Estimation of instantaneous rates of tag shedding for school shark, *Galeorhinus galeus*, and gummy shark, *Mustelus antarcticus*, by conditional likelihood

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Abstract.–Fish and other animals are often tagged to estimate their abundance as well as rates of growth, fishing mortality, natural mortality, and movement. Results of these studies are biased if tags are not retained permanently and if tag loss is not taken into account. In this paper, we develop a simple tag shedding model to account for the effects of time at liberty, sex, and other factors and use one of its special cases to estimate the instantaneous tag shedding rate from data based on two double-tagging experiments on the school shark, *Galeorhinus galeus*, and gummy shark, *Mustelus antarcticus*, off southern Australia. For either species, tag shedding rate could vary with tag type, position of tag on fish, and sex of fish, but not with length at release or time at liberty. The shedding rate of Petersen disc fin tags was well above 50%/yr. Dart tags were shed at a higher rate (41%/yr for school shark; 63%/yr for gummy shark) than either "Roto" or "Jumbo" fin tags (8%/yr for school shark; 6%/yr for gummy shark). For either species of shark, the shedding rate of dart tags anchored in the basal cartilage of the dorsal fin was about half that of dart tags anchored in the dorsal musculature.

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Tags are markers placed on or in animals to identify an individual. Animals are tagged to estimate their abundance as well as rates of growth, fishing mortality, natural mortality, and movement. In many studies, a tagged animal is assumed to retain its tag permanently. This assumption, however, is not valid for certain types of tags. Consequently, many attempts have been made to estimate tag shedding rates (e.g. Davis and Reid, 1982; Francis, 1989; Faragher and Gordon, 1992; Treble et al., 1993; Hampton, 1996; Xiao, 1996a).

Tag shedding models are of three main types; all are based on Beverton and Holt's (1957, p. 205, equations 14.32–14.37) model for a double-tagging experiment. Some models are conditional on the number of recaptured fish with a single tag, as well as the number of recaptured fish with both tags as a function of time at liberty, and use the least squares method (Gulland, 1955, 1963; Chapman, 1961; Paulik, 1963; Chapman et al., 1965; Bayliff and Mobrand, 1972; Russell, 1980; Kirkwood, 1981; Alt et al., 1985) or more generally the maximum likelihood method (Robson and Regier, 1966; Seber, 1973; Seber and Felton, 1981; Wetherall, 1982; Kremers, 1988; Fabrizio et al., 1996) for estimation of parameters. Other models are conditional on the number of recaptured fish retaining at least one tag as a function of time at liberty and on the exact times at liberty (Wetherall, 1982). Use of these types of models in data analysis requires grouping recaptured fish by time at liberty because of an insufficient number of recaptures for a particular (exact) time at liberty, especially in small-scale tagging experiments. Still other models are conditional only on the exact times at liberty (Kirkwood and Walker, 1984; Hampton and Kirkwood, 1989; Hearn et al., 1991; Xiao, 1996a). These models 1) use the exact times at liberty in model fitting, 2) use probabilities of tag retention directly rather than using the often statistically undesirable ratios as the dependent variable in regression analysis, 3) apply to both small (but see below) and large numbers of recaptures, and 4) yield estimates of tag shedding rates independent of instantaneous fishing mortality, natural mortality, and mortalities due to all other causes. Almost all previous tag shedding models have considered only the effects of fish time at liberty on shedding rates, ignoring effects of other equally or potentially more important factors, such as fish sex and size.

School shark *Galeorhinus galeus* (Linnaeus) and gummy shark *Mustelus antarcticus* (*sensu* Last and Stevens, 1994) are major species in the Australian southern shark fishery—a commercial fishery that extends from Western Australia through South Australia to Bass Strait and Tasmania in the east and that has an annual landed value of $A15.6 million (Walker et al., 1996). Two tagging studies were undertaken to study the growth (Moulton et al., 1992), natural mortality (Grant et al., 1979), and local movements of these two species within Bass Strait and off eastern Tasmania (T. I. Walker, Marine and Freshwater Resources Institute, PO Box 114, Queenscliff, Vic 3225 Australia, unpubl. data). These studies suggest that school shark are highly migratory, compared with gummy shark, but they provide little quantitative information about their rates of movements beyond these areas, where most sharks were tagged and released. Also, fishing effort was too poorly documented at the time of Grant et al.'s (1979) tagging program (1940s and 1950s) to be adequate for quantifying the rates of movement for these two species. Finally, predominant use of gill nets with large mesh sizes (8 inches) off the southern coast of Western Australia and off South Australia at the time of T.I. Walker's tagging study (1970s) led to a low level of fishing effort and a small number of recaptures. Such a lack of quantitative information on rates of movement hampered stock assessment. Consequently, a large-scale tagging experiment was designed (Xiao, 1996b) and implemented to fill in this gap. In that study, thousands of individuals were released; each individual was tagged with an easily attachable and highly visible external tag (a Roto tag or a dart tag), the shedding rate of which was to be determined through an accompanying double-tagging experiment (see below).

In this paper, we develop a simple tag shedding model to account for the effects of fish sex, size, and factors other than time at liberty and use a special case to estimate the instantaneous tag shedding rate for the two species of sharks.

Materials and methods

Tagging experiments

Two double-tagging experiments were performed on *G. galeus* and *M. antarcticus*. In the first experiment (Olsen, 1953; Walker, 1989; Table 1), a total of 2597 school and 363 gummy sharks with a respective total length range of 31–164 (85 ±43, n=2586) cm and 32–179 (102 ±24, n=362) cm were captured by longline hooks, measured to the nearest centimeter, tagged with an internal and external tag, and released in inshore waters off Victoria, South Australia, and Tasmania, Australia, from 22 May 1949 to 10 July 1954. Internal tags were either 50 mm long and 23 mm wide (J-tag), or 50 mm long and 22 mm wide (L-tag), or 35 mm long and 10 mm wide (S-tag) and were inserted into the body cavity through an incision on the left flank parallel to the muscles in the lower half of the body immediately below the posterior half of the first dorsal fin. External tags were a white (W-tag) or gray Petersen disc (G-tag); both were 16 mm in diameter and 1 mm thick and were placed in the midcentral part of the first dorsal fin. Of those released, 417 school and 20 gummy sharks were recaptured within 42.5 years. Their respective total length at recapture ranged from 43 to 175 (127 ±35, n=267) cm and from 83 to 152 (125 ±19, n=12) cm; their respective times at liberty ranged from 31 to 15,510 (2761 ±2758, n=417) d, and from 52 to 3900 (1771 ±1159, n=20) d.

In the second double-tagging experiment (Table 2), as part of a major tagging experiment (see above), 291 school and 731 gummy sharks with a respective total length range of 38–168 (134 ±17, n=291) cm and 40–176 (108 ±20, n=729) cm were captured in gill nets, measured to the nearest millimeter, tagged with two external tags (a Roto tag and a dart tag) either in the lower half or basal cartilage of the first dorsal fin, and released off southern Australia, from 15 December 1993 to 24 April 1996. Two types of Roto tags were used: either a 45-mm-long and 18-mm-wide Jumbo (Roto) tag, or a 36-mm-long and 9-mm-wide Roto tag (Daltons of New South Wales, Australia). The dart tag was 95 mm long and 2 mm in diameter (Hallprint of South Australia, Australia). As of 1 May 1997, 48 school and 207 gummy sharks were recaptured. Their respective total length at recapture ranged from 85 to 179 (135 ±18, n=38) cm and from 66 to 167 (115 ±17, n=150) cm; their respective times at liberty ranged from 31 to 633 (269 ±163, n=48) d, and from 1 to 1138 (275 ±244, n=207) d.

