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# MORTALITY ESTIMATES FOR JUVENILE DUSKY SHARKS *CARCHARHINUS OBSCURUS* IN SOUTH AFRICA USING MARK-RECAPTURE DATA

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A maximum likelihood model is developed, using mark-recapture data, to estimate total and fishing mortality rates for the dusky shark *Carcharhinus obscurus* in South Africa. The model accounts for tag-shedding, non-reporting of recaptured tags, the multiple release and single recapture nature of the study and the usage of two different types of tags (sheep-ear and ORI tags). Tag shedding was quantified as tags washed up on beaches and fouling of tags in protective shark nets, which amounted to 17% of all tags recovered between 1986 and 1993. The ORI tag had a higher tag-shedding rate than the sheep-ear tag. Assuming a 75% reporting rate for recaptured dusky sharks, an instantaneous fishing mortality rate was estimated to be $0.27 \cdot \text{year}^{-1}$, with a 95% confidence level ranging between 0.19 and $0.44 \cdot \text{year}^{-1}$.

In KwaZulu-Natal, elasmobranch research was initiated by the Oceanographic Research Institute (ORI) in 1959, with various studies investigating the taxonomy, distribution and biology of sharks being undertaken (Bass *et al*. 1973). In 1964, a tagging programme aimed at gaining insight into the growth and migrations of sharks was initiated (Davies and Joubert 1966). In that study, 726 dusky sharks *Carcharhinus obscurus,* most of which were <1 m long, were tagged and released off Durban. Of that total, 322 (44%) were recaptured. Davies and Joubert (1966) speculated that the high rate of recapture was partially as a result of a reward system for returned tags, which encouraged anglers to target dusky sharks, and partially because many sharks were recaptured before they were able to move away from the area of tagging (mean time-at-liberty = 26 days). Bass *et al.* (1973) continued the study by tagging and releasing a further 2 316 dusky sharks, of which 97 (4.2%) were recaptured. Tag returns from that study showed a distinct geographical segregation of dusky sharks in terms of sex and size, and the southern KwaZulu-Natal coast was identified as a primary nursery area for juvenile dusky sharks.

Van der Elst (1979) investigated claims from recreational anglers that a proliferation of small sharks (including dusky sharks) in the nearshore zone was having a negative effect on the teleost composition of their catches. The analysis from that study showed an increase in the number of small sharks caught during shore-angling competitions, with a simultaneous reduction in the number of teleosts caught per outing.

In 1984, ORI initiated another tagging programme (with commercial and conservationist sponsorship) to obtain fisheries-related parameters such as growth and mortality of finfish, sharks and batoids. Recreational anglers participate in this tagging programme and details are outlined in Van der Elst (1990). From 1986 to 1993, a total of 3 629 dusky sharks was marked and released along the KwaZulu-Natal and Eastern Cape coasts. Sharks were mainly marked by members of the tagging programme, but tag recoveries were reported by personnel servicing shark nets (Cliff and Dudley 1992), anglers and the general public. In all, 345 (9.5%) tags were recovered. These included tags that were washed up on the shore and those recovered from shark nets. Recaptures of tagged sharks alone amounted to 7.7%, which is nearly double the recapture rate reported by Bass *et al.* (1973).

In the current study, total and fishing mortality rates for the dusky shark are estimated from information based on the tagging programme mark-recapture data. A model that considers the nature of multiple releases (marking of sharks found throughout the study) and single recapture of dusky sharks (recaptured tagged sharks are usually not again released) is developed. Aspects such as the fouling of tags on shark gill nets, wash-up of tags on the shore, non-reporting of recaptures and the fact that two different types of tags were used in the study are incorporated into the model. These mortality estimates are required for assessment of the status of the stock of dusky sharks.

