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Population dynamics and movements of skipjack tuna (*Katsuwonus pelamis*) in the Maldivian fishery: analysis of tagging data from an advection-diffusion-reaction model

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Abstract

An advection diffusion reaction model was used to estimate movement and tag attrition parameters from skipjack tuna tagging data off the Maldives. Two sets of data were available from the experiments carried out during two distinct periods: 1990–1991 and 1993–1995. The results of the analysis were compared with the previous analyses and discussed in relation to management of skipjack fisheries in the Maldives and in the Indian Ocean. The movements were found to be highly variable in space and time, and few consistent patterns were observed between the two data sets. Similarly, significantly different estimates of fishing and natural mortality rates were observed from the two data sets. These differences were found, in part, to be due to the uneven distribution of tag releases in both space and time. Estimates of movement and attrition rates show that emigration from the Maldivian fishery to the rest of the Indian Ocean's was small. The exploitation rate was found to be substantial, contributing about 30-40% of the total attrition in the fishery area. Such levels of localized exploitation may be maintained by steady immigration from outside of the Maldives, but more extensive tagging is required to be certain. The impact of tuna fisheries elsewhere in the Indian Ocean on the domestic Maldivian fishery cannot be determined until a comprehensive large-scale tagging program, including all the fisheries in the Indian Ocean, is completed.

Résumé

Dynamique des populations et déplacements du listao (*Katsuwonus pelamis*) dans la pêcherie des Maldives : analyse des données de marquage au moyen d'un modèle d'advection-diffusion-réaction. Un modèle d'advection-diffusion-réaction est utilisé pour évaluer les paramètres de déplacements et de pertes de poissons marqués, à partir des marquages de listao effectués au large des Maldives. Deux séries de données étaient disponibles, provenant des expériences menées lors de deux périodes distinctes 1990-1991 et 1993-1995. Les résultats de l'analyse sont comparés avec ceux des précédentes analyses, en relation avec la gestion des pêches du listao aux Maldives et dans l'océan Indien. Les déplacements observés sont très variables dans l'espace et dans le temps, et on observe peu de schémas identiques entre les deux séries de données. De manière similaire, les estimations des taux de mortalité naturelle et par pêche, pour ces deux séries de données, diffèrent significativement. Les différences observées sont dues, en partie, à la distribution irrégulière des marquages, à la fois dans l'espace et dans le temps. L'estimation des taux de déplacements et de pertes de poissons marqués montrent que l'émigration des listaos des Maldives vers le reste de l'océan Indien est faible. Le taux d'exploitation observé est élevé, contribuant à 30-40% de la perte totale des listaos dans la zone de pêche. De tels niveaux d'exploitation locale peuvent être maintenus par une immigration continue vers les Maldives, mais une augmentation des marquages est nécessaire pour en avoir la certitude. L'impact des autres pêcheries de l'océan Indien sur la pêcherie locale des Maldives ne pourra être déterminé qu'avec la réalisation d'un programme de marquage complet à grande échelle, impliquant toutes les pêcheries de l'océan Indien.

Keywords: Tagging data analysis; Maldives tuna fishery; Diffusion models; Skipjack tuna; Fishery management

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1. Introduction

Skipjack tuna, *Katsuwonus pelamis*, is the most important species caught in the Maldivian tuna fishery, comprising more than 80% of the total tuna landings in the Maldives (MPHRE, 1998). The fishery has been in existence for nearly a millennium (Adam et al., 1997) and despite the economic diversification in recent years, tuna fishing remains the main economic activity in the outer islands. In recent years, catches of skipjack tuna were of the order of 80,000 metric tons annually and in 1999 a record catch of 92,888 metric tons was reported (MOFAMR[1], unpublished data).

Skipjack tuna are also caught in increasing numbers by the industrial purse-seine fishery in the west and south of the Maldives, the neighboring Sri Lankan gillnet fishery to the northeast, and to a lesser extent in the pole-and-line fishery in the Laccadive archipelago to the north of the Maldives. In the purse-seine fishery, skipjack tuna are often caught in mixed schools of juvenile yellowfin (*Thunus albacares*) around drifting logs and, increasingly, around fish aggregating devices (FADs) specifically released for the purpose. The total Indian Ocean catch of skipjack, including the Maldives', during the latter-part of the 1990s was around 300×10^3 metric tons annually (Anon, 2000), the Maldivian catch representing 25–30%. With this increased and widespread fishing both in the Maldives and in the Indian Ocean, greater understanding of tuna movement dynamics and fishery interaction has become an important issue in the region (Anon, 1999).

Tagging experiments provide a valuable source of information on movement and stock dynamics. In the Indian Ocean, major tagging experiments on skipjack tuna have been conducted in the Maldivian fishery only, although some releases have been made to the central Indian Ocean by the National Research Institute of Far Seas Fisheries (NRIFSF), Japan (Yano, 1991). However, the recoveries from the NRIFSF releases have been few (32 in total). As part of the ongoing tuna research in the Maldives, two tagging experiments were conducted in the Maldives during 1990–1991 and between 1993 and 1995. The main target in both the programs was skipjack tuna. Description of these programs and the tagging methodology are given in Yesaki and Waheed (1992) and Anderson et al. (1996).

Analyses of the Maldivian tagging data have been carried out by Yesaki and Waheed (1992), Bertignac et al. (1994), Bertignac (1994), Anderson et al. (1996) and Adam (1999). While these analyses have highlighted important population dynamic features, a comprehensive integrated analysis of the data has not been done. Here we report the analysis of these data using the advection diffusion reaction model developed by Sibert et al. (1999). The results of the analysis are discussed in terms of fishery interaction and management of the resource.