Table 1

Description of the first double-tagging experiment for gummy and school sharks. The number of recaptures includes, consecutively and in parentheses, that with two tags, with tag A only, and with tag B only. "—" indicates unknown or not computable.

Row	Species	Tag A	Tag B	Sex	Number released	Mean length at release (cm)	Length range at release (cm)	Number recaptured	Mean length at recapture (cm)	Length range at recapture (cm)	Mean time at liberty (d)	Range of time at liberty (d)
1	gummy	L-tag	W-tag	M	11	110 ±07	99–122	—	—	—	—	—
2	gummy	L-tag	W-tag	F	1	90 ± –	90–090	—	—	—	—	—
3	gummy	L-tag	G-tag	M	128	108 ±12	79–144	6(0,6,0)	131 ±16	114–145	2224 ±1154	1209–3900
4	gummy	L-tag	G-tag	F	129	112 ±20	77–179	13(0,13,0)	128 ±15	106–152	1698 ±1104	80–3531
5	gummy	S-tag	W-tag	M	32	86 ±28	33–136	—	—	—	—	—
6	gummy	S-tag	W-tag	F	14	65 ±20	38–102	—	—	—	—	—
7	gummy	S-tag	G-tag	M	27	88 ±22	39–119	1(0,1,0)	83 ±–	83–083	52 ± –	52–52
8	gummy	S-tag	G-tag	F	21	63 ±25	32–117	—	—	—	—	—
9	school	J-tag	W-tag	M	59	127 ±26	62–154	18(2,15,1)	146 ±11	125–155	5039 ±4369	705–15251
10	school	J-tag	W-tag	F	41	128 ±33	60–164	14(1,13,0)	152 ±15	113–167	3260 ±2333	319–8380
11	school	L-tag	W-tag	M	32	145 ±07	116–160	7(1,6,0)	155 ±14	143–174	4382 ±3142	841–9539
12	school	L-tag	W-tag	F	15	148 ±15	106–160	4(0,4,0)	161 ±08	155–167	3809 ±5548	546–12114
13	school	L-tag	G-tag	—	4	137 ±18	112–155	2(0,2,0)	152 ±–	152–152	2971 ±0769	2427–3515
14	school	L-tag	G-tag	M	521	141 ±12	71–163	127(4,123,0)	147 ±12	114–175	3858 ±3100	82–15510
15	school	L-tag	G-tag	F	292	137 ±17	73–164	71(6,65,0)	149 ±12	112–167	3142 ±2341	89–9107
16	school	S-tag	W-tag	—	2	67 ±09	60–073	—	—	—	—	—
17	school	S-tag	W-tag	M	14	48 ±06	40–057	2(0,2,0)	83 ±–	83–083	2652 ±2456	915–4389
18	school	S-tag	W-tag	F	14	54 ±06	43–065	5(0,5,0)	107 ±40	57–141	2566 ±1944	260–5262
19	school	S-tag	G-tag	—	15	57 ±12	32–067	2(1,1,0)	—	—	377 ±0434	70–684
20	school	S-tag	G-tag	M	781	54 ±13	31–148	86(7,79,0)	97 ±35	43–159	1568 ±1604	31–7555
21	school	S-tag	G-tag	F	807	53 ±12	31–148	79(13,64,2)	95 ±33	51–159	1221 ±1512	35–6200

Table 2

Description of the second double-tagging experiment for gummy and school sharks. The number of recaptures includes, consecutively and in parentheses, that with two tags, with tag A only, and with tag B only. "—" indicates unknown or not computable; tagging position refers to tag B's position.

Row	Species	Tag A	Tag B	Tagging position	Sex	Number released	Mean length at release (cm)	Length range at release (cm)	Number recaptured	Mean length at recapture (cm)	Length range at recapture (cm)	Mean time at liberty (d)	Range of time at liberty (d)
1	gummy	Jumbo	dart	fin	M	68	115 ±08	97–140	13(9,3,1)	117 ±08	107–130	192 ±119	64–386
2	gummy	Jumbo	dart	fin	F	66	125 ±21	80–176	19(17,1,1)	122 ±10	108–145	119 ±083	13–309
3	gummy	Jumbo	dart	muscle	M	101	109 ±14	87–144	41(22,19,0)	112 ±14	86–148	278 ±232	5–818
4	gummy	Jumbo	dart	muscle	F	164	119 ±21	68–175	43(19,24,0)	123 ±20	91–167	340 ±273	6–1138
5	gummy	Roto	dart	muscle	—	1	106 ± –	106–106	1(0,1,0)	—	—	83 ± –	83–83
6	gummy	Roto	dart	muscle	M	151	96 ±18	45–135	37(20,15,2)	106 ±17	66–148	309 ±262	2–1059
7	gummy	Roto	dart	muscle	F	180	99 ±18	40–136	53(26,26,1)	112 ±14	78–138	278 ±256	1–886
8	school	Jumbo	dart	fin	M	46	135 ±14	108–168	3(3,0,0)	136 ±13	123–149	136 ±089	34–202
9	school	Jumbo	dart	fin	F	81	139 ±12	108–167	15(11,3,1)	141 ±12	110–157	306 ±130	123–546
10	school	Jumbo	dart	muscle	M	77	134 ±11	100–158	12(9,2,1)	140 ±20	107–179	263 ±201	33–633
11	school	Jumbo	dart	muscle	F	53	140 ±14	100–164	9(6,3,0)	142 ±10	122–155	272 ±179	31–551
12	school	Roto	dart	muscle	M	13	108 ±23	71–152	3(3,0,0)	110 ±22	85–124	317 ±164	146–474
13	school	Roto	dart	muscle	F	21	110 ±29	38–160	6(2,4,0)	115 ±15	100–136	229 ±172	34–468

Model

Consider a (single) fish i that is captured, double tagged, and released at time $t_0(i)$. The index i can be used to examine the effects of any factor on the instantaneous tag shedding rate. Let A and B indicate the two types of tags and