## MATERIAL AND METHODS

### Mortality model

The model developed is similar to Hilborn's (1990) general movement model. The model estimates rates of fishing and total mortality from mark-recapture

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Table I: Tagging programme mark-recapture data for *Carcharhinus obscurus* tagged off the Eastern Cape and KwaZulu-Natal coasts during the period 1986–1993

| Year | Number tagged | Sheep-ear tags | | | Number tagged | ORI tags | | |
|---|---|---|---|---|---|---|---|---|
| | | Recoveries | | | | Recoveries | | |
| | | Wash-ups + net fouling | Recaptures | Total | | Wash-ups + net fouling | Recaptures | Total |
| 1986 | 470 | 5 | 41 | 47* | 0 | 0 | 0 | 0 |
| 1987 | 481 | 6 | 38 | 45* | 0 | 0 | 0 | 0 |
| 1988 | 299 | 4 | 55 | 59 | 0 | 0 | 0 | 0 |
| 1989 | 246 | 2 | 22 | 25† | 55 | 2 | 0 | 2 |
| 1990 | 85 | 0 | 12 | 12 | 253 | 12 | 18 | 30 |
| 1991 | 66 | 3 | 3 | 6 | 299 | 2 | 18 | 20 |
| 1992 | 27 | 0 | 3 | 3 | 517 | 13 | 25 | 38 |
| 1993 | 73 | 1 | 9 | 10 | 758 | 10 | 36 | 48*† |

* Includes one tag found in the stomach of a predatory shark
† Includes one tag from a dead specimen

data. Initially, the model is developed for a single tag type and is then extended to include another tag type. Each model has three main components:

(i) a population dynamics component that describes how tagged individuals survive over time;
(ii) an observation component that describes the capture of marked individuals; and
(iii) a component specifying the likelihood of recoveries.

Mark-recapture data for *C. obscurus* between 1986 and 1993 are summarized in Table I. The model is based on the following assumptions and equations. It is assumed that dusky sharks are marked in the middle of each year, whereas recaptures occur at the end of each year. Assuming that $N_t$ dusky sharks (which were marked in the previous time interval) survive to the end of time $t$, and if a further $T$ animals are marked and released during time interval ($t$+1), then the number of sharks surviving to the end of this interval can be expressed as

$$N_{t+1} = N_t\,\mathrm{e}^{-Z} + T_{t+1}\,\mathrm{e}^{-Z/2} \qquad , \qquad (1)$$

where $Z$ is the instantaneous total loss rate for dusky sharks and is assumed to be constant for the study period. Equation 1 describes the number of marked dusky sharks alive at the end of time $t$+1 as dependent on those surviving from the previous time interval and the number of newly tagged sharks. In this model, tag-induced mortality is considered negligible. In a tank study of marked *C. obscurus*, Davies and Joubert (1966) reported that no dusky sharks suffered mortality that could be attributed to the presence of a tag. From 1986 to 1993, only five tags were recovered that could possibly be considered as tag-induced mortalities (Table I).

The following equations model the recapture of marked dusky sharks (observation model). Using the Baranov catch equation (Ricker 1975), the number of marked dusky sharks recaught ($r$) at the end of time interval $t$ is expressed as

$$r_t = N_{t-1}\frac{F}{Z}(1-\mathrm{e}^{-Z}) + T_t\frac{F}{Z}(1-\mathrm{e}^{-Z/2}) \qquad , \qquad (2)$$

where $F$ is the instantaneous rate of fishing mortality and is assumed to be constant for the study period. However, not all recaptures are reported. A constant fraction ß is assumed to be reported, therefore,

$$R_t = \beta r_t \qquad , \qquad (3)$$

where $R$ is the reported number of recaptures. Similarly, it can be shown that the number of wash-ups ($W$), which includes tags that have been washed ashore as well as those fouled in the shark nets, in interval $t$ can be expressed as

$$W_t = N_{t-1}\frac{\beta K}{Z}(1-\mathrm{e}^{-Z}) + T_t\frac{\beta K}{Z}(1-\mathrm{e}^{-Z/2}) \qquad , \qquad (4)$$

where $K$ is the instantaneous tag-loss rate. For Equations 1 – 4, $Z = F + K + O$, where $O$ is the sum of the instantaneous rates of natural mortality and emigration.