Table 1
Summary of skipjack tuna release and recoveries (with known date of recapture) by tagging experiment and the combined data stratified by the calendar month. Nº days is the duration of tag-release period in the month.

Experiment/month	Nº days	Nº released	Nº recovered
Experiment 1: (1990)	49	8033	1407 (17.5%)
Experiment 2: (1993–1994)	56	6474	553 (8.5%)
Combined	105	14 507	1960 (13.5%)
January 1990	1	13	8 (61%)
January/February 1990	9	994	192 (19%)
March 1990	8	853	258 (30%)
May 1990	8	785	103 (13%)
June 1990	1	174	27 (15%)
September 1990	8	469	106 (23%)
October 1990	6	3069	555 (18%)
November 1990	8	1676	158 (9%)
September 1993	12	643	17 (3%)
January/February 1994	13	2082	126 (6%)
April 1994	13	1317	97 (7%)
August 1994	18	2432	313 (13%)

2. Materials and methods

2.1. Data

The data analyzed in this study consists of skipjack tuna released and recaptured in the Maldivian pole-and-line fishery only. The tagging was conducted from local fishing vessels from which skipjack were captured with pole-and-line gear using the live-bait technique (see Yesaki and Waheed [1992] and Anderson et al. [1996] for details). A total of 14,507 skipjack tuna, of size range 30–70 cm FL, were tagged and released from both the programs, and 1,960 (13.5%) were recovered (Table 1). Of the total recoveries, 97.3% were recovered from the Maldivian fishery. The 53 recoveries from the overseas fisheries and the 60 fish reported without date and/or location were not included in the analysis (see below).

The tagging database contains release and recovery positions identified to 0.5°-grid squares. The catch and effort data, however, are available only by atoll. Therefore, the effort data were transformed into 0.5°-grid format using estimates of the proportion of effort expended by any given atoll to the neighboring 0.5° grids (Adam, 1999). The resulting average monthly efforts by half-degree grids are given in Fig. 1c. For the purposes of this analysis, a release cohort is defined as all releases in a calendar month, stratified by release grid. Recoveries from each such cohort were stratified by month and by recovery grid. The total numbers released and recovered in each 0.5°-grid over the entire period are shown in Figs 1a, b.

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[1] Ministry of Fisheries, Agriculture and Marine Resources, Republic of Maldives.

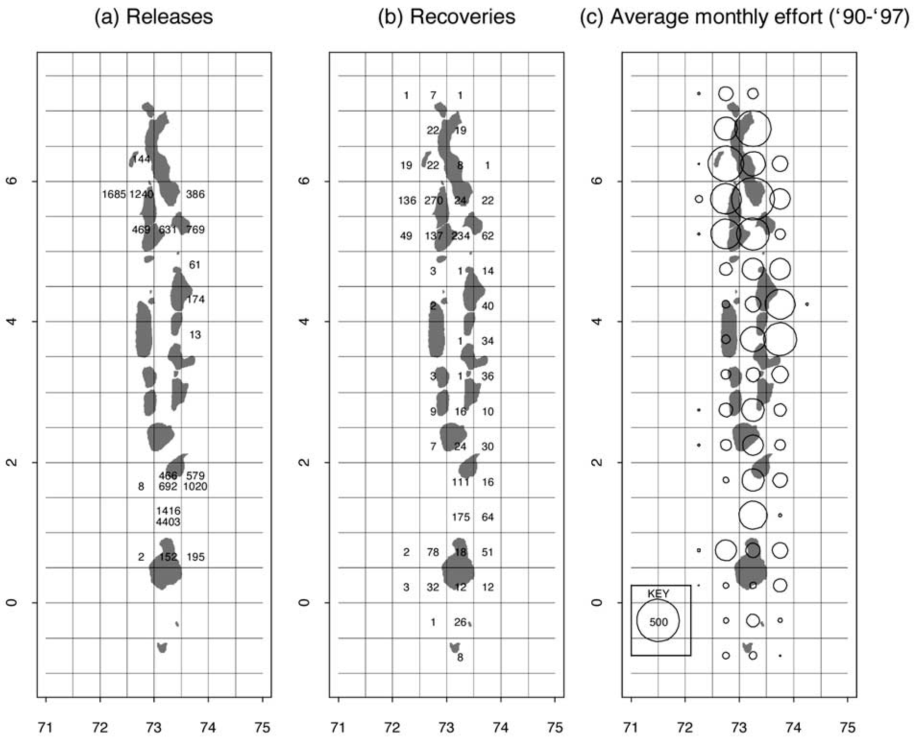

Fig. 1. Summary of tag releases **(a)**, recoveries **(b)**, and the average monthly fishing effort (days) during 1990–1997 **(c)**. The numbers in the upper half of the grids in **(a)** are the numbers released during the first experiment, and the numbers below during the second experiment. The diameters of the circles in **(c)** are proportional to the average monthly days fished in each grid as indicated. The shaded regions represent the atoll boundaries of the Maldives.