$P(i,A,B,t(i))$ = probability of retaining both tags at time $t(i)$;
$P(i,A,0,t(i))$ = probability of retaining only tag A at time $t(i)$;
$P(i,0,B,t(i))$ = probability of retaining only tag B at time $t(i)$;
$P(i,0,0,t(i))$ = probability of retaining neither tag at time $t(i)$;
$\dot{C}(i,A,B,t(i))$ = probability that it is caught at time $t(i)$ and reported given that it has retained both tags;
$\dot{C}(i,A,0,t(i))$ = probability that it is caught at time $t(i)$ and reported given that it has retained only tag A;
$\dot{C}(i,0,B,t(i))$ = probability that it is caught at time $t(i)$ and reported given that it has retained only tag B;
$\dot{C}(i,0,0,t(i))$ = probability that it is caught at time $t(i)$ and reported given that it has retained neither tag;
$\dot{U}(i,A,B,t(i))$ = probability that it is caught at time $t(i)$ but not reported given that it has retained both tags;
$\dot{U}(i,A,0,t(i))$ = probability that it is caught at time $t(i)$ but not reported given that it has retained only tag A;
$\dot{U}(i,0,B,t(i))$ = probability that it is caught at time $t(i)$ but not reported given that it has retained only tag B;
$\dot{U}(i,0,0,t(i))$ = probability that it is caught at time $t(i)$ but not reported given that it has retained neither tag;
$\dot{D}(i,A,B,t(i))$ = probability that it is dead at time $t(i)$ given that it has retained both tags;
$\dot{D}(i,A,0,t(i))$ = probability that it is dead at time $t(i)$ given that it has retained only tag A;
$\dot{D}(i,0,B,t(i))$ = probability that it is dead at time $t(i)$ given that it has retained only tag B;
$\dot{D}(i,0,0,t(i))$ = probability that it is dead at time $t(i)$ given that it has retained neither tag;
$\pi(i)$ = probability that it remains alive after type-I mortality (i.e. mortality due to the immediate effects of tagging and handling);
$\rho(i,j)$ = probability that it retains tag j ($j=A,B$) after type-I shedding (i.e. tag shedding due to the immediate effects of tagging and handling);
$F(i,t(i))$ = instantaneous rate of fishing mortality at time $t(i)$;
$M(i,t(i))$ = instantaneous rate of natural mortality at time $t(i)$;
$R(i,A,B,t(i))$ = probability of reporting given that it is caught at time $t(i)$ and that it has retained both tags;
$R(i,A,0,t(i))$ = probability of reporting given that it is caught at time $t(i)$ and that it has retained only tag A;
$R(i,0,B,t(i))$ = probability of reporting given that it is caught at time $t(i)$ and that it has retained only tag B;
$R(i,0,0,t(i))$ = probability of reporting given that it is caught at time $t(i)$ and that it has retained neither tag;
$\lambda(i,A,t(i))$ = instantaneous shedding rate of tag A at time $t(i)$; and
$\lambda(i,B,t(i))$ = instantaneous shedding rate of tag B at time $t(i)$.

We assume that, in the time interval $[t(i),t(i)+\Delta t]$, the probability that fish i retaining both tags is caught is $F(i,t(i))\Delta tP(i,A,B,t(i))+O(\Delta t)$, the probability that it is dead is $M(i,t(i))\Delta tP(i,A,B,t(i))+O(\Delta t)$, the probability that it sheds tag A is $\lambda(i,A,t(i))\Delta tP(i,A,B,t(i))+O(\Delta t)$, and the probability that it sheds tag B is $\lambda(i,B,t(i))\Delta tP(i,A,B,t(i))+O(\Delta t)$, where $O(\Delta t)\to 0$ as $\Delta t\to 0$. It is also assumed that these events are independent with no more than one event occurring in the time interval. Under these assumptions, the probability that fish i retains both tags at time $t(i)+\Delta t$ given that it has retained both tags at time $t(i)$ is given by

$$P(i,A,B,t(i)+\Delta t)=[1-F(i,t(i))\Delta t-M(i,t(i))\Delta t-\lambda(i,A,t(i))\Delta t-\lambda(i,B,t(i))\Delta t]\ P(i,A,B,t(i))+O(\Delta t).$$

Taking the limit $\Delta t\to 0$ and letting the dot above a quantity denote the first derivative of that quantity with respect to $t(i)$ yields

$$\dot{P}(i,A,B,t(i))=-[F(i,t(i))+M(i,t(i))+\lambda(i,A,t(i))+\lambda(i,B,t(i))]\ P(i,A,B,t(i)).$$

This and similar arguments yield a tag shedding model of the form

$$\begin{cases} \dot{P}(i,A,B,t(i)) = -\left[F(i,t(i)) + M(i,t(i)) + \lambda(i,A,t(i)) + \lambda(i,B,t(i))\right]P(i,A,B,t(i)) \\ \dot{P}(i,A,0,t(i)) = -\left[F(i,t(i)) + M(i,t(i)) + \lambda(i,A,t(i))\right]P(i,A,0,t(i)) + \lambda(i,B,t(i))P(i,A,B,t(i)) \end{cases} \quad (1)$$

$$\begin{cases}
\dot{P}(i,0,B,t(i)) = -\left[F(i,t(i)) + M(i,t(i)) + \lambda(i,B,t(i))\right]P(i,0,B,t(i)) + \lambda(i,A,t(i))P(i,A,B,t(i)) \\
\dot{P}(i,0,0,t(i)) = -\left[F(i,t(i)) + M(i,t(i))\right]P(i,0,0,t(i)) + \lambda(i,A,t(i))P(i,A,0,t(i)) + \lambda(i,B,t(i))P(i,0,B,t(i)) \\
\dot{C}(i,A,B,t(i)) = F(i,t(i))R(i,A,B,t(i))P(i,A,B,t(i)) \\
\dot{C}(i,A,0,t(i)) = F(i,t(i))R(i,A,0,t(i))P(i,A,0,t(i)) \\
\dot{C}(i,0,B,t(i)) = F(i,t(i))R(i,0,B,t(i))P(i,0,B,t(i)) \\
\dot{C}(i,0,0,t(i)) = F(i,t(i)) = R(i,0,0,t(i))P(i,0,0,t(i)) \\
\dot{U}(i,A,B,t(i)) = F(i,t(i))\left[1 - R(i,A,B,t(i))\right]P(i,A,B,t(i)) \\
\dot{U}(i,A,0,t(i)) = F(i,t(i))\left[1 - R(i,A,0,t(i))\right]P(i,A,0,t(i)) \\
\dot{U}(i,0,B,t(i)) = F(i,t(i))\left[1 - R(i,0,B,t(i))\right]P(i,0,B,t(i)) \\
\dot{U}(i,0,0,t(i)) = F(i,t(i))\left[1 - R(i,0,0,t(i))\right]P(i,0,0,t(i)) \\
\dot{D}(i,A,B,t(i)) = M(i,t(i))P(i,A,B,t(i)) \\
\dot{D}(i,A,0,t(i)) = M(i,t(i))P(i,A,0,t(i)) \\
\dot{D}(i,0,B,t(i)) = M(i,t(i))P(i,0,B,t(i)) \\
\dot{D}(i,0,0,t(i)) = M(i,t(i))P(i,0,0,t(i))
\end{cases} \qquad \left[t_0(i) \le t(i)\right] \qquad \begin{matrix}(1)\\ \text{continued}\end{matrix}$$

with initial conditions

$$\begin{cases}
P(i,A,B,t_0(i)) = \pi(i)\rho(i,A)\rho(i,B) \\
P(i,A,0,t_0(i)) = \pi(i)\rho(i,A)\left[1-\rho(i,B)\right] \\
P(i,0,B,t_0(i)) = \pi(i)\left[1-\rho(i,A)\right]\rho(i,B) \\
P(i,0,0,t_0(i)) = \pi(i)\left[1-\rho(i,A)\right]\left[1-\rho(i,B)\right] \\
C(i,A,B,t_0(i)) = 0 \\
C(i,A,0,t_0(i)) = 0 \\
C(i,0,B,t_0(i)) = 0 \\
C(i,0,0,t_0(i)) = 0 \\
U(i,A,B,t_0(i)) = 0 \\
U(i,A,0,t_0(i)) = 0 \\
U(i,0,B,t_0(i)) = 0 \\
U(i,0,0,t_0(i)) = 0 \\
D(i,A,B,t_0(i)) = 0 \\
D(i,A,0,t_0(i)) = 0 \\
D(i,0,B,t_0(i)) = 0 \\
D(i,0,0,t_0(i)) = 0
\end{cases}$$