The third model component specifies the likelihood ($L$) of the number of recoveries being reported if the population dynamics and observation model are true. Hilborn (1990) has shown that the sampling distribution of the tag recoveries can be approximated by a Poisson distribution. The likelihood of the expected number of recoveries $\hat{R}_t$ and $\hat{W}_t$, given the observed number of tag recoveries $R_t$ and $W_t$ are

$$L(R_t/\hat{R}_t) = \frac{e^{-\hat{R}_t}\hat{R}_t^{\,R_t}}{R_t!} \tag{5}$$

and

$$L(W_t/\hat{W}_t) = \frac{e^{-\hat{W}_t}\hat{W}_t^{\,W_t}}{W_t!} \tag{6}$$

respectively.

The total likelihood of observing all $R_t$ and $W_t$ recoveries, given the corresponding $\hat{R}_t$ and $\hat{W}_t$ values, are the products of the individual likelihoods:

$$L(\boldsymbol{R}/\hat{\boldsymbol{R}}) = \prod_t (e^{-\hat{R}_t}\hat{R}_t^{\,R_t}/R_t!) \tag{7}$$

and

$$L(\boldsymbol{W}/\hat{\boldsymbol{W}}) = \prod_t (e^{-\hat{W}_t}\hat{W}_t^{\,W_t}/W_t!) \quad , \tag{8}$$

so that

$$\begin{aligned} L(\boldsymbol{R},\boldsymbol{W}/\hat{\boldsymbol{R}},\hat{\boldsymbol{W}}) &= L(\boldsymbol{R}/\hat{\boldsymbol{R}})\, L(\boldsymbol{W}/\hat{\boldsymbol{W}}) \\ &= \prod_t (e^{-\hat{R}_t}\hat{R}_t^{\,R_t}/R_t!) \prod_t (e^{-\hat{W}_t}\hat{W}_t^{\,W_t}/W_t!) \quad . \end{aligned} \tag{9}$$

For computational convenience, the negative of the log-likelihoods was calculated and forms the quantity to be minimized:

$$\begin{aligned} -\ell\text{n}(L(\boldsymbol{R}/\hat{\boldsymbol{R}})) - \ell\text{n}(L(\boldsymbol{W}/\hat{\boldsymbol{W}})) &= \sum_t \hat{R}_t - \sum_t R_t\,\ell\text{n}(\hat{R}_t) + [\sum_t R_t!] \\ &+ \sum_t \hat{W}_t - \sum_t W_t\,\ell\text{n}(\hat{W}_t) + [\sum_t W_t!] \quad . \end{aligned} \tag{10}$$

Note that the terms within square brackets are ignored when estimating the model parameters, because they are constants and independent of the model parameters.

## Tag type

During the first year of the tagging study by Davies and Joubert (1966), large sheep-ear tags were used on juvenile dusky sharks. Note that the tag was a larger version of the sheep-ear tag that was commonly used then to tag small livestock (Davies and Joubert 1966). However, based on results of tag-evaluation experiments started at ORI in 1962 (Davies and Joubert 1966), use of the large sheep-ear tags was discontinued after the first year of the tagging study in favour of specially designed ORI tags. The difference between the tags is in their shape; the large sheep-ear tag is elongated, whereas the ORI tag is round. The shape of the ORI tag is believed to reduce vertical movement in the water and supposedly increases tag retention time (Van der Elst 1990). The tagging programme issued members with large sheep-ear tags for tagging sharks up until 1989. Subsequently, only ORI tags have been issued for the purpose, but members who still possessed sheep-ear tags continue to use them. Some anglers also incorrectly use tags that have been designed for use on other fish, but these incorrectly marked dusky sharks were excluded from the present analysis. However, because of the change in tags, there has been a marked increase in the number of wash-ups and of tags recovered from the shark nets (Table I). In this study, the hypothesis that the shedding rate of ORI and large sheep-ear tags is the same was tested.