2.2. *The model*

The details of the advection diffusion model and its implementation to estimate the movement and attrition parameters are given in Bills and Sibert (1997) and Sibert et al. (1999). Only the pertinent features will be mentioned here. Simply put, the advection-diffusion-reaction model equation captures the horizontal movements and attrition of tagged fish (interchangeably used as tags herein after) over time in a defined geographic boundary. The basic advection-diffusion-reaction equation can be written as

$$\frac{\partial N}{\partial t} = \frac{\partial}{\partial x}\left(D\frac{\partial N}{\partial x}\right) + \frac{\partial}{\partial y}\left(D\frac{\partial N}{\partial y}\right) - \frac{\partial}{\partial x}(uN) - \frac{\partial}{\partial y}(vN) - ZN \qquad (1)$$

The equation separates the rate of the change in tag density at point x,y into diffusive (D) and advective (u and v) movements. u is the east-west component of directed movement (positive toward the east) and v is the north-south component (positive towards north). Initial conditions must be specified to solve the equation. Let $R_{rij}^{t_r}$ be he number of tagged fish released into the $0.5^{\circ} \times 0.5^{\circ}$ computational element (ij) in release month t_r where r is the index of the monthly tag release cohorts $r = 1,\ 2,\ldots\ r_{\max}$. For the 'combined' data set $r_{\max} = 33$. The initial conditions can be specified as

$$N_{rij}^{0} = \begin{cases} \beta R_{rij}^{t_r} & \text{tag release site} \\ 0 & \text{otherwise} \end{cases} \qquad (2)$$

where β is the proportion of tags effectively put out to sea or remain available in the tagging experiment. Explicitly, $\beta = (1–\alpha)(1–\Phi)$ where α is the proportion of tags that are lost immediately following release (= 0.0289), estimated independently from a double tagging experiment that was carried along with the second tagging experiment (Adam and Kirkwood, 2001). Φ is the proportion of recoveries that was not used in the analysis. This includes the proportion of recoveries with no usable information (= 0.0270) and the proportion of recoveries from the overseas fisheries (= 0.0305). These give β a value of 0.91, which was fixed in the analyses. All the recaptured tags were assumed to be reported (Adam, 1999).

The last term, Z, in the equation (1) is the total instantaneous tag attrition rate and includes components due to fishing mortality (F), natural mortality (M) and tag shedding (λ).

$$Z = M + F + \lambda\ . \qquad (3)$$

λ (=0.018 per month [pm]) have been estimated from a double tagging experiment (Adam and Kirkwood, 2001) that was conducted along with the second tagging experiment. The fishing mortality rate F was re-parameterized by relating it to the fishing effort, E_{ij} through proportionality constant, q, also known as the catchability coefficient.

$$F = q\tilde{E}^n_{ij} \tag{4}$$

Here $\tilde{E}^n_{ij}$ is the normalized fishing effort at computational grid (ij) in month n as given by $\tilde{E}^n_{ij} = E^n_{ij}/\bar{E}$, where E^n_{ij} is the observed fishing effort in month n and $\bar{E}$ is the fishing effort averaged over the whole area for the period 1990-1997, the duration of the tagging experiment. Since the mean of $\tilde{E}^n_{ij}$ is 1.0, q is equivalent to the average fishing mortality.

The movement parameters were re-parameterized into regions (space) and seasons (time) to avoid having to estimate the movement parameters at each grid point. In order to achieve this, assume a matrix R in the ij plane with region numbers in each element and a vector T with season numbers in each element. These two will then map the model domain into 'regions' and 'seasons' to estimate the parameters in the specified regions and seasons. Thus the model parameters are specified at each point by

$$u^n_{ij} = U_{[R_{ij}][T^n]} \tag{5}$$

$$v^n_{ij} = V_{[R_{ij}][T^n]}$$

$$D^n_{ij} = D_{[R_{ij}][T^n]}$$

Although the islands' and atolls' boundaries would affect skipjack movement in the area (e.g., Kleiber and Hampton, 1994), we were not able to deal with them in the model. Closing the atoll boundaries in the model would mean closing of the grids with atoll boundaries. This would require for both release and recovery data to be fictitiously shifted to adjacent grid cells. For the available resolution of the data (30 by 30 nautical miles), the amount of such shifting that is required would make the data questionable for this analysis. For these reasons, island and atoll boundaries were made 'invisible' to the model. In other words, movements were unrestricted across the atolls and islands. However, the boundaries at the continental landmasses (India and Sri Lanka) were closed.

The predicted number of tag returns in the time step n is given by

$$\hat{C}^n_{ij} = \frac{F}{Z}(1 - \exp(-Z\,\Delta t))\,N^n_{rij} \tag{6}$$

N^n_{rij} in (6) satisfies equation (1), which is solved numerically using the ADI algorithm with the 'upwind' finite difference approximations (Press et al., 1992; Sibert et al., 1999). The boundary conditions can be specified to be open or closed. Open boundaries are appropriate if the model domain represents a subset of the known habitat and there are reasons to believe that fish emigrate from the model domain. Closed boundaries are justified if the model domain includes the entire habitat, or if there are reasons to believe that fish do not move out of the model domain. Both these cases were tested in the analysis.

The parameters (U,V,D,q,M) were estimated by minimizing the negative log of a Poisson likelihood function that relates the observed (C^n_{ij}) and predicted ($\hat{C}^n_{ij}$ from equation (6)) recoveries.

$$L(U,V,D,q,M \mid C^n_{rij},\tilde{E}^n_{ij}) = \prod_{r}^{r_{\max}} \prod_{n=t_r}^{t_r+36} \prod_{ij} \left(\frac{e^{-\hat{C}^n_{rij}} \hat{C}^{n\;C^n_{rij}}_{rij}}{C^n_{rij}\,!} \right) \tag{7}$$

The minimum of -log L was found using a quasi-Newton numerical function minimizer, which in turn depends on the gradient of partial derivatives, computed using adjoint functions and portions of the ADModel Builder non-linear optimization package (Otter Research Ltd., 2000). Different starting values of the parameters were used to avoid local minima.