Solution of this system of ordinary differential equations as an initial value problem gives

$$
\begin{cases}
P(i,A,B,t(i)) = \pi(i) e^{-\int_{t_0(i)}^{t(i)} [F(i,s)+M(i,s)]ds} \rho(i,A)\rho(i,B) e^{-\int_{t_0(i)}^{t(i)} [\lambda(i,A,s)+\lambda(i,B,s)]ds} \\
P(i,A,0,t(i)) = \pi(i) e^{-\int_{t_0(i)}^{t(i)} [F(i,s)+M(i,s)]ds} \rho(i,A) e^{-\int_{t_0(i)}^{t(i)} \lambda(i,A,s)ds} \left[1-\rho(i,B) e^{-\int_{t_0(i)}^{t(i)} \lambda(i,B,s)ds}\right] \\
P(i,0,B,t(i)) = \pi(i) e^{-\int_{t_0(i)}^{t(i)} [F(i,s)+M(i,s)]ds} \left[1-\rho(i,A) e^{-\int_{t_0(i)}^{t(i)} \lambda(i,A,s)ds}\right] \rho(i,B) e^{-\int_{t_0(i)}^{t(i)} \lambda(i,B,s)ds} \\
P(i,0,0,t(i)) = \pi(i) e^{-\int_{t_0(i)}^{t(i)} [F(i,s)+M(i,s)]ds} \left[1-\rho(i,A) e^{-\int_{t_0(i)}^{t(i)} \lambda(i,A,s)ds}\right] \left[1-\rho(i,B) e^{-\int_{t_0(i)}^{t(i)} \lambda(i,B,s)ds}\right] \\
C(i,A,B,t(i)) = \int_{t_0(i)}^{t(i)} F(i,s)R(i,A,B,s)P(i,A,B,s)ds \\
C(i,A,0,t(i)) = \int_{t_0(i)}^{t(i)} F(i,s)R(i,A,0,s)P(i,A,0,s)ds \\
C(i,0,B,t(i)) = \int_{t_0(i)}^{t(i)} F(i,s)R(i,0,B,s)P(i,0,B,s)ds \\
C(i,0,0,t(i)) = \int_{t_0(i)}^{t(i)} F(i,s)R(i,0,0,s)P(i,0,0,s)ds \\
U(i,A,B,t(i)) = \int_{t_0(i)}^{t(i)} F(i,s)[1-R(i,A,B,s)]P(i,A,B,s)ds \\
U(i,A,0,t(i)) = \int_{t_0(i)}^{t(i)} F(i,s)[1-R(i,A,0,s)]P(i,A,0,s)ds \\
U(i,0,B,t(i)) = \int_{t_0(i)}^{t(i)} F(i,s)[1-R(i,0,B,s)]P(i,0,B,s)ds \\
U(i,0,0,t(i)) = \int_{t_0(i)}^{t(i)} F(i,s)[1-R(i,0,0,s)]P(i,0,0,s)ds \\
D(i,A,B,t(i)) = \int_{t_0(i)}^{t(i)} M(i,s)P(i,A,B,s)ds \\
D(i,A,0,t(i)) = \int_{t_0(i)}^{t(i)} M(i,s)P(i,A,0,s)ds \\
D(i,0,B,t(i)) = \int_{t_0(i)}^{t(i)} M(i,s)P(i,0,B,s)ds \\
D(i,0,0,t(i)) = \int_{t_0(i)}^{t(i)} M(i,s)P(i,0,0,s)ds
\end{cases}
\qquad (2)
$$

This tag shedding model follows essentially the same line of thought as Xiao's (1996a) and can be readily phrased in the standard terminology of competing risks in survival analysis (David and Moeschberger, 1978). Also, notice that the left-hand side of Equation 1 sums to zero; the left-hand side of Equation 2 sums to $\pi(i)$.

When a single fish is double tagged and released at time $t_0(i)$, one of 16 mutually exclusive events can happen at time $t(i)$ (Equation 1 or 2). However, only three events are actually observable: the fish has, upon recapture, retained both tags, retained tag A and lost tag B, or lost tag A and retained tag B, with respective probabilities of $\dot{C}(i,A,B,t(i))$, $\dot{C}(i,A,0,t(i))$ and $\dot{C}(i,0,B,t(i))$. The event that it has shed both tags upon recapture, with a probability of $\dot{C}(i,0,0,t(i))$, cannot be observed, for when both tags are shed, a fish cannot be reliably distinguished from one that was never tagged. A likelihood function can be constructed to estimate parameters in Equation 1 or 2 by following arguments in standard competing risk analysis, but these estimates are substantially biased. To overcome this problem, we estimated model parameters by conditioning on observations of three events only, i.e. by maximizing the conditional likelihood function for all reported recaptures with at least one tag retained

$$L = L_1 \cdot L_2 \cdot L_3,$$

with

$$\begin{aligned}
L_1 &= \prod_{h=1}^{n} \frac{\dot{C}(h,A,B,t(h))}{\dot{C}(h,A,B,t(h)) + \dot{C}(h,A,0,t,(h)) + \dot{C}(h,0,B,t(h))} \\
&= \prod_{h=1}^{n} \frac{R(h,A,B,t(h))\theta(h,A,B,t(h))}{R(h,A,B,t(h))\theta(h,A,B,t(h)) + R(h,A,0,t(h))\theta(h,A,0,t(h)) + R(h,0,B,t(h))\theta(h,0,B,t(h))} \\
L_2 &= \prod_{j=1}^{m} \frac{\dot{C}(j,A,0,t(j))}{\dot{C}(j,A,B,t(j)) + \dot{C}(j,A,0,t(j)) + \dot{C}(j,0,B,t(j))} \\
&= \prod_{j=1}^{n} \frac{R(j,A,0,t(j))\theta(j,A,0,t(j))}{R(j,A,B,t,(j))\theta(j,A,B,t(j)) + R(j,A,0,t(j))\theta(j,A,0,t(j)) + R(j,0,B,t(j))\theta(j,0,B,t(j))} \\
L_3 &= \prod_{k=1}^{p} \frac{\dot{C}(k,0,B,t(k))}{\dot{C}(k,A,B,t(k)) + \dot{C}(k,A,0,t(k)) + \dot{C}(k,0,B,t(k))} \\
&= \prod_{k=1}^{n} \frac{R(k,0,B,t(k))\theta(k,0,B,t(k))}{R(k,A,B,t(k))\theta(k,A,B,t(k)) + R(k,A,0,t(k))\theta(k,A,0,t(k)) + R(k,0,B,t(k))\theta(k,0,B,t(k))}
\end{aligned} \tag{3}$$