It is defensible to assume that sharks tagged with either of the tag types are harvested at the same rate, i.e. $F$ is the same for each tag type. For this case (Model 1), the objective function to be minimized is the sum of the negative log-likelihoods (Equation 10) for each tag type, with $F$ and $\beta$ being constant for each tag type, i.e.

$$\begin{aligned} &-\ell\text{n}(L(\boldsymbol{R}^s/\hat{\boldsymbol{R}}^s)) - \ell\text{n}(L(\boldsymbol{W}^s/\hat{\boldsymbol{W}}^s)) \\ &-\ell\text{n}(L(\boldsymbol{R}^o/\hat{\boldsymbol{R}}^o)) - \ell\text{n}(L(\boldsymbol{W}^o/\hat{\boldsymbol{W}}^o)) \quad , \end{aligned} \tag{11}$$

where the superscripts $s$ and $o$ index the sheep-ear and ORI tags respectively. In this model, there are five parameters to be estimated ($F$, $K^s$, $K^o$, $\beta$ and $O$). In the following analysis (Model 2), the assumption that the rate of tag loss is the same for each tag type, i.e. the instantaneous rate of tag loss is assumed to be the same for sheep-ear and ORI tags ($K^s = K^o$), is examined. This reduces the number of parameters to be estimated to four ($F$, $K$, $\beta$ and $O$). Note that Model 2 is a special case (nested within) of Model 1.

All models were implemented on a spreadsheet, which was programmed with a function-optimization routine. Given the number of sharks marked and the tag returns reported in each time interval, estimates of the parameters can be obtained by use of a non-linear minimization routine that finds optimum parameter estimates that satisfy the required minimization criteria.

## Model selection

The likelihood-ratio test was used to test whether a model fit is improved by the inclusion of an extra free parameter. When Model 1 has one more parameter than Model 2 and Model 2 is nested within Model 1, the criterion is

$$2(-\ell\text{n}(\hat{\boldsymbol{P}}_2)) - 2(-\ell\text{n}(\hat{\boldsymbol{P}}_1)) \geq 3.84 \quad , \tag{12}$$