2.3. Approach of the analysis

The matrix R and the vector T (equation (5)) can be used to set various configurations of seasons and regions to describe alternative movement patterns. For the full model, we specified two regions and two seasons consistent with the idea that fishery dynamics is different in the north and south (Anderson, 1992) and during northeast and southwest monsoon seasons (Anderson et al., 1998). The division between the regions was set at 2.5ºN (Anderson, 1992), and various combinations of season starting months (September to December for the northeast and March to May for the southwest season) were tested to find the best starting month combination of the seasons. The model domain was constrained within the geographic region of 66ºE to 80ºE and 5ºS to 14.5ºN (Fig. 2). This choice was a compromise to allow unrestricted movement within the model domain and to exclude neighboring fisheries for which there are no readily available data. Various model configurations ($MqD_{(R,T)}V_{(R,T)}U_{(R,T)}$) can be represented by the numbers of parameters to estimate. The full model $MqD_{(2,2)}V_{(2,2)}U_{(2,2)}$ has 14 parameters to estimate. 'Nested' submodels of the full model can be specified by estimating common parameters for both regions or seasons (see Hilborn and Mangel, 1997). The four-model configuration and the number of parameters (p) to estimate are given in table 2. For brevity, they will be referred by model number in the text as given in the table.

Model 1 is nested with models 2 and 3 which are, in turn, nested with the full model 4, allowing the use of likelihood ratio tests (Brownlee, 1965) to determine best fitting model to the data.

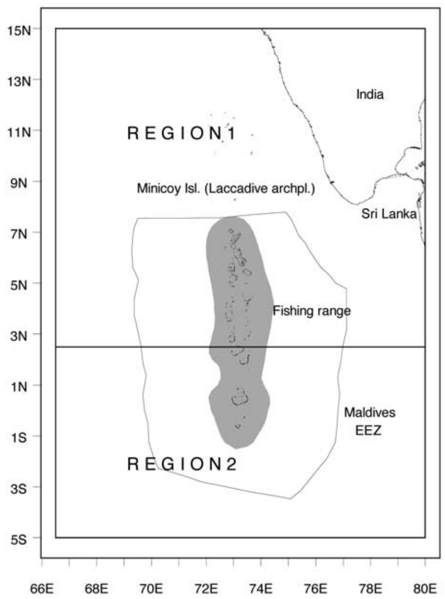

Fig. 2. Map of the central Indian Ocean showing the model area, the two regions, the approximate range of the Maldivian fishery (shaded), and the 200-mile Exclusive Economic Zone of the Maldives (thin line).

3. Results

Due to the time lag between the two tagging experiments, the combined data set was compared with the data from the two experiments analyzed separately. For all three data sets, model 4 was found to fit better than all submodels (Table 3). For the two-season models (2 and 4), the best starting month combination was found by fitting the model using all possible starting month combinations for the northeast and southwest monsoon seasons. For the first experiment data highest log *L* was obtained for April and September whereas in the second experiment it was for May and December. In the combined data set, the best combination was found to be May and October. These results indicate that skipjack movement varies between seasons and may also vary between years.

In order to see if there are significant differences between the parameter estimates between years, that is, between individual data sets in comparison to the combined analysis, a likelihood ratio test was performed on the aggregated model (first experiment + second experiment) versus the combined data set. The aggregated value of log *L* for model 4 was –2650.9 with 28 estimated parameters. The aggregated model compared with the model 4 of the combined data set ($\chi^2_{(14)} = 449.7$) was found to be highly significantly different ($P < 0.0001$), suggesting that movement and mortality were different during the periods covered by the two experiments. These differences are reflected in different numerical values of the parameters as well as in the starting months of the seasons.

For model 4, the predicted tag returns by calendar month since recovery show reasonably good agreement with the observed numbers (Fig. 3, right panels) for all the data sets. The tag attrition curves also show good agreement with observed and predicted tag recoveries over time, even for the short-term recovery periods (Fig. 3, left panels).

Table 4 shows the estimates of the advection and diffusion parameters for the three data sets. Also shown in Table 4 are the magnitudes of the resultant directed component (*V'*) of *U* and *V*. The values of *D* have been corrected for the 'numerical dispersion' introduced by the use of the upwind differencing (Sibert et al., 1999).

The estimates of *D* range from 500 to about 4000 square nautical miles per month (sq Nmi pm), and the estimates of *V'* range from 2 to 44 Nmi pm, except during the northeast monsoon season in the northern region where it was 134 Nmi)pm (Table 4). The relative degree of importance

Table 2
Model configurations and the numbers of parameters to estimate

Model #	Configuration	*P*
1	$MqD_{(1,1)}V_{(1,1)}U_{(1,1)}$	5
2	$MqD_{(2,1)}V_{(2,1)}U_{(2,1)}$	8
3	$MqD_{(1,2)}V_{(1,2)}U_{(1,2)}$	8
4	$MqD_{(2,2)}V_{(2,2)}U_{(2,2)}$	14

P = number of parameters

Table 3
Likelihood ratio tests for model selection. *p* indicates the number of estimated parameters; log *L* is the log likelihood; χ^2 is the likelihood ratio; *df* is the increase in number of parameters over the previous model; *P* is the significance level of the χ^2 (*df*) test. The numbers in the parenthesis beside the model number indicate the season starting months