$$\begin{cases}
\theta(i,A,B,t(i)) = \rho(i,A)\rho(i,B)e^{-\int_{t_0(i)}^{t(i)} [\lambda(i,A,s)+\lambda(i,B,s)]ds} \\[2ex]
\theta(i,A,0,t(i)) = \rho(i,A)e^{-\int_{t_0(i)}^{t(i)} \lambda(i,A,s)ds} \left[1 - \rho(i,B)e^{-\int_{t_0(i)}^{t(i)} \lambda(i,B,s)ds} \right]
\end{cases}$$

$$\begin{cases} \theta(i,0,B,t(i)) = \left[1-\rho(i,A)e^{-\int_{t_0(i)}^{t(i)}\lambda(i,A,s)ds}\right]\rho(i,B)e^{-\int_{t_0(i)}^{t(i)}\lambda(i,B,s)ds} \\ \theta(i,0,0,t(i)) = \left[1-\rho(i,A)e^{-\int_{t_0(i)}^{t(i)}\lambda(i,A,s)ds}\right]\left[1-\rho(i,B)e^{-\int_{t_0(i)}^{t(i)}\lambda(i,B,s)ds}\right], \end{cases} \tag{3 continued}$$

where h, j, and k index fish recaptures with both tags retained, with tag A only, and with tag B only; n, m , and p are the total numbers of fish recaptures with both tags retained, with tag A only, and with tag B only.

In the estimation, we assumed that $t_0(i)=0$, there was no type-I tag shedding (i.e. $\rho(i,A)=\rho(i,B)=1$), and $R(i,A,B,t(i))=R(i,A,0,t(i))=R(i,0,B,t(i))$. The latter assumption makes Equation 3 independent of probability of reporting at time $t(i)$. We also set the instantaneous shedding rate of tag j (j=A,B) as a function of fish total length at release $L(i)$ and time at liberty $t(i)$ of the form $\lambda(i,j,t(i))=\beta_0(j)+\beta_1(j)L(i)+\beta_2(j)t(i)$, where $\beta_0(j)$, $\beta_1(j)$ and $\beta_2(j)$ are parameters to be estimated. Thus, $\lambda(i,j,t(i))$ has three terms and seven (2^3–1) nested models, since each term can be included or excluded in a nested model and a nested model has at least one term. Under these assumptions, Equation 3 becomes

$$L=L_1 \cdot L_2 \cdot L_3, \tag{4}$$

with

$$L_1 = \prod_{h=1}^{n} \frac{\theta(h,A,B,t(h))}{\theta(h,A,B,t(h))+\theta(h,A,0,t(h))+\theta(h,0,B,t(h))}$$

$$L_2 = \prod_{j=1}^{n} \frac{\theta(j,A,0,t(j)}{\theta(j,A,B,t(j))+\theta(j,A,0,t(j))+(\theta(j,0,B,t(j))}$$

$$L_3 = \prod_{k=1}^{n} \frac{\theta(k,0,B,t(k))}{\theta(k,A,B,t(k))+\theta(k,A,0,t(k))+\theta(k,0,B,t(k))}$$

$$\begin{cases} \theta(i,A,B,t(i)) = e^{-[\beta_0(A)+\beta_1(A)L(i)+\beta_0(B)+\beta_1(B)L(i)]t(i)-\frac{1}{2}[\beta_2(A)+\beta_2(B)]t(i)^2} \\ \theta(i,A,0,t(i)) = e^{-[\beta_0(A)+\beta_1(A)L(i)]t(i)-\frac{1}{2}\beta_2(A)t(i)^2}\left[1-e^{-[\beta_0(B)+\beta_1(B)L(i)]t(i)-\frac{1}{2}\beta_2(B)t(i)^2}\right] \\ \theta(i,0,B,t(i)) = \left[1-e^{-[\beta_0(A)+\beta_1(A)L(i)]t(i)-\frac{1}{2}\beta_2(A)t(i)^2}\right]e^{-[\beta_0(B)+\beta_1(B)L(i)]t(i)-\frac{1}{2}\beta_2(B)t(i)^2} \\ \theta(i,0,0,t(i)) = \left[1-e^{-[\beta_0(A)+\beta_1(A)L(i)]t(i)-\frac{1}{2}\beta_2(A)t(i)^2}\right]\left[1-e^{-[\beta_0(B)+\beta_1(B)L(i)]t(i)-\frac{1}{2}\beta_2(B)t(i)^2}\right] \end{cases}$$

For the first experiment, $\lambda(i,A,t(i))=0$ because internal tags (tag A)were inserted into the shark's body cavity and were not shed, except under very unusual circumstances. For the same reason, although three recaptured school sharks appeared to have shed their internal tags (rows 9 and 21, Table 1), these events were actually due to failure to detect the tag upon recapture. Consequently, both tags were assumed to be present for these recaptures. Also, tag shedding rates of white and gray Petersen discs were estimated, singly or in combination, to examine their possible differences (Table 3). Data on $\lambda(i,A,t(i))$(Roto tags)

Table 3

Instantaneous rate of tag shedding for school shark estimated from data based on the first double-tagging experiment assuming that the shedding rates of internal tags (tag A) are zero, i.e., $\lambda(i,A,t(i))=\beta_0(A)=0$, and those of external tags (tag B) depend only on their types, i.e., $\lambda(i,B,t(i))=\beta_0(B)$; n is the number of recaptures. $-\log(L)$ gives values of the negative of the logarithm of the likelihood function; "—" indicates not applicable or not computable. J = J-tag; L = L-tag; S = S-tag; W = W-tag; G = G-tag. The word "and" indicates pooling of data: J and L for pooling data from J-tag and L-tag; M and F for pooling data from males and females. Estimates for tag A of J and L and tag B of G are the same as those for tag A of L and tag B of G; estimates for tag A of J and S and tag B of G are the same as those for tag A of S and tag B of G.

Row	Tag A	Tag B	Sex	n	$\beta_0(B)$ (SE)/yr	$-\log(L)$
1	J	W	M and F	32	0.3718(0.1089)	9.4439
2	J	W	M	18	0.2829(0.1104)	5.4509
3	J	W	F	14	0.5816(0.2946)	3.3332
4	L	W	M and F	11	0.6446(0.3609)	2.3503
5	L	W	M	7	0.3617(0.2605)	1.3295
6	L	W	F	4	—	—
7	L	G	M and F	200	0.7347(0.1012)	45.4817
8	L	G	—	2	—	—
9	L	G	M	127	1.1439(0.2534)	14.3301
10	L	G	F	71	0.5202(0.1016)	27.4639
11	S	W	M and F	7	—	—
12	S	W	—	0	—	—
13	S	W	M	2	—	—
14	S	W	F	5	—	—
15	S	G	M and F	167	3.0653(0.4739)	47.9105
16	S	G	—	2	1.2692(1.5899)	0.3407
17	S	G	M	86	4.5992(1.0705)	18.1029
18	S	G	F	79	2.3509(0.4955)	26.9553
19	L	W and G	M and F	211	0.7291(0.0974)	47.8580
20	L	W and G	—	2	—	—
21	L	W and G	M	134	1.0272(0.2119)	16.8622
22	L	W and G	F	75	0.5466(0.1040)	28.3971
23	S	W and G	M and F	174	3.0857(0.4735)	48.0298
24	S	W and G	—	2	1.2692(1.5899)	0.3407
25	S	W and G	M	88	4.5993(1.0702)	18.1029
26	S	W and G	F	84	2.3912(0.4975)	27.1604
27	J and L	W	M and F	43	0.4165(0.1084)	12.1642
28	J and L	W	M	25	0.2993(0.1016)	6.8258
29	J and L	W	F	18	0.7464(0.3367)	4.0018
30	J and L	W and G	M and F	243	0.6460(0.0780)	59.5387
31	J and L	W and G	—	2	—	—
32	J and L	W and G	M	152	0.7457(0.1255)	27.0143
33	J and L	W and G	F	89	0.5508(0.0979)	31.7369
34	J and S	W	M and F	39	0.4434(0.1207)	11.6709
35	J and S	W	—	0	—	—
36	J and S	W	M	20	0.3162(0.1168)	6.1176
37	J and S	W	F	19	0.7587(0.3557)	4.4422
38	J and S	W and G	M and F	206	1.6579(0.2133)	80.2783
39	J and S	W and G	—	2	1.2692(1.5899)	0.3407
40	J and S	W and G	M	106	1.5043(0.2682)	45.5600
41	J and S	W and G	F	98	1.8729(0.3550)	34.0001