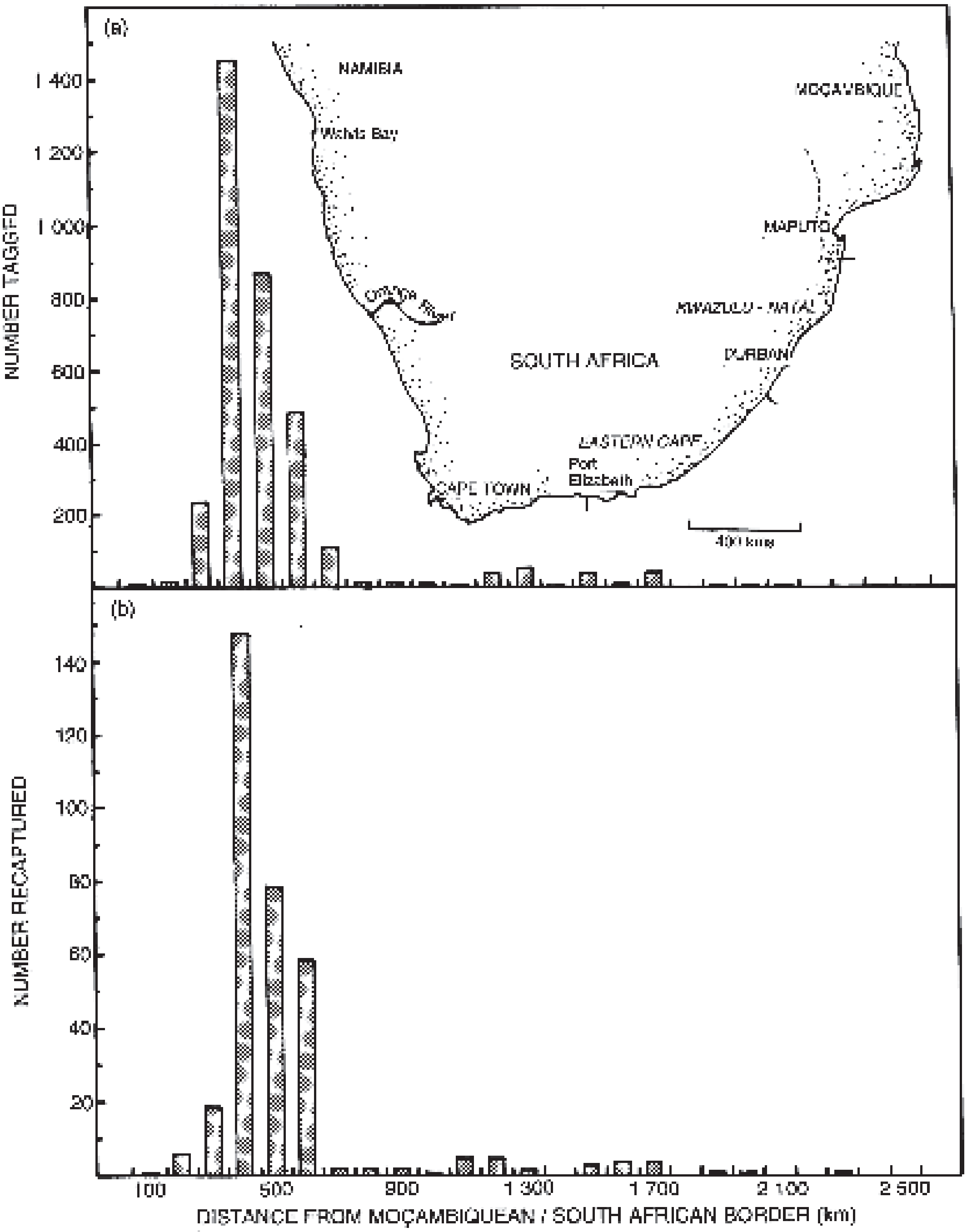

Fig. 1: The mark-recapture data (1986-1993) of *Carcharhinus obscurus* tagged off the Eastern Cape and KwaZulu-Natal coasts, showing the location of (a) the number tagged and (b) the number recaptured relative to distance (km) from the border between Moçambique and South Africa

Table II: Estimates of model parameters for fixed values of $\beta$ (reporting rate) and the 95% confidence intervals (*CI*) for $\beta = 0.75$ and model negative log-likelihood values ($-\ell n\ L$). Numbers in square brackets indicate annual rates

| Parameter | Value | | |
|---|---|---|---|
| | $-\ell nL = -689.856$<br>$\beta = 1$ | $-\ell nL = -689.999$<br>$\beta = 0.75$ (*CI*) | $-\ell nL = -690.290$<br>$\beta = 0.5$ |
| | | *Model 1* | |
| $F$ ($\cdot$year$^{-1}$) | 0.21 | 0.27 (0.19–0.44) | 0.41 |
| $K^s$ ($\cdot$year$^{-1}$) | 0.029 | 0.039 (0.0219–0.072)[4%] | 0.058 |
| $K^o$ ($\cdot$year$^{-1}$) | 0.060 | 0.080 (0.051–0.135)[8%] | 0.12 |
| $O$ ($\cdot$year$^{-1}$) | 2.22 | 2.14 (1.45–3.58) | 1.99 |
| | | *Model 2* | |
| $F$ ($\cdot$year$^{-1}$) | 0.22 | 0.29 (0.20–0.48) | 0.47 |
| $K$ ($\cdot$year$^{-1}$) | 0.047 | 0.062 (0.040–0.106)[6%] | 0.093 |
| $O$ ($\cdot$year$^{-1}$) | 2.39 | 2.30 (1.54–3.96) | 2.12 |

where $-\ell n(\hat{\boldsymbol{P}}_j)$ is the negative log-likelihood of the vector $\hat{\boldsymbol{P}}_j$ of best parameter estimates of model $j$ and 3.84 is the value of the $\chi^2$ distribution, with 1*df* at the 95% confidence level. If Equation 12 is true, Model 2 is rejected in favour of Model 1 .