Data	Model number	*p*	log *L*	Test	χ^2	*df*	*P*
Exp. 1	1	5	–1672.61				
	2 (4,9)	8	–1584.75	2 vs. 1	187.7	3	<0.0001
	3	8	–1595.81				
	4 (4, 9)	14	–1528.90	4 vs. 2	99.7	6	<0.0001
Exp. 2	1	5	–1216.40				
	2 (5, 12)	8	–1191.09				
	3	8	–1142.48	3 vs. 1	147.8	3	<0.0001
	4 (5, 12)	14	–1122.07	4 vs. 3	40.8	6	<0.0001
Combined	1	5	–3013.65				
	2 (5, 10)	8	–2982.05	2 vs. 1	243.2	3	<0.0001
	3	8	–3053.30				
	4 (5, 10)	14	–2875.83	4 vs. 2	212.4	6	<0.0001

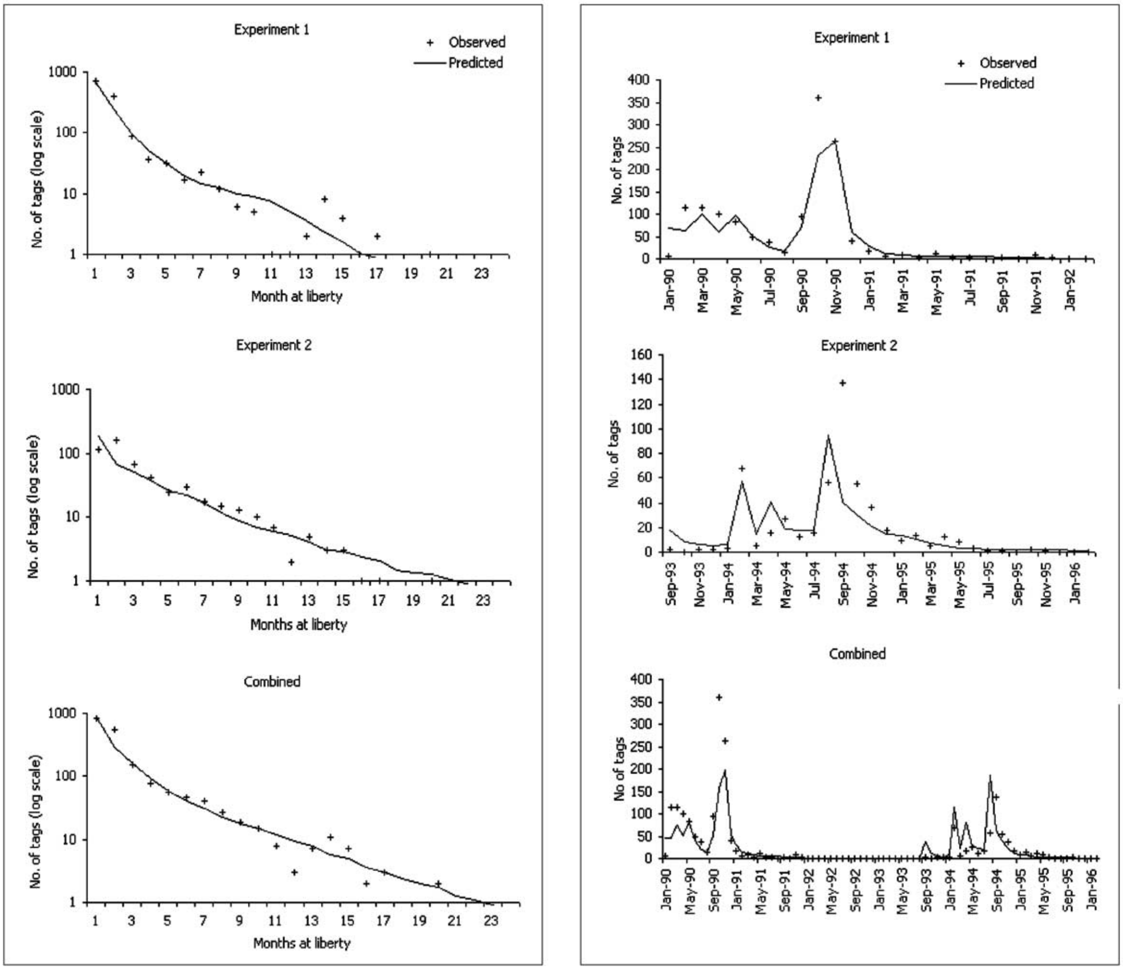

Fig. 3. Observed (crosses) and the predicted number of recaptures (continuous lines) by calendar months since releases (right panels) and observed and predicted number of tags over the life of the cohorts summed over the model area (left panels) for the two experiments and the combined data set.

of advective and diffusive movement can be estimated from the Peclet number (Sibert et al., 1999). This is the ratio of advection over diffusion multiplied by the characteristic movement length *l* which, in this case has been taken as the model resolution (i.e., 30 Nmi). Values greater than unity indicate that directed movements are more important than the diffusive movement over a range of 30 Nmi.