continued

were too limited from the second experiment (Table 2) to estimate two or more parameters. We estimated $\beta_0(A)$ only, which can, however, be scaled to $\beta_1(A)$ or $\beta_2(A)$ given $L(i)$ and $t(i)$. For tag B (Petersen discs or dart tags), all seven nested models of $\lambda(i,B,t(i))$ were fitted, where possible, to data from each tagging experiment. The final and most parsimonious model was decided by the χ^2 statistic (Seber and Wild, 1989, p.196–197). All parameters were estimated by minimizing $-\log(L)$ by using the simplex algorithm by a FORTRAN 77 program (available on request).

Results

Maximization of Equation 4 for both sets of tagging data yielded estimates of shedding rate for various (independent) combinations of fish sex, tag type, and tag position, and their (asymptotic) standard errors (Tables 3 and 4). If a tag was retained in all recaptured fish, we assumed that its shedding rate was zero in order to estimate other parameters of the model. Because shedding rates must be nonnegative, the assumption of zero shedding rate will lead to an underestimate of the parameter concerned and introduce a positive bias into the estimates of other parameters. The extent of such bias could be assessed by simulation studies but is beyond the scope of this work.

Fish length at release or time at liberty, or both, entered certain final models for $\lambda(i,B,t(i))$, only when the number of fish recaptured was small. By contrast, whenever there were many fish recaptures (e.g. rows 14–15 and 20–21, Table 1), neither factor entered the final model. Therefore, we conclude that fish length at release or time at liberty, or both, did not significantly affect tag shedding rates; and their inclusion in certain models was a result of too few recaptures.

Fish sex affected tag shedding rates of Petersen discs for some combinations of tag type and tag position. For a combination of a 50-mm-long and 23-mm-wide internal tag (J-tag) with a white Petersen disc (external) tag (W-tag) (rows 1–3, Table 3), $\lambda(i,B,t(i))$=0.3718 (±0.1089)/yr if data are pooled for both sexes of school shark, with a –log-likelihood of 9.4439. For the sex-specific model, $\lambda(i,B,t(i))$=0.2829 (±0.1104)/yr for males; $\lambda(i,B,t(i))$=0.5816 (±0.2946)/yr for females, with a (male and female) combined –log-likelihood of 8.7841 (=5.4509+3.3332). The increase in value of the –log-likelihood function for an extra parameter is, in this case, negligible ($\chi^2_{1,0.2507}$=2×(9.4439–8.7841)=1.3196), suggesting no statistically significant differences in tag shedding rates between sexes for white Petersen discs.

Table 3 (continued)

Row	Tag A	Tag B	Sex	n	$\beta_0(B)$ (SE)/yr	$-\log(L)$
42	L and S	W	M and F	18	0.9094(0.4251)	3.4541
43	L and S	W	—	0	—	—
44	L and S	W	M	9	0.4791(0.3116)	1.7664
45	L and S	W	F	9	—	—
46	L and S	G	M and F	367	1.2892(0.1331)	116.1464
47	L and S	G	—	4	1.2729(1.5769)	0.3409
48	L and S	G	M	213	2.1071(0.3520)	41.2981
49	L and S	G	F	150	0.9537(0.1327)	67.8985
50	L and S	W and G	M and F	385	1.2679(0.1274)	119.8703
51	L and S	W and G	—	4	1.2729(1.5769)	0.3409
52	L and S	W and G	M	222	1.8674(0.2992)	45.8682
53	L and S	W and G	F	159	0.9818(0.1336)	68.9822
54	J and L and S	W	M and F	50	0.4753(0.1168)	14.1985
55	J and L and S	W	—	0	—	—
56	J and L and S	W	M	27	0.3252(0.1063)	7.4610
57	J and L and S	W	F	23	0.8956(0.3763)	4.8981
58	J and L and S	G	M and F	367	1.2892(0.1331)	116.1464
59	J and L and S	G	—	4	1.2729(1.5769)	0.3409
60	J and L and S	G	M	213	2.1071(0.3520)	41.2981
61	J and L and S	G	F	150	0.9537(0.1327)	67.8985
62	J and L and S	W and G	M and F	417	1.0891(0.1026)	137.7412
63	J and L and S	W and G	—	4	1.2729(1.5769)	0.3409
64	J and L and S	W and G	M	240	1.2738(0.1761)	63.3863
65	J and L and S	W and G	F	173	0.9478(0.1251)	72.8067

Table 4

Instantaneous rate of tag shedding for gummy and school sharks estimated from data based on the second double-tagging experiment assuming that $\lambda(i,A,t(i))=\beta_0(A)$ and $\lambda(i,B,t(i))=\beta_0(B)$. Tagging position refers to tag B's position; n is the number of recaptures; –log(L) gives values of the negative of the logarithm of the likelihood function; "—" indicates not applicable or not computable. The word "and" indicates pooling of data: Jumbo and Roto for pooling data from Jumbo tag and Roto tag; M and F for pooling data from males and females.