### Likelihood profile method

Confidence bounds for the parameters of the mortality model were determined by the likelihood profile method (Schnute 1989, Lebreton *et al.* 1992). The 95% confidence interval for a parameter $P_i$ of vector $\boldsymbol{P}$ ($i = 1,2,..., k$) is determined by minimizing the negative log-likelihood for a range of values of $P_i$, with the remaining ($k$–1) parameters being free. The 95% confidence point values of $P_i$ are equal to the upper and lower boundary values of the range of $P_i$ that satisfies the inequality

$$2(-\ell n\, L\,(\hat{\boldsymbol{P}})) - 2(-\ell n\,(L\,(\hat{\boldsymbol{P}}_{best})) \le 3.84 \qquad (13)$$

where $-\ell n\ L\,(\hat{\boldsymbol{P}}_{best})$ is the negative log-likelihood of the best estimate of $\boldsymbol{P}$, with all $k$ parameters free, and $-\ell n\ L\,(\hat{\boldsymbol{P}})$ is the negative log-likelihood of the best estimate of $\boldsymbol{P}$, with $k$–1 parameters free and parameter $P_i$ fixed.

## RESULTS

The number of dusky sharks tagged and released along the eastern and south-eastern coasts of South Africa are shown in Figure 1. The majority of sharks were tagged and recaptured in KwaZulu-Natal, especially near Durban, approximately 400 km south of the Moçambican border. Times-at-liberty ranged between 0 and 521 days, with a mean value of 65 days (*SD* = ± 83).

Estimation of the model parameters was difficult. Despite the global minimum being attained, unique values for $F$, $\beta$, $K^o$ and $K^s$ could not be obtained, because some of the parameters (e.g. $F$ and $\beta$) are confounded in the models. In other words, although an estimate of the product of the parameters (e.g. $F\beta$) was obtainable, there was insufficient information in the data to obtain separate and unique parameter values for the product coefficients. As $\beta$ is confounded with three parameters ($F$, $K^o$ and $K^s$), it was fixed for a range of values which reduced the number of free parameters by one in each model. Estimates of the parameters, their 95% confidence intervals and the negative log-likelihoods for each model are given in Table II. Based on the likelihood- ratio test, Model 1 ($K^s$ not equal to $K^o$) best describes the data. In Table III, the observed and predicted numbers of recaptures and wash-ups and their associated residuals are given. Figure 2 shows the fit of Model 1 to the observed data (with $\beta = 0.75$).

## DISCUSSION

The fact that most dusky sharks tagged and released along the KwaZulu-Natal coast were juveniles is not surprising, because the area has been identified as a nursery area for that species (Bass *et al.* 1973). Most recaptures occurred within the area of tagging, which is probably a result of the short time of two months between tagging and recapture.

The best fit to the observed data was obtained by Model 1, i.e. tag retention is not the same for ORI and

Table III: Observed and Model 1 predictions of recaptures of *Carcharhinus obscurus* and wash-ups for sheep-ears and ORI tags. The non-reporting rate for recaptures and wash-ups was assumed to be 25% ($\beta = 0.75$)

| Year | Sheep-ear tags | | | ORI tags | | |
|---|---|---|---|---|---|---|
| | Observed | Predicted | Residual | Observed | Predicted | Residual |
| *Recaptures* | | | | | | |
| 1986 | 41 | 28 | 13.211 | – | – | – |
| 1987 | 38 | 39 | –0.958 | – | – | – |
| 1988 | 55 | 29 | 25.656 | – | – | – |
| 1989 | 22 | 22 | –0.236 | 0 | 3 | –3.225 |
| 1990 | 12 | 11 | 0.810 | 18 | 16 | 1.974 |
| 1991 | 3 | 6 | –3.333 | 18 | 23 | –5.104 |
| 1992 | 3 | 3 | -0.282 | 25 | 37 | –12.244 |
| 1993 | 9 | 5 | 3.935 | 36 | 56 | –20.204 |
| *Wash-ups* | | | | | | |
| 1986 | 5 | 4 | 1.057 | – | – | – |
| 1987 | 6 | 6 | 0.473 | – | – | – |
| 1988 | 4 | 4 | –0.163 | – | – | – |
| 1989 | 2 | 3 | –1.155 | 2 | 1 | 0.782 |
| 1990 | 0 | 2 | –1.588 | 12 | 5 | 7.298 |
| 1991 | 3 | 1 | 2.102 | 2 | 7 | –4.780 |
| 1992 | 0 | 1 | –0.466 | 13 | 11 | 2.072 |
| 1993 | 1 | 1 | 0.281 | 10 | 16 | –6.492 |