The magnitudes of *V'* and *D* are shown in graphical form in Fig. 4. In the first experiment, diffusive movement dominates over advection, suggesting that fish did not prefer

Table 4
Model 4 estimates of advection and diffusion parameters and the Peclet numbers (see text). The units *V*, *U* and *V'* (the magnitude of the resultant directed movement component of *U* and *V*) are in nautical miles per month; D is in square nautical miles per month. Parentheses adjacent to to the season number indicate the starting month of the season; southwest (SW) and northeast (NE). Estimates of *D* are corrected for numerical dispersion as discussed in the text

Data set	Season	Region	*V*	*U*	*D*	*V'*	Peclet number
Exp. 1	1 (4, SW)	1 (north)	–13.14	–3.42	1742	13.58	0.23
	1 (4, SW)	2 (south)	1.12	13.47	2210	13.52	0.18
	2 (9, NE)	1 (north)	1.90	–24.09	574	24.16	1.26
	2 (9, NE)	2 (south)	–36.96	–10.25	2348	38.35	0.45
Exp. 2	1 (5, SW)	1 (north)	132.71	16.90	2244	133.78	1.77
	1 (5, SW)	2 (south)	1.57	0.02	795	1.57	0.06
	2 (12, NE)	1 (north)	13.05	48.67	926	50.39	1.58
	2 (12, NE)	2 (south)	–3.90	–43.46	1512	43.64	0.86
Combined	1 (5, SW)	1 (north)	17.42	–25.19	4338	30.63	0.17
	1 (5, SW)	2 (south)	3.64	4.26	1141	5.60	0.11
	2 (10, NE)	1 (north)	–4.37	–19.02	534	19.51	1.07
	2 (10, NE)	2 (south)	–24.87	–20.00	2667	31.92	0.28

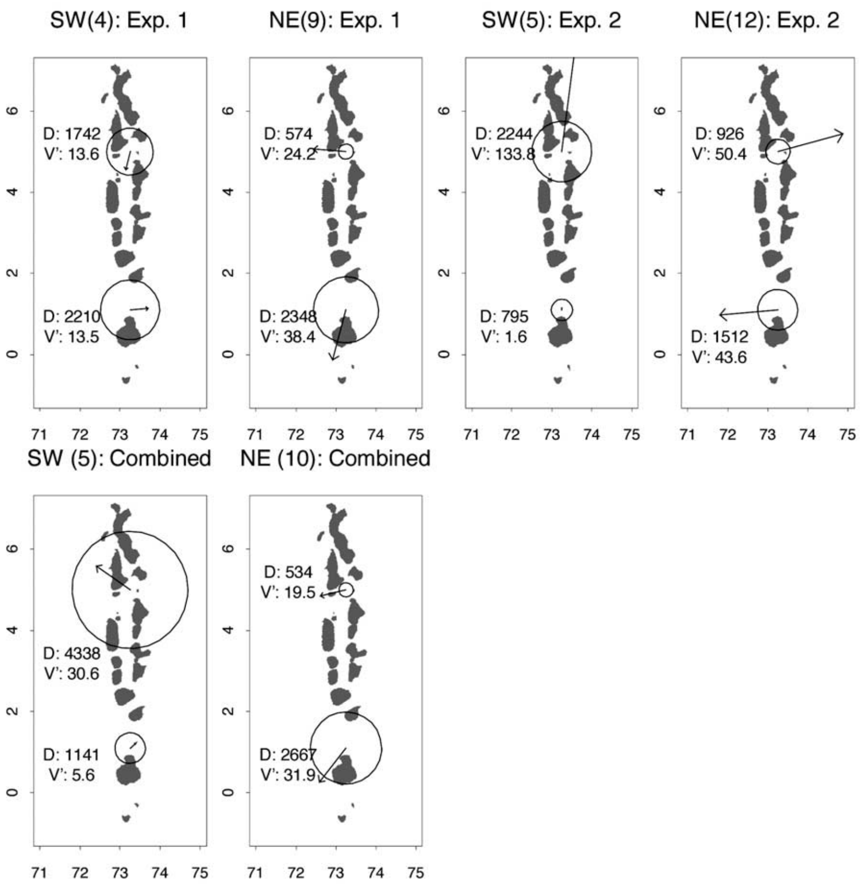

Fig. 4. Model four estimates of diffusive (circles) and adjective (directed arrows) movements by regions (north and south) and seasons (southwest, SW and northeast, NE, monsoons, starting calendar month in parentheses). The unit of *D* is sq Nmi pm and *V'* in Nmi pm. Note *D* and *V'* are not drawn to scale in relation to the geographic map of the Maldives, represented here by atoll boundaries.

any particular direction over the movement length considered. For the northeast monsoon season in the north, however, advective component was dominant. Unlike the first experiment, the second experiment data showed that advective movements were more important than diffusion with the exception in the southern region during the southwest monsoon (Fig. 4). During the southwest monsoon season, in the south, the directed movements are towards north and northeast in all three data sets (Fig. 4), but the dominant movement in all these three cases was diffusion (Table 4).

Table 5 shows the estimates of *M* and *q* for the data sets along with their standard deviations. The estimate of *M* from the first experiment data was 0.13 per month and for the second experiment it was very low at 0.008 pm. The estimate from the combined data set was 0.08 pm, a value in between the first and the second experiment's estimate. Estimates of *q* range from 0.02 to 0.07 pm per grid area. Since the fishing effort was normalized, *q* is also a estimate of average fishing mortality rate (see equation (4)). The lower estimates of *M* and *q* from the second experiment data appears to be due to the more persistent nature of the fish indicated by the more gradual and extended attrition curve compared with the first experiment data (Fig. 3).

A useful statistic often calculated from the estimates of the attrition rates is the harvest ratio (HR). This is the ratio of fishing mortality rate to the total attrition rate, a measure of fishing impact on the population.

$$HR = \frac{F}{\lambda + F + M} \tag{8}$$

Kleiber et al. (1987) suggested that for skipjack like species a value of 0.5 would be a reasonable reference point

Table 5

Estimates of natural mortality rate, *M* (per month), and catchability coefficient, *q* (per month per grid area), along with their ± standard deviation. The harvest ratio, HR, is the fraction of fishing mortality expressed as total attrition. The tag shedding rate, λ (per month), is from Adam and Kirkwood (2001).