Row	Species	Tag A	Tag B	Position of tag	Sex	n	$\beta_0(A)$ (SE)/yr	$\beta_0(B)$ (SE)/yr	–log(L)
1	gummy	Jumbo	dart	fin	M and F	32	0.1912(0.1349)	0.3770(0.1886)	19.5193
2	gummy	Jumbo	dart	fin	M	13	0.2133(0.2125)	0.5642(0.3260)	10.98
3	gummy	Jumbo	dart	fin	F	19	0.1771(0.1770)	0.1890(0.1890)	8.0212
4	gummy	Jumbo	dart	muscle	M and F	84	—	0.9239(-)	67.5957
5	gummy	Jumbo	dart	muscle	M	41	—	0.8550(0.2021)	34.5527
6	gummy	Jumbo	dart	muscle	F	43	—	0.9902(-)	32.9376
7	gummy	Roto	dart	muscle	M and F	91	0.1304(0.0747)	1.0502(0.1712)	71.5838
8	gummy	Roto	dart	muscle	—	1	—	—	—
9	gummy	Roto	dart	muscle	M	37	0.1581(0.1110)	0.8183(0.2187)	31.8327
10	gummy	Roto	dart	muscle	F	53	0.0918(0.0913)	1.2111(0.2563)	37.1817
11	gummy	Jumbo	dart	fin and muscle	M and F	116	0.0569(0.0402)	0.8278(0.1243)	91.8731
12	gummy	Jumbo	dart	fin and muscle	M	54	0.0586(0.0584)	0.8042(0.1749)	47.2285
13	gummy	Jumbo	dart	fin and muscle	F	62	0.0555(0.0553)	0.8503(0.1766)	44.6251
14	gummy	Jumbo and Roto	dart	muscle	M and F	175	0.0641(0.0369)	0.9828(0.1121)	141.3449
15	gummy	Jumbo and Roto	dart	muscle	—	1	—	—	—
16	gummy	Jumbo and Roto	dart	muscle	M	78	0.0809(0.0570)	0.8379(0.1484)	67.8238
17	gummy	Jumbo and Roto	dart	muscle	F	96	0.0447(0.0446)	1.0948(0.1656)	70.9707
18	gummy	Jumbo and Roto	dart	fin and muscle	M and F	207	0.0857(0.0381)	0.9172(0.1012)	164.2892
19	gummy	Jumbo and Roto	dart	fin and muscle	—	1	—	—	—
20	gummy	Jumbo and Roto	dart	fin and muscle	M	91	0.1011(0.0580)	0.8083(0.1361)	79.4274
21	gummy	Jumbo and Roto	dart	fin and muscle	F	115	0.0692(0.0487)	0.9989(0.1474)	82.5257
22	school	Jumbo	dart	fin	M and F	18	0.0973(0.0972)	0.2646(0.1530)	11.0858
23	school	Jumbo	dart	fin	M	3	—	—	—
24	school	Jumbo	dart	fin	F	15	0.1104(0.1103)	0.2948(0.1706)	10.6735
25	school	Jumbo	dart	muscle	M and F	21	0.1041(0.1038)	0.4262(0.1917)	14.7690
26	school	Jumbo	dart	muscle	M	12	0.1727(0.1725)	0.3219(0.2282)	6.6030
27	school	Jumbo	dart	muscle	F	9	—	0.5484(0.3201)	7.3704
28	school	Roto	dart	muscle	M and F	9	—	0.7845(0.3967)	8.5426
29	school	Roto	dart	muscle	M	3	—	—	—
30	school	Roto	dart	muscle	F	6	—	1.6867(0.8865)	5.6360
31	school	Jumbo	dart	fin and muscle	M and F	39	0.1003(0.0708)	0.3466(0.1230)	26.0748
32	school	Jumbo	dart	fin and muscle	M	15	0.1421(0.1419)	0.2700(0.1912)	7.0831
33	school	Jumbo	dart	fin and muscle	F	24	0.0773(0.0772)	0.3831(0.1571)	18.7670
34	school	Jumbo and Roto	dart	muscle	M and F	30	0.0798(0.0796)	0.5339(0.1793)	24.0789
35	school	Jumbo and Roto	dart	muscle	M	15	0.1188(0.1188)	0.2263(0.1602)	7.5881
36	school	Jumbo and Roto	dart	muscle	F	15	—	0.8882(0.3425)	14.0341
37	school	Jumbo and Roto	dart	fin and muscle	M and F	48	0.0876(0.0619)	0.4254(0.1233)	35.8236
38	school	Jumbo and Roto	dart	fin and muscle	M	18	0.1038(0.1037)	0.1997(0.1414)	7.9368
39	school	Jumbo and Roto	dart	fin and muscle	F	30	0.0746(0.0745)	0.5510(0.1755)	26.7306

However, for a combination of a 50-mm-long and 22-mm-wide internal tag (L-tag) with a gray Petersen disc (external) tag (G-tag) (rows 7–10, Table 3), $\lambda(i,B,t(i))$= 0.7347 (±0.1012)/yr if data are pooled for both sexes, with a –log-likelihood of 45.4817. For the sex-specific model, $\lambda(i,B,t(i))$=1.1439 (±0.2534)/yr for males; $\lambda(i,B,t(i))$=0.5202 (±0.1016)/yr for females, with a (male and female) combined –log-likelihood of 41.7940 (=14.3301+27.4639). The increase in value of the –log-likelihood function for an extra parameter is statistically significant ($\chi^2_{1,0.0066}$=2×(45.4817–41.7940)= 7.3754), suggesting significant differences in tag shedding rates between sexes for gray Petersen discs. Similarly, for a combination of a 35-mm-long and 10-mm-wide internal tag (S-tag) with a gray Petersen disc (external) tag (rows 15–18, Table 3), $\lambda(i,B,t(i))$=3.0653 (±0.4739)/yr if data are pooled for both sexes, with a –log-likelihood of 47.9105. For the sex-specific model, $\lambda(i,B,t(i))$=4.5992 (±1.0705)/yr for males; $\lambda(i,B,t(i))$= 2.3509 (±0.4955)/yr for females, with a (male and female) combined –log-likelihood of 45.0582 (=18.1029+ 26.9553). The increase in value of the –log-likelihood function for an extra parameter is, again, statistically significant ($\chi^2_{1,0.0169}$=2×(47.9105–45.0582)=5.7046), again suggesting significant differences in tag shedding rates between sexes for gray Petersen discs. Notice, in these cases, that tag shedding rates for males nearly doubled those for females. For the second tagging experiment, no differences in tag shedding rates were found among sexes for either species of shark (Table 4).

The shedding rate of Petersen discs for the school shark was very high. When combined with a 50-mm-long and 23-mm-wide internal tag (J-tag), white Petersen disc (W-tag) had a shedding rate of $\lambda(i,B,t(i))$=0.2829(±0.1104)/yr or $100\times(1-e^{-0.2829}) \approx$ 24.64%/yr for males, and $\lambda(i,B,t(i))$=0.5816(±0.2946)/yr or 44.10%/yr for females (rows 1–3, Table 3). When combined with a 50-mm-long and 22-mm-wide internal tag (L-tag), gray Petersen disc (G-tag) had a shedding rate of $\lambda(i,B,t(i))$=1.1439 (±0.2534)/yr or 68.14%/yr for males and $\lambda(i,B,t(i))$=0.5202 (±0.1016)/yr or 40.56%/yr for females (rows 7–10, Table 3). When combined with a 35-mm-long and 10-mm-wide internal tag (S-tag), gray Petersen disc (G-tag) had a shedding rate of $\lambda(i,B,t(i))$=4.5992 (±1.0705)/yr or 98.99%/yr for males and $\lambda(i,B,t(i))$=2.3509 (±0.4955)/yr or 90.47%/yr for females (rows 15–18, Table 3). Other combinations of tag type and tagging position for the first tagging experiment did not yield reliable (in accuracy and precision) estimates of tag shedding rate because of insufficient data.

For the second tagging experiment, tag shedding rates varied considerably for both species of sharks (rows 1–10 and 22–30, Table 4). However, dart tags had a higher shedding rate than either Roto or Jumbo tags. For example, for male gummy shark tagged in the fin, dart tags had an instantaneous shedding rate of 0.5642 (±0.3260)/yr and Jumbo tags 0.2133 (±0.2125)/yr (row 2, Table 4). For either gummy or school shark, the shedding rate of dart tags placed in the fin was about half that of dart tags placed in the muscle (rows 1–10 and 22–30, Table 4).