sheep-ear tags. With $\beta = 0.75$, the overall fit of Model 1 to the observed recaptures is reasonable, as depicted by the small residual values, except for the years 1986, 1988, 1992 and 1993 (Table III, Fig. 2a). However, the parameters $K^s$, $K^o$, $O$ and $F$ (for $\beta = 0.75$) have fairly wide confidence bounds (Table II). A possible reason for the poor estimate of $F$ is that the assumption of constant fishing mortality during the study was violated. The assumption of a constant fishing mortality could have been relaxed if effort data for the dusky shark fishery were available. Such effort data only exist for the shark-net fishery. For the recreational dusky shark fishery, only effort indices in KwaZulu-Natal are available, but these are regarded as unreliable. Furthermore, the shark-net effort data are not directly comparable to effort indices of the recreational fishery because the latter is a hook-and-line fishery, whereas the former is a net fishery.

The estimates of rates of fishing mortality and tag-shedding are very sensitive to the choice of reporting rate (Table II) and are a result of the confounding of parameters in the model. In this tagging study, a preliminary reporting rate of 75% for recaptured sharks and finfish, based on angler surveys (ORI unpublished data), has been assumed. Based on competition angler surveys, Van der Elst (1979) found a non-reporting rate of only 3%, but this rate is considered here to be too low for application to the entire spectrum of anglers who might capture a tagged animal. The reporting rate in this study, however, excludes an unknown percentage of recaptured dusky sharks that are not identified as tagged individuals by anglers. Tag recognition by anglers is often reduced as a result of heavy algal growth on the tag and the practical difficulties of handling a live shark. If the number of overlooked tags is negligible, and assuming a non-reporting rate of 25%, an instantaneous fishing mortality ($F$) rate of approximately $0.27 \cdot \text{year}^{-1}$ for dusky sharks is obtained (Table II). Off KwaZulu-Natal, dusky sharks are caught by both sport anglers and by shark-netting operations (Van der Elst 1979), whereas off the Eastern Cape they are mainly fished by sport anglers (Smale 1991). All these fishing operations participated in the mark-recapture study, and therefore estimates of fishing mortality represent a combined assessment.

Because the tagging programme relies on the participation of the general public and field identification of sharks can be difficult (Bass *et al*, 1973), there is a potential for misidentification of sharks. Juvenile *C. obscurus* can be confused with the milkshark *Rhizoprionodon acutus*, but the percentage of anglers misidentifying those sharks is likely to be small. Van der Elst (1979) reported that only 4.3% of *R. acutus* captured during fishing competitions were misidentified as *C. obscurus*. The same author also showed that the mass frequency distributions of anglers' catches of *C. obscurus* and *R. acutus* closely resembled those described by Bass *et al.* (1973), substantiating the anglers' ability to distinguish between the species.

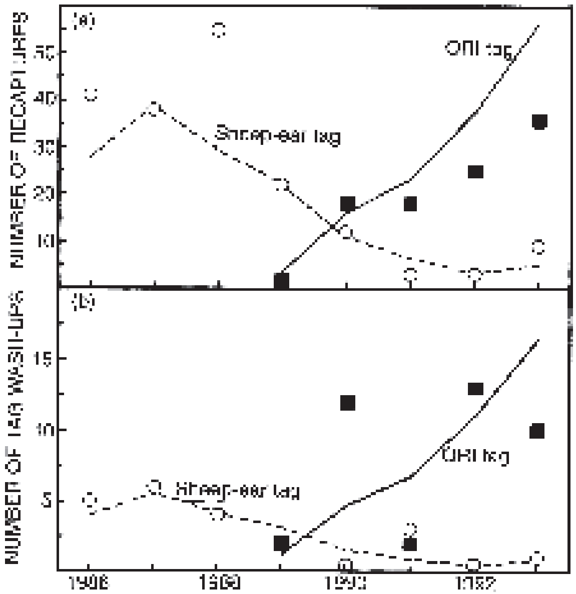

Fig. 2: Fit of Model 1 (with = 0.75), showing the trends in (a) the number of tagged *Carcharhinus obscurus* recaptured and (b) the number of tag wash-ups for the sheep-ear and ORI tags