Parameter	Experiment 1	Experiment 2	Combined
λ	0.018 ± 0.013	0.018 ± 0.013	0.018 ± 0.013
M	0.131 ± 0.009	0.008 ± 0.003	0.079 ± 0.006
$q\ (\equiv F)$	0.069 ± 0.003	0.021 ± 0.0004	0.046 ± 0.001
HR	0.32	0.44	0.32

for a fishery approaching full exploitation. The values ranging from 0.32 to 0.44 (Table 5) suggest that the fishery was approaching full exploitation.

4. Discussion

The overall picture of movement and attrition emerging from this integrated analysis is that details of skipjack tuna dynamics off the Maldives are more variable in space and time than have shown in previous analyses. Based on the calendar months of overseas recoveries with respect to the release season in the Maldivian fishery, Yeasaki and Waheed (1992) and Anderson et al. (1996) observed that skipjack in the Maldives tend to move westward during the northeast monsoon season, and eastward during the southwest monsoon, in phase with the prevailing surface currents in the area. A more detailed analysis by Adam (1999), however, showed that they were more complex and such simple east-west patterns were not significant in the data. Adam (1999) also showed that there were considerable differences in the east-west orientations between the northern and southern regions. Although our results would not be strictly comparable with Adam's (1999) analysis, this view is supported by our results. It should be noted that we excluded the data from the overseas recoveries and so the only east-west movement would be from within the narrow range of the local fishery (see Fig. 2). It could be that skipjack do indeed behave differently when close to the island chains and FADs (e.g., Kleiber and Hampton, 1994) but respond to such monsoon-related east-west orientation outside the range of the local fishery. Yesaki and Waheed's (1992) and Anderson et al.'s (1996) observation of east-west movement were indeed based on the recoveries from the overseas fisheries.

There was a strong signal of the northward movement during the southwest monsoon in the second set of experiment data in the northern region. Closer examination of the data revealed that this was due to the persistent northward movement of the release cohort during August 1994. Similar northward movement was not observed in the first experiment data or indeed for runs of the model even for a selection of cohorts released only to the south during the southwest monsoon (May and December).

The estimate of $M = 0.131$ pm from the first experiment data and $M = 0.079$ pm in the combined data set are similar to the estimate made by Sibert et al. (1999) for the skipjack tuna in the Pacific Ocean from tagging conducted around 1980 using the same method of analysis. Hampton (2000) estimated a size-dependent M of skipjack tuna in the Pacific Ocean from tagging conducted 10 years later. Hampton's (2000) estimates of natural mortality rates were 0.13, 0.10 and 0.17 pm, for the three size-class 41–50, 51–60 and 61–70 cm respectively. In the first Maldivian tagging experiment, more than 95% fish were in the size range 41–70 cm at recapture, and our estimate of about 0.1 pm is consistent with Hampton's (2000) estimate.

The estimate of attrition components, especially M in the second tagging experiment, appear to be anomalously low, but there was clear signal in the data. Part of the reason for this observation is the more gradual and extended attrition curve estimated for the second experiment data. The predicted recoveries in the first experiment indicate there was no recoveries after the 16th month-at-liberty whereas in the second experiment the predicted recoveries extended until the 21st month-at-liberty, although in both the experiments, recoveries were observed until the 20th month-at-liberty (Fig. 3). In the first experiment, 82% of the recoveries were made within the first 2 months of release compared with only 53% in the second tagging experiment, enabling a larger proportion to remain vulnerable in the subsequent months for an extended period in the second experiment. This resulted in a sharp decline in the overall recovery rate in the second experiment compared with the first (8.5% vs. 17.5%), thus estimating a lower overall attrition rate.

The geographical distribution of the releases may also account for both the lower recapture and attrition rates. Most of the releases in the second tagging experiment were released to one particular 0.5° grid, a seamount locally known as *Sathoraha*, the most popular fishing ground in the south. Fishing from *Sathoraha* requires about 5–6 hours of steaming and since fishing is conducted on daytrips it is not economical for the fishermen to go there unless fishing is good and the weather is fine. These factors would contribute to a lower overall fishing mortality rate for the releases made there. The releases in the first tagging experiment were to the north, to a wider area and much closer to the islands where the fishing effort was high (Fig. 1). This resulted in a higher overall fishing mortality rate compared with the second experiment.

One of the main objectives of the tagging experiments in the Maldives was to understand the fishery interaction and its effects on the management actions taken locally. Assuming that all the recoveries from the overseas fisheries were reported, the 53 recoveries represent only a small fraction that was vulnerable in the overseas fisheries. Some idea of emigration may be gained from the estimates obtained by keeping the model boundaries open compared with estimates obtained by keeping them closed. For the case of the open boundaries, any fish leaving the area is considered to be an emigrant. The parameter estimates obtained with open boundaries were very similar to those obtained with closed boundaries for all data sets, justifying our assumption of the closed boundary model. For the first experiment, the estimates of movement parameters were very similar, with virtually no difference in M and q, and the value of log Ls were almost the same (Table 6).