Discussion

We developed a simple tag shedding model (Equations 1–4) to account for the effects of time at liberty, sex, size, tag position, and other factors and used a special case to estimate the instantaneous shedding rates of Petersen discs, Roto tags, and dart tags in two species of sharks. It can be used to estimate the shedding rates of two tags, singly or in combination, and has two interesting features. In Equation 1, both $F(i,t(i))$ and $M(i,t(i))$ are independent of the 16 state variables. This independence ensures that $P(i,A,B,t(i))$, $P(i,A,0,t(i))$, $P(i,0,B,t(i))$ and $P(i,0,0,t(i))$ are all expressible as a product (Equation 2), which in turn ensures that terms involving $F(i,t(i))$ and $M(i,t(i))$ in the likelihood function (Equation 3 or 4) are cancelled out. Thus, as in Xiao (1996a), our tag shedding model applies, even when $F(i,t(i))$ and $M(i,t(i))$ are arbitrary functions of time $t(i)$. On the other hand, if fishing and natural mortalities depend on the state variables of tags A and B, then terms in $P(i,A,B,t(i))$, $P(i,A,0,t(i))$, $P(i,0,B,t(i))$ and $P(i,0,0,t(i))$ involving four fishing mortalities $F(i,A,B,t(i))$, $F(i,A,0,t(i))$, $F(i,0,B,t(i))$ and $F(i,0,0,t(i))$ and four natural mortalities $M(i,A,B,t(i))$, $M(i,A,0,t(i))$, $M(i,0,B,t(i))$ and $M(i,0,0,t(i))$ cannot be factored out. Then, for estimation of parameters by maximizing Equation 3, particular functional forms of all the eight mortalities must be hypothesized. This tag shedding model is more general but more data-demanding. The other interesting feature of our tag shedding model is that Equation 3 is independent of probabilities of reporting $R(i,A,B,t(i))$, $R(i,A,0,t(i))$, $R(i,0,B,t(i))$ and $R(i,0,0,t(i))$ if these probabilities are identical, arbitrary functions of time $t(i)$ because of the way they enter Equation 3.

Statistically significant differences in shedding rates of Petersen discs between male and female school sharks were detected when many fish were recaptured. We do not know why such differences existed but we postulate that male sharks have a higher tag shedding rate because they are more active and would tend to rub off the tags and that female sharks have a lower tag shedding rate because they are larger and have thicker fins. An external fin tag, such as a Petersen disc, is shed only after its pin or locking mechanism has cut through the fin. The larger the tagged fish, the thicker is its fin and hence the farther the distance its pin or locking mechanism has to cut through to the posterior edge of the fin. Consequently, larger animals have lower shedding rates. Thus, sex is confounded in its effects with size. That is probably why the length at release of school sharks did not affect the shedding rates of Petersen discs within a wide size range examined, although the loss of anchor tags (Floy tags) was size-dependent for striped bass *Morone saxatilis* (Waldman et al., 1990) but size-independent for lake trout *Salvelinus namaycush* (Fabrizio et al., 1996). We could not detect differences between sexes with fewer recaptures, however, because the use of Equation 1 or 2 to resolve sexual differences in tag shedding rate requires many recaptures (see below).

Shedding rates of Petersen discs, Roto tags, and dart tags did not change with time at liberty. Some tagged fish have higher shedding rates than others, because tags that are less securely attached are shed earlier. The proportion of less securely attached tags decreases with increasing time at liberty. This will yield an apparent decrease in tag shedding rate with time at liberty. A similar argument applies when tag shedding rates vary among individuals. The lack of a trend may indicate negligible tag losses from improper attachment, insignificant individual variability in tag shedding rate, or insufficient data (see below).

Estimates of tag shedding rates in Tables 3 and 4 must be used cautiously because only those that are based on many recaptures are reliable, whereas those that are based on few recaptures are unreliable. For example, the estimates of tag shedding rates for a combination of a 50-mm-long and 22-mm-wide internal tag (L-tag) with a white Petersen disc (W-tag, external) (rows 4–6, Table 3) were based on only 11 recaptures (rows 11 and 12, Table 1), only one of which had retained both tags (row 11, Table 1), and hence are unreliable. No estimates could even be obtained for a combination of a 35-mm-long and 10-mm-wide (S-tag) internal tag with a white Petersen disc (W-tag, external) (rows 11–14, Table 3), despite seven recaptures, none of which had retained both tags (rows 16–18, Table 1). Similarly, no estimates could be obtained, for any tag combinations, from data on gummy sharks from the first double-tagging experiment, despite 20 recaptures, none of which had retained both tags (rows 1–8, Table 1). Equally unreliable estimates of tag shedding rates could also result from pooling of information while ignoring differences in its sources. For example, estimates from pooling all three internal tags (i.e. J-tag, L-tag and S-tag) (rows 54–65, Table 3) should be treated cautiously because of sexual differences inferred above. By contrast, for both sexes of school sharks, the estimates of shedding rates of gray Petersen discs are reliable for its combination with a 50-mm-long and 22-mm-wide internal tag (L-tag) (rows 9 and 10, Table 3) or with a 35-mm-long and 10-mm-wide (S-tag) internal tag (rows 17 and 18, Table 3) because information from many fish recaptures was used in their estimation. Much less reliable estimates were obtained for dart tags on gummy sharks (rows 5, 6, 9, and 10, Table 4). Although rather high in all cases, all these shedding rates are actually underestimated, as will be shown and published elsewhere.

Although we have examined only the effects of tag type, sex, length at release, and time at liberty on tag shedding, many other factors, such as tagging operator (Hampton, 1996), can also affect tag shedding rate. However, hundreds or even thousands of fish need to be recaptured (many more need to be released) to estimate effects of tagging operators reliably. Such a great demand of data is well expected of Equation 1 or 2, which is a compartmental model. The solution of a compartmental model can be given by a linear combination of exponentials and is known to yield bad ill-conditioning (Seber and Wild, 1989, p. 118–119). Indeed, for some compartmental models, no amount of data is sufficient for identifying model parameters. Similarly, the "best" model of all possible models of a general model is identifiable only by a sufficient volume of data. As mentioned above, fish length at release or time at liberty, or both, entered certain "best" models for $\lambda(i,B,t(i))$, when the number of fish recaptured was small, but did not, when there were many fish recaptures. This finding suggests that fewer data than sufficient cannot identify the "best" model. To detect and address problems with parameter and model identifiability for a particular general model (e.g. Equation 1 or 2), one might generate as large a set of data as necessary, for example, by duplicating each record of an existing set of data from a double-tagging experiment a necessary number of times, analyse it, and design one's tagging experiment accordingly (e.g. to determine the number of fish to be released and the expected number of fish to be recaptured).

Results of our study have major implications for future double-tagging experiments for estimating instantaneous tag shedding rate and for analysis of tagging data. Because estimation of a single parameter requires many fish recaptures and hence incurs considerable financial resources, use of an easily detected and permanent tag eliminates a need for considering tag loss and is preferred in any tagging experiment. However, with a commercially or recreationally harvested species, problems of tag reporting remain. Use of two readily detectable, identical tags with a moderate shedding rate in a double-tagging experiment reduces the number of parameters to be estimated by one half. A moderate shedding rate is necessary because too low a shedding rate requires some recaptures after a long time at liberty for reliable estimation of parameters; too high a shedding rate renders the tag useless for some applications.

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