In this study, 1.7% of marked dusky sharks (17% of all tags recovered) had their tags ripped from their dorsal fins, washed up on beaches or fouled in the shark nets. Because most tagged dusky sharks were <1 m long and shark nets are not designed to catch sharks <1.5 m (Cliff and Dudley 1992), small, tagged dusky sharks are able to pass through the nets, increasing the chance of tag fouling. Reporting on the first year of their tagging programme using sheep-ear tags, Davies and Joubert (1966) estimated that 4% of tagged dusky sharks shed their tags as a result of fouling in shark nets. The same proportion of sheep-ear tags was shed per year in the present study. Davies and Joubert (1966) considered that, as a result of fin growth, it was unlikely that the tags would be shed within the first three years of tagging. However, it is not certain if tag shedding is only a result of interaction with shark nets.

Tag-induced mortality was considered to be negligible and was not accounted for in the model. Over the study period, five tags were recovered by methods other than recaptured animals, fouling in shark nets or wash-ups (Table I). Of these, three were recovered from the stomachs of predatory sharks, and were considered as natural mortality, and two were recovered from dead tagged specimens that were at liberty for 2 and 81 days. Even if both mortalities are assumed to have been tag-induced, this factor is negligible considering the number of dusky sharks that were tagged and released annually.

Note that an assumption of Equations 1–4 is that the reporting rates of tags recovered from recaptured sharks, wash-ups and those from shark nets are the same. This is probably unlikely, because the reporting rate of tags fouled and from tagged sharks recaptured in the nets is probably higher than those from tagged sharks recaptured by anglers or wash-ups. This is because personnel servicing the nets are more aware of the tagging programme and are more likely to report all tags recovered in shark nets. The magnitude of this difference in reporting rate is unknown.

The ORI tags have a shedding rate double that of the sheep-ear tags (Table II). From 1989, the use of sheep-ear tags was changed in favour of the ORI tag, in the belief that the ORI tag was retained longer in sharks (Van der Elst 1990). However, the present results show that the annual mean tag-shedding rate has increased by 4% since the introduction of the ORI tag. It is suggested that the sheep-ear tags be retained in combination with the ORI tags, because future studies may explain the mechanism by which tag retention is improved with a change in tag shape.

Natanson *et al.* (1995) reported an age-at-maturity of 21 years for female dusky sharks. Substituting this value in the Rikhter and Efanov (1977) mortality equation indicates a natural mortality rate (*M*) of 0.015·year$^{-1}$. This value is much smaller than the current estimate for *F* of 0.27·year$^{-1}$. It is the general belief that overfishing occurs at fishing rates where *F*»*M*. Substitution of lower age-at-maturity for dusky sharks of 11 years, according to Van der Elst (1979), results in an *M* value of 0.116·year$^{-1}$, which is still smaller than the current value of *F*. The fact that *F*»*M*, coupled with the relatively low fecundity of dusky sharks (6–14 pups, Bass *et al.* 1973) and the late age-at-maturity (Natanson *et al.* 1995, Van der Elst 1979), is cause for concern and future research should be directed at addressing this issue.

Cliff and Dudley (1992) reported that between 1981 and 1990 an average annual total of 283 dusky sharks was captured in shark nets off the KwaZulu-Natal coast. At least 10% of these were found alive in the nets and were usually tagged and released. The catch by sport anglers is unknown. However, use of data of competition sport anglers Van der Elst (1979) showed that the catch rates of dusky sharks (mostly juveniles) increased sharply between 1956 and 1976. Most of those sharks were killed because they were regarded as "pests" by anglers. However, there has been a move recently towards promoting the release of sharks alive (and tagged if possible), which is the result of an increase in conservation awareness among anglers. This conservation practice could augur well for the future of the fishery.

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