Using dispersion rates calculated from various subsets of data (releases in the north, south, and releases to the 0.5° grids with no land) from Jones' (1976) method, Adam (1999) showed that less than 15% of tagged fish would

Table 6
Likelihood value and parameter estimates for the first experiment data for open and closed boundary conditions. The first subscript in the parameters refers to the region followed by season

Parameter	Open	Closed
$D_{1,1}$	1493.4	1469.3
$D_{2,1}$	184.5	184.2
$D_{1,2}$	1991.6	2123.6
$D_{2,2}$	1730.1	1788.2
M	0.150	0.150
q	0.069	0.069
$U_{1,1}$	–0.114	–0.091
$V_{1,1}$	–0.438	–0.456
$U_{2,1}$	–0.803	–0.802
$V_{2,1}$	0.063	0.072
$U_{1,2}$	0.449	0.169
$V_{1,2}$	0.037	0.047
$U_{2,2}$	–0.342	–0.093
$V_{2,2}$	–1.232	–1.256
log L	–1528.9	–1529.5

survive to reach the 200-mile Exclusive Economic Zone boundary. The result obtained here supports the view that emigration to the overseas fisheries is low.

An alternative approach to estimate their persistence in the fishery is to compute their ‘half-life’ (Skellam, 1951; Jones, 1959). Half-life is the time required for half the population to disappear from the specified area and time. In simple situations, the half-life can be computed analytically from the movements and mortality parameters (e.g., Holland et al., 1999; Sibert et al., 2000). In our model, the movement parameters vary in time and space. Therefore simple analytical approaches are inappropriate. We estimate the half-life numerically using the numerical solution to equation (1). By setting the initial tag density to one tag per computational element, the time at which tag density in each square decreased to less than 0.5 was noted. The half-life was estimated by linear interpolation between this time and the previous time step. Seasonal variability in movement requires that the simulation be run for each of the 12 possible starting months in a year. The average half-life was computed by averaging the estimates in each grid over the 12 possible starting months. The average half-life for a region can be calculated by averaging the average estimate over any given area. The estimates of half-life obtained using the estimates of the attrition and movement parameters for the first and the second experiment data are given in Table 7.

The result show that within the range of the fishery, half-lives were less than a month. The half-life was higher for the second experiment data, supporting the earlier interpretation of the results. As expected, the average half-life increased when the fish move outside the range of the fishery, i.e., to areas of low fishing mortality. The effect on the half-life in the absence of fishing can be shown by setting q equal to zero in the model. When this was done, the estimate of half-life within the fishery area increased by an order of magnitude. This suggests that fishing mortality is relatively high and the current catches are maintained by high immigration.

Table 7
Half-life of skipjack tuna estimated for various areas in the model region using the estimates of parameters from model 4

		Half-life (months)	
Data set	Region	with q	q set to 0
Experiment 1	Whole model area	3.6	4.3
	Region 1 (north)	3.5	4.0
	Region 2 (south)	3.8	4.7
	Fishery range	0.6	3.2
Experiment 2	Whole model area	6.4	8.3
	Region 1 (north)	5.6	6.7
	Region 2 (south)	7.3	10.3
	Fishery range	0.9	7.6

A tagging experiment is a ‘snapshot’ of the fishery during the time of the experiment. The Maldivian fishery has undergone noticeable changes since the mid-1990s. The last few years have seen a trend in larger vessels capable of steaming farther offshore into areas that were not previously exploited. These vessels are capable of catching more fish per unit of fishing effort (1 day) compared with the relatively smaller vessels prevalent during early 1990s, during the time of the experiments. Together with improvements in bait fishing and holding techniques, this increases the effective fishing effort and the range of exploitation. The relatively high overall harvest ratio and the estimates of relatively large proportion of half-life on the fishing grounds attributable to fishing mortality suggest that the Maldivian skipjack fishery was approaching high exploitation levels in the mid-1990s. The potential impact of further increases in local fishing mortality should be evaluated very carefully.

The Maldives tagging studies have provided valuable estimates of local fishing mortality and suggest low emigration rates from the Maldives to other areas. However, local tagging experiments restricted to the Maldives archipelago cannot provide critical information on immigration rates from other areas into the Maldivian fishery. In the absence of such information, it is difficult estimate the impact of the large-scale tuna fisheries in the Indian Ocean on the Maldivian domestic fishery. Low levels of immigration would suggest a more discrete stock, and increases in local catch rates would lead only to local depletion. On the other hand, if immigration rates were found to be higher, the Maldivian domestic fishery would depend more heavily on stocks in the rest of the Indian Ocean. In this case, the effect on abundance of local increases in exploitation rate by the domestic fishery would be minimal, but the productivity of the domestic fishery could potentially be impacted by large scale fisheries in other areas. Such impacts already appear to be observable in the catch-effort data. For instance, Adam and Anderson (1998) and Adam (1999) showed negative correlation between the total Indian Ocean skipjack catch and the Maldives' since the inception of the purse seine fishery in the mid-1980s.

A coordinated tagging effort both within the Maldives and in other areas of the Indian Ocean is necessary to address issues of tuna immigration and interaction between the Indian Ocean fisheries and the Maldives domestic fishery in a consistent manner (e.g., Anganuzzi, 1996). The Indian Ocean Tuna Commission has planned a large-scale tagging program starting in 2002 that includes skipjack tuna (IOTC, 2001). The Maldives with their experience and expertise in conducting successful tagging programs can play an important role in creating a well-integrated tagging program in the Indian Ocean. The data generated from such a tagging program would enable the issue of immigration to the Maldivian fishery to be rigorously addressed. Given the developments currently taking place in the Maldivian fishery and in the Indian Ocean tuna fishery in general, it is prudent that policies intended to manage local fisheries include considerations of immigration and fishery interaction.

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