable than others, a Peterson tagging experiment is apt to overemphasize the vulnerable ones both in respect to tags put out and recaptures made; hence the estimate of rate of exploitation is too high and the population estimate is too low." Future analysis stratifying the data by age at release would help to answer some questions that arise because of the migratory behavior of bluefin. We suggest cohort analysis in the fashion of Bayliff (1971) as a productive method of analysis.